Influence of ecosystem variability on the demography and reproductive performance of two *Eudyptes* penguins, Macaroni and Eastern Rockhopper Penguins, at sub-Antarctic Marion Island, 1994–2019

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Dissertation presented for the degree of Master of Science

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January 2022

DECLARATION

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Acknowledgements

I thank my supervisors Dr Azwianewi Makhado and Professor Peter Ryan for their extensive input into my thesis, directing and advising me to the finishing line. The creative freedom they allowed me, and their motivation prompted the publication of my first paper from Chapter 3 in the Africa Journal of Marine Science (July 2021). The paper had 5 co-authors, I took the lead in writing up the manuscript, performed all the analytical calculations and numerical simulations. AB Makhado and PG Ryan supervised the findings of this work and helped with the interpretation of the results and discussion. BM Dyer contributed to sample preparation, RJM Crawford and PA Pistorius provided critical feedback for the research.

I thank my friends and colleagues at Department of Forest Fisheries and the Environment (DFFE) for making my stay within the department as a student an experience to remember. Special mention goes to Bruce Dyer and Makhudu Masotla for the field trips and the insurmountable knowledge they were always willing to provide, showing me the ropes in marine science monitoring. Field trips with the department were long but with these two on board you laughed your way through them, walking long distances looking for birds and all sorts of reptiles.

I thank everyone from the FitzPatrick Institute of African Ornithology for the interesting talks, morning tea and lunch talks that help during a long day of research. Hilary Buchanan who helped with my logistics at UCT, thank you.

This project was possible because of the data collected over the last 26 years by DFFE through the South African National Antarctic Programme (SANAP). Funding for SANAP projects is administered by the National Research Foundation.

Thank you to all my friends and family for their support and love. I thank my aunt Pretty Gomba and her family for always being there for me and being a supporting pillar in Cape Town when I missed my family back home. My mother, Tariro and Tendai have always allowed me to explore different things and have never held me back but have always been there for me every time I fell, the sparks that lit the fire.

Abstract

Penguins are among the most important avian predators in the Southern Ocean, consuming large amounts of prey. Macaroni Penguins *Eudyptes chrysolophus* and Eastern Rockhopper Penguins *E. filholi* are listed as Vulnerable due to large-scale population declines across their distributions. The aim of my thesis is to update trends in the breeding populations of Macaroni and Eastern Rockhopper Penguins at Marion Island from 1994–2019. The breeding population of Macaroni Penguins has decreased more or less consistently at an average rate of 1.9% per year since 1994, whereas Eastern Rockhopper Penguins showed a rapid initial decline of 13% per year from 1994–2001, then stabilised to fluctuate between 55 000 and 80 000 pairs. I assess the long-term trends in pre-breeding condition (arrival dates and mass on arrival for breeding) and breeding performance (breeding success and fledgling mass) of both Macaroni and Eastern Rockhopper Penguins. I also compare within and between these variables to explain trends in the breeding population of both penguins for the last two decades.

There was inter-annual variation in pre-breeding variables (arrival dates and mass on arrival) and breeding variables (breeding success and fledging mass) in both penguins which could indicate variability in prey availability and climatic conditions across the breeding seasons from 1994–2019. Over the study period, Macaroni Penguins arrived to breed 3–5 weeks earlier than Eastern Rockhopper Penguins on Marion Island. There was no consistent trend in mass on arrival among male or female Macaroni Penguins but Eastern Rockhopper Penguin mass on arrival decreased from 1994 to 2007 and then had an increasing trend post 2007 for both sexes. Breeding success of Macaroni Penguins fluctuated annually with no obvious trend, whereas the breeding success of Eastern Rockhopper Penguins increased at all three study locations. This increase in body condition and breeding success could explain the stabilising population of Eastern Rockhopper Penguins at Marion Island. Breeding variables (breeding success, fledgling mass) of both penguins were related to pre-breeding variables (arrival dates and mass at arrival). The breeding performance of both penguins is not only affected by localised prey availability and climatic conditions during breeding, but the effect might potentially be at a broader scale, before the onset of breeding.

I used diet samples collected from these two species during breeding to determine inter-annual variation in prey composition to assess whether long-term changes in diet might explain trends in their breeding populations. The population size of the two penguins at Marion Island is more evenly matched compared to any other location where the two *Eudyptes* penguins breed sympatrically. They are expected to exhibit a level of segregation in their biology to allow their co-existence, from selection of breeding grounds, foraging strategies, diet and response to changing oceanographic conditions. I also tested for differences in preferred prey species. Both penguins mainly fed on euphausiids *Thysanoessa vicina* and *Euphausia vallentini*. Myctophid fishes (mainly *Krefftichthys anderssoni* and *Protomyctophum tenisoni*) were more important in the diet of Macaroni than Eastern Rockhopper Penguins. There was no long-term change in their diets that could explain their decreasing population trends at Marion Island. However, the more diverse diet of Macaroni Penguins could potentially allow them to compensate for years of low euphausiid availability compared to Eastern Rockhopper Penguins. The considerable overlap in diet between the two penguins suggests potential competition of resources between the two penguins, during breeding.

Variation in breeding performance of both Macaroni and Eastern Rockhopper Penguins was related to breeding diet composition. Macaroni Penguins had higher breeding success when they fed more on myctophids, whereas Eastern Rockhopper Penguins fledged lighter chicks when they preyed on myctophids. Macaroni Penguins are more efficient at foraging on myctophids compared to Eastern Rockhopper Penguins and hence, foraging on myctophids could have opposing effects on duration of foraging, provision rate and parental care between the two penguin species.

Variation in the diet composition when breeding was related to the latitudinal position of the oceanic fronts. Macaroni and Eastern Rockhopper Penguins fed on more fish *Protomyctophum tenisoni* when the Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF) were further away from Marion Island and fed on more crustaceans *Thysanoessa vicina* when the fronts were closer to the island. The variable latitudinal position of the fronts is known to influence species composition and oceanographic conditions around the Island.

Variation in breeding performance was not readily explained by large-scale oceanographic conditions or local scale oceanographic conditions except for sea surface height (SSH). Macaroni Penguins tended to fledge heavier chicks in years of low SSH, associated with more upwelling and mesoscale eddies, whereas Eastern Rockhopper Penguins tended to fledge heavier chicks in years of higher SSH associated with less upwelling and fewer mesoscale eddies. This indicates the difference in habitat preference and response to oceanographic conditions between the two penguin species: Macaroni Penguins forage in cooler waters compared to Eastern Rockhopper Penguins.

In summary, this study reports trends in the population size, breeding performance and diet of two sympatric penguin species and how they respond to their environment. Both penguins' populations have been decreasing since 1994 but for the Eastern Rockhopper Penguin most of the decline happened before 2001 and their population has since stabilised. The two-closely related penguins manage to segregate some aspects of their ecology to facilitate co-existence on the same island while foraging in broadly the same area and feeding on the same prey. Macaroni Penguins arrive on the Island 3–5 weeks earlier than Eastern Rockhopper Penguins, which reduces competition for resources during breeding. Macaroni Penguins have a more diverse diet and feed on more fish compared to Eastern Rockhopper Penguins. The breeding performance of Macaroni Penguins responded positively to fish in their diet while Eastern Rockhopper Penguin chick condition was negatively affected by fish in their diet. The breeding biology and diet of the two penguins responded to changes in oceanographic settings around Marion Island, showing the possible effect of climate change on these two species.

Chapter 1: General Introduction

Seabird as indicators

Seabirds are a diverse group of species made up of approximately 359 species worldwide, 3.5% of all birds (Croxall et al. 2012a, Dias et al. 2019). Their distribution across the world's oceans and their dependence on both land and marine resources to breed make them good indicators of marine ecosystem health (Parsons et al. 2008, Hazen et al. 2019). Seabirds are top marine predators and important consumers of marine resources. They consume >18 million tonnes annually, removing large quantities of biomass from the world oceans, acting as biological pumps in marine ecosystems because they reflect changes in lower trophic levels (Brooke 2004). Consumption of large marine biomass by seabirds has the capability to affect primary and secondary production which is transferred through the food web, a cascading effect in influencing the number and type of primary and secondary consumers in marine ecosystems (Reyes-Arriagada et al. 2015).

Seabirds spend most of their lives at sea but have to return to land to breed, this makes them easy to study compared to other fully marine predators and hence useful as sentinels of the marine environment (Boersma 2008). Most studies of seabird biology have been carried out during the short period of their annual cycle when they are on land (Parsons et al. 2008). Seabirds aggregate in large colonies during breeding, this allows for the enumeration of their population abundance which has been used by most scientists to inform conservation policy makers (governmental departments) to assess seabird conservation status (Cairns 1988, Kharitonov and Siegel-Causey 1988, Diamond and Devlin 2003, Piatt et al. 2007). The aggregation of seabirds during breeding also allows for the measurement of other demographic and behavioural parameters like breeding productivity, diet, foraging behaviour and survival which can be useful as indicators of prey availability and environmental change (Cairns 1988). These parameters can be linked to oceanographic variables such as El Niño-Southern Oscillation (ENSO) and reflect the ecological impacts of changes in oceanographic conditions (Forcada and Trathan 2009, Baylis et al. 2012). The observation of short-term and long-term trends in seabird populations allows for the identification of local environmental changes and ocean productivity (Bost and Le Maho 1993).

Seabirds forage at sea to sustain themselves and provide for their young. The survival of adults and offspring is determined by the parent being able to locate and return with sufficient high nutrient prey. During breeding, seabirds are constrained by the need to return to their colonies to provision for their young and relieve their partners that are incubating eggs (Elliott et al. 2009). To minimise the cost of foraging while provisioning for their chicks, seabirds must balance the energy required to locate prey and bring it back to the colony with the energy content of the prey (Ballance et al. 2001). Seabirds optimise their intake and delivery rate of prey by minimising travelling distances between colonies and prey by foraging in areas closer to their colonies during breeding, while trying to manage their own energy uptake and meeting the energy demands of their rapidly growing chicks (Pyke 1984, Fauchald 2009). The foraging range of seabirds is limited by their physiology, physical and dynamic oceanographic conditions (bathymetry, sea-surface temperature, chlorophyll, sea surface height) which influence prey distribution and availability. Marine top predators tend to aggregate in areas where prey is abundant such as at frontal zones, the edge of sea ice and upwelling zones (Ballance et al. 2001, Weimerskirch 2007, Hindell et al. 2020).

Due to the energy cost associated with breeding, constraints of central place foraging and unpredictable marine environments, most seabirds have developed a conservative life history strategy, offsetting low reproductive rates and the delayed onset of breeding with high adult survival (Lack 1968, Ricklefs 1990). Trends in seabird biology have been used in detecting impacts of climate change and its influence on marine ecosystems (Croxall 2002). Climate change affects weather and oceanographic conditions like sea level rising and sea surface temperature which influence prey distribution. This in turn is reflected by changes in seabird breeding, distribution and population trends (Chambers et al. 2011, Sydeman et al. 2012).

Penguin life history, breeding and foraging ecology

Penguins (family Spheniscidae) are flightless species restricted to land and sea, hence their movements are more energetically demanding compared to most seabirds (Borboroglu and Boersma 2015). Like most seabirds, penguins have a conservative life history, which means they have long parental care, late sexual maturity, long life span and small clutch size (Borboroglu and Boersma 2015). Apart from the *Aptenodytes* penguins, all penguins lay two eggs which are often of different size. The crested penguins (*Eudyptes*) and Adélie Penguins *Pygoscelis adeliae* lay asymmetrical eggs with the second egg (B-egg) laid on average 4 days later being larger than the first laid egg (A-egg). In most penguins the first egg is larger than the second one but genus *Eudyptes* the second egg is 20–78% larger than the first (Croxall and Davis 1999, Ancel et al. 2013, Borboroglu and Boersma 2015, Cerchiara 2018). Generally, only one chick survives and the situation in which the second chick survives along with the first chick in years of abundant food resource is a classic case of facultative brood reduction in penguins (Cassady St Clair 1990). When resources are very low it is potentially a mechanism for increasing reproductive effort in penguins (Croxall and Davis 1999, Favaro and Pichegru 2018).

Both parents participate in the incubation and provisioning of the chicks (Favaro and Pichegru 2018). Penguin chicks are semi-altricial with limited mobility and thermoregulatory capacity, which makes them prone to mortality from exposure to the environment (temperature and storms, Trathan et al. 2015), starvation (Ropert-Coudert et al. 2019) and predation threat (Horswill et al. 2014) and hence cannot be left unattended when young. The growth of the chicks is dependent on the frequency and quality of the food provisioned by their parents and that in turn is determined by the proximity, availability and amount of prey from the breeding colony and environmental conditions (Cerchiara 2018). Once the chick hatches, they are guarded (guard stage) by a parent. The chick's continued growth and increased thermal independence comes with an increase for food requirement making it difficult for one parent to meet the requirements of the now larger chick. Hence both parents leave to forage, and the chicks are left unattended and aggregate into creches for protection from predators and exposure to the environment. As the chicks mature into semi-independent fledglings in creches with continued provisioning they continue to grow and gain weight. While the fledglings are restricted to their breeding grounds, they must develop waterproof, insulating feathers to go out and forage on their own. After the breeding season, once their chicks have fledged the adults go to sea to regain their fat reserves and initiate moulting shortly after to maintain their feathers for good insulation against environmental conditions at sea and on land. Moulting requires an extended period of fasting as penguins undergo catastrophic moulting where all feathers are replaced in one go (Williams 1995, Davis and Renner 2003, Borboroglu and Boersma 2015). The survival of penguins is thus dependant on the seasonal peak abundance of food around their colony prior to their moulting and in some instances if resources are scarce, penguins abandon their chicks in order to fatten up and ensure they survive their moult (Boersma 2008, Favaro and Pichegru 2018).

Due to their adaptation to both land and sea, much of their ecology is dependent on their distribution and range at sea and whether they are inshore or offshore foragers (Davis and Renner 2003). How far a bird must travel to find its food will affect how much time it spends at the nest and how much energy it uses (Davis and Renner 2003). Migratory and offshore penguins such as Macaroni and King Penguins *Aptenodytes patagonicus* arrive at breeding colonies with large body reserves following feeding from a considerable distance from their colony and then undergo extended fasting periods compared to inshore species like Gentoo Penguins *Pygoscelis papua* (Morrison 2015). There is also evidence of a correlation between the foraging trips of penguins during chick rearing and the duration of the fast of the first incubation shift between the parent penguins (Croxall and Davis 1999). The foraging range of penguins also supports why sympatric breeding penguins like inshore (Gentoo) and offshore (Macaroni) penguin species utilise and react to prey abundance around South Georgia Island differently (Waluda et al. 2012, 2017). Both preferentially feed on Antarctic Krill (*Euphausia superba*), but Macaroni Penguins feed on more krill than Gentoo Penguins. When krill is scarce, Macaroni Penguins compensate by eating more amphipods *Themisto gaudichaudii* whereas Gentoo Penguins increase the proportion of fish in their diet. In both cases their diets reflect the availability of prey in their foraging ranges which could potentially have an impact on fledgling mass and breeding success (Croxall and Davis 1999, Waluda et al. 2012, 2017). Long-term studies are crucial to understand the population processes (abundance and breeding rate) of seabird species and determining trends in their population and in this study, I try to explain the factors behind the population process of two *Eudyptes* penguins at Marion Island.

***Eudyptes* penguins**

The *Eudyptes* or crested penguins are the largest penguin genus with seven species. Most of the genus' global population is largely accounted for by Macaroni and Rockhopper Penguins (Oehler et al. 2008). *Eudyptes* penguins cover the largest geographical area with a circumpolar distribution and are mostly found on the sub-Antarctic Islands and in temperate regions within the Southern Ocean (Williams 1995, Borboroglu and Boersma 2015). According to the IUCN *Eudyptes* penguins species are either classified as Near Threatened, Vulnerable or Endangered, with the majority of the crested penguins species around the world in decline (IUCN 2021). Most of the drivers of decline have been attributed to climate change (Cunningham and Moors 1994, Horswill et al. 2014, Morrison 2015, Niemandt et al. 2016), predation pressure (Cuthbert et al. 2009, Ryan and Kerr 2012, Hiscock and Chilvers 2014, 2016), fisheries pressure (Hilton et al. 2006, Trathan et al. 2012, 2015), pollution (Borboroglu et al. 2008) and diseases (de Lisle et al. 1990, Cooper et al. 2009).

Eudyptes penguins have a unique two egg clutch size with a reverse egg size dimorphism and reverse hatching synchrony in which the second-laid egg (B-egg) is significantly larger than the first egg (A-egg) (Warham 1972, Williams 1995). The B-egg receives preferential incubation and the A-egg is often ignored once the B-egg hatches (Warham 1975, Poisbleau et al. 2008). The chick from B-egg takes most of the food, leaving the chick from the A-egg to starve. The reason why *Eudyptes* penguins have a two-egg clutch but only fledge one is thought to be a maladaptive canalised trait, which means that they have a fixed phenotypic behaviour (clutch size) and only raise one chick regardless of the change and effect of environmental conditions (Stein and Williams 2013, Morrison et al. 2016). The causality behind the evolution of a smaller A-egg compared to the B-egg is not well understood. *Eudyptes* are also known for having an exceptionally long incubation/guard period compared to other penguins. The chicks are guarded by the male for 3–5 weeks compared to other penguins, which alternate guarding duties between sexes avoiding the long fasting period endured by male *Eudyptes* penguins. Males guard their chick for an extended fasting period while the females forage for the chick (Warham 1975, Morrison 2015).

Macaroni Penguin

Macaroni Penguins are the most abundant penguin species with a global population of 6.3 million breeding pairs (Birdlife International 2021a). The population has declined by >47% over the past 50 years from approx. 11.3 million breeding pairs in the 1970s (Crossin et al. 2013, Birdlife International 2021a). Due to this decline Macaroni Penguins are ranked as Vulnerable under the IUCN Red list and they are also considered a priority species under the CCAMLR Ecosystem Monitoring Program (CEMP), which monitors this species within the Southern Ocean. The largest population decline of Macaroni Penguin species was observed at South Georgia, decreasing by >70% from 5.4 million breeding pairs in the late 1970s to about 1 million breeding pairs in the early 2000s (Trathan et al. 2012). It has been hypothesised that the reduction in Macaroni Penguin population is due to the recovery and increase of the Antarctic Fur Seal *Arctocephalus gazella* population on the island because of the cessation of harvesting in the 18th and 19th centuries. This resulted in competition between Antarctic Fur Seals and Macaroni Penguins for the principal prey, Antarctic Krill *Euphausia superba* (Trathan et al. 2012). Forcada and Trathan (2009) also attributed the population decline to shifts in food resources caused by climate change (sea surface temperature warming). Horswill et al. (2016) suggest a combination of factors could have affected the population of Macaroni Penguins at South Georgia including predation pressure by giant petrels species, competition with Antarctic Fur Seal and climate factors like ENSO events and local warming. In contrast, numbers of Macaroni Penguins have been increasing on three colonies at Kerguelen for the past 50 years and they have been stable at the Crozet Islands for the past 10 years (Barbraud et al. 2020).

Macaroni Penguins’ diet are usually dominated by krill (euphausiid), although the dominant species differ among colonies. At South Georgia and Bouvet Island they prey on *Euphausia superba* (Waluda et al. 2012, Niemandt et al. 2016), at Marion, Crozet, Kerguelen and Heard islands they commonly prey on *E. vallentini* and *Thysanoessa vicina* (Brown and Klages 1987, Ridoux 1994, Deagle et al. 2007). The dominant prey species also varies between breeding seasons, with their diet dominated by mesopelagic fish (myctophids) and squid in some years, potentially reflecting prey availability around their colonies during breeding (Waluda et al. 2012). At some breeding colonies the proportions of prey in their diet has been linked to changes in reproductive performance (Crawford et al. 2003a, Waluda et al. 2017). At Marion Island fledgling mass was attributed increases in fish intake (Crawford et al. 2003a), and at Bird Island Macaroni Penguins fledged heavier chicks when the diet was dominated by euphausiids, particularly Antarctic Krill, and lighter chicks when more amphipods were eaten (Waluda et al. 2017).

Macaroni Penguins are offshore feeders that travel 50–500 km from the colony during their breeding season to find prey, however this varies across different colonies and time during breeding (Brown 1987, Green et al. 1998, Barlow and Croxall 2002a, Whitehead et al. 2016, 2017). Constrained by their breeding duties, their foraging range is mostly determined by the energy requirement of their chicks. Macaroni Penguins generally forage closer to the island during the earlier parts of the chick-rearing period <50 km and increase their range as the chicks grow older and are capable of diving at depths of >100 m (Crossin et al. 2013). Foraging depth of the penguins within the ocean is also determined by the choice in prey and myctophids are diel migrators, moving closer to the surface at night and then deeper during the day. Macaroni Penguin are visual feeders dependent on light, thus they carry out most of the diving and feeding during the day however they do dive during the night making shallower dives (Green et al. 1998, Crossin et al. 2013, Whitehead et al. 2016, 2017).

At Marion Island, numbers of Macaroni Penguins decreased by 30% between 1994–2009 as a result of a disease outbreak and low breeding success (Crawford et al. 2009). Using GPS loggers on Macaroni Penguins at Marion Island, their foraging behaviour and diet was shown to be sensitive to sea surface temperature, local geostrophic flow and position of oceanic fronts (Whitehead 2017). When cooler water persisted within their foraging ground during breeding Macaroni Penguins performed deeper dives, fed on more fish, and arrived in better condition (Whitehead 2017). The poor breeding success of Macaroni Penguins has been related to body condition on arrival and there has been an observed increase in sea surface temperature and shift in marine food webs at Marion Island (Hunt et al. 2001, Mélice et al. 2003, Crawford and Dyer 2006). The drivers of the population decrease in these penguins remain poorly understood at Marion Island, but a changing environment can alter prey availability and affect how Macaroni Penguins provision their chicks. In this study I try to explain the long-term trends in two *Eudyptes* penguin breeding population at Marion Island using their diet, breeding biology and understand how these variable change in response to climatic and oceanographic variables.

Rockhopper Penguin

Rockhopper Penguins were previously described as a single species with three subspecies: the Southern Rockhopper Penguin *Eudyptes c. chrysocome*, which breeds on the Falklands, and Islands around South America; the Eastern Rockhopper Penguin *Eudyptes c. filholi*, which breeds on sub-Antarctic Islands in the Indian Ocean sector of the Southern Ocean and south of New Zealand (Prince Edwards, Crozet, Kerguelen, Macquarie, Auckland, Antipodes and Campbell Islands); and the Northern Rockhopper Penguin *E. c. moseleyi*, which breeds on Tristan da Cunha, Gough Island, St Paul Island and Amsterdam Island. Using genetics, morphology and behavioural studies, Rockhopper Penguins were reclassified into two species, the Northern Rockhopper Penguin *E. moseleyi* and the Southern Rockhopper Penguin (sometimes referred to as the Western Rockhopper Penguin, comprising two subspecies *E. c. chrysocome* and *E. c. filholi;* Jouventin et al. 2006). Recent studies suggest further splitting the Southern Rockhopper Penguin into Western *E. chrysocome* and Eastern *E. filholi* Rockhopper Penguins (Banks et al. 2006, de Dinechin et al. 2009, Frugone et al. 2018, Cole et al. 2019). The taxonomic classification of rockhopper penguins complicates the assessment of their conservation status (Mays et al. 2019). In this study I follow Cole et al (2019) and Banks et al(2006) and identify the three Rockhopper Penguins as three separate species and this study treats the Eastern Rockhopper Penguin as a full species. From here on Eastern Rockhopper penguin is referred to as Rockhopper penguin and all other species are referred by their full names unless otherwise stated.

The global population of all Western/Eastern Rockhopper Penguins and Northern Rockhopper Penguins have decreased globally by 34% and 57%, respectively in the last four decades (Morrison et al. 2015, Mattern and Wilson 2018). The Eastern Rockhopper Penguin is still classified as a sub-species of the Southern Rockhopper Penguin by the IUCN and listed as Vulnerable. In the early 20th century, Campbell Island used to host the largest population of Eastern Rockhopper Penguins, with some 1.6 million breeding pairs. The population experienced a drastic decline of 94% from 1942 to 1984 and further decreased by 22% from 1984 to 2012 (Moors 1986, Cunningham and Moors 1994, Hull et al. 2004, Morrison et al. 2015). Cunningham and Moors (1994) suggested that this decline was caused by increases in ocean temperature, which may have affected prey availability resulting in reduced adult survival. Reduction of other Rockhopper Penguins has been observed on other islands. The Falkland Islands used to support the largest population of Southern Rockhopper Penguins (approx. 1.5 million breeding pairs), which decreased by approximately 91% from the 1930s to 2001. However, the population then increased by 51% from 2005–2010 (Pütz et al. 2002, Baylis et al. 2013). This fluctuation in the population of Southern Rockhopper Penguin was due to low breeding success in the earlier years and then an increase in juvenile and adult survival between 2006-2010 (Dehnhard et al. 2013a). Northern Rockhopper Penguins also experienced a drastic decline in their population of >90% since the 1950s at Gough Island (Guinard et al. 1998, Cuthbert et al. 2009). However, due to limited study of Northern Rockhopper Penguins during the earlier years there was no identified cause of their population decline (Cuthbert et al. 2009). The population of Northern Rockhopper penguins decreased by 50% from 1971-1993 at Amsterdam Island (Guinard et al. 1998). Recent factors that have been identified to impact these penguins at both Gough and Amsterdam Island include competition for prey with other top predators (Guinard et al. 1998, Barlow et al. 2002), landslips (Ryan 1993), predation by fur seals (Ryan and Kerr 2012) and incidental catches by fishing vessels (Ryan and Cooper 1991, Cuthbert et al. 2009).

Like Macaroni Penguins, Rockhopper Penguins extensively feed on krill but also feed on other species including mesopelagic fish and squids. At Marion Island they dominantly feed on *E. vallentini* and *T. vicina* (Brown and Klages 1987), whereas at Crozet, Campbell and Kerguelen Islands they mainly feed on *E. vallentini* (Brown and Klages 1987, Tremblay and Cherel 2003). During breeding, Rockhopper Penguins travel <500 km from their colonies. They travel <50 km at Marion Island during the brood guard stage, increasing their foraging distances to >100 km from the colonies during creche after the guard stage (Hull 1999, Tremblay and Cherel 2003, Rey and Schiavini 2005). This however changes at each stage of their breeding, with Rockhopper Penguins foraging farther offshore during creche compared to guard stage at Crozet, Kerguelen and Marion Island (Brown 1987, Tremblay and Cherel 2005, Whitehead et al. 2016, 2017). Rockhopper Penguins like Macaroni Penguins are visual feeders and mostly forage during the day. They usually dive to depths of <30 m although they have been recorded to dive to depths >100 m at Crozet, Kerguelen, Marion and Macquarie island (Brown 1987, Tremblay and Cherel 1999, 2000, 2003, Hull 2000, Whitehead et al. 2016, 2017).

Marion Island supported 42 000 pairs of Rockhopper Penguins which decreased by 70% from 1994–2008 (Crawford et al. 2009). Like Macaroni Penguins, Crawford et al. (2006) attributed the decline at Marion Island to low breeding success, producing fewer chicks than is needed to maintain a stable population (Crawford et al. 2003b). In the context of competitive exclusion theory, the two *Eudyptes* species have to segregate certain aspects of their ecology to facilitate co-existence on the same Island, when resources are limiting (Kneitel 2008). Macaroni and Rockhopper Penguins feed on the same species (euphausiids) but Macaroni Penguins forage farther, dive deeper and have been observed to feed on more fish compared to Rockhopper Penguins during breeding (Brown 1987, Brown and Klages 1987, Whitehead et al. 2017). Little is known about how these two species segregate their ecology and facilitate sympatric breeding on the island.

Study site

The sub-Antarctic Prince Edward Islands (PEIs) archipelago (46°52′ S, 37°51′ E) is comprised of two islands about 19 km apart, Marion Island (290 km^2) and Prince Edward Island (45 km^2). The two islands rise from a depth >3000 m and are connected by a shallow inter-island shelf ~200 m deep (Hanel and Chown 1998, Pakhomov and Froneman 1999). The closest landfall is Crozet Island 950 km to the east (Fig. 1.1, Ansorge et al. 2012).

The islands are volcanic in origin and are mostly surrounded by steep, cliff-faced coastlines, with only a few rocky, boulder or pebble beaches (Hanel and Chown 1998). The islands provide breeding and moulting sites for more than 5 million marine predators (seals and seabirds) including four species of penguins: King Penguin, Gentoo Penguin, Macaroni Penguin and Rockhopper Penguin (Ryan and Bester 2008). Apart from Gentoo Penguins, these species aggregate in large colonies and have a significant influence on the marine and terrestrial ecosystems at the islands, with penguins estimated to import more than 30 000 tons of guano, feathers, carcasses and eggs to Marion Island each year (Williams and Berruti 1978, Cooper and Brown 1990, Ryan and Bester 2008).

The Prince Edward Island archipelago lies in the path of the Antarctic Circumpolar Current (ACC), between the Sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front farther (APF) to the south in a transition zone called the Antarctic Polar Frontal Zone, separating warm sub-Antarctic surface waters from cooler Antarctic surface water (Fig. 1.1, Pakhomov et al. 2000, Ansorge et al. 2009). The dynamic variability in the latitudinal position of these fronts results in the mixing and interchanges of Antarctic and sub-Antarctic water masses creating a blend of sub-Tropical, sub-Antarctic and Antarctic species which affects the oceanographic and biological processes in the vicinity creating a diverse distribution of phytoplankton, zooplankton, benthic and demersal communities around the islands (Ansorge and Lutjeharms 2003, Durgadoo et al. 2010, Ansorge et al. 2012). The interaction of ACC with the shallow South-West Indian Ridge results in the advection of cyclonic and anticyclonic eddies eastwards directing them past the Prince Edwards Islands vicinity, which enhance local macro and mesoscale oceanographic environment around the Island and that is crucial for the survival of the high density of predators on the islands (Pakhomov and Froneman 1999, Pakhomov and Chown 2003, Lutjeharms and Ansorge 2008, Durgadoo et al. 2010, Ansorge et al. 2012).

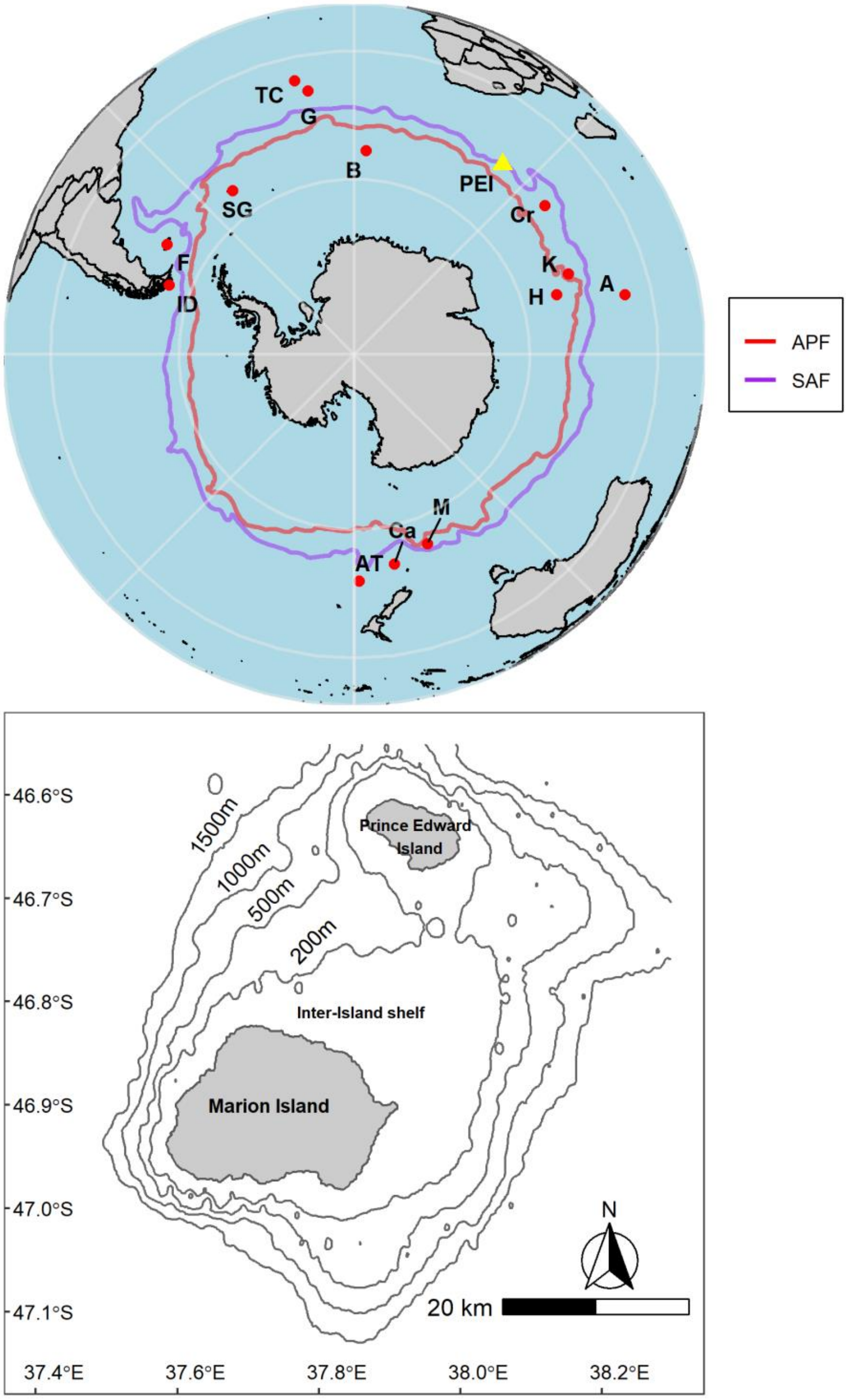


Figure 1.1: Top; The locations of major Macaroni and Rockhopper Penguin breeding islands (red circles) in relation to the Antarctic Polar Front (APF) and Sub-Antarctic Polar Front (SAF); Crozet (Cr), Kerguelen (K), Amsterdam (A), Heard (H), Macquarie (M), Campbells (C), Antipodes (AT), Ildefonse and Diego Ramirez (ID), Falkland (F), South Georgia (SG), Tristan da Cunha (TC), Gough (G), Bouvetoya (B), Prince Edwards Islands (PEI, yellow triangle). **Bottom;** The Prince Edwards Islands, comprising Marion and Prince Edward Island and surrounding bathymetry.

Thesis structure

The thesis is divided into three main chapters. These report the population trends and breeding biology of the two penguins (Chapter 2), their diet (Chapter 3) and relates inter-annual changes in their breeding biology and diet to environmental data (Chapter 4) to provide insights into potential drivers of their population dynamics. Data presented in the thesis cover a 26-year span from 1994–2019. Each chapter is written as a stand-alone chapter to facilitate publication, which leads to some duplication across the chapters.

Chapter 2 reports trends in the populations Macaroni and Rockhopper Penguins at Marion Island (updating Crawford et al. 2009), as well as key breeding performance parameters (breeding success, arrival date, body condition on arrival and fledgling mass; Crawford et al. 2006). From the late 1980s to the late 2000s, the population of Macaroni and Rockhopper Penguins has been decreasing at Marion Island (Cooper et al. 1997, Crawford and Dyer 2006). I assess whether changes in breeding biology parameters might explain the observed trends in both penguin population sizes.

Objectives:

1. Update the status of Macaroni and Rockhopper Penguins population trends at Marion Island.
2. Explore inter-annual variation and long-term trends in pre-breeding conditions (arrival dates and mass on arrival) and breeding performance (fledging mass and breeding success) of the two penguins.
3. Compare within and between pre-breeding (arrival dates and mass on arrival) and breeding variables (breeding success and fledgling mass) to explain trends in population sizes.

In chapter 3 I describe long-term trends in the diet of Macaroni and Rockhopper Penguins and whether changes in their diet can explain trends in their population at Marion Island. What penguins feed on is crucial to understanding how they interact with the environment around them and how their population responds to environmental changes (Boersma 2008, Trathan et al. 2015). Little is known about long-term variation in penguin diets at most breeding colonies. Macaroni and Rockhopper Penguins breeding at Marion Island mainly prey on crustaceans (krill), fish (myctophids) and cephalopods (squids) (Brown and Klages 1987). The two *Eudyptes* species breed sympatrically at the island, hence a level of segregation is expected to reduce competition for resources. Chapter 3 provides the first long-term diet study on Macaroni and Rockhopper Penguins at Marion Island to assess how these two closely related species limit competitions for resources.

Objectives:

1. Describe the long-term diet composition of the two penguins.
2. Compare diet composition between the two penguins.

Comparing diet to breeding performance can be used to understand predator response to prey availability (Waluda et al. 2012). Diet potentially reflects relative prey abundance within an ecosystem, and each prey type provides varying energy content (Boyd and Murray 2001). Ansorge et al. (2012) shows that the assemblage and abundance of marine organisms around the Prince Edward Islands are influenced by adjacent frontal latitudinal variability. This can be reflected by changes in prey composition of the two penguins in relation to the fronts. Climate variability affects penguins through changes in environmental conditions and prey availability, which is reflected through changes in their breeding and population dynamics (Bost and Le Maho 1993, Sydeman et al. 2012). Investigating how Macaroni and Rockhopper Penguin breeding performance responds to climatic signals is important to better understand how climate change could affect these species. The aims of Chapter 4 are three-fold for both Macaroni and Rockhopper Penguins.

Objectives:

1. Investigate the influence of inter-annual variation in diet in relation to breeding performance.
2. Explore large scale and local scale environmental drivers of variation in breeding performance and body condition on arrival.
3. Model diet composition in relation to the latitudinal position of the oceanic fronts.

In Chapter 5, I summarise the main findings of the thesis, how the two penguins facilitate co-existence on the same island in such large numbers. I identify other areas of further research concerning the two *Eudyptes* penguins at Marion Island.

Chapter 2: Long-term variation in the population size and reproductive performance of Macaroni and Eastern Rockhopper Penguins at Marion Island

Abstract

The population size and breeding performance of Macaroni and Rockhopper Penguins has been monitored annually at sub-Antarctic Marion Island since 1994, which has allowed for the assessment of population trends of these Vulnerable species. In this chapter I update the long-term population trends of these two penguin species and assess inter-annual variability in their breeding biology from their arrival dates, body condition on arrival, breeding success and fledgling mass, which could explain changes in their populations since 1994. Populations of Macaroni and Rockhopper Penguin declined by 45% and 66% respectively, at Marion Island from 1994–2019. Macaroni Penguin numbers decreased steadily at 1.9% per year, whereas Rockhopper Penguins decreased at 13% per year from 1994–2001, then stabilized, fluctuating between 55 000 and 85 000 pairs.

There was high inter-annual variability in arrival dates with no obvious trend. Male and female mass on arrival was correlated within each species, suggesting that both sexes foraged in broadly the same area prior to returning to the island to breed. There was no consistent trend in mass on arrival of Macaroni Penguins, but arrival masses of Rockhopper Penguins decreased from 1994 to the mid-2000s and then increased to 2019. Arrival date was negatively correlated with mass on arrival for both species, which meant the penguins were generally in better condition when they arrived early to breed. There was no trend in Macaroni Penguin breeding success, but breeding success of Rockhopper Penguins increased at all monitored colonies, which could explain why the population stabilized from 2001. Fledging mass of Macaroni and Rockhopper Penguins were more influenced by mass on arrival of males than females, which likely indicates sex specific provisioning rate in *Eudyptes* penguins. Fledgling mass was positively correlated to breeding success for Macaroni Penguins but not Rockhopper Penguins. This shows that larger and heavier chicks are likely to survive, and relatively small chicks have higher risk of mortality. Mass on arrival was positively correlated with breeding success for both Macaroni and Rockhopper Penguins. Pre-breeding condition could potentially be carried over to the breeding season, reflecting the importance of wintering conditions of both Macaroni and Rockhopper Penguins on their breeding performance at Marion Island. The high inter-annual variability in breeding performance of both species is probably shaped by environmental conditions before and during the breeding season.

Introduction

Penguins are one of the main consumers in the Southern Ocean and useful for monitoring ecosystem health (Borboroglu and Boersma 2015). Regular monitoring of penguins is important to assess population status, trends and detection of potential causes of population change such as climate change, habitat degradation, competition for prey resources, predation, diseases and other threats (Barbraud et al. 2020). Long-term trend analysis of penguins is important to determine their conservation status and predict their responses to environmental variation (Boersma et al. 2020). Research on their population dynamics can provide insights into variability of the ocean systems and changes occurring within the Southern Ocean (Boersma 2008). Environmental constraints are especially well-defined during breeding when adults must find sufficient food close to their breeding colonies.

Long term declines in the numbers of Macaroni and Rockhopper Penguins have been reported at most breeding islands where they have been studied over the past 50 years, resulting in both species being listed as Vulnerable (Weimerskirch et al. 1989, Williams and Croxall 1991, Cooper 1992, Cunningham and Moors 1994, Cooper et al. 1997, Woehler and Croxall 1997, CCAMLR 2000, Crawford et al. 2003a, 2003b, Putz et al. 2003, Lynnes et al. 2004, Kirkwood et al. 2007, Oehler et al. 2008, Biuw et al. 2010, Hiscock and Chilvers 2014, Horswill et al. 2014, 2016, Morrison et al. 2015, Barbraud et al. 2020, IUCN 2021) (Table 2.1). It is important to understand the reason behind these declines, especially given the lack of obvious drivers of decreases among *Eudyptes* penguins (e.g. competition with fisheries, bycatch, oil pollution, etc.) (Ropert-Coudert et al. 2019). In contrast, increase in the populations of both species have been observed at Crozet and Kerguelen Island. (Weimerskirch et al. 1989, Barbraud et al. 2020). However, these trends have only been observed at selected colonies, which may not reflect trends in the entire island populations. Recent population trends of these two species are not known at most breeding sites.

The Prince Edward Islands (larger Marion Island and smaller Prince Edward Island) supported 300 000 and 80 000 pairs of Macaroni and Rockhopper Penguins in 2008, representing 4% and 17% of the global population respectively (Crawford et al. 2009). This is unusual in that where the numbers of the two species are most similar compared to other islands where two *Eudyptes* species breed together (Jouventin et al. 1984, Weimerskirch et al. 1989, Kirkwood et al. 2007, Hiscock and Chilvers 2014). A level of segregation between the two species must exist to facilitate their coexistence in such large numbers on the island (Hardin 1960). Breeding populations at Marion Island have been monitored annually since the late 1980s as a contribution to the CCAMLR Ecosystem Monitoring Program (CEMP). The two penguin species are considered as key top predators and indicators of environmental change under CEMP (Cooper and Brown 1990, Cooper et al. 1997, CCAMLR 2000). The most recent published data from Marion Island indicated a decrease in the population of these two *Eudyptes* penguins (Crawford et al. 2003, 2009). In 2008/09, the island supported approximately 290 000 pairs of Macaroni and 42 000 pairs of Rockhopper Penguins, which was 30% and 70% less respectively, than population estimates made in 1994/95 (Crawford et al. 2009). These population declines at Marion Island have been attributed to inadequate breeding success, producing fewer chicks than is needed to maintain the population and climate-induced changes in prey availability around the island during the breeding season (Crawford et al. 2003a, 2003b, Crawford and Dyer 2006).

Macaroni Penguins leave Marion Island between late March and early April after molting ashore for 3–4 weeks. They remain at sea for six months to replenish their body condition before returning to breed, usually arriving in early October (Williams 1980). Males arrive roughly one week earlier than females, during which time they re-establish territories and start to build nests. A fasting period of 3–4 weeks occurs when courtship, mating and laying of two eggs occurs. Incubation lasts 34–40 days from early November to early December, with both sexes taking turns to incubate the eggs (Williams 1980). Once the egg hatches, the males guard the chicks for 20–24 days while the females forage for the chicks until they are old enough to thermoregulate and aggregate into creches. The chicks lose their down feathers 60–70 days after hatching, and fledge in mid-February (Williams 1980, Crawford and Dyer 2006). The adults then return to sea for 2–3 weeks to fatten up ahead of their annual molt (Williams 1980, Whitehead et al. 2017). The annual cycle of Rockhopper Penguins is similar, except it is delayed by 3–4 weeks. The incubation period lasts 28–32 days from late November to late December, and the chicks fledge in early March (Williams 1980, Crawford and Dyer 2006).

This study updates long-term data collected on Macaroni and Rockhopper Penguins' breeding population size and population trends at Marion Island. I report long term trends and inter-annual variability in their pre-breeding condition (arrival dates, mass on arrival) and breeding performance (fledgling mass, breeding success). I compare the relationships within and across pre-breeding and breeding performance, to explore possible reasons for the decrease in the population of Macaroni and Eastern Rockhopper Penguins at Marion Island from 1994–2019.

Table 2.1: Trend in the breeding populations of Macaroni and Eastern Rockhopper Penguins at their different breeding locations.

	Macaroni		Eastern Rockhopper			
Island	Breeding number	Trend	Breeding number	Trend	Reference	Data Year
Crozet	2 200 000	Decreasing	152 000	decreasing	(Woehler and Croxall 1997)	1962 - 85
Kerguelen	1 800 000	Decreasing	85 000	decreasing	(Weimerskirch et al. 1989)	1984 - 87
Heard and McDonald	1 000 000	Decreasing	10 000	decreasing	(Birdlife International 2021b, 2021a)	
Campbell	-	-	33 200	decreasing	(Morrison 2015)	2012
Antipodes	-	-	2 988	decreasing	(Hiscock and Chilvers 2014)	2011
Auckland	-	-	2 700–3 600	decreasing	(Cooper 1992)	1992
Ildefonso and Diego Ramirez	21 260	decreasing	219 100	decreasing	(Kirkwood et al. 2007)	2002
South Georgia	1 000 000	decreasing	-	-	(Birdlife International 2021a)	
Bouvetoya	1 100	decreasing	-	-	(Biuw et al. 2010)	2007 - 08
Prince Edward	302 000	decreasing	80 000	decreasing	(Crawford et al. 2009)	2008

Methods

Breeding population trends

The number of breeding pairs of Macaroni Penguins were counted annually around the island between late November and early December from 1994 to 2019 when all pairs were presumed to be incubating. Counts were done using tally counters and binoculars, making use of natural features like terraces to demarcate the colonies into smaller sections, the counts were repeated at least 2–3 times per colony to estimate a confidence interval. Fixed concrete markers with numbered riser poles were placed 2 m outside the edges of the two largest Macaroni Penguin colonies at Bullard North (n = 45) and Kildalkey Bay (n = 40), to track changes in the area occupied by the penguins at the colonies (Fig. 2.1a). Fourteen 5 m × 5 m randomly-selected fixed quadrats were marked with concrete blocks and riser poles sited at the Bullard North colony and 18 at Kildalkey Bay (Crawford et al. 2003a). The riser poles allow these quadrats to be readily located in each colony. Active nests were counted by approaching each quadrat slowly and cautiously to minimise disturbance during counts. The number of breeding pairs for each colony was estimated, from the mean density of nests in the quadrats and the total colony area. The methods used were consistent over time, so any error in area estimation were unlikely to influence relative changes in population estimates. Counts of breeding pairs of Macaroni Penguins were also made each year at Macaroni Bay (North), Archway Bay, Van den Boogaard and Bullard South. Counts in 2001 were conducted three weeks later than in other years, hence the counts were multiplied by a correction factor of 1.3 based on the number of active nests counted at Macaroni Bay (North) decreasing from 207 pairs in late November to 161 pairs on 18 December (Fig. 2.1a, Crawford et al. 2003a).

For Rockhopper Penguins, counts of breeding pairs were carried out annually from 1994 to 2019 at Trypot Fault, Trypot Hole and Van den Boogaard in the north-eastern part of Marion Island (Fig. 2.1b). These counts were undertaken from outside the colonies and are unlikely to have disturbed the breeding birds. The counts were estimated at all visible localities using tally counter and binoculars. A correction factor was also applied to Rockhopper Penguins counts in 2001 as with Macaroni Penguins (Crawford et al. 2003b). Counts were also made along two sectors of the island, from Storm Petrel Bay to Hansen Point and Rook's Bay to Swartkop Point (excluding Toffee Lava, Fig. 2.1b) in 1994 and annually from 1996 to 2019. These sectors were chosen because of the relatively greater ease of counting colonies in these coastal sectors around Marion Island. The two sectors account for approximately 24–36% of the total population (Crawford et al. 2003b). In 1994, 1996, 2001 and from 2008–2019, active nests of Rockhopper Penguins were counted at all breeding localities (excluding Toffee Lava and Santa Rosa) around Marion Island between late November and mid-December.

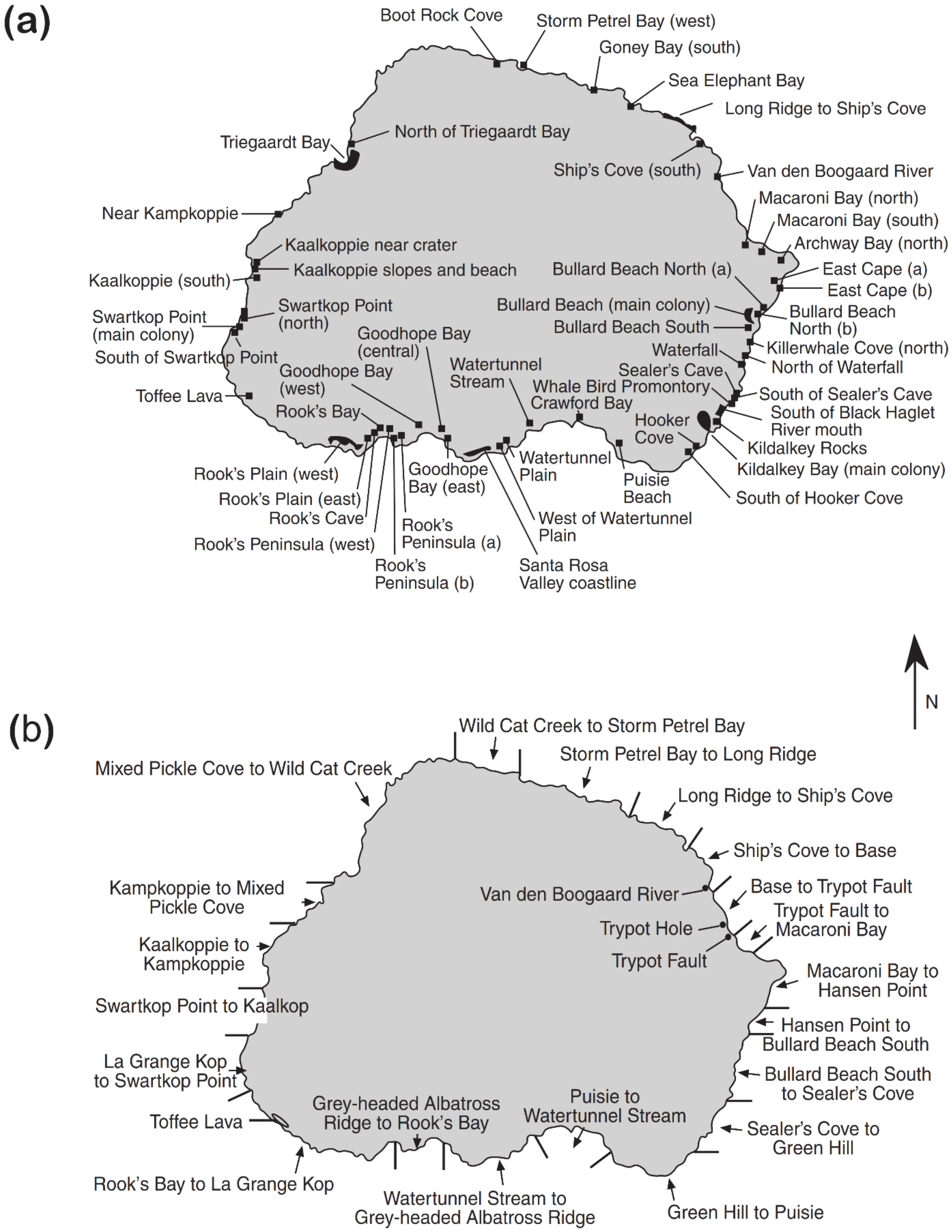


Figure 2.1: Marion Island showing the breeding colonies observed for Macaroni Penguins (a) and the sections of the breeding colonies for Eastern Rockhopper Penguins (b).

Arrival dates and weights

Observations of penguin first arrival dates at Marion Island commenced at the beginning of October for Macaroni Penguins and at the end of October for Rockhopper Penguins each year. The observations were done daily ahead of the anticipated arrival to be confident that the penguins have arrived. The dates of weighing of males and females *Eudyptes* penguins at Bullard beach were used as surrogates of the timing of their arrival at the island. The penguins were weighed on their arrival.

The “mass on-arrival” of adult male, female penguins and pre-departure mass of fledgling penguins were measured at Bullard North for Macaroni Penguins, and between Duiker’s Point and Kildalkey Beach along the east coast for Rockhopper Penguins. Sexes of adults were discriminated using bill measurements. Males are larger than females, have longer, deeper bills and arrive at colonies earlier than do females (Warham 1972, Marchant and Higgins 1990, Williams and Croxall 1991).

A sample of approximately 100 males and 100 females were weighed on arrival and 250 chicks were weighed at fledgling for Macaroni and Rockhopper Penguins each year (Supplementary Table S1). The masses of adults and chicks at fledgling were measured by catching the bird, placing it in a harness, which was then suspended from a spring balance and weighed to an accuracy of 0.1 kg. After weighing, each bird was marked with a green dye to avoid reweighing the same individual. Means of the body mass of adults and chicks at fledging were calculated ± standard deviation (SD) each year.

Breeding success

Breeding success of Macaroni Penguins was monitored from 1994/95–2019/20 at four localities: Van den Boogaard, Macaroni Bay, Archway Bay and Bullard South, a section of the Bullard North Beach colony south of the other colonies. All four colonies are on the north-eastern side of Marion Island for ease of access from the research station. Van den Boogaard and Macaroni Bay are both small colonies (10–40 pairs per year), Archway Bay is slightly larger (100–200 pairs) and Bullard South is the largest (1000–3000 pairs). Hatching success (number chicks hatched per pair) at these colonies was estimated from counts of hatched chicks (as close as possible to 4 January) and breeding success (number of chicks fledged per pair) from counts of chicks in crèches (as close as possible to 28 February about the time that the last chicks enter crèches (Crawford *et al.* 2003b), assuming that chicks that reach the creche stage would survive to fledge (Cooper et al. 1997). Each count was made three times on the same day by the same observer and the mean was used.

Breeding success of Rockhopper Penguins was monitored at three sites on the northeastern coast of Marion Island: Van den Boogaard, Trypot Fault and Trypot Hole. Counts of the number of newly hatched chicks and chicks in creches were made as close as possible to 4 January for Macaroni Penguins and 28 February for Rockhopper Penguins (Cooper et al. 1997).

Data Analysis

The Trends and Indices for Monitoring Data (TRIM, *rtrim*) package in R was used to determine trends with 95% confidence intervals in populations of Macaroni and Rockhopper Penguins on Marion Island (Bogaart et al. 2020). The *rtrim* model annual counts using a Poisson distribution, accounting for serial correlation, data overdispersion and can handle data with high proportion of missing counts. Imputing the missing counts estimated based on the absolute value of the specific colony and the general trend of the whole group of colonies in that year (Pannekoek and Van Strien 2005). Linear models were used concurrently to determine the rate of change in numbers of breeding pairs presented ± standard error. The island breeding pair counts are presented ± 95% confidence intervals for Macaroni Penguins. For Rockhopper Penguins, counts of breeding pairs in the two large coastal sections was used to estimate the overall breeding pairs trend. The breeding pairs counts of the two sections are presented ± 95% confidence intervals.

The study made use of time series datasets, thus before each analysis the datasets were checked for autocorrelation errors using *acf()* and *pcf()* plots and stationarity using the Augmented Dickey Fuller test (ADF Test) and the KPSS test (Shumway and Stoffer 2017). Penguin arrival dates were converted to Julian day for analysis with correction for leap years by adding a day for non-leap years. Student t-tests were used to assess difference between two univariate datasets; the data were first tested for normality using qqplot and Shapiro-Wilks's test and if the data were not normal, they were transformed and if normality was not achieved non- parametric test, Mann-Whitney U-tests were used. Post-hoc pairwise comparisons of breeding sites were done with a Bonferroni correction.

A cross correlation function *ccf () and a simple linear correlation test* was used to assess whether there is a relationship between two time series (at lag 0). If the time series was not stationary, the time series X (independent) were pre-whitened using Arima (1,0,0). I then filtered and transformed each time series according to the Arima model into x and y where x becomes white noise (independent of autocorrelation errors and stationary), then I ran *ccf (x, y, lag = 0)*.

Results

Population trends

The overall estimated number of Macaroni Penguin breeding pairs decreased by 45% from 430 000 pairs (95% CI: 401 221–468 289) in 1994/95 to 238 000 pairs (95% CI: 216 878–267 354) in 2019/20 at a rate of 1.9 ± 0.25% per year (linear regression, $t_{1,24} = 7.41$, $p < 0.01$) per year (Fig. 2.2). Most of the breeding pairs of Macaroni Penguins (80–92%) were found at Bullard North and Kildalkey Bay, and the rates of decline at these two colonies reflected the overall island trend. At Bullard North the estimated number of breeding pairs decreased from 170 000 to 84 000 pairs from 1994/95 to 2019/20 (1.8 ± 0.38% per year; linear regression, $t_{1,24} = 4.8$, $p < 0.01$). At Kildalkey the number of breeding pairs decreased from 184 000 to 124 000 pairs (1.5 ± 0.34% per year; linear regression, $t_{1,24} = 3.9$, $p < 0.01$, Fig. 2.2). Inter-annual variation in the numbers of breeding pairs at the two colonies were positively correlated ($r = 0.47$, $p = 0.01$, $df = 24$) over the length of the study period. The number of breeding pairs at all the other smaller colonies (excluding Kildalkey Bay and Bullard North) decreased from 79 000 pairs (95% CI: 66 917–94 527) to 29 000 pairs (95% CI: 23 625–42 251) at a rate of 3.3 ± 0.6% (linear regression, $t_{1,24} = 5.8$, $p < 0.01$, Fig. 2.2).

The combined number of breeding pairs of Macaroni Penguins at Archway Bay, Bullard South, Macaroni Bay and Van den Boogaard decreased from about 4 000 pairs in 1994/95 to 1 300 pairs in 2019/20 by 68% at a rate of 5.5 ± 0.72% per year (linear regression, $t_{1,24} = 7.52$ $p < 0.01$). Macaroni Bay had the largest decrease from 411 to 34 pairs (92%) followed by Van den Boogaard (33–4 pairs, 88%), Bullard South (3 680–1 259 pairs, 66%) and Archway Bay (210–84 pairs, 60%, Fig. 2.3). There was a positive and significant relationship in inter-annual variation of breeding numbers between the monitored colonies of Macaroni Penguins ($p < 0.01$, $r_{24} = 0.51–0.90$) with the strongest relationship being between Macaroni Bay and Van den Boogaard. The breeding numbers of Macaroni and Rockhopper Penguins were positively correlated between all the four monitored colonies, Archway Bay-Bullard South ($r_{24} = 0.56$, $p = 0.03$), Archway Bay-Macaroni Bay ($r_{24} = 0.66$, $p < 0.01$), Archway Bay-Van den Boogaard ($r_{24} = 0.68$, $p < 0.01$), Bullard South-Macaroni Bay ($r_{24} = 0.67$, $p < 0.01$), Bullard South-Van den Boogaard ($r_{24} = 0.51$, $p = 0.007$), Macaroni Bay-Van den Boogaard ($r_{24} = 0.90$, $p < 0.01$).

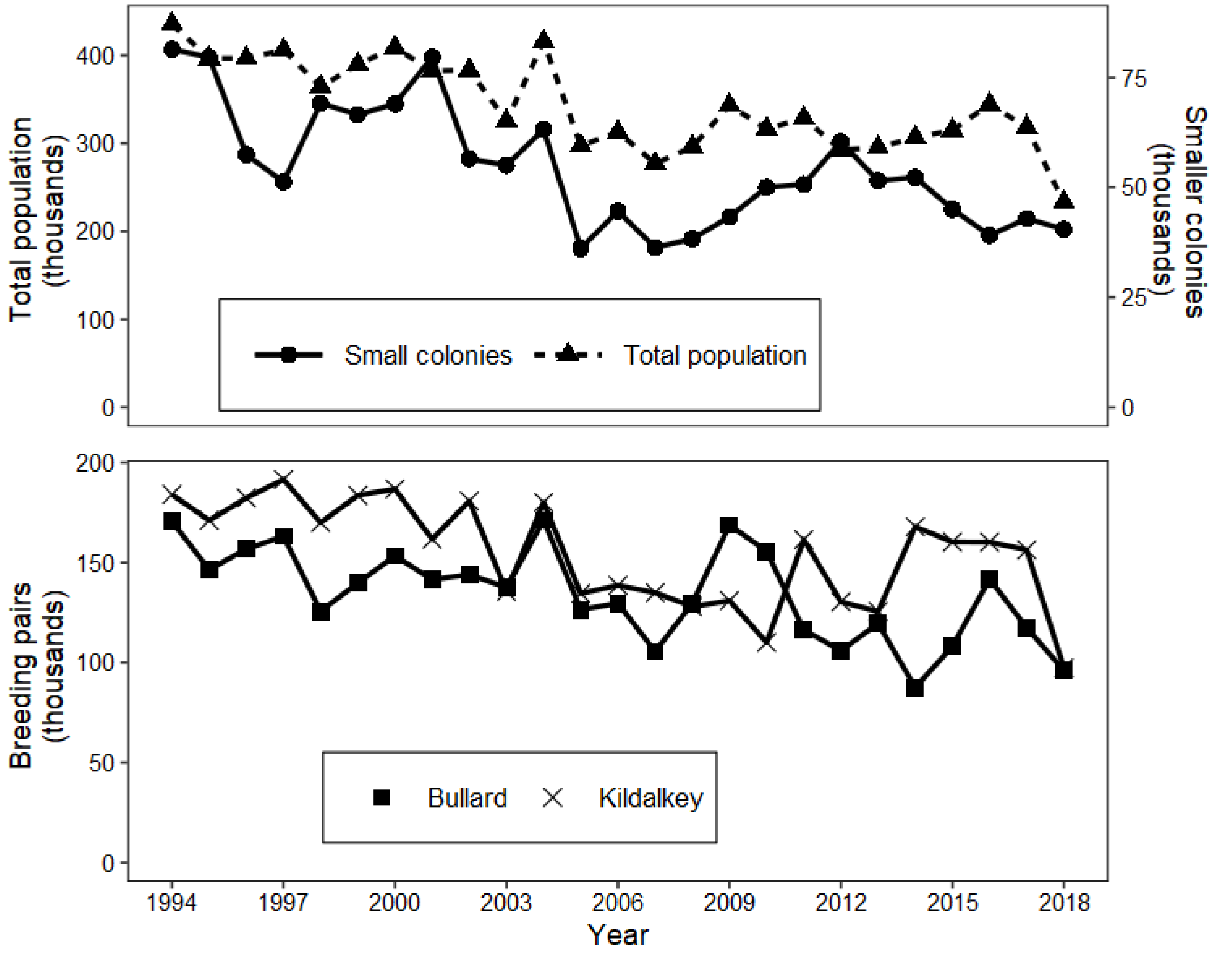


Figure 2.2: Trends in the number of breeding pairs of Macaroni Penguins at all monitored colonies on Marion Island from 1994/95–2018/19.

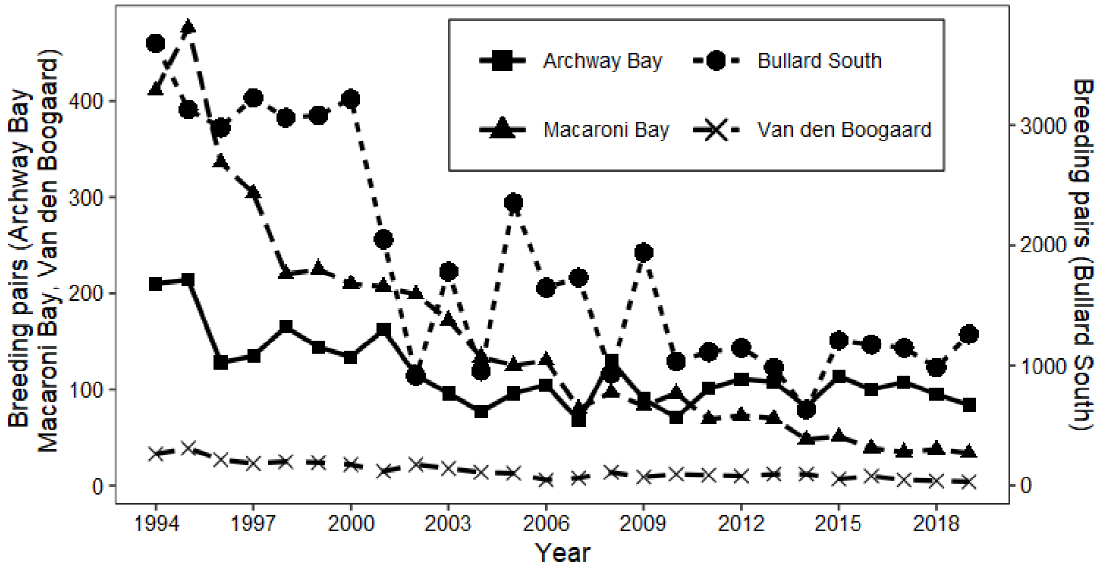


Figure 2.3: Trends in the number of breeding pairs of Macaroni Penguins at Archway Bay, Bullard South, Macaroni Bay and Van den Boogaard.

The estimated number of Rockhopper Penguin breeding pairs in the two regularly monitored coastal sections of Marion Island decreased by 59% from 43 000 (95% CI: 34 321–50 587) pairs to 19 000 (95% CI: 13 475–24 450) pairs from 1994/95 to 2001/02 at a rate of 8.4 ± 2.1% per year (linear regression, $t_{(1,6)}$ = 4.1, p = 0.01) and was relatively stable from 2002/03–2019/20, with a non-significant decrease of 0.9 ± 0.5 % per year (linear regression, $t_{1,16}$ = 2.03, p = 0.06, Fig. 2.4). The total estimated population of Rockhopper Penguins breeding at Marion Island decreased by 66% from 173 000 pairs (95% CI: 154 193 - 190 996) in 1994/95 to 53 000 pairs (95% CI: 44 377 - 65 677) in 2019/20 (Fig. 2.4). Most of this decrease occurred before 2002, when the population decreased by 13.0 ± 2.6% per year (linear regression, $t_{1,6}$ = 5.1, p = 0.01). Thereafter, the population stabilized with a non-significant decrease of 1.1 ± 0.5% per year (linear regression, $t_{1,16}$ = 2.2, p = 0.05, Fig. 2.4), fluctuating between 55 000–85 000 pairs (Fig. 2.4).

There was a significant decrease in the combined number of breeding pairs of Rockhopper Penguins at Trypot Fault, Trypot Hole and Van den Boogaard from 306 pairs in 1994/95 to 128 pairs 2019/20, at 4.2 ± 0.93% per year (linear regression, $t_{1,24}$ = 4.47, p < 0.01). Van den Boogaard had the highest number of breeding pairs while Trypot Hole and Trypot Fault were generally similar (Fig. 2.5). Trypot Hole had the largest decrease (69%) from 80 pairs to 25 pairs followed by Van den Boogaard (57%, 157–67 pairs) and Trypot Fault (48%, 69–36 pairs; Fig. 2.5). The number of breeding pairs of Rockhopper Penguins were positively related between all three monitored colonies: Trypot Hole-Trypot Fault (r_{24} = 0.62, p = 0.001), Trypot Hole-Van den Boogaard (r_{24} = 0.51, p = 0.01) and Trypot Fault-Van den Boogaard (r_{24} = 0.75, p < 0.01).

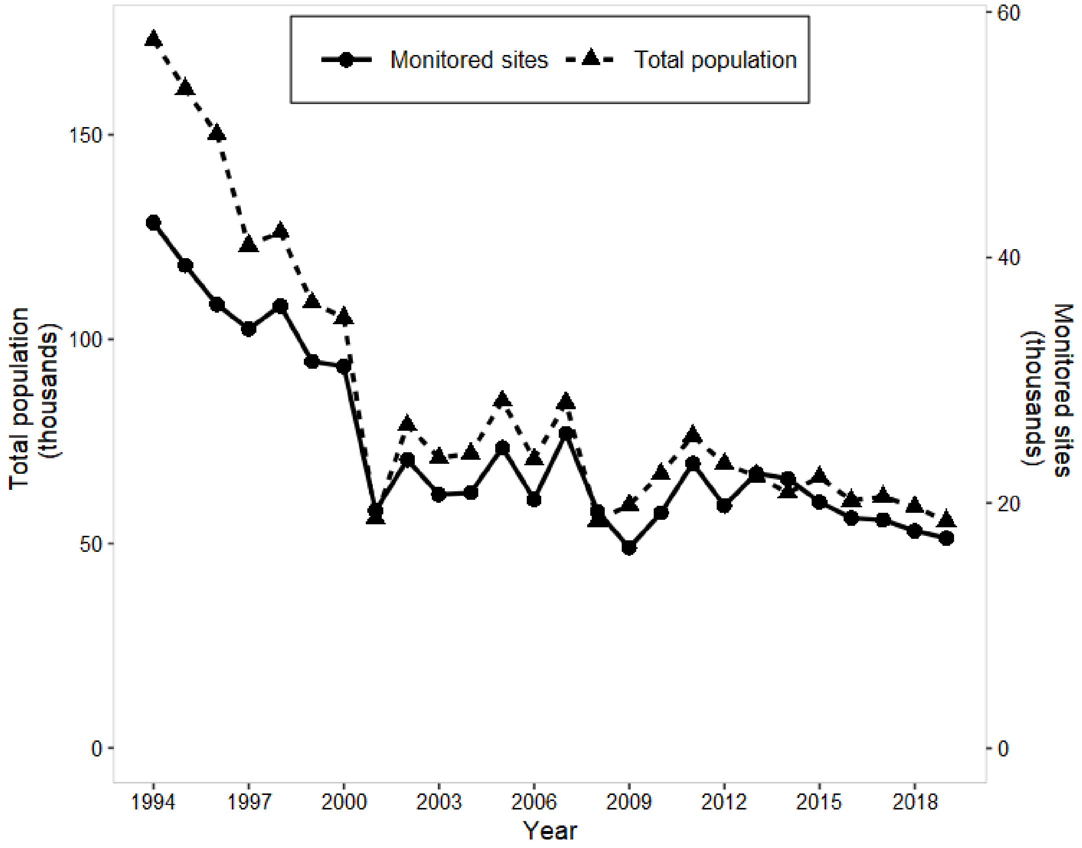


Figure 2.4: Trend in the number of breeding pairs of Eastern Rockhopper Penguins at all colonies and the regularly monitored sites at Marion Island from 1994/95–2018/19.

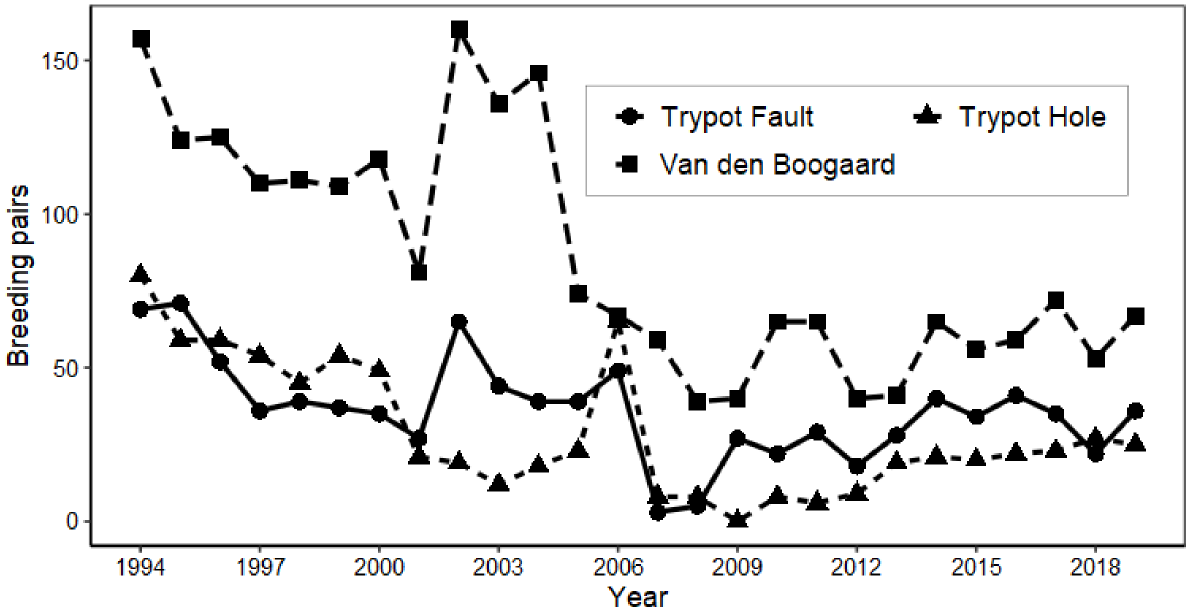


Figure 2.5: Trends in the number of breeding pairs of Eastern Rockhopper Penguins at Trypot Fault, Trypot Hole and Van den Boogaard from 1994/95–2018/19.

Breeding success

Among Macaroni Penguins, breeding success generally was highest at Bullard South and lowest at Macaroni Bay, with complete breeding failure at the latter colony in 2010, 2011, 2013 and 2015. Breeding success averaged 0.55 ± 0.17 chicks/pair at Bullard South, 0.45 ± 0.13 chicks/pair at Archway Bay, 0.38 ± 0.26 chicks/pair at Van den Boogaard and 0.17 ± 0.14 chicks/pair at Macaroni Bay (Table 2.2). There was no significant long-term trend in breeding success of Macaroni Penguins at any of the monitored sites ($p > 0.05$) except at Van den Boogaard (generalised least squares, $t_{24} = -4.03$, $p = 0.001$) where breeding success decreased over the study period. There was a positive but not significant relationship in inter-annual variation of breeding success between the monitored colonies of Macaroni Penguins ($p > 0.05$), except between Archway and Bullard South ($r_{21} = 0.39$, $p = 0.051$), which was the strongest relationship found between the monitored colonies. Hatching success and fledging success were negatively correlated at Archway Bay ($r_{24} = -0.43$, $p < 0.03$), Bullard South ($r_{24} = -0.33$, $p = 0.12$) and Van den Boogaard ($r_{24} = -0.18$, $p = 0.37$) but not Macaroni Bay ($r_{24} = 0.38$, $p = 0.06$) and only Archway Bay had a significant relationship.

Table 2.2: Summary of the hatching success (hatched per pair), fledgling success (fledged per hatch) and breeding success (fledged per pair) of Macaroni and Eastern Rockhopper Penguins at the monitored sites (mean ± SD).

Site	Hatching success	Fledging success	Breeding success
Macaroni Penguin			
Archway Bay	0.52 ± 0.15	0.88 ± 0.21	0.45 ± 0.12
Bullard South Beach	0.71 ± 0.17	0.80 ± 0.21	0.54 ± 0.16
Macaroni Bay	0.31 ± 0.25	0.52 ± 0.34	0.18 ± 0.15
Van den Boogaard	0.60 ± 0.27	0.62 ± 0.43	0.37 ± 0.27
Overall	0.61 ± 0.22	0.79 ± 0.19	0.49 ± 0.16
Eastern Rockhopper Penguin			
Trypot Fault	0.63 ± 0.27	0.67 ± 0.39	0.44 ± 0.26
Trypot Hole	0.62 ± 0.25	0.67 ± 0.50	0.42 ± 0.29
Van den Boogaard	0.69 ± 0.18	0.82 ± 0.28	0.55 ± 0.19
Overall	0.67 ± 0.14	0.77 ± 0.24	0.52 ± 0.17

Combined breeding success of the four Macaroni Penguin colonies ranged from 0.15 (1996/97) to 0.85 (2014/15) chicks/pair, with an overall mean of 0.49 ± 0.16 (n = 26, Fig. 2.6). There was tendency for breeding success to increase over the study period, but this was not significant (generalised least squares, $t_{24} = 1.26$, $p = 0.220$, Fig. 2.6).

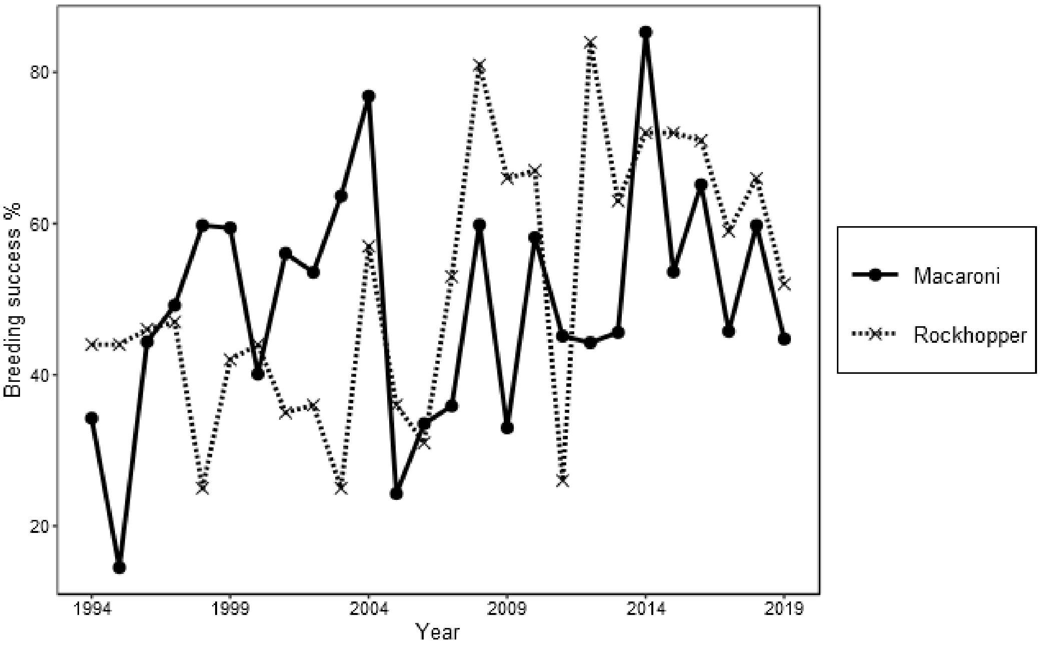


Figure 2.6: Trends in the breeding success (chicks fledged per breeding pair) of Macaroni and Eastern Rockhopper Penguins at Marion Island between 1994/95–2018/19.

The breeding success of Rockhopper Penguins averaged 0.55 ± 0.19 chicks/pair at Van den Boogaard, 0.44 ± 0.26 chicks/pair at Trypot Fault and 0.42 ± 0.29 chicks/pair at Trypot Hole with an increasing trend at all three sites (Trypot Hole: generalised least squares, $t_{24} = 2.13$, $p = 0.04$; Trypot Fault: $t_{24} = 3.65$, $p = 0.001$; Van den Boogaard: $t_{24} = 0.93$, $p = 0.361$). Inter-annual variation in breeding success at the monitored colonies were similar and strongest between the nearby colonies of Trypot Fault and Trypot Hole ($r_{24} = 0.63$, $p = 0.003$) and not significant between Trypot Fault and Van den Boogaard ($r_{24} = 0.33$, $p = 0.315$) and between Van den Boogaard and Trypot Hole ($r_{24} = 0.10$, $p = 0.65$). Hatching success and fledging success of Rockhopper Penguins was not significantly correlated at all three colonies: Trypot Fault ($r_{24} = 0.30$, $p < 0.14$), Trypot Hole ($r_{24} = 0.14$, $p < 0.49$) and Van den Boogaard ($r_{24} = -0.11$, $p = 0.60$).

Overall breeding success of all the three colonies ranged from 0.25 (1998/99, 2003/04) to 0.84 (2012/13) chicks/pair, with an overall mean of 0.52 ± 0.17 (n = 26, Fig. 2.6). Over the entire study period, Rockhopper Penguins showed a significant increase in breeding success (t_{24} = 3.30, p = 0.003; Fig. 2.6).

Adult arrival date

The mean arrival date of Macaroni Penguin males was 9 October (± 4 days, range 2–17 October), 7 ± 4 days earlier than females (16 October ± 5 days, range 06–25 October, $t_{49.8}$ = -5.41, $p < 0.001$). The latest arrival date was in 2007 for both male and females. Annual arrival dates were significantly correlated between males and females (r_{24} = 0.66, p = 0.001). There was no significant trend in the arrival dates of either male (generalised least squares, t_{24} = -0.99, p = 0.332) or female (t_{24} = -1.29, p = 0.208) Macaroni Penguins over the years (Fig. 2.7). Macaroni Penguins overall breeding success was negatively correlated with arrival dates, breeding success was high when they arrived early to breed, however, this relationship was only significant for females (r_{24} = -0.48, p = 0.02) and not males (r_{24} = -0.33, p = 0.12).

Rockhopper Penguins arrived 27 ± 5 days later than Macaroni Penguins (n = 26 years). The longest difference in arrival between the two species was 37 days in 2002 for males and 38 days in 2019 for females and the shortest difference was males (19 days, 1994) and females (12 days, 2009). There was no significant trend in the interval between arrival of the two species for both male (generalised least squares, t_{24} = 1.48, p = 0.15) and female (t_{24} = 01.05, p = 0.31) over the study period. The mean date of arrival of Rockhopper Penguin males was 05 November (± 4 days, range 28 October–13 November), female: 8 November (± 3 days, range 3–14 November). There was no significant trend in the arrival dates against time for either males (generalised least squares, t_{24} = 0.47, p = 0.645) or females (t_{24} = -0.49, p = 0.628) Rockhopper Penguins over the entire study period (Fig. 2.7). The latest arrival date was in 2006 for males and 1998 and 2002 for females. Male and females arrived on the Island at the same time between 2005–2011, 2013–2015 and 2017–2018. On the years they didn't arrive on the same day the annual arrival dates between males and females were significantly correlated (r_{24} = 0.84, $p < 0.001$). There was negative but non-significant relationship between overall breeding success and arrival dates of both male (r_{24} = -0.19, p = 0.357) and female (r_{24} = -0.17, p = 0.418) Rockhopper Penguins.

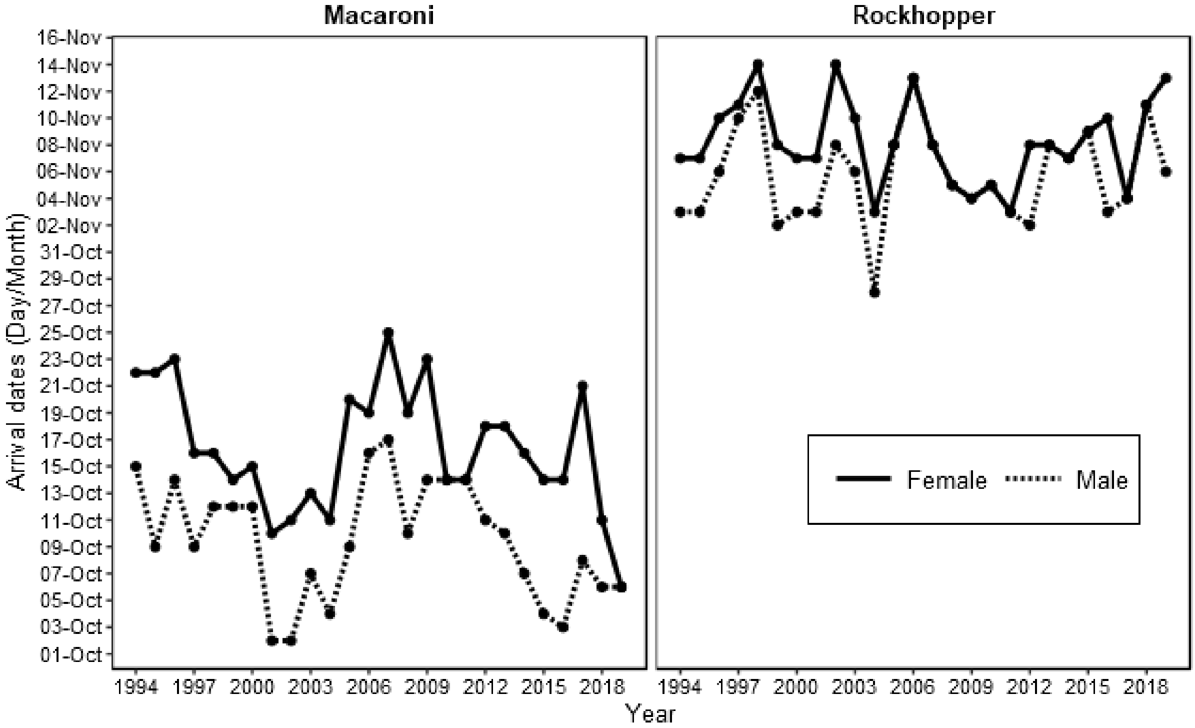


Figure 2.7: Annual arrival dates of male (dashed line) and female (solid line) Macaroni and Eastern Rockhopper Penguins on Marion Island 1994/95–2019/20.

Mass on arrival of adults

The mass on arrival for both male and female Macaroni Penguins had no significant trend over time (Fig. 2.8). There was no difference in mass on arrival between male and female Macaroni Penguins ($t_{49.9}$ = 1.48, p = 0.14) and inter-annual variation in their weights was positively correlated (r_{23} = 0.69, p < 0.001). Mass on arrival of adults had a negative but non-significant relationship against arrival dates for both male (r_{24} = - 0.27, p = 0.19) and female (r_{24} = -0.25, p = 0.21) Macaroni Penguins were generally lighter when they arrived late. Mass on arrival had a positive relationship against overall breeding success but it was only significant for females (r_{24} = 0.40, p = 0.046) and not males (r_{24} = -0.36, p = 0.07). Macaroni Penguins tended to have a higher breeding success when the parent weighed more on arrival.

There was no difference in arrival mass between male and female Rockhopper Penguins ($t_{49.6}$ = -0.85, p = 0.40) and their weights were positively correlated (r_{24} = 0.72, p < 0.001). The mass on arrival decreased from 1994 to 2007 for both male (generalised least squares, t_{14} = -3.68, p = 0.003) and female (generalised least squares, t_{14} = -2.24, p = 0.04) Rockhopper Penguins, when the lowest mass was recorded (males: 2.59 ± 0.31 kg; females: 2.56 ± 0.34 kg, both n = 100). Thereafter, the average mass on arrival of both sexes tended to increase, fluctuating between 3.0–3.5 kg, but this pattern was not statistically significant for both males (generalised least squares, t_{24} = -18, p = 0.86) or females (generalised least squares, t_{13} = 0.503, p = 0.63, Fig. 2.8). There was a negative correlation between mass on arrival against arrival dates, but this was only significant for males (r_{24} = - 0.55, p = 0.003), not females (r_{24} = -0.31, p = 0.12). Similarly, mass on arrival was positively correlated with overall breeding success but this was only significant for males (r_{24} = 0.53, p = 0.01) and not females (r_{24} = 0.34, p = 0.09).

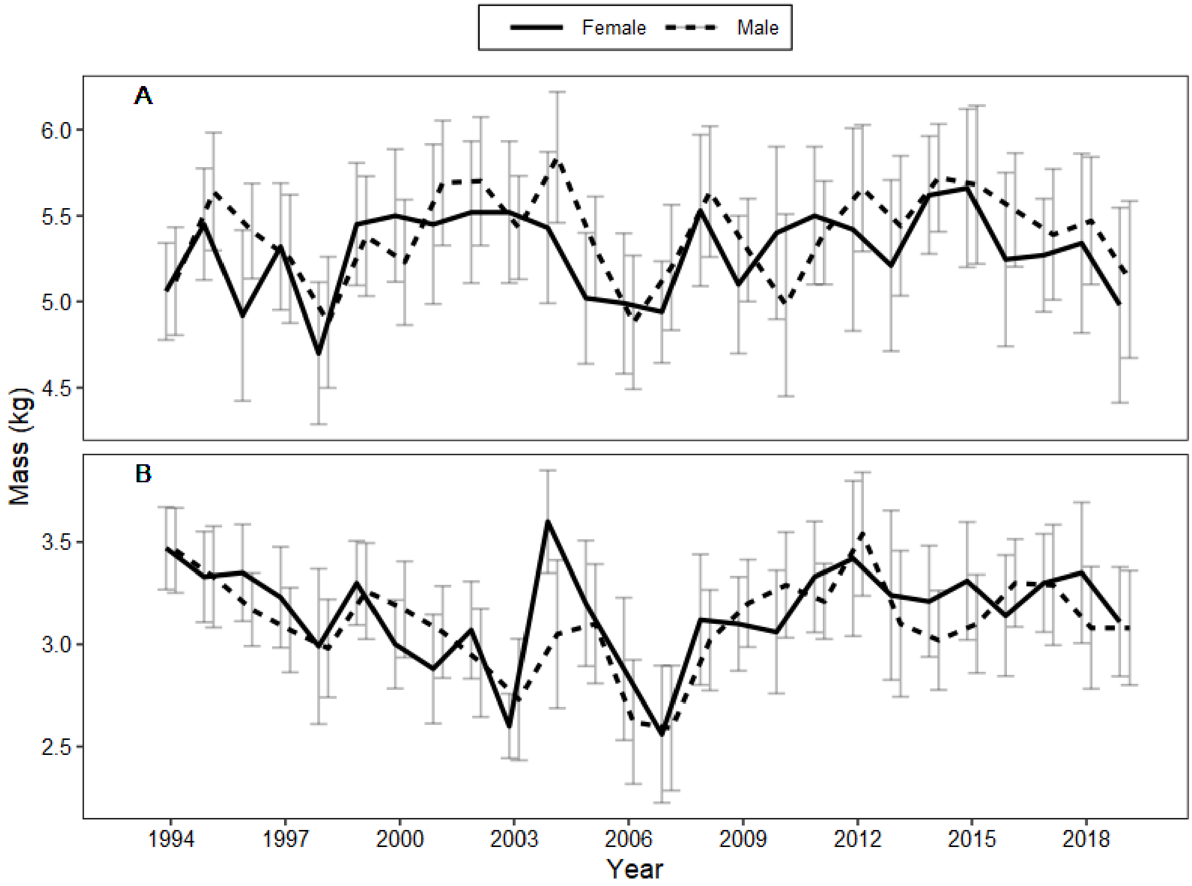


Figure 2.8: Trends in the mass on arrival of Macaroni (A) and Eastern Rockhopper (B) Penguins at Marion Island 1994/95–2019/20

Fledgling weights

Average fledgling mass of Macaroni Penguins ranged from 2.13 ± 0.60 kg (2006) to 4.15 kg ± 0.57 kg (2004), with no clear trend over time (Fig. 2.9). Fledgling weights of chicks were positively correlated with male arrival weights (r_{24} = 0.40, p = 0.04) but there was no relationship with female arrival weights (r_{24} = -0.06, p = 0.79). Fledgling weights of Macaroni Penguins were negatively correlated with arrival date, but the relationship was only significant for males (r_{24} = -0.54, p = 0.01) not females (r_{24} = -0.22, p = 0.29). Macaroni Penguins fledged heavier chicks when the parents arrived earlier and weighed more. There was a positive relationship between overall breeding success of Macaroni Penguins and fledgling mass (r_{24} = 0.40, p = 0.04).

Average fledgling mass of Rockhopper Penguins ranged from 1.32 ± 0.30 kg (2006) to 2.13 ± 0.25 kg (1997), with no clear trend over time (Fig. 2.9). There was no significant relationship between fledgling weight and arrival mass of both male (r_{24} = 0.25, p = 0.25) and female (r_{24} = 0.14, p = 0.50) Rockhopper Penguins. There was no significant relationship between fledgling weight and arrival dates of both males (r_{24} = -0.02, p = 0.89) and females (r_{24} = -0.24, p = 0.25). There was no significant relationship between fledgling mass and breeding success (r_{24} = 0.12, p = 0.57).

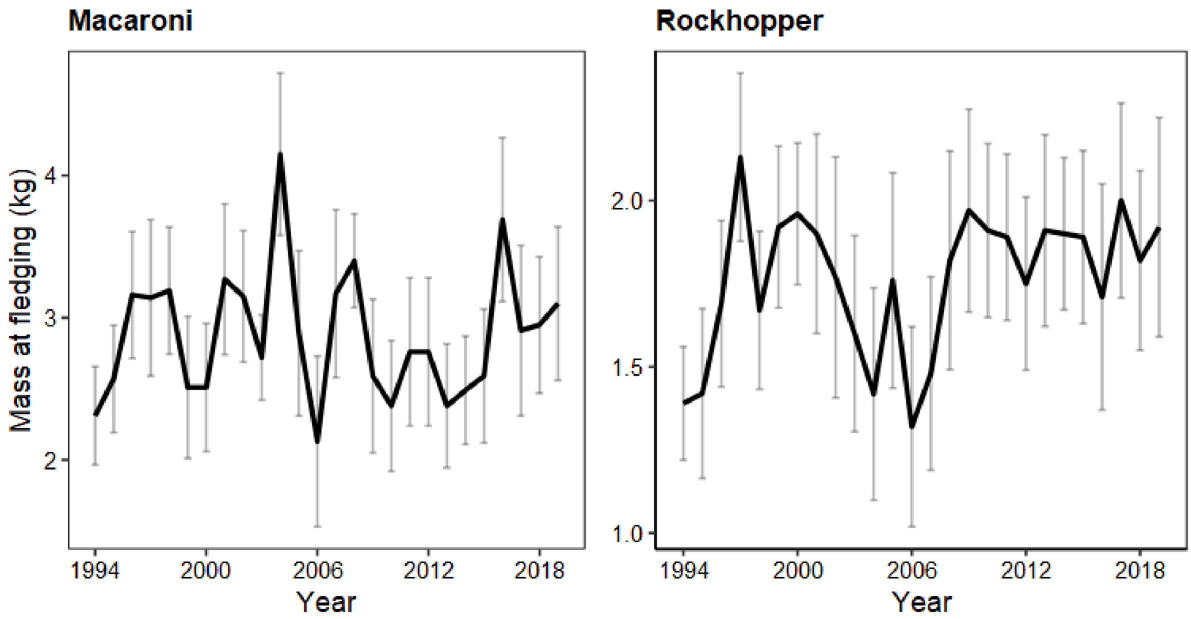


Figure 2.9: Trends in the mass of chicks at fledging of Macaroni and Eastern Rockhopper Penguins at Marion Island 1994/95–2019/20.

Discussion

This study expands on the work done by Crawford and Dyer (2006), however it is the longest research on these *Eudyptes* species' inter-annual variation in breeding population and breeding performance at Marion Island since (Cooper et al. 1997). In the early 1983 and 1984 there was an estimated 405 084 and 144 235 pairs of Macaroni and Rockhopper Penguins breeding at Marion Island, respectively (Watkins 1987, Cooper and Brown 1990). Counts of similar sections were carried out in 1994/95 and the breeding population increased to 433 723 and 173 077, however the increasing trend since the 1980s was not statistically significant. By

2003 a decreasing trend of 18% and 61% of Macaroni and Rockhopper Penguins, respectively was reported at Marion from 1994–2003 (Crawford et al. 2003a, 2003b). In 2009 the population of the two *Eudyptes* penguins was reducing at a faster rate of 30% and 70% from 1994/95 to 2009 (Crawford et al. 2009). My current study maintains the methods of collection carried out by Crawford (2009) and are in consensus with the continued decrease in the population of these two species since 1994, with the overall breeding population of Macaroni and Rockhopper Penguins decreasing by 45% (434 000–238 000) and 66% (173 000–53 000) from 1994/95–2019/20.

The breeding population of Macaroni Penguins in 2019/20 is almost half the estimated population in 1984 and over the study period the species has been decreasing at a rate of 1.9 ± 0.25% per year. The overall trend in Macaroni Penguin population is determined by the two main colonies Bullard Beach and Kildalkey where 80–92% of Macaroni Penguins were found breeding over the study period. Outside these two main colonies Macaroni Penguins decreased at 3.3 ± 0.6% per year, almost twice the rate of decline compared to the two main breeding colonies. This is possibly due to increased chances of adults and offspring survival in large colonies because a reduced proportion of breeders are exposed to the vulnerable colony edge in larger colonies which negates the effect of predation (e.g.by Brown Skuas *Stercorarius antarcticus* and Giant petrels) and climate which is possibly compounded in smaller colonies (Tenaza 1971, Robertson 1986, Jackson et al. 2005, Wilson et al. 2010, Schmidt et al. 2021).

Macaroni Penguins have experienced severe declines at South Georgia, where most of the world's population of this species used to be found at >5 million in the 1970s (Croxall and Prince 1979). According to Trathan et al. (2012), recovery in Antarctic Fur Seal numbers since their exploitation in the last century has exacerbated the reduction in numbers of Macaroni Penguin. This has also increased the overlap in fishing grounds between these two species and a resultant competition for Antarctic Krill *Euphausia superba* within the Scotia Sea. This contrast in population trend between two top predators has also been observed at Marion Island. There has been an increase in the populations of sub-Antarctic Fur Seals *Arctocephalus tropicalis* and Antarctic Fur Seals which breed sympatrically at Marion Island, during the same period in which the population of the two *Eudyptes* penguins found at Marion Island were observed to be decreasing (Hofmeyr et al. 2006, Crawford et al. 2009, Wege et al. 2016). Further research is required to determine the relationship between seals and penguins on Marion Island. Penguins have been reported in the diet of seals at Marion Island and there has been reported predation on penguins on land by Antarctic and sub-Antarctic Fur Seals but this has only been documented on King Penguins (Hofmeyr and Bester 1993, Reisinger et al. 2018).

In contrast to the decreasing number of Macaroni Penguins at Marion Island, penguins at Kerguelen Islands have been increasing for the past 50 years, however the ecological factors contributing to their increase remain unknown. The population of Macaroni Penguins at the Crozet Islands has remained stable for the past 10 years but this trend is based on a small sample size and could possibly not fully reflect the entire Island's population (Barbraud et al. 2020). At South Georgia the population of Macaroni Penguins reduced by approximately 70% between 1985 and early 2010, their survival rates were largely affected by top down factors (predation pressure from giant petrels) and bottom up factors (climate change) (Horswill et al. 2016).

The breeding population of Rockhopper Penguin is almost a third of the estimated population in 1984, however their decline at Marion Island has not been constant throughout the study. The overall breeding population of Rockhopper Penguins declined at a rate almost eight times as much as Macaroni Penguins and at a rate almost five times as much at the regularly monitored sites before 2001. From 2002 the overall breeding pairs of Rockhopper Penguins stabilised with inter-annual variation in overall breeding pairs fluctuating between 55 000–85 000 pairs. The stability in the population of Rockhopper Penguins at Marion Island mirrors that of the population at the Crozet islands which has been stable from the late 2000s to late 2010s. In contrast to Marion Island the population of Rockhopper Penguins at Kerguelen Island has been increasing since the 1960s (Barbraud et al. 2020). Rockhopper Penguins have also experienced a drastic decline at Campbell Island, reducing by 94% from 1942–1984 (Cunningham and Moors 1994). However, Morrison et al. (2015) show that the same population continued to decline at a slower rate by 21.8% from 1984–2012, with most of the decline occurring from 1984–1996 and the population had an increasing trend from 1996–2012. The slower rate in decline of Rockhopper Penguins at Campbell Island in the late 20th century compared to the 1940s has been a result of increased food availability of Southern Whiting *Micromesisteus australis* and higher reproductive success from 1990–2009 (Dunn and Hanchet 2014 from Morrison et al. 2015). More so, the growth rate of Rockhopper Penguins at Campbell Island after 1996 coincided with cooler and lower than average sea surface temperature from 1990–2012 during their breeding period (Morrison et al. 2015).

Breeding success

Compared to the early 1990s and early 2000s, Macaroni and Rockhopper Penguins at Marion Island exhibited more inter-colony variability in breeding success and less inter-colony variability in breeding penguin numbers across the monitored colonies (Cooper et al. 1997, Crawford and Dyer 2006). Out of the six pairwise comparison in breeding success of the four monitored colonies of Macaroni Penguins, only Archway and Bullard South had a significant positive relationship. For Rockhopper Penguins only Trypot Fault and Trypot Hole had a significant positive relationship in breeding success out of the three pairwise comparison of the three monitored colonies. Pairwise comparison in breeding penguins' number of all the colonies yielded a strong positive relationship for both Macaroni and Rockhopper Penguins, however the number of breeding penguins also reduced drastically at all the monitored colonies for both species during the same period. According to Cooper (1997) this shows that the breeding of both these species is possibly influenced by environmental variable before the onset of breeding and/or during the laying of eggs. Due to the strong relationships in breeding success of Macaroni Penguins between monitored colonies, Crawford (2006) and Cooper (1997) conclude that Macaroni Penguins' breeding success is affected by wider environmental variables compared to Rockhopper Penguins, however from 1994/95–2019/20 breeding success relationship between the monitored colonies was not as strong.

From 1994/95–2002/03 the overall breeding success of Macaroni and Rockhopper Penguins averaged 0.46 and 0.40 fledged chicks per pair respectively, Crawford et al (2003a, b) concluded that this is not sufficient to maintain the population at Marion Island. In this study from 1994/95–2019/20 the overall breeding success of both Macaroni and more so of Rockhopper Penguins were higher compared to the previous study, Macaroni Penguins breeding success ranged from 0.15–0.85 chicks/pair with an average 0.49 chicks/pair and that of Rockhopper Penguins ranged from 0.25–0.84 chicks/pair and averaged 0.52 chicks/pair. Despite the higher breeding success by 2019/20 of both penguins at Marion Island they are still lower than the 0.64 chick/pair suggested by Guinard et al (1998) for the population to remain in equilibrium. However, this equilibrium value is not for Marion Island and study on survival rates of the two *Eudyptes* penguins is still lacking at Marion Island. Rockhopper Penguins had a significant increasing trend in their breeding success since 1994/95, fledging more chicks in the later years of the study at all the three monitored colonies. This could explain the reduced rate of decline of Rockhopper Penguins post the early 2000s at Marion Island.

Arrival dates

Over the past 25 years Macaroni Penguins arrived at Marion Island on 10 October ± 4 days for males and 16 October ± 5 days, with males significantly arriving 1 week earlier than the females. Rockhopper Penguins arrived on 5 November ± 4 days and females arrived 8 November ± 3 days. The arrival dates varied annually but generally there was no long-term trend in arrival date of both penguins at Marion Island, ruling out arrival dates a possible suspect for the decline of these species over the past 25 years.

Spatial and temporal segregation among closely related species is important to reduce competition for resources (Thiebot et al. 2013). Post breeding Macaroni and Rockhopper Penguins from Marion Island forage in different areas during the early overwintering period, with Macaroni Penguins foraging in cooler waters compared to the warmer waters near the sub-Antarctic Front used by Rockhopper Penguins (Enticott 1986, Whitehead 2017). Later in the wintering period as Macaroni and Rockhopper Penguins prepare to return to the Island there is increased overlap in foraging ground which suggests competition for resources prior to breeding, if resources are limited. Whitehead (2017) showed that Rockhopper Penguins in 2013 and 2014 moved to cooler more productive waters in October preceding their breeding season, when Macaroni Penguins return to Marion Island. This is emphasised by the difference in arrival between Macaroni and Rockhopper Penguins from 1994/95–2019/20 in this study. Rockhopper Penguins arrived on average 27 ± 5 days later than Macaroni Penguins. This temporal segregation allows Rockhopper Penguins to minimise competition with Macaroni Penguins and forage in their absence preparing to breed and get enough body reserves for reproduction due to prolonged fasting periods (Thiebot et al. 2013, Whitehead 2017).

Mass on arrival and fledgling weights

Penguins are both income and capital breeders, but among crested penguins, males are more capital breeders and females are more income breeders (Meijer and Drent 1999). The male characteristically initiates the fasting period during incubation while the female goes out to forage then both become income breeders when they simultaneously go to forage to provision for their chicks (Meijer and Drent 1999, Green et al. 2007, Dehnhard et al. 2015). They are dependent on their lipid reserves during breeding to survive the long fasting period hence their body condition determines parental investment with some penguins opting not to breed due to low mass upon returning to the colony, and deserting nesting site and breeding if they reach a critical minimum threshold (Williams and Rodwell 1992, Williams 1995, Croxall and Davis 1999, Robinson et al. 2005, Dehnhard et al. 2015). Body condition is important in both male and female *Eudyptes* penguins to survive fasting periods during courtship, mating, laying of eggs and males guarding eggs during brood until the females return. *Eudyptes* penguin lose weight as they progress further into breeding hence it would be expected that initial body condition would affect the breeding performance of the penguins more in males than females. In this study body condition of Macaroni and Rockhopper Penguins was positively related to breeding success. This agrees with previous work at Marion Island, Campbell Island and South Georgia where poor body condition was related to poor reproductive performance in these two species, potentially affecting their population processes (Crawford and Dyer 2006, Morrison 2015, Horswill et al. 2016).

Macaroni Penguins showed inter-annual variation in mass on arrival over the years with no detectable trend over time. This is potentially indicative of changing in prey availability in each season within their foraging ground due to environmental variability and years with higher mass of arrival reflecting abundant prey at overwintering foraging grounds. Male and female Macaroni and Rockhopper Penguins' mass on arrival was positively correlated suggesting that their foraging areas are similar before breeding, or environmental conditions are similar at different foraging locations. During winter when Macaroni and Rockhopper Penguins are not breeding they expand their foraging range and follow mesoscale eddies and sub-mesoscale filaments. This is because of the high productivity and elevated concentration of zooplankton and mesopelagic fish, preferring cooler water over warmer waters which could explain the penguins' variability in their body conditions on arrival (Ansorge et al. 2009, Thiebot et al. 2013, Ratcliffe et al. 2014, Whitehead 2017).

For Rockhopper Penguins a distinctive decrease in mass on arrival was reported by Crawford (2008) from 1985/86–2007/08. This trend is also evident in our study. Post 2007/08 Rockhopper Penguins' mass on arriving increased despite the trend not being significant for the weights of both males and females fluctuated between 3.0–3.5 kg up to the end of the study. Along with the breeding success of Rockhopper Penguins, the changing trend in mass on arrival could explain the stabilising population of Rockhopper Penguins at Marion Island. Like Macaroni Penguins the mass on arrival of male Rockhopper Penguins was correlated to female Rockhopper Penguins suggesting that they forage in the same area during winter. Contrary to Whitehead (2017), sex specific foraging strategies during late winter was observed for Rockhopper Penguins at Marion Island in 2013–14 with female Rockhopper Penguins feeding on higher trophic level prey (higher fish content) compared to males which preyed on lower trophic level prey (high krill content). There is no long-term study on the foraging biology of both Macaroni and Rockhopper Penguins during winter that could elucidate on the trend in their feeding biology prior to breeding hence further research is required to support variability in body condition of *Eudyptes* penguins at Marion Island.

The body condition of both male and female Macaroni and Rockhopper Penguins were negatively related with time of arrival which infers that those penguins which arrived earlier to breed were generally in better condition. However, the relationship was only significant in male Rockhopper Penguins. Similarly at Bird Island, South Georgia, Macaroni Penguins that arrived late commenced egg laying late, had lower weights and the breeding population was negatively impacted. Conversely, in the following year, Macaroni Penguins arrived early and breeding population was higher (Williams and Croxall 1991). In the closely related Northern Rockhopper Penguins *Eudyptes moseleyi* a similar negative relationship between body mass and arrival was observed at Amsterdam Island from 1994–2016 (Delord et al. 2021).

Chick size and body mass of penguins is affected by parental provision efficiency (quality, quantity and frequency of meals) through environmentally induced prey availability around a colony during breeding (Salihoglu et al. 2001, Barlow and Croxall 2002a, Mattern and Wilson 2018). Thus, chick body condition is indirectly affected by environmental variability until they become independent and must forage for their own and variability in chick mass can reflect prey availability around a colony within and beyond a breeding season. Chicks with a high body mass and good condition have better survival rates (between fledgling and sexual maturity) and are likely to reach first time breeding and recruit into the breeding population (Saraux et al. 2011). There was high inter-annual variability in fledgling mass for both Macaroni and Rockhopper Penguins with no significant trend from 1994/95–2019/20 at Marion Island. The variation in mass at fledgling was positively correlated with adult male body mass for both Macaroni and Rockhopper Penguins however only Macaroni Penguins had a significant relationship. This shows that the chicks respond to the good body condition of male Macaroni Penguins to survive the fasting period which likely resulted in increased parental expenditure and provisioning to the growing chicks. Male crested penguins undergo long fasting periods, incubate and guard the chick up to creche and the female solely provisions for the chick at that time and after that both sexes provision the chick until it fledges (Williams 1980, 1995).

Barlow and Croxall (2002) show at Bird Island that although the male Macaroni Penguins fed chicks at a lower rate than females the added biparental investment in feeding the chicks increased the provisioning rate during creche stage by 65% compared to the guard stage when only the female is feeding the chick. The provision rate of males had a significant effect on increased chick growth rate while female provision was critical for the survival of the chicks up to the guard stage. This is likely the same case with Macaroni Penguins at Marion Island. This is highlighted by the very high fledgling success (fledged chicks per hatch) of Macaroni Penguins at all the four monitored colonies compared to the hatching success (Table 2.2). Heavier fledgling chicks have a higher probability of survival than lighter chicks (Dehnhard et al. 2014, Horswill et al. 2014). This is potentially reflected by the relationship between breeding success and fledgling weight of Macaroni Penguins in this study where higher fledging mass resulted in higher breeding success. Macaroni Penguin fledgling survival rate at Bird Island was sensitive to fledgling mass and increased with fledging heavier chicks (Horswill et al. 2014). There was no significant relationship between fledgling mass and breeding success in

Rockhopper Penguins showing that other factors could be masking this relationship on the Island.

In 1983–84 during breeding at Marion Island Macaroni Penguins were shown to feed on higher trophic level prey (myctophid fish) and increase the amount of fish in their diet as their chicks grew, compared to Rockhopper Penguins which had diet dominated with krill (Brown and Klages 1987). More so, Crawford (2006) shows that Macaroni Penguins fledged heavier chicks when there was more fish in the diet of adults during breeding. Quality of prey could have a significant effect on the growth of chicks during breeding at Marion Island.

Outside arrival dates, adult body condition on arrival, mass at fledgling and breeding success, the population size of penguins is also affected by the juvenile survival rates up to sexual maturity and adult survival rates (Horswill et al. 2014, 2016). Once parental care ceases young penguins have to transition from a terrestrial habitat to forage independently in a marine habitat with patchily distributed prey (Horswill et al. 2014, Hinke et al. 2020). Most seabirds have high adult survival rates thus their population sizes are more sensitive to adult survival (Morrison 2015). Long-lived (K-selected) species like penguins will theoretically allocate more energy towards their own survival to ensure future reproduction and adult survival (Furness and Monaghan 1987). Long-term juvenile and adult survival rates of Macaroni and Rockhopper Penguins are lacking at Marion Island possibly because of the time-consuming effort required to collect the data. Further research is required on these survival rates. This could potentially shed light on factors that are regulating the population dynamics of the two *Eudyptes* penguin populations at Marion Island from top down control from predation and bottom up control from prey availability (Baum and Worm 2009, Schwarz et al. 2013, Horswill et al. 2016).

In conclusion, results from our study show a decline in long term population trends of both Macaroni and Rockhopper Penguins at all the monitored colonies, in 26 years they have decreased by 45% and 66% from 1994//95–2019/20, respectively. For Macaroni Penguins the decline has been constant while most of the Rockhopper Penguin population decline happened from 1994 to the early 2000s, thereafter the population stabilised with inter-annual variation fluctuating between 55 000–85 000 pairs up to the end of the study. The observed change in Rockhopper Penguin numbers is attributed to improved body condition on arrival and increasing trend of their breeding success throughout the study. Crawford (2006) concludes that the population decline of both species is because of inadequate breeding success to maintain the population; despite the improved breeding success of Rockhopper Penguins the breeding success of both penguins is still inadequate to maintain an equilibrium and more so for Macaroni Penguins. Following the large-scale ENSO (El Niño Southern

Oscillation) of 1997/98 both Macaroni and Rockhopper Penguins had a decrease in their mass on arrival in 1998/99, showing the possible impact of environmental variables on these species. There is high inter-annual variation in the arrival dates, body condition on arrival and fledgling mass which likely reflects the changes in prey availability and environmental variables around Marion Island. The relationship between pre-breeding parameters (mass on arrival, arrival dates) and breeding parameters (fledgling weight, breeding success) show the carry over effect of wintering conditions into the breeding seasons. Penguins might not only be affected by local scale food availability and environmental conditions during breeding, but this could be at a broader scale before the onset of breeding, when their foraging range is expanded.

Chapter 3: Long-term variation in the breeding diets of Macaroni and Eastern Rockhopper Penguins at Marion Island

Abstract

In this chapter I examine the diet of Macaroni and Rockhopper Penguins at Marion Island during their breeding period. This study involves the longest time series on the diet of these two species at Marion Island with the last assessment on their diet having been done in the early 1980s. There was substantial overlap in the diets of the two species, with crustaceans, dominated by the euphausiids *Thysanoessa vicina* and *Euphausia vallentini*, together making up >80% of the diets by number and >60% by mass over the study period in both Macaroni and Rockhopper Penguins. The lanternfishes *Krefftichthys anderssoni* and *Protomyctophum tenisoni* were the most-commonly consumed fish in the diet of breeding Macaroni Penguins and dominated their diet in three of the 25 years (1994, 1998 and 2014); they were also the most consumed fish by Rockhopper Penguins. Macaroni Penguins consume more of the amphipod crustacean *Themisto gaudichaudii* and the lanternfish *Electrona carlsbergi* as well as a greater diversity of and larger-sized fish than did Rockhopper Penguins. The Horsefish *Zanclorhynchus spinifer* was found in substantial amounts in the diet of Rockhopper Penguins in 1996 and 1997. Despite annual variations in relative prey contributions to the diets, there were no significant long-term changes in the diet of either penguin species over the study period or when compared with an earlier assessment in 1982. I conclude that changes in the relative proportions of prey in the diets of these penguin species during breeding are unlikely to account for the recent declines in these penguin populations.

Introduction

Long-term studies on the diet of seabirds allow for better understanding of ecosystem structure and functioning and provide information on prey preferences and foraging behavior (Brown 1987, Cairns 1988, Hull 1999, Cury et al. 2011). The proportion of a prey species in the diet of a seabird is likely to reflect the abundance of that prey within their foraging range (Green et al. 2015). By monitoring seabird diet over several years, one can therefore assess relative shifts in prey availability, and predator responses to ecosystem changes (Boersma 2008, Croxall et al. 2012a). Linking seabird diet with reproductive performance parameters and population trends can be integral to seabird conservation. It can furthermore provide information about the at-sea foraging conditions and ecosystem processes that are central to the health of upper-trophic-level predators within the commuting range (Wanless et al. 2005, Camphuysen et al. 2012, Karnovsky et al. 2012, Kowalczyk et al. 2014).

Breeding penguins are constrained by their need to forage within the commuting range of their colonies, so that they can return regularly to relieve their partners of nest duties or provision their chicks. This constraint allows for their study at breeding colonies, and the fact that their diet can be reflective of prey availability, potentially makes them good indicators of ecosystem change (Woehler et al. 2001, Forcada and Trathan 2009). Among sub-Antarctic seabirds, penguins consume the largest quantity of pelagic prey, with Macaroni Penguins being the leading consumer, previously estimated to consume 8 million tons of prey per year (Brooke 2004). After Macaroni Penguins, Rockhopper Penguins (*sensu lato*) are the most abundant crested penguins globally. Both have circumpolar distributions within the Southern Ocean, with their breeding ranges overlapping at several sub-Antarctic islands (Wilson 1983, Woehler and Croxall 1997, Woehler et al. 2001, Kooyman 2002). The two *Eudyptes* species mainly feed on swarming crustaceans, with krill species (euphausiids) typically dominating their diet, but they also eat some mesopelagic fish and cephalopods (Brown and Klages 1987, Ridoux 1994, Tremblay and Cherel 2003, Deagle et al. 2007, Waluda et al. 2012).

When closely-related predators breed sympatrically, the competitive exclusion principle dictates divergent resource use which might be presented through their foraging behavior and diet composition (Kneitel 2008, Bertolin 2012, Bertolin and Casaux 2019). During the non-breeding season, when there are no central-place foraging constraints, *Eudyptes* species breeding at the same locality can disperse more widely to forage in different areas, reducing foraging overlap and interspecific competition (Brown 1987, Barlow and Croxall 2002b, Thiebot et al. 2013, Ratcliffe et al. 2014, Whitehead 2017). However, while breeding, with foraging constrained to the vicinity of the colony, morphological differences among *Eudyptes* penguins promote niche partitioning, allowing them to coexist (Ratcliffe et al. 2014). Macaroni

Penguins are larger than Rockhopper Penguins, and they can dive deeper and feed on larger prey, so a level of differentiation would be expected between the diet of these two species breeding on the same island (Brown 1987, Whitehead 2017). Macaroni Penguins also breed 3–4 weeks earlier than Rockhopper Penguins at Marion Island and they often have longer foraging trips, travelling farther from the island, thus facilitating some degree of temporal and spatial separation of food demand over the breeding season (Crawford and Dyer 2006, Whitehead 2017).

The global decrease of *Eudyptes* penguin populations since the early 1980s has been attributed to climate change and its impact on food abundance. For example, the reduction in numbers of Rockhopper Penguins at Campbell Island in the early 1980s was attributed to increased ocean temperatures, which reduced the availability of euphausiids around the island (Cunningham and Moors 1994). Similarly, at South Georgia, variations in Macaroni Penguin breeding performance from 1989 to 2010 were related to changes in the proportions of euphausiids in their diet (Waluda et al. 2012). At Marion Island, the breeding populations of Macaroni and Rockhopper Penguins decreased by 45% and 66% respectively, from 1994 to 20019. Crawford et al. (2003a, 2003b) suggested that these population declines may have been related to inadequate reproduction linked to reduced prey availability and showed a significant relationship between the number of fish in the diet of Macaroni Penguins and their reproductive performance.

The diets of the two *Eudyptes* penguins breeding at Marion Island have been monitored during chick-rearing from 1983/84–1984/85 as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (Brown and Klages 1987, Agnew 1997, CCAMLR 2000). Studies in the 1980s found that the diets of both species were dominated by two euphausiids, *Euphausia vallentini* and *Thysanoessa vicina*, with the myctophid fish *Krefftichthys anderssoni* and *Protomyctophum tenisoni* making up most of the fish component of the diet (Williams and Laycock 1981, Brown and Klages 1987, Brown et al. 1990). The caridean shrimp *Nauticaris marionis* was also found to be an important constituent of the diet in 1983/84 (Brown and Klages 1987, Brown et al. 1990). Considering the limited knowledge on the reasons for the declines of both these *Eudyptes* penguins, a reassessment of their trophic ecology at the Prince Edward Islands is timely. This study describes their diets during the period 1994/95–2018/19, quantifying inter-annual variability in diet composition. I also assess population changes in these two crested-penguin species in relation to temporal patterns in their diet composition.

Methods

Diet sample collection

Diet samples were collected from adult *Eudyptes* penguins provisioning chicks at Marion Island during each austral summer from 1994/95 to 2018/19, except for 2002/03 when Macaroni but no Rockhopper Penguin diet samples were collected. Diet samples were collected from presumed breeding adults returning from foraging trips (i.e., heading from the water's edge to the colony). Adults were caught before entering the colony, restrained and stomach contents were obtained using a water offloading technique adapted from Wilson (1984), outlined by CCAMLR (2014). After diet samples were collected, the penguins were measured, marked with a harmless food colorant so that they would not be sampled a second time, and released into the colony. During each breeding season, for Macaroni Penguins at least 10 diet samples were collected in December and 15 in January and February from the Bullard North colony on the east coast of Marion Island (Fig. 3.1, Supplementary Table S3.2). For Rockhopper Penguins, 5–21 samples were collected monthly from January-March at colonies along the island's northeast coast between Ship's Cove and Archway (Fig. 3.1, Supplementary Table S3.2).

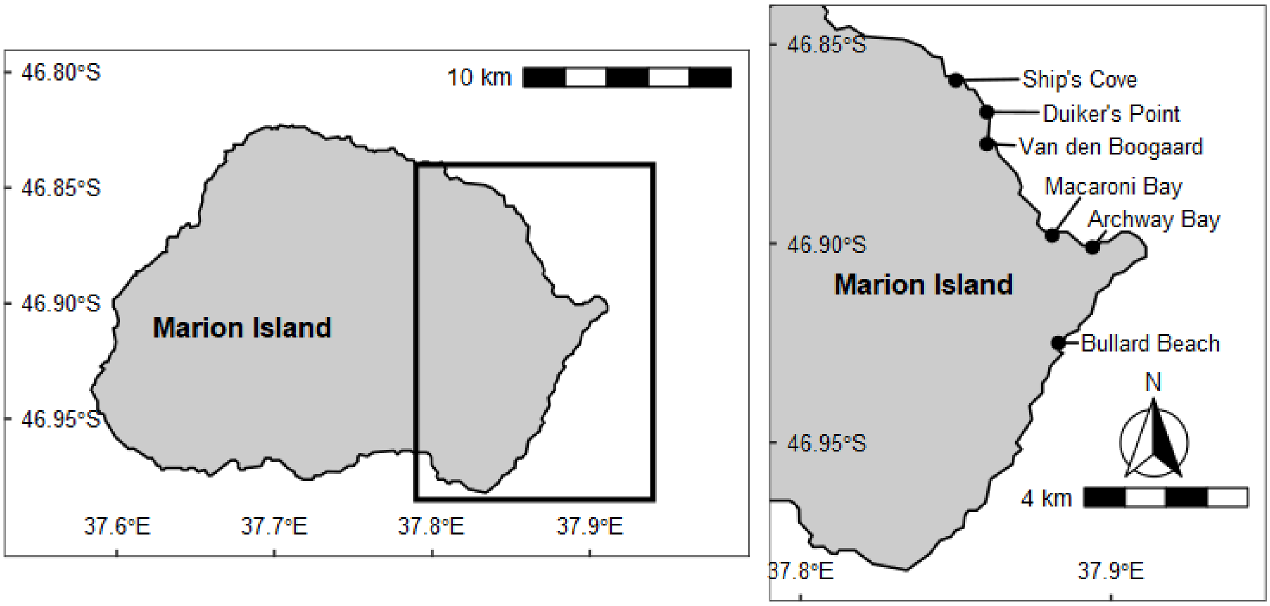


Figure 3.1: Map showing the sites sampled for diet of Macaroni Penguins and Eastern Rockhoppers Penguins at Marion Island

Prey samples were drained, sorted and weighed according to methods outlined by CCAMLR (2014). All samples collected were either frozen or fixed in ethanol (90%) until later analysis (Crawford et al. 2003a). In the laboratory, the samples were drained through a sieve and the wet weight of each whole sample was recorded. The sample was then sorted to remove fish and cephalopod remains, including all fish otoliths and cephalopod beaks. Any unusual prey items were also removed and weighed. Generally, a sub-sample of 10–20% of the whole sample weight of the crustacean component was selected at random and sorted to species level and if the sample weighted < 50 g the entire sample was processed. Numbers of individuals of each crustacean species were counted and the crustacean component was weighed. Fish otoliths and cephalopod beaks were identified to species level where possible. The longest axis of each otolith was measured through a dissecting microscope with the aid of a calibrated graticule. Regressions were used to estimate the mass of fish from the otolith length (Hecht 1987, Brown et al. 1990, Williams and McEldowney 1990, Smale et al. 1995, Reid 1996, Makhado et al. 2013).

Diet analysis

For each prey item or group found in the diet I calculated its (i) percentage frequency of occurrence (%FO), i.e. the percentage of the number of samples collected in which it was represented; (ii) percentage numerical abundance (%NA), i.e. the percentage an individual prey species in a sample contributed to all prey items in all sample; and (iii) percentage mass (%M), i.e. the proportion that the item contributed to the total mass of all prey items in all samples. To determine the important prey items in the diet, an integrative percentage index of relative importance (%IRI, Pinkas et al. 1971) was calculated, where:

$$\%IRI = \frac{(\%NAi + \%Mi) \text{ x } \%FOi}{\sum_{i=1}^{n}(\%NAi + \%Mi) \text{ x } \%FO\, i}\, x\, 100$$

i = prey and *n* = number of prey.

Reconstituted mass was used to investigate annual variability in diet composition. Each species in the diet was ranked through contribution by mass, numerical abundance, and frequency of occurrence as well as by the index of relative importance.

Statistical analyses

The data were tested for normality before analysis using visual tools (histograms and qqplots), or Shapiro-Wilks tests. If normality assumptions were violated, the data were log or square root transformed (adding a constant if the data had any zeros when log transforming [log (x+1)]). If normality was not achieved, an alternative non-parametric test was used. The *rich()* package was used to test for differences in species richness among diet samples from Macaroni and Rockhopper Penguins with 999 randomisations tests and bootstrap estimations (Rossi 2011). Wilcoxon rank tests were used to assess differences in the lengths of fish prey consumed by the two penguin species. To assess whether there were long-term differences in diet composition between the two species, the data were pooled into 5-year bins and visualized using non-metric multidimensional scaling (nMDS) in the vegan package, function metaMDS with 1000 permutations (Oksanen et al. 2020). A 95% confidence interval ellipse function (*state_ellipse*) was applied in the nMDS plots to further distinguish differences between groups. nMDS was also used to visualise the differences between species. A permutational multivariate analysis of variance (PERMANOVA) was used with the *Adonis* function in the vegan package to distinguish a statistically significant difference from the null hypothesis that prey composition did not differ among groups (temporal changes, and/or between species) compared with 1000 permutations of the different groups (Anderson 2001, Lemieux-Labonté et al. 2016). This multivariate test is sensitive to unbalanced designs and data dispersion within-group and assumes homogeneity within groups (Anderson and Walsh 2013). Thus, a further analysis of multivariate homogeneity (PERMDISP) using function betadisper (vegan package) was undertaken to test for a significant difference in within-group variation against 1000 permutations. The null hypothesis of this test was that within-group dispersion was the same. The results of the PERMANOVA, PERMDISP and the nMDS were used to infer the strength of the *p*-value in the PERMANOVA analysis and reach a conclusion. All analyses were carried out using the statistical package R version 3.6.1 (R Core Team 2019).

Results

A total of 1005 and 664 regurgitation samples were collected from adult Macaroni and Rockhopper Penguins, respectively, from 1994/95 to 2018/19. Over this 25-year study period, Macaroni Penguins fed on a higher number of species (richness) per sample (c2m randomization test, Macaroni - Rockhopper = 0.72, p = 0.001, nrandom = 999) and had a greater range of prey (51 species: 17 crustaceans, 30 fish and at least 4 cephalopods) than Rockhopper Penguins (37 species: 10 crustaceans, 22 fish and 5 cephalopods). The mean annual sample mass recovered from Macaroni Penguins ranged between 27 ± 25 g [SD] (2010/11) and 435 ± 373 g (1994/95) and from Rockhopper Penguins between 20 ± 19 g (2005/06) and 202 ± 145 g (1994/95) (Supplementary Fig S3.1). The mean annual masses recovered from the two species were positively correlated with each other (log transformed data; r = 0.76, $p < 0.01$), with a consistent decrease in mean mass from 1994/95 to 2010/11, then an increase to 2018/19.

Crustaceans dominated the diets of both species, being present in 98% of Macaroni Penguin diet samples and >99% of Rockhopper Penguin samples. The euphausiids *Thysanoessa vicina* and *Euphausia vallentini* were the two most important prey species for both penguin species, comprising 59% and 76% of the diet by mass and 89% and 95% by number of preys for all Macaroni and Rockhopper Penguins, respectively (Table 3.1). *T. vicina* occurred in 85% of Macaroni Penguin samples, followed by *E. vallentini* (47%) and the amphipods *Themisto gaudichaudi* (44%) and *Primno macropa* (15%; Table 3.1). (Note: Table 3.1 is a subset of Supplementary Table S3.1 which lists all the prey species identified over the course of the study.). *T. vicina* also was most frequently encountered in Rockhopper Penguin samples (78%) but it was almost matched by *E. vallentini* (77%); the amphipods *Primno macropa* (17%) and *Themisto gaudichaudi* (14%) were recorded less frequently than in Macaroni Penguin diet (Table 3.1).

Fish species were more often present in the diet of Macaroni Penguins (77%) than Rockhopper Penguins (58%). Two myctophid species, *Krefftichthys anderssoni* and *Protomyctophum tenisoni*, were the most frequently recorded fish species (Table 3.1). Although they only accounted for 3% (Macaroni) and 1% (Rockhopper) of the number of prey items, they contributed 21% and 4% to their respective diets by mass (Table 3.1). *Protomyctophum choriodon* occurred in 7% and 3% and *Protomyctophum bolini* in 2% and 0.05% of Macaroni and Rockhopper Penguins' samples, respectively. Macaroni Penguins fed on more fish species than Rockhopper Penguins, and the fish eaten were significantly larger (Fig. 3.2). The mean standard length (± SD) of *K. anderssoni* eaten by Macaroni Penguins (44.0 ± 8.5 mm) was significantly larger than for Rockhopper Penguins (24.8 ± 17.2 mm; Wilcoxon test, Z = 43.2, $p < 0.001$). *K. anderssoni* eaten by Rockhopper Penguins had a bimodal distribution in length, with most fish < 25 mm, whereas Macaroni Penguins seldom ate fish < 25 mm (Fig. 3.2). *P. tenisoni* consumed by Macaroni Penguin (40.1 ± 4.7 mm) were significantly larger than those eaten by Rockhopper Penguins (38.5 ± 4.7 mm; Z = 12.41, $p < 0.001$), but the difference may not be biologically meaningful. *E. carlsbergi* eaten by Macaroni Penguins averaged slightly longer (66.5 ± 7.0 mm) than those eaten by Rockhopper Penguins (64.7 ± 7.3 mm; Z = 3.078, p = 0.002), but this was driven by a few larger fish eaten by Macaroni Penguins and the modal length was similar for both penguin species (Fig. 3.2). The average standard length of *Z. spinifer* preyed on by Rockhopper Penguins was (173.9 ± 2.1 mm, n = 41); only one individual was found in Macaroni Penguin diet samples.

Cephalopods were found in smaller quantities than crustaceans and fish, occurring in 54% of Macaroni Penguin and 42% of Rockhopper Penguin diet samples (Table 3.1). Most cephalopods could not be identified (78% of all cephalopod prey items by number from Macaroni Penguins and 54% from Rockhopper Penguins). Of those that could be identified to species level, *Kondokovia longimana* (Macaroni 5% FO and Southern Rockhopper 2% FO) and *Moroteuthis ingens* (4% and 6%, respectively) occurred most frequently within the penguins' diets (Table 3.1).

Table 3.1: Selected prey species identified from diet samples of adult Macaroni Penguins and Eastern Rockhopper Penguins feeding chicks at Marion Island 1994–2018, as percentages of frequency of occurrence (%FO), numerical abundance (%NA), mass (%M) and index of relative importance (%IRI). For the complete list of prey species see Supplementary Table S3.1

	Macaroni Penguins				Eastern Rockhopper Penguins			
	%FO	%NA	%M	%IRI	%FO	%NA	%M	% RI
Crustacean	98.0	96.8	64.6		99.7	98.0	81.6	
Thysannoesa vicina	85.4	63.9	39.4	68.2	77.7	58.1	39.6	56.3
Euphausia vallentini	47.6	24.7	19.9	16.4	77.1	37.5	35.4	41.8
Themisto gaudichaudi	43.7	7.4	4.7	4.1	14.2	0.8	0.6	0.2
Primno macropa	15.1	0.6	0.4	0.1	16.8	0.7	0.4	0.1
Nauticaris marionis	2.1	0.1	0.2	<0.1	9.2	0.7	0.6	0.1
Euphausia lucens	0.6	<0.1	<0.1	<0.1	5.2	0.6	0.3	0.1
E. longispina	0.1	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
E. superba	0.1	<0.1	<0.1	<0.1	-	-	-	-
E. longirostra	0.02	<0.1	<0.1	<0.1	0.8	<0.1	<0.1	<0.1
Fish	77.0	3.1	33.6		57.5	1.1	16.5	
Krefftichthys andersoni	51.4	1.7	13.4	6.0	28.9	0.6	1.3	0.4
Protomyctophum tenisoni	51.9	1.0	8.0	3.6	14.3	0.3	2.3	0.3
Electrona carlsbergi	13.5	0.2	8.4	0.9	2.0	<0.1	0.7	<0.1
E. subaspera	0.4	<0.1	0.1	<0.1	0.2	<0.1	0.1	<0.1
Zanclorhynchus spinifer	0.1	<0.1	0.1	<0.1	1.9	<0.1	8.5	0.1
Protomyctophum. Bolini	1.5	<0.1	1.0	<0.1	0.5	<0.1	<0.1	<0.1
P. choriodon	7.2	<0.1	1.1	0.1	3.1	<0.1	1.7	0.1

P. normani	0.5	<0.1	<0.1	<0.1	-	-	-	-
P. parallelum	0.2	<0.1	<0.1	<0.1	-	-	-	-
Gymnoscopelus fraseri	0.5	<0.1	0.1	<0.1	0.8	<0.1	0.1	<0.1
G. piabilis	0.1	<0.1	0.1	<0.1	-	-	-	
G. nicholsi	0.1	<0.1	<0.1	<0.1	0.3	<0.1	0.1	<0.1
Gobionotothen marionensis	0.2	<0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
G. angustifrons	0.1	<0.1	<0.1	<0.1	-	-	-	-
Lepidonothen larseni	0.3	<0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Notothenia spp.	1.9	<0.1	0.3	<0.1	11.9	0.1	0.5	0.1
Paranotothenia magellanica	-	-	-	-	0.2	<0.1	<0.1	<0.1
Cephalopod	54.4	0.1	1.7		41.8	0.4	1.9	
Kondokovia longimana	5.4	<0.1	0.2	<0.1	1.9	<0.1	<0.1	<0.1
Moroteuthis ingens	3.9	<0.1	0.2	<0.1	5.7	0.2	0.8	<0.1
Martialla hyadesi	1.9	<0.1	0.1	<0.1	1.2	<0.1	0.1	<0.1

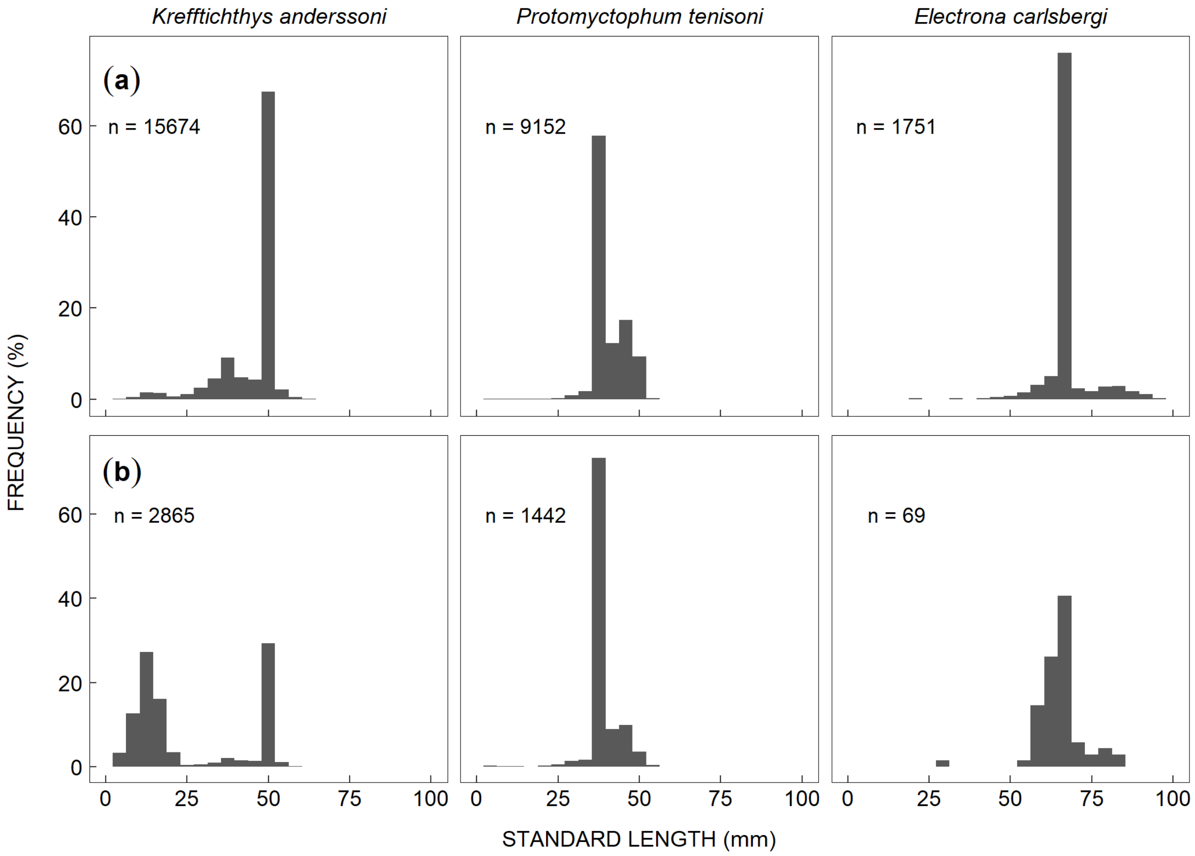


Figure 3.2: Size-frequency distributions of dominant fish species in the diets of (a) Macaroni Penguins and (b) Eastern Rockhopper Penguins at Marion Island (n = sample size)

Inter-annual variability in diet

Crustaceans dominated (>50%) the diet by mass in most years, except for in Macaroni Penguins in 1994, 1998, 2014 and 2015 and in Rockhopper Penguins in 1997, when fish dominated the diet (Fig. 3.3 and 3.4). *Thysanoessa vicina* and *Euphausia vallentini* were present in all 25 years for Macaroni Penguins and in all 24 years for Rockhopper Penguins. *Protomyctophum tenisoni* was present in 24 years for Macaroni Penguins and in 19 years for Rockhopper Penguins (Supplementary Table S3.1). *Krefftichthys anderssoni* was present in all 25 years for Macaroni Penguins and in 20 years for Rockhopper Penguins. *Notothenia* spp. occurred in 14 years for Macaroni Penguins and in 21 years for Rockhopper Penguins. *Thysanoessa vicina* and *E. vallentini* together dominated 21 out of the 25 years of Macaroni Penguin diet and 22 out of the 24 years of Rockhopper Penguin diet. The myctophids *Electrona carlsbergi*, *K. anderssoni* and *P. tenisoni* dominated the remaining four years in Macaroni Penguin diet (Fig. 3.4a). The only time Antarctic Krill *Euphausia superba* was recorded in the diet of Macaroni Penguins at Marion Island during the study was in 2013 (Table 3.1, Supplementary Table S3.1).

In the first four years of the study Rockhopper Penguins fed on fish prey other than the two common myctophid species (Fig. 3.4b). In 1994, the largest proportions of fish by mass in their diet were *Protomyctophum choriodon* (12%) and *Protomyctophum tenisoni* (13%). In 1995, they fed on *K. anderssoni* (11%) and *Z. spinifer* (3%) and unidentified euphausiids (58%) (Fig. 3.4b). The Horsefish *Zanclorhynchus spinifer* was found less often in the diet of Macaroni Penguins in one year (1996) than in the diet of Rockhopper Penguins (five years, Supplementary Table S3.1) and was found in substantial amounts in the diet by mass of Rockhopper Penguins in 1996 and 1997. *Notothenia* spp. made up 9% of the diet by mass of Rockhopper Penguins in 2007 and 27% in 2008.

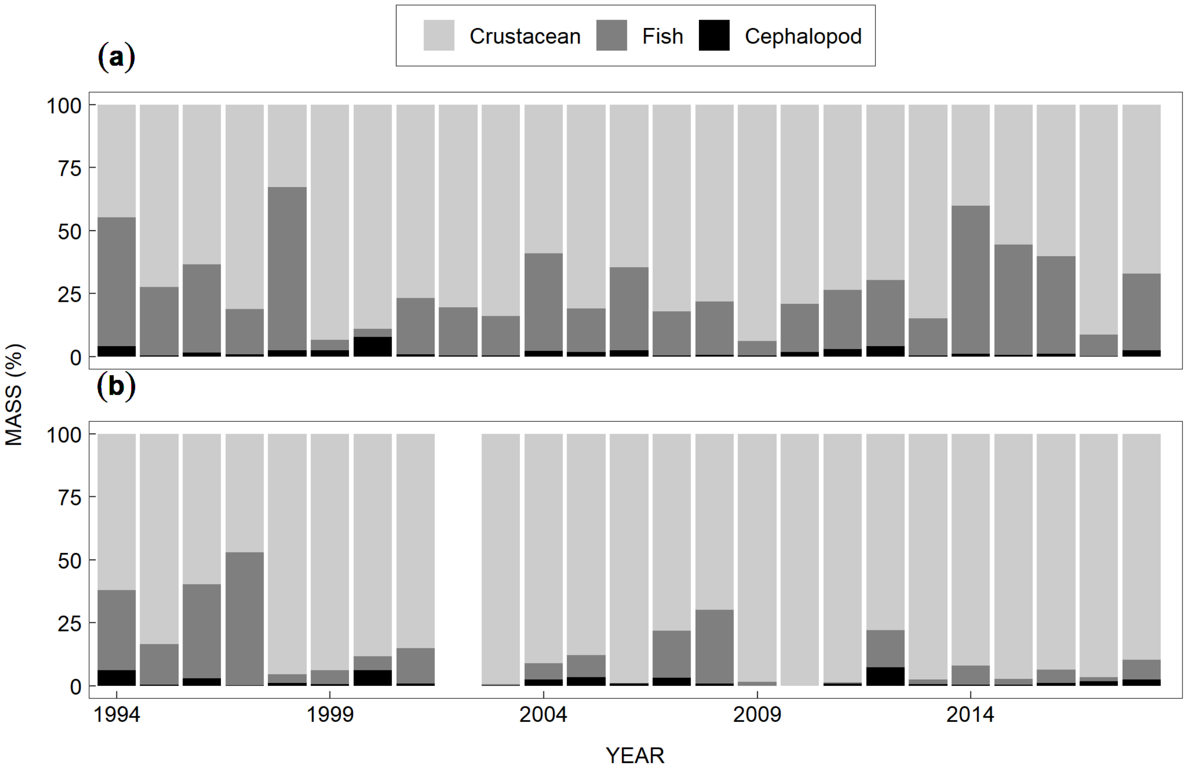


Figure 3.3: Annual variability in diet composition (percentage mass of prey group) for (a) Macaroni Penguins and (b) Eastern Rockhopper Penguins at Marion Island from 1994/95 to 2018/19 (no data were gathered for Eastern Rockhopper Penguins in 2002)

Figure 3.4: The annual relative contributions by mass of the dominant prey species in the diets of (a) Macaroni Penguins and (b) Eastern Rockhopper Penguins during the chick-rearing period, from 1994/95 to 2018/19 (no data were gathered for Eastern Rockhopper Penguins in 2002)

Long-term changes in penguin diets

For Macaroni Penguins, there were significant differences in diets between the pooled five-year groups (*permanova*, F = 19.64, $R^2 = 0.07$, p = 0.001), but this explained only 7% of the variation in prey composition. Rockhopper Penguins also exhibited significant differences in diet between the pooled five-year groups (*permanova*, F = 10.45, R^2 = 0.06, p = 0.001), but again this explained only 6% of the variation in prey composition. There was no multivariate homogeneity between the pooled groups for either species (*betadisper*, F = 14.603, p = 0.001 and F = 27.18, p = 0.001, respectively), which could influence the significance of the PERMANOVA test. There were thus no substantial long-term changes in the diet of either Macaroni or Rockhopper Penguins. This conclusion is supported by the ordination plots, which show no distinction in prey composition between the pooled groups (Fig. 3.5). However, there was a significant difference between the two penguins' diet at a species level (*permanova*, F = 106.93, R^2 = 0.06, p = 0.001), but again the grouping only explained 6% of the variation and there was no multivariate homogeneity between the two species groups (*betadisper*, F = 4.2, p = 0.035). Thus, there was no difference between the diet of the two species, but extensive overlap as shown by the ordination plots (Fig. 3.6).

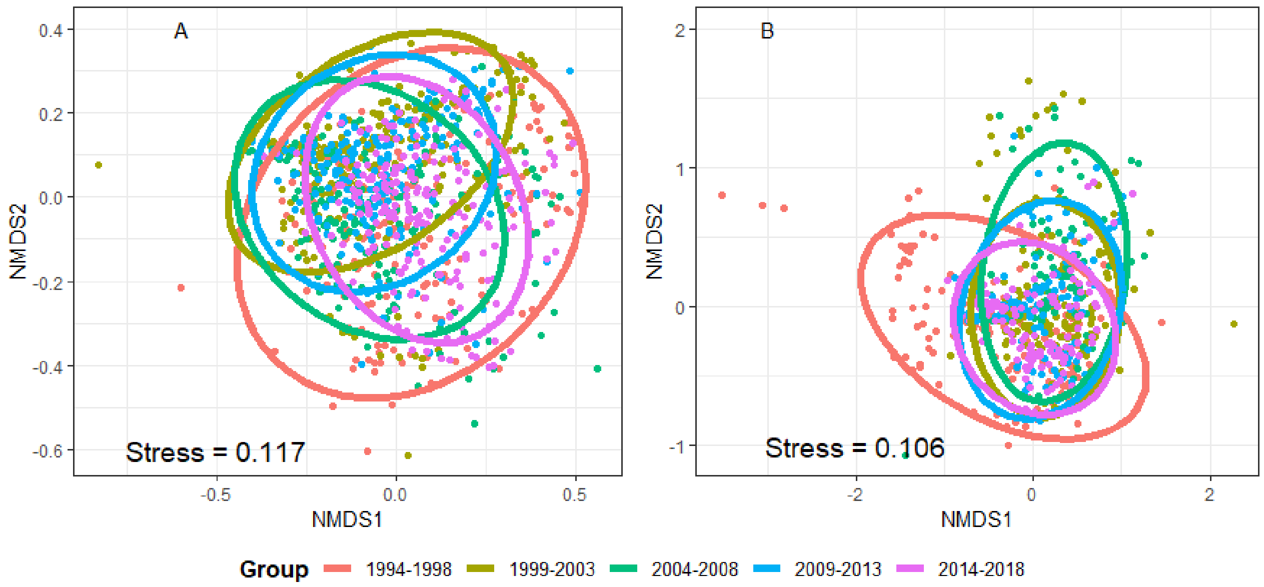


Figure 3.5: Non-metric multidimensional scaling of difference in five-year cluster prey composition of penguins between years (five years) of Macaroni (A) and Eastern Rockhopper (B) Penguins. Each point represents a single sample.

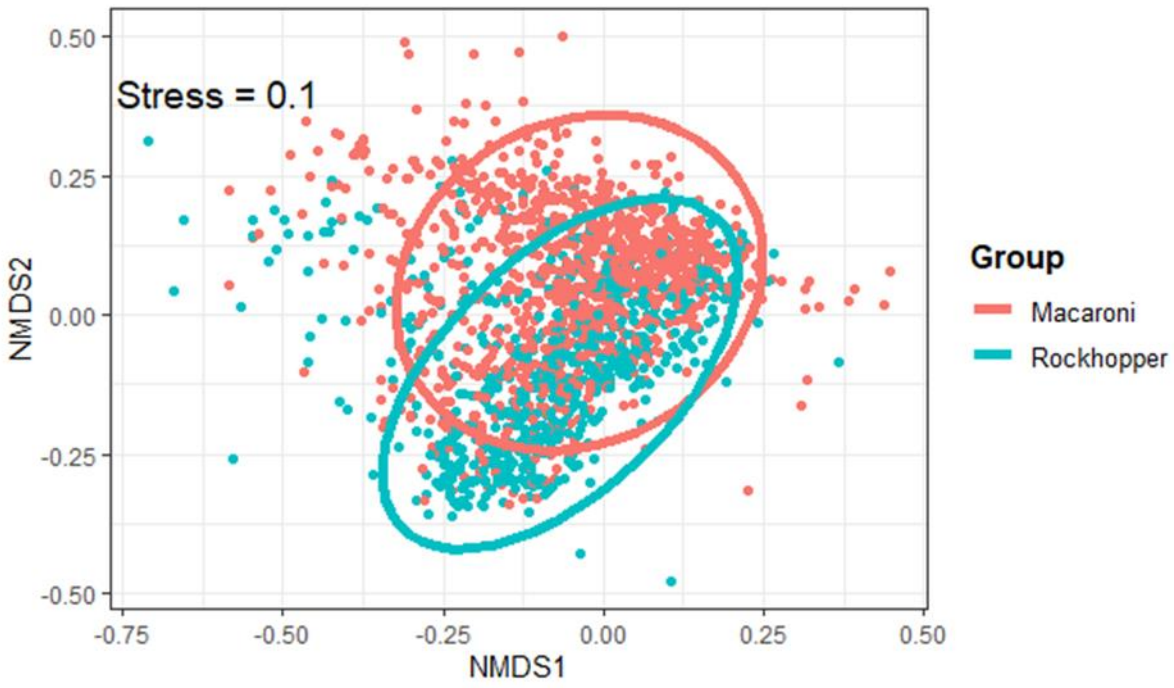


Figure 3.6: Non-metric multidimensional scaling of prey composition without grouping, showing differences between diet samples of Macaroni Penguins (red circles) and Eastern Rockhopper Penguins (blue circles).

Discussion

This is the first long-term study of the diet of Macaroni and Rockhopper Penguins breeding on Marion Island, building on the initial study of the diet of these two species by Brown and Klages (1987). Crustaceans dominated the diet of both Macaroni and Rockhopper Penguins, with euphausiids *T. vicina* and *E. vallentini* being the most frequently consumed prey species, comprising >80% by number in the diet of both penguins over 25 years. Macaroni Penguins consumed more fish than Rockhopper Penguins over the full period with the myctophids *K. anderssoni* and *P. tenisoni* the most commonly eaten fish prey species.

In a previous study at Marion Island, crustaceans, especially the euphausiids *T. vicina* and *E. vallentini*, were found to dominate the diet of both species in 1984/85 (Brown and Klages 1987). However, in 1983/84 their diets were dominated by the decapod *Nauticaris marionis* (Brown and Klages 1987), which never exceeded 11% annually in the diet of either species during our study. *Nauticaris marionis* is a key component of the benthic ecosystem around the PEIs (Perissinotto and McQuaid 1990, Haley et al. 2017) and was recorded in small amounts in the diet in 13 of 24 years for Rockhopper Penguins and 7 of 25 years for Macaroni Penguins, suggesting that it is often available to the penguins. Its relatively small contribution to the diet of the two penguins after 1983/84 suggests that other prey may have been scarce in that season. The two euphausiids that normally dominate the penguins' diets are the most abundant components of the macro zooplankton within waters of the Antarctic Polar Frontal Zone located between the sub-Antarctic Front and the Antarctic Polar Front and are the most abundant euphausiids on the inter-island shelf at the PEIs (Hunt and Pakhomov 2003). Our study is consistent with diet studies of Macaroni and Rockhopper Penguins at other breeding colonies, with crustaceans dominating their diet, but with more fish in the diet of Macaroni than Rockhopper Penguins (Supplementary Table S4).

Rockhopper Penguins breeding at Marion Island fed largely on euphausiid species compared to Macaroni Penguins, whereas their sympatric counterparts, utilised the amphipod *Themisto gaudichaudii* and fish to a greater extent (Fig. 3.4), which suggests some level of segregation in diet between the two species. *Themisto gaudichaudii* is potentially available to all penguins at Marion Island and is the most abundant amphipod distributed in the Southern Ocean (Jażdżewski 1981). However, only Macaroni Penguins seem to utilise *T. gaudichaudii* at Marion Island, making up 5% of their diet by mass over the 25 years, but is almost totally absent (<1%) in the diets of Rockhopper Penguins, King Penguins and Gentoo Penguins (Brown and Klages 1987, Adams and Klages 1989, Brown et al. 1990, Carpenter-Kling et al. 2019).

Of the most important fish species recorded in the diet of Macaroni Penguins, *K. anderssoni*, *P. tenisoni* and *E. carlsbergi* were among the 10 most frequently occurring species in myctophid surveys in the southern Indian Ocean (Koubbi et al. 2011). Similar species of fish have been found in the diets of other predators at Marion Island, including King Penguins, Gentoo (Adams and Klages 1989, Carpenter-Kling et al. 2019), and sub-Antarctic Fur Seals and Antarctic Fur Seals (Makhado et al. 2008, 2013, Reisinger et al. 2018).

Krefftichthys anderssoni, P. tenisoni and *E. carlsbergi* mature at about 54 mm SL, 45 mm SL and 83 mm SL, respectively (Gon and Heemstra 1990). The otoliths collected in this study showed that the two *Eudyptes* penguins mainly fed on juvenile *K. anderssoni*. Rockhopper Penguins fed on a bimodal distribution of *K. anderssoni*, 80% of which were <25 mm SL. About 80% and 60% of *P. tenisoni* found in the diet of Macaroni and Rockhopper Penguins, respectively, were <45 mm, i.e., immature. Both penguin species fed on juvenile *E. carlsbergi*, with 80% <75 mm SL. Macaroni Penguins preyed on more *E. carlsbergi* than did its congener, a further contrast in fish consumption between the two species. The size-frequency distribution of fish consumed indicates that Rockhopper Penguins preyed on smaller fish (<30 mm SL) than Macaroni Penguins (Fig. 3.2). Macaroni Penguins forage deeper and perform significantly more dives to depths >80 m than Rockhopper Penguins (Whitehead et al. 2016). Macaroni Penguins have a larger bill size than Rockhopper Penguins and thus can exploit larger prey (Agnew and Kerry 1995, Whitehead 2017). With regard to fish in the diet, it should be noted that, being more rapidly digested than crustaceans or squid (Jackson and Ryan 1986), fish could be under represented by weight in our diet samples.

Kondokovia longimana and *M. ingens* were the cephalopods most frequently eaten by the two *Eudyptes* penguins at Marion Island. However, cephalopods were found in smaller quantities in the diets than were crustaceans and fish. Their consumption may be a result of opportunistic feeding by the penguins when both cephalopods and penguins target aggregating krill. Brown and Klages (1987) suggest that *K. longimana* that are preyed on by Macaroni and Rockhopper Penguins are juveniles, given that *K. longimana* spawns at a dorsal mantle length >500 mm (Clarke 1980).

Inter-annual variability in diet

The diets of Macaroni and Rockhopper Penguins at Marion Island showed no substantial long-term changes over the 25 years of monitoring, although their populations decreased over the study period by 45% and 66%, respectively (see Chapter 2). Similarly, no long-term dietary changes were found in the diets of sub-Antarctic and Antarctic Fur Seals on Marion Island over the period 1989–2010 although their diet varied seasonally and annually (Reisinger et al. 2018). Macaroni and Rockhopper Penguins exhibited annual variability in their diet, which suggests fluctuations in local prey availability and that the diets of some breeding seabirds are affected by local conditions around Marion Island (Brown and Klages 1987). Changes in the composition of the diet of the two *Eudyptes* species have been attributed to interannual oceanographic variability, which can alter prey availability around the island (Brown et al. 1990). There is a need for further studies linking the diets of Macaroni Penguins and Rockhopper Penguins with oceanographic conditions at Marion Island to elucidate environmental impacts on prey availability.

For Macaroni Penguins, although there was no long-term trend in diet composition, there was considerable inter-annual variation in the importance of fish, in particular (Fig. 3.4). The only time Antarctic Krill *Euphausia superba* was recorded in the diet of Macaroni Penguins at Marion Island during the study was in 2013 (Table 3.1). This species tends to occur well south of the PEIs, dominating the diets of Macaroni Penguins at more southerly breeding localities, e.g. South Shetland, South Georgia and Bouvet Islands (Croxall and Furse 1980, Waluda et al. 2012, Niemandt et al. 2016). The macro and mesoscale oceanographic environment near Marion Island is influenced by the dynamic latitudinal position of the sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) (Perissinotto et al. 2000, Ansorge and Lutjeharms 2002). When the SAF is located far north of the island there is a reduced flow rate of the Antarctic Circumpolar Current (ACC) around Marion Island, which allows for the formation of eddies and periodic intrusion of Antarctic species. In contrast, when the SAF is positioned southward, closer to the island, there is increased flow rate which impedes the formation of eddies and the settlement of nutrients around the island (Hunt et al. 2001, Ansorge and Lutjeharms 2002, Hunt and Pakhomov 2003). However, 2013/14 was characterised by warmer sea surface temperatures when there was a southward shift in the SAF towards the island (Whitehead 2017). Thus, the presence of *E. superba* in their diet may suggest that Macaroni Penguins foraged farther south that year.

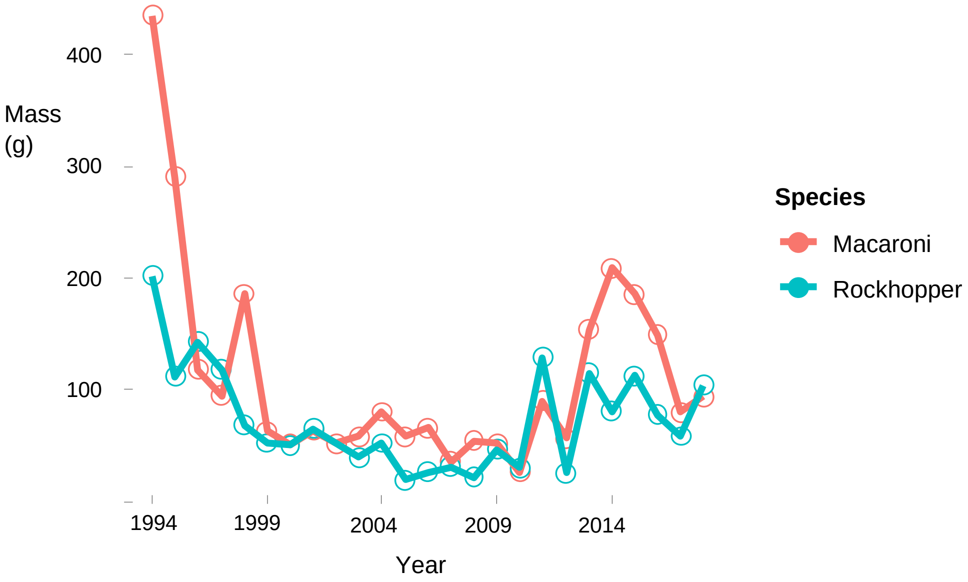
The greater variability and diversity in the diet of Macaroni Penguins compared with Rockhopper Penguins at Marion Island is consistent with the findings of an earlier study (Adams and Brown 1989), and this greater flexibility is facilitated by the greater foraging range and dive depth of Macaroni Penguins. In particular, the higher proportions of myctophids in their diet may reflect their ability to dive deeper than Rockhopper Penguins (Whitehead 2017). During the breeding period of 2011/12–2013/14 at Marion Island, Macaroni Penguins (143 [SD 14] s) dived for longer than Rockhopper Penguins (113 [SD 16] s), spent more time feeding at the bottom (70 [SD 14] s vs 42 [SD 10] s) and had a higher bottom-time dive efficiency (0.38 [SD 0.08] vs 0.28 [SD 0.06]). Myctophids undergo diel vertical migrations, which means they are closer to the surface at night and migrate to the bottom during the day (Robison 2003), but penguins are visual foragers diving mainly during the day (Wilson et al. 1993). At Marion Island, >80% of dives by Macaroni and Rockhopper Penguins occurred during the day in the 2012/13 breeding period (Whitehead 2017).

Rockhopper Penguins exhibited some inter-annual variability in their diet. In the mid-1990s, fish contributed substantially, especially *Zanchlorhynchus spinifer* (1996 and 1997) and *Protomyctophum tenisoni* and *P. choriodon* (1994), but this did not correspond to a year of high fish consumption in the diet of Macaroni Penguins (Fig. 3.3 and 3.4). Small numbers of *P. choriodon* were found in the diets of Antarctic and sub-Antarctic fur seals on Marion Island, where *P. tenisoni* made up >25% by mass in the diet of these two seals (Reisinger et al. 2018), suggesting that *P. choriodon* is not common around the island. Also, Rockhopper Penguins preyed on more *Notothenia* spp. than did Macaroni Penguins (Table 3.1). Notothenids occurred in high proportions by mass in their diets in 2007 (9%) and 2008 (27%). Adams and Brown (1989) suggested that Rockhopper Penguins are inefficient feeders on fish, but repeated instances of high occurrence of fish in their diet show them to be opportunistic and efficient feeders on available forage resources. The presence of *Z. spinifer* in their diet in 1996/97 and 1997/98 coincided with the large-scale climatic perturbation caused by the ENSO event of 1997/98 (Surman and Nicholson 2009). Interestingly, in 1997 Rockhopper Penguins fledged heavier chicks than usual at Marion Island (Crawford et al. 2003b). Clausen and Pütz (2002) showed an increase of different fish species in the diet of Rockhopper Penguins in the Falkland Islands during the same period. ENSO-driven oceanographic variability has been linked to changes in prey availability, breeding success (Chastel et al. 1993, Surman and Nicholson 2009) and survival (Hodder and Graybill 1985) of seabirds. However, the relationship between fledgling mass, oceanographic conditions and the diet of the two penguin species was not investigated in this study. The large size of *Z. spinifer* (170–180 mm) preyed on by Rockhopper Penguins indicates that they preyed on pelagic post-larval fish (Gon and Heemstra 1990). *Zanchlorhynchus spinifer* was recorded in the diet of Rockhopper Penguins at Macquarie Island in 1982,1985 and 1993 (Horne 1985, Hindell 1988, Hull 1999). From 1997, Rockhopper Penguins at Marion Island had a diet dominated by *E. vallentini* and *T. vicina*, despite the rapid climate changes around the island (Rouault et al. 2005). There was a 1.4 °C increase in mean sea-surface temperature around Marion Island from 1949 to 2003 (Mélice et al. 2003), which could have influenced the availability of prey.

Macaroni Penguins breed 3–5 weeks earlier than Rockhopper Penguins at Marion Island, helping to reduce the temporal and spatial overlap in foraging between the species (Crawford and Dyer 2006, Chapter 2) and hence reducing potential competition for food. The foraging range and duration of both penguins increases as their chicks develop (Brown 1987, Brown and Klages 1987; Whitehead et al. 2017). By the time the Rockhopper Penguins arrive, Macaroni Penguins are incubating their eggs (Brown 1987), and by the time the chicks of Rockhopper Penguins hatch and are being fed frequently, Macaroni Penguins are foraging further offshore. As the breeding period continues, there is a period of about three weeks when both Macaroni and Rockhopper Penguins are provisioning large chicks during the same period, and this may increase competition between the species. According to Whitehead (2017), between 2011/12 and 2013/14 Macaroni Penguins at Marion Island (49 [SD 22] km) travelled 12 (SD 5) km farther than Rockhopper Penguins (37 [SD 21] km) and spent more hours at sea (29 [SD 17] and 27 [SD 15] hours, respectively), with both species foraging farther and for longer as the chicks developed during the guard period. However, during the creche period, the penguins performed their trips in less than one day but occasionally performed long self-provisioning trips of 5–14 days. Both species perform frequent dives of 40–60 m, which suggests pelagic foraging, with Macaroni Penguins making more frequent deeper dives than Rockhopper Penguins (Brown and Klages 1987, Whitehead et al. 2017).

In years of low krill availability near Marion Island, the annual variability and high incidence of fish in the diet of Macaroni Penguins suggest that they could outperform Rockhopper Penguins by switching from a krill to a fish dominated diet. This could explain their large numbers than Rockhopper Penguins at the island (Crawford et al. 2009). Crawford et al. (2003a) suggest the ongoing, long-term decline of both species is because of insufficient breeding success to maintain the population. In conclusion, substantial overlap was found between the diets of the two *Eudyptes* penguins and, overall, no apparent long-term changes in dietary compositions were evident. This suggests considerable competition for resources between these two sympatric species during breeding, when their foraging range is constrained, and they have potentially overlapped foraging grounds. Mean sample mass between Macaroni and Rockhopper Penguins was positively correlated, which could indicate a similar impact on the two species of prey availability around Marion Island. Based on sampling in 1984/85, Adams and Klages (1989), concluded that the dietary segregation of the two *Eudyptes* penguins on Marion Island is incomplete. This study, based on a 25-year time series, largely supports this conclusion. Further studies are required to better understand the specific responses of these sympatric species to changes in prey availability and their ecological roles in the Southern Ocean.

Supplementary material



Supplementary Figure S3.1: Mean annual samples mass recovered from Macaroni and Eastern Rockhopper Penguins at Marion Island from 1994–2018 (no data was collected for Eastern Rockhopper Penguins in 2002).

Supplementary Table S3.1: All prey species identified in the diet samples of Macaroni Penguins and Eastern Rockhopper Penguins at Marion Island 1994–2018.

	Macaroni Penguin				Eastern Rockhopper Penguin			
	% Frequency	% Number	% Mass	% IRI	% Frequency	% Number	% Mass	% IRI
Crustacean	98.0	96.8	64.6		99.7	98.0	81.6	
Thysanoessa vicina	85.4	63.9	39.4	68.2	77.7	58.1	39.6	56.3
Euphausia vallentini	47.6	24.7	19.9	16.4	77.1	37.5	35.4	41.8
Themisto gaudichaudii	43.7	7.4	4.7	4.1	14.2	0.8	0.6	0.2
Primno macropa	15.1	0.6	0.4	0.1	16.8	0.7	0.4	0.1
Nauticaris marionis	2.1	0.1	0.2	<0.1	9.2	0.7	0.6	0.1
Euphausia lucens	0.6	<0.1	<0.1	<0.1	5.2	0.6	0.3	0.1
E. longispina	0.1	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
E. superba	0.1	<0.1	<0.1	<0.1	-	-	-	-
E. longirostra	0.2	<0.1	<0.1	<0.1	0.8	<0.1	<0.1	<0.1
Hyperiella antarctica	-	-	-	-	0.8	<0.1	<0.1	<0.1
Calanus propinquus	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Nematocarcinus longirostris	0.1	<0.1	<0.1	<0.1	-	-	-	-
Pasiphaea longispina	0.1	<0.1	<0.1	<0.1	-	-	-	-
Cyllopus spp.	0.2	<0.1	<0.1	<0.1	-	-	-	-
Grammarid spp.	0.2	<0.1	<0.1	<0.1	-	-	-	-
Hyperiella spp.	1.1	<0.1	<0.1	<0.1	-	-	-	-
Lanceola spp.	0.1	<0.1	<0.1	<0.1	-	-	-	-
Unidentified euphausiid	0.5	0.01	<0.1	<0.1	4.3	<0.1	4.7	0.2
Unidentified isopod	0.1	<0.1	<0.1	<0.1	0.3	<0.1	<0.1	<0.1
Unidentified prawn	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Unidentified amphipod	1.3	<0.1	<0.1	<0.1	1.5	0.01	0.01	<0.1
Unidentified decapod	0.5	<0.1	<0.1	<0.1	-	-	-	-

Fish	77.0	3.1	33.6		57.5	1.1	16.5	
Krefftichthys anderssoni	51.4	1.7	13.4	6.0	28.9	0.6	1.3	0.4
Protomyctophum tenisoni	51.9	1.0	8.0	3.6	14.3	0.3	2.3	0.3
Electrona carlsbergi	13.5	0.2	8.4	0.9	2.0	<0.1	0.7	0.01
E. subaspera	0.4	<0.1	0.1	<0.1	0.2	<0.1	0.1	<0.1
Zanclorhynchus spinifer	0.1	<0.1	0.1	<0.1	1.9	<0.1	8.5	0.1
Protomyctophum choriodon	7.2	<0.1	1.1	0.1	3.1	<0.1	1.7	0.1
P. bolini	1.5	<0.1	1.0	<0.1	0.5	<0.1	<0.1	<0.1
P. normani	0.5	<0.1	<0.1	<0.1	-	-	-	-
P. parallelum	0.2	<0.1	<0.1	<0.1	-	-	-	-
Gymnoscopelus fraseri	0.5	<0.1	0.1	<0.1	0.8	<0.1	0.1	<0.1
G. piabilis	0.1	<0.1	0.1	<0.1	-	-	-	-
G. nicholsi	0.1	<0.1	<0.1	<0.1	0.3	<0.1	0.1	<0.1
Gobionotothen marionensis	0.2	<0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Lepidonothen larseni	0.3	<0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Notothenia spp.	1.9	<0.1	0.3	<0.1	11.9	0.1	0.5	0.1
Paranotothenia magellanica	-	-	-	-	0.2	<0.1	<0.1	<0.1
Maurolicus meulleri	-	-	-	-	0.3	<0.1	<0.1	<0.1
Channichthys rhinoceratus	-	-	-	-	0.2	<0.1	0.3	<0.1
Micromesistius australis	-	-	-	-	0.2	<0.1	<0.1	<0.1
Ceratoscopelus warmingii	-	-	-	-	0.2	<0.1	<0.1	<0.1
Lampanyctus intricarius	3.5	0.02	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Arctozenus risso	0.2	<0.1	<0.1	<0.1	0.7	<0.1	<0.1	<0.1
Magnisudis prionosa	1.3	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Notolepis coatsi	1.6	<0.1	0.2	<0.1	0.3	<0.1	0.1	<0.1

Bathylagus antarcticus	0.1	<0.1	<0.1	<0.1	-	-	-	-
Sio nordenskjoldii	0.1	<0.1	<0.1	<0.1	-	-	-	-
Paradiplospinus glacilis	0.1	<0.1	<0.1	<0.1	-	-	-	-
Antimora rostrata	0.1	<0.1	<0.1	<0.1	-	-	-	-
Metelectrona ventralis	0.2	<0.1	<0.1	<0.1	-	-	-	-
Gymnoscopolus spp.	0.1	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Electrona spp.	0.8	0.01	<0.1	<0.1	-	-	-	-
Bathylagus spp.	0.2	<0.1	<0.1	<0.1	-	-	-	-
Nansenia spp.	0.3	<0.1	<0.1	<0.1	-	-	-	-
Trematomus spp.	0.3	<0.1	-	-	-	-	-	-
Unidentified fish	11.1	<0.1	0.8	0.1	20.8	0.1	1	0.2
Cephalopod	54.4	0.1	1.7		41.8	0.4	1.9	
Kondokovia longimana	5.4	<0.1	0.2	<0.1	1.9	<0.1	<0.1	<0.1
Moroteuthis ingens	3.9	<0.1	0.2	<0.1	5.7	0.2	0.8	0.1
Martialla hyadesi	1.9	<0.1	0.1	<0.1	1.2	<0.1	0.1	<0.1
Gonatus antarcticus	-	-	-	-	0.3	<0.1	<0.1	<0.1
Moroteuthis spp.	-	-	-	-	0.2	<0.1	<0.1	<0.1
Octopus spp.	1.6	<0.1	<0.1	<0.1	4.5	<0.1	0.1	<0.1
Unidentified squid	-	-	-	-	33.2	0.3	0.9	0.3

Supplementary Table S3.2: Number of samples collected monthly and yearly of Macaroni and Eastern Rockhopper Penguins at Marion Island 1994–2018.

Year	Macaroni Penguin				Eastern Rockhopper Penguin			
	December	January	February	Total	January	February	March	Total
1994/95	7	11	12	30	13	11	7	31
1995	7	15	15	37	14	8	7	29
1996	15	14	14	43	15	15	0	30
1997	15	15	15	45	15	14	15	44
1998	17	12	11	40	0	13	21	34
1999	30	15	0	45	15	15	15	45
2000	15	15	16	46	15	14	15	44
2001	9	17	6	32	16	16	9	41
2002	11	13	11	35	0	0	0	0
2003	15	14	15	44	9	21	0	30
2004	16	22	11	49	10	8	1	19
2005	10	15	20	45	6	10	0	16
2006	10	0	15	25	0	15	0	15
2007	15	10	15	40	5	10	9	24
2008	10	15	14	39	5	0	6	11
2009	10	15	15	40	5	10	10	25
2010	9	15	15	39	5	10	10	25
2011	10	15	15	40	5	12	10	27
2012	10	15	16	41	5	9	7	21
2013	10	20	15	45	5	10	10	25
2014	0	30	15	45	5	10	10	25
2015	10	15	15	40	5	11	10	26
2016	10	15	15	40	5	10	10	25
2017	10	15	15	40	6	10	11	27
2018/19	10	15	15	40	5	10	10	25
Total	291	373	341	1005	189	272	203	664

Supplementary Table S3.3: The number of years in which prey species was found in the diet of Macaroni and Eastern Rockhopper Penguins at Marion Island.

Species	Macaroni Penguin		Eastern Rockhopper Penguin	
	Years present in diet	N years	Years present in diet	N years
Crustaceans				
Thysanoessa vicina	1994–2018	25	1994–2001, 2003–18	24
Euphausia vallentini	1994–2018	25	1994–2001, 2003–18	24
Themisto gaudichaudii	1994–2018	25	1994–97, 1999–2001,2005–07, 2010–18	19
Primno macropa	1995–2002, 2004–18	23	1997–2001, 2005–08,2010–18	18
Nauticaris marionis	1995–96, 1998–99, 2004, 07, 18	7	1995, 1998–99, 2001,04 ,2006–07,2010–11,2014–16,18	13
Euphausia lucens	1998, 2001–02, 05, 10, 11	6	1998–2000, 05, 07, 09, 11, 13, 16	9
Euphausia longispina	1998	1	1999	1
Euphausia superba	2013	1		
Euphausia longirostra	1998, 2004	2	2005, 2007, 2011	3
Hyperiella antarctica			1999, 2001, 2005, 2009	4
Calanus propinquus	2006	1	2006	1
Nematocarcinus Longirostris	1998	1	–	–
Pasiphaea longispina	2014	1	–	–
Cyllopus spp.	1998	1	–	–
Grammarid spp.	2001	1	–	–
Hyperiella spp.	1997–1999,2001, 07, 09, 11, 15	8	–	–
Lanceola spp.	1998	1	–	–
Unidentified euphausiid	1996, 1998, 2001, 2012	4	1994–96, 1998	4
Unidentified isopod	1996	1	1996, 2001	2
Unidentified prawn	2009, 2016	2	2016	1
Unidentified amphipod	1997–1999, 2012, 2015–2018	8	1998, 2001, 2016, 2018	4
Unidentified decapod	1995, 1998, 2014–2016	5	–	–
Fish				
Krefftichthys anderssoni	1994–2018	25	1994–2001, 2003–05, 2007–08, 11, 2013–18	20

Protomyctophum tenisoni	1994–2001, 2003–2018	24	1994–2001, 2003–05, 08, 11, 2013–18	19
Electrona carlsbergi	1994–1999, 2003–2018	22	1994, 96, 98, 2000–01, 04, 11, 14, 16	9
Electrona subaspera	1996, 1998, 2006, 2014	4	1994	1
Zanclorhynchus spinifer	1997	1	1994–1997, 2018	5
Protomyctophum Choriodon	1994–98, 2002, 04, 06, 08, 10, 12, 14, 16, 18	14	1994, 98, 2004, 14, 2016–17	6
Protomyctophum bolini	1994–95, 97, 2002, 13, 2015–18	9	1998, 2007	2
Protomyctophum normani	2004, 2016	2	–	–
Protomyctophum Parallelum	2010, 2014	2	–	–
Gymnoscopelus fraseri	1994, 1998, 2004, 2018	4	1996, 1999, 2007	3
Gymnoscopelus piabilis	2002	1	–	–
Gymnoscopelus nicholsi	1998	1	1999	1
Gobionotothen Marionensis	1994, 1995	2	1996, 1998	2
Lepidonothen larseni	2001, 2008, 2014	3	1995, 1998, 2005, 2007	4
Notothenia spp.	1994, 2001, 2006–08, 2010–18	14	1994–99, 2001, 2004–09, 2011–18	21
Paranotothenia Magellanica	–	–	2017	1
Maurolicus meulleri	–	–	2013, 2015	2
Channichthys Rhinoceratus	–	–	2001	1
Micromesistius australis	–	–	1996	1
Ceratoscopelus warmingii	–	–	2007	1
Lampanyctus intricarius	2004, 2010, 2012–16, 2018	8	2013, 2015	2
Arctozenus risso	1998, 2011	2	1995, 2011	2
Magnisudis prionosa	1994–95, 1997–98, 2001 2008–09, 13, 2015–16	10	2017	1
Notolepis coatsi	1995, 2002–04, 07, 2012–16, 18	11	1999, 2017	2
Bathylagus antarcticus	1994, 1995	2	–	–
Sio nordenskjoldii	1997	1	–	–
Paradiplospinus glacilis	1994	1	–	–
Antimora rostrata	1997	1	–	–

Metelectrona ventralis	1994, 2003	2	–	–
Gymnoscopelus spp.	1994	1	1996	1
Electrona spp.	1994, 1996, 2010	3	–	–
Bathylagus spp.	1995, 1996	2	–	–
Nansenia spp.	1996, 1999, 2013	3	–	–
Trematomus spp.	1998, 2016	2	–	–
Unidentified fish	1994–2018	25	1994–01, 2004–18	22
Cephalopods				
Kondokovia longimana	1994–2001, 04, 07, 2008–10, 12	14	1994–96, 1998–2000, 12	7
Moroteuthis ingens	1994–99, 2001, 03, 05, 2008–10,12	13	1994–98, 2001, 06, 08, 12	8
Martialla hyadesi	1995, 1997–99, 2001, 04, 08, 2012–13	9	2000–01, 04, 2011–12	5
Gonatus antarcticus	–	–	1994	1
Moroteuthis spp.	–	–	1994	1
Octopus spp.	1994, 97, 99, 2001–02, 04, 09, 2011–14	11	1996–99, 2001, 06, 07, 09, 13,15, 2016–17	12
Unidentified squid	–	–	1994–2001, 2003–18	22

Supplementary Table S3.4: Summary of breeding diet (percentage by mass) of Macaroni and Easter/Western Rockhopper Penguins at various breeding sites.

Site	Year	Species	Crustaceans	Fish	Cephalopods	Source
Bird Island	1989–2010	Macaroni	90.7	9.1	0.2	(Waluda et al. 2012)
Bouvet	1997, 1999, 2001, 2008	Macaroni	28, 22, 48, 57	73, 77, 53,42	1, <1, <1, <1	(Niemandt et al. 2016)
Crozet	1980–1981	Macaroni	60.9	28.7	9.8	(Ridoux 1994)
		Eastern Rockhopper	71	17	11	
Crozet	1998–1999	Eastern Rockhopper	95	4	1	(Tremblay and Cherel 2003)
Falkland	1980	Western Rockhopper	45	53	2	(Croxall et al. 1985)
Heard	1986–1987	Macaroni	76.7	23.2	0.1	(Klages et al. 1989)
		Eastern Rockhopper	99.3	0.7	<0.1	
Heard	1992	Macaroni	58.6	41.4	-	(Green et al. 1998)
Macquarie	1984–1986	Eastern Rockhopper	69.3	28.6	1.7	(Hindell 1988)
Marion	1983/84 and 84/85	Macaroni	87–62.1	4.9–24.7	8.1–13.2	(Brown and Klages 1987)
		Eastern Rockhopper	91.6–80.8	3.8–14	4.6–5.2	
Marion	1994–2018	Macaroni	64.6	33.6	1.9	Present study
		Eastern Rockhopper	81.6	16.5	1.7	
South Shetland (Clarence)	1977	Macaroni	100	-	-	(Croxall and Furse 1980)
South Shetland (Gibbs)		Macaroni	37	63	-	(Croxall and Furse 1980)

Chapter 4: Effect of oceanographic variation on diet and reproductive performance of Macaroni and Eastern Rockhopper Penguins

Abstract

The need to understand the factors that affect the population processes of long-lived species which live in a dynamic marine ecosystem creates a challenge for conservation management. Macaroni and Rockhopper Penguins have shown a decrease in their population and high inter-annual variability in their breeding biology and diet since their monitoring under CCMALR started in 1994. However, the reasons for the annual variability have not been explored in the context of the changing environmental climate. In this study I try to find a link between their diet, breeding performance, climatic and oceanographic variables, to assess whether there is a relationship which could explain the decrease in the population of Macaroni and Rockhopper Penguins at Marion Island since 1994.

Macaroni Penguins had higher breeding success when they fed on myctophids, while Rockhopper Penguins fledged lighter chicks when they fed more on myctophids. This might be linked to the difference in vertical foraging between the two penguin species. Macaroni Penguins have greater diving abilities, and they are more efficient at reaching deep myctophid prey than Rockhopper Penguins. Macaroni Penguin fledgling mass decreased with increasing sea surface height while Rockhopper Penguin fledgling mass increased with increasing sea surface height similarly with male Rockhopper Penguin mass on arrival. The contrasting response to sea surface height indicates the differentiation in foraging adaptations between these two sympatric penguin species around Marion Island before the onset of breeding and during breeding when their foraging range is constrained.

Macaroni Penguin diet was associated with the position of the Antarctic Polar Front (APF) while Rockhopper Penguins responded to both the position of the APF and the Sub-Antarctic Front (SAF). Macaroni Penguins fed more on myctophid prey (*Protomyctophum tenisoni*) when APF was farther away from the Island and conversely Macaroni Penguins fed on crustacean prey (*Thysannoesa vicina*) when APF was closer to the island. Similarly, Rockhopper Penguins fed on myctophid prey (*P. tenisoni*) and amphipods (*Themisto gaudichaudi*) when SAF was further away from the island and fed on crustacean *T. vicina* when SAF was closer to the Island.

The variation in male and female mass on arrival, fledgling mass and breeding success was not significantly explained by Sea Surface Temperature (SST), Southern Oscillation Index (SOI), Southern Annular Mode (SAM) and Sea Level Anomalies (SLA). However, the fledgling mass of both penguins was explained by Sea Surface Height (SSH).

Introduction

Seabirds and Environmental change

Marine ecosystems are increasingly being affected by climate change, excessive fishing, pollution, predation and other disturbances over the range of their geographical distribution through space and time (Southwell et al. 2017). As a physical driver of ecosystem functioning, climate change has the potential to influence seabird demography and population dynamics, generally by affecting food availability and distribution (Cury et al. 2011, Oro et al. 2014) . Seabirds are central place foragers while breeding, due to their need to provision their offspring within a limited time. This restricts their foraging range at sea in relation to their breeding colony (Lowther et al. 2014). Seabirds interact with both terrestrial and marine ecosystems, coming on land for their breeding and going back to sea to forage and provision for their growing chicks (Weller et al. 2016). This makes them good bioindicators of their immediate environments and can be particularly useful in understanding changes in ecosystems where lower trophic levels are not well monitored (Boersma 2008, Durant et al. 2009). The constraint of central place foraging also puts them at risk when they have limited breeding sites which could constrain their ability to respond to shifting climate variables by moving their breeding sites.

Observing different biological parameters of seabirds like breeding success, survival, population trends, diet and foraging parameters will help identify large and small-scale changes in the marine environment surrounding breeding colonies (Cunningham 2017). There has been a marked increase in global average temperature, affecting trophic dynamics, species interaction and shifting marine food webs resulting in decreasing trends in many seabird populations, including penguins (Hilton et al. 2006, Baylis et al. 2012, Croxall et al. 2012a, Trathan et al. 2012, Dehnhard et al. 2013a, 2013b, Constable et al. 2014, Horswill et al. 2014, Delord et al. 2021). However other factors like the continued exploitation of resources by fisheries, by-catch from fisheries activities, predation pressure from seals and giant petrels and diseases have had a direct effect on seabird population declines at other sites (Cooper et al. 2009, Cuthbert et al. 2009, Morrison et al. 2015, Ropert-Coudert et al. 2019).

Large-scale climatic variation, such as El Niño-Southern Oscillation ENSO (Surman and Nicholson 2009, Surman et al 2012) and localised physical conditions (frontal movements, wind strength, and sea surface temperature (SST) influence primary production and consumer abundance (Frederiksen et al. 2004, Jaquemet et al. 2007, Bost et al. 2015). This happens through the influence of climatic variables on ocean and atmosphere interaction propagating the dynamics of marine ecosystem structures (Baylis et al. 2012, Cimino et al. 2014).

Marion Island is positioned along the Antarctic Circumpolar Current (ACC) sandwiched by two fronts, Sub-Antarctic Front (SAF) to the north and Antarctic Polar Front (APF) to the south. The variability in their latitudinal position has been linked with changes in phytoplankton blooms, zooplankton prey composition and abundance around the water of Marion Island (Ansorge and Lutjeharms 2003, Hunt and Pakhomov 2003, Ansorge et al. 2009, 2012). *Eudyptes* penguins feed on low trophic level prey euphausiids (*Thysanoessa vicina* and *Euphausia vallentini*), fish and squids at Marion Island (Chapter 3) They are likely to be influenced by changes in oceanographic conditions that affect primary productivity and biomass especially during breeding when their foraging is constrained. The diet of Gentoo penguins at Marion Island has been linked to the latitudinal position of both the APF and the SAF at (Carpenter-Kling et al. 2019).

The proportion of penguins that engage in reproduction is linked to their body condition, affected by the amount of food available (Vleck and Vleck 2002). The growth rate and recovery of a breeding population from negative effects is sensitive to juvenile survival, adult survival and breeding performance (Williams 1995, Borboroglu and Boersma 2015). Considering the complex interactions, size, and dynamic nature of the marine ecosystem it is difficult to only attribute trends in population to just on factor. In the case of *Eudyptes* penguins at Marion Island there is very limited human induced disturbance such as commercial fishing and pollution in the region and none that directly impact the penguins or their prey, hence fewer factors could affect them.

According to the global assessment of seabird populations by the IUCN Red list of threatened species, half of the seabird species are known to be declining and one third are threatened with extinction (Croxall et al. 2012, Paleczny et al. 2015). Penguins are one of the most threatened families of seabirds and *Eudyptes* penguins are the most abundant genus within the penguin family. Most *Eudyptes* penguins are globally threatened including Macaroni and Rockhopper Penguins (Borboroglu and Boersma 2015, Dias et al. 2019, Birdlife International 2021a). At Marion Island there has been a decline in the two *Eudyptes* penguins, Macaroni and Rockhopper Penguins since the early 1980s and the two Penguins species have been monitored at Marion Island annually under CCMALR since 1994 (Cooper et al. 1997, CCAMLR 2000) (Chapter 2). In this chapter I try to explain the dramatic decline in their population by using data from the last 26 years of their reproductive performance (fledgling mass and breeding success) and body condition before breeding to address the following questions: does diet influence their reproductive performance? (2) are their diet and reproductive performance and body condition prior to breeding affected by climatic and environmental conditions?

Methods

For data collection on breeding success and adult mass on arrival, see the Methods section in Chapter 2. For the data collection on diets, see Methods section in Chapter 3.

Environmental Variables

Large-scale climatic variability within the Southern Ocean is usually characterized by the Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) (Table 1). The SOI is based on the difference in atmospheric pressure between Tahiti (17°33'S,149°37'W), in the Pacific, and Darwin (12°28'S, 130°51'E) in northern Australia. The positive values of SOI indicate warm phases of ENSO events (La Niña) while negative values of SOI indicate cold phases of ENSO events (Baylis et al. 2012).

The SAM results from internal atmospheric dynamics in middle latitudes and is associated with a meridional shift in the position and intensity of westerly winds in the Southern Ocean (Forcada and Trathan 2009). Both environmental indices are associated with changes in Sea Surface Temperature (SST) and Sea Surface Height (SSH), Sea Level Anomaly (SLA) throughout the Southern Ocean (Forcada and Trathan 2009, Surman et al. 2012).

Meso-scale climatic variability was characterised by satellite-derived monthly mean measurements of SST, SSH, SLA. These parameters are often used as proxies of marine environmental conditions which can affect prey distribution and availability around Marion Island (Table 4.1). Prey might be found in specific temperatures and depth, which may be targeted by marine top predators as productive areas (Forcada and Trathan 2009). The analysis of environmental variables against reproductive variables of Macaroni and Rockhopper Penguins was exploratory in that there was no prior assumption on how and which variable was to influence the reproductive variables of the penguins before breeding, adult mass on arrival and during breeding, fledgling mass, and breeding success (chicks fledged per pair).

For adult mass on arrival, the marine environmental variables were summarised as annual seasonal averages prior breeding, Macaroni (Aug–Oct) and Rockhopper (Sep–Nov), between 45–55°S, 30–45°E. The gap is accounting for the 3–5 weeks difference in arrival between the two penguins at Marion Island (see Chapter 2). For fledgling mass and breeding success, environmental variables were summarised over a smaller range because their foraging range is reduced during breeding, between 46–48°S, 37–40°E (Brown 1987, Whitehead 2017). Fledgling mass was summarised after hatching of the chicks to fledgling before pre-moult Macaroni (Dec–Feb) and Rockhopper (Jan–Mar). Breeding success was summarised from egg laying to fledgling before pre-moult, to span the entire breeding period, Macaroni (Nov–Feb), Rockhopper (Dec–Mar).

Ocean fronts where two water masses with different environmental characteristics meet, divide the Southern Ocean into several distinct habitats with different biophysical properties (Chapman et al. 2020). Oceanic fronts are identified as areas of high marine productivity, attracting marine predators as favourable predictable feeding grounds with elevated prey availability (Bost et al. 2009). Marion Island is sandwiched by two fronts, the Sub-Antarctic Front (SAF) to the north and Antarctic Polar Front to the south (APF, Chapter 1, Fig. 1.1).

In previous studies the position of the fronts within the Southern Ocean have been identified and inferred from Sea Surface Height (SSH, Table 4.1) maps using methods adapted from Swart et al. (2010) and Sokolov and Rintoul (2009). Sea surface temperature values were used to identify the position of the middle- Sub-Antarctic Front (M-SAF, 0.03) and southern Sub-Antarctic Front (S-SAF, -0.17), and the northern-Antarctic Polar Front (N-APF, -0.3) and middle Antarctic Polar Front (M-APF, -0.48) according to Swart et al. (2010). Both limits of the fronts were used to cover the highly variable foraging grounds of both Macaroni and Rockhopper Penguins which are offshore foragers.

Data analysis

To assess the influence of oceanographic variability on adult mass on arrival, fledgling mass and breeding success of Macaroni and Rockhopper Penguins, I used a general additive model (GAM) with the ‘gam’ function in the R package ‘mgcv’ (Wood 2011). The models were fitted with a Gaussian error distribution. I used a penalized cubic regression spline and smoothing parameters were estimated using restricted maximum likelihood (REML). To avoid multicollinearity, univariate models were run to compare the relationship between adult mass on arrival of both male and female, fledgling mass, and breeding success against the individual environmental variables (Table 4.1).

Table 4.1: Table showing environmental variables used to indicate large-scale and meso-scale climatic variability around Marion Island.

Variable	Abbreviation	Temporal Resolution	Spatial Resolution	Source
Southern Oscillation Index	SOI	Monthly	-	NCDC/NOAA[a]
Southern Annular Mode	SAM	Monthly	-	Marshall Southern Annular Mode (SAM) Index (Station based)[b]
Sea Surface Temperature	SST	Monthly	0.5° x 0.5°	NOAA NCEP EMC CMB GLOBAL Reyn_SmithOIv2[d]
Sea Surface Height	SSH	Monthly	0.08° x 0.08°	MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012[c]
Sea Level Anomaly	SLA	Monthly		SEALEVEL_GLO_PHY_CLIMATE_L4_REP_OBSERVSTIONS_008_057[C]
Ocean fronts		Daily	0.25° x 0.25°	SEALEVEL_GLO_PHY_CLIMATE_L4_REP_OBSERVSTIONS_008_057[C]

[a] National Centres for Environmental Information (https://www.ncdc.noaa.gov/)

[b] Climate data guide (https://climatedataguide.ucar.edu/); Produced by Marshall (2003).

[c] Copernicus Marine Service Information (https://marine.copernicus.eu/) GLOBAL OCEAN BIOGEOCHEMISTRY HINDCAST.

[d] National Oceanic and Atmospheric Administration http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/ /.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.sst/; Produced by Reynolds et al. (2002).

The Dharma package in R was used to test for autocorrelation in GAM model residuals with function ‘testTemporalAutocorrelation’ (Hartig and Lohse 2020). If autocorrelation was detected, function ‘gamm’ was used instead with an autoregressive correlation structure and the ‘auto.arima’ function in the R package ‘forecast’ was used to selected the best autocorrelation order for the autoregressive model (Hyndman and Khandakar 2008).

A multiple linear regression with a Gaussian link was used to determine a possible relationship between diet and fledgling mass. A beta regression model generated in R with package ‘betareg’ (Zeileis et al. 2020) was used to determine a possible relationship between diet and breeding success because breeding success assumes proportional values between 0 and 1.

Residual plots were examined to assess model fit and variance inflation factors (VIF) were used to check relationships between covariates. The models were compiled separately for each prey group in the diet of Macaroni and Rockhopper Penguins (see Chapter 2). Model 1 only contained dominant species preyed on by the two penguins: two euphausiids (*Thysanoessa vicina, Euphausia vallentini*) and three myctophids (*Electrona carlsbergi, Krefftichthys anderssoni, Protomyctophum tenisoni*). Model 2 contained all euphausiids, myctophids and amphipods. Model 3 contained all prey species, crustaceans, cephalopods, and fish. The models were compiled separately to avoid multicollinearity between variables because they are derived from the same diet. A forest plot was made to present the results of the models and show the effect size (beta coefficients) on fledgling mass and breeding success (Long 2020).

A beta regression was used to determine a relationship between percentage annual composition of dominant prey species in the diet of the two penguins (*Thysanoessa vicina, Euphausia vallentini, Electrona carlsbergi, Krefftichthys anderssoni, Protomyctophum tenisoni*) against the mean annual latitudinal position of the fronts during the breeding period of Macaroni and Rockhopper Penguins from 1994–2018.

Results

Link between diet and reproductive performance

Breeding success

A positive relationship was found between Macaroni Penguin breeding success and the mass of myctophids in the diet (beta regression = 2.45, p = 0.01) and mean mass of all fish in the diet (beta regression, z = 2.33, p = 0.02; Table 4.2 Figs 4.1 and 4.2). The uptake of *E. vallentini* and amphipods had a negative effect on both penguins breeding success and in contrast there was a positive response to the uptake of myctophids and lanternfish (*P. tenisoni* and *K anderssoni*) however not significant (Table 4.2).

Table 4.2: The influence of diet on breeding success of Macaroni and Eastern Rockhopper Penguins on Marion Island from 1994–2019 using beta regression models.

Model		Macaroni			Eastern Rockhopper		
		Pseudo R^2	z-value	p-value	Pseudo R^2	z-value	p- value
1	*T. vicina*	0.30	0.29	0.77	0.11	-0.76	0.45
	E. vallentini		-1.35	0.18		-0.79	0.43
	E. carlsbergi		-1.34	0.18		-0.67	0.51
	K. anderssoni		1.05	0.29		0.09	0.93
	P. tenisoni		1.20	0.23		0.81	0.42
2	All euphausiids	0.29	0.36	0.72	0.05	-0.41	0.68
	All myctophids		2.45	0.01*		-0.34	0.73
	All amphipods		-0.32	0.19		-0.68	0.50
3	All crustaceans	0.25	-0.32	0.75	0.05	-0.88	0.38
	All cephalopods		-0.34	0.73		0.66	0.51
	All fish		2.33	0.02*		-0.11	0.91

(*) indicates significant value p<0.05

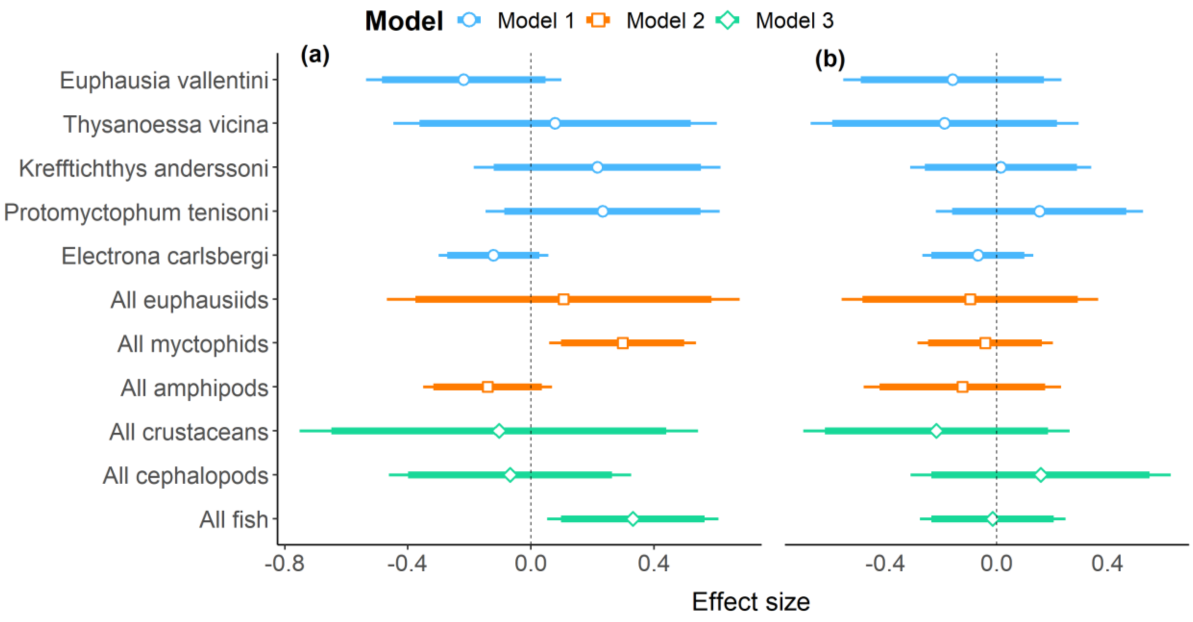


Figure 4.1: Forest plot summarizing beta regression models of mean annual diet components (predictors) against breeding success of Macaroni (a) and Eastern Rockhopper Penguins (b). Bars show standardized coefficient estimates (effect size) of predictor variables and 90 and 95% confidence intervals.

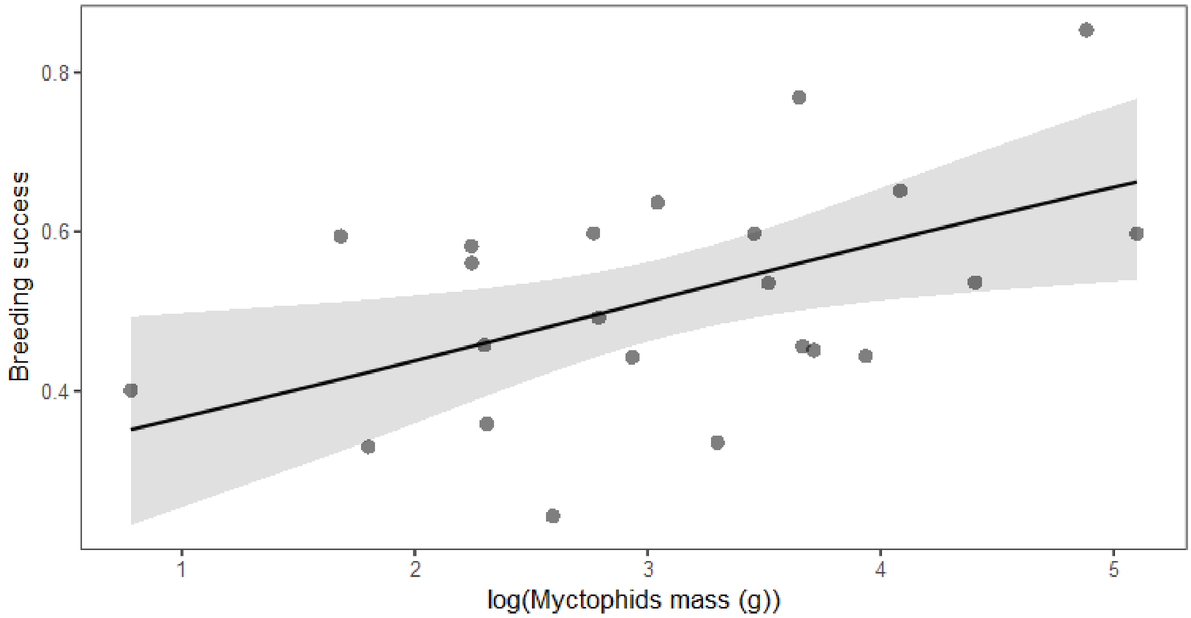


Figure 4.2: The relationship between the mean mass of myctophids in the diet of Macaroni Penguins at Marion Island and breeding success (chicks fledged/pair) from 1994 to 2019.

Fledgling mass

There was a tendency for an increase in fledgling mass with increase in uptake of fish, myctophids and *K. anderssoni* by Macaroni Penguins, however the relationship was not significant (Table 4.3, Fig. 4.3). Rockhopper Penguin fledgling mass decreased as the mass of myctophids in the diet increased (t = -2.47, p = 0.02, Fig. 4.4). In contrast there was a tendency for an increase in fledgling mass with uptake of crustaceans, all euphausiids *and E. vallentini* by Rockhopper Penguins howbeit the relationship was not significant (Table 4.3).

Table 4.3: The influence of diet on fledgling mass of Macaroni and Eastern Rockhopper Penguins using linear regression models.

Model		Macaroni			Eastern Rockhopper		
		R^2	t-value	p-value	R^2	t-value	p- value
1	*T. vicina*	0.23	0.29	0.78	0.14	-0.39	0.94
	E. vallentini		-2.05	0.05		1.06	0.31
	E. carlsbergi		-1.32	0.19		-0.08	0.94
	K. anderssoni		0.98	0.34		-1.06	0.30
	P. tenisoni		0.002	0.99		-0.45	0.66
2	All euphausiids	0.09	-1.08	0.29	0.24	1.23	0.23
	All myctophids		0.99	0.33		-2.47	0.02*
	All amphipods		0.37	0.71		0.29	0.77
3	All crustaceans	0.07	-1.17	0.26	0.056	0.60	0.55
	All cephalopods		-0.79	0.44		-0.93	0.36
	All fish		1.09	0.29		-0.27	0.79

(*) indicates significant value $p<0.05$

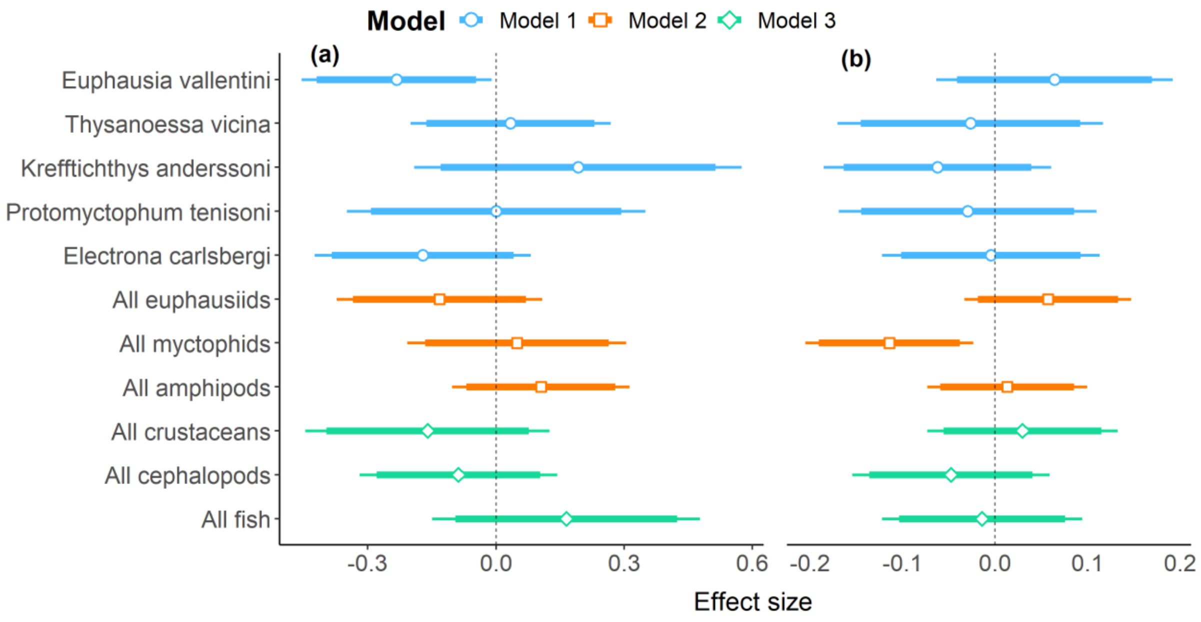


Figure 4.3: Forest plot summarizing multiple linear regression models of mean annual diet components (predictors) against fledgling mass of Macaroni (A) and Eastern Rockhopper (B) Penguins. Conventions as Fig. 4.2.

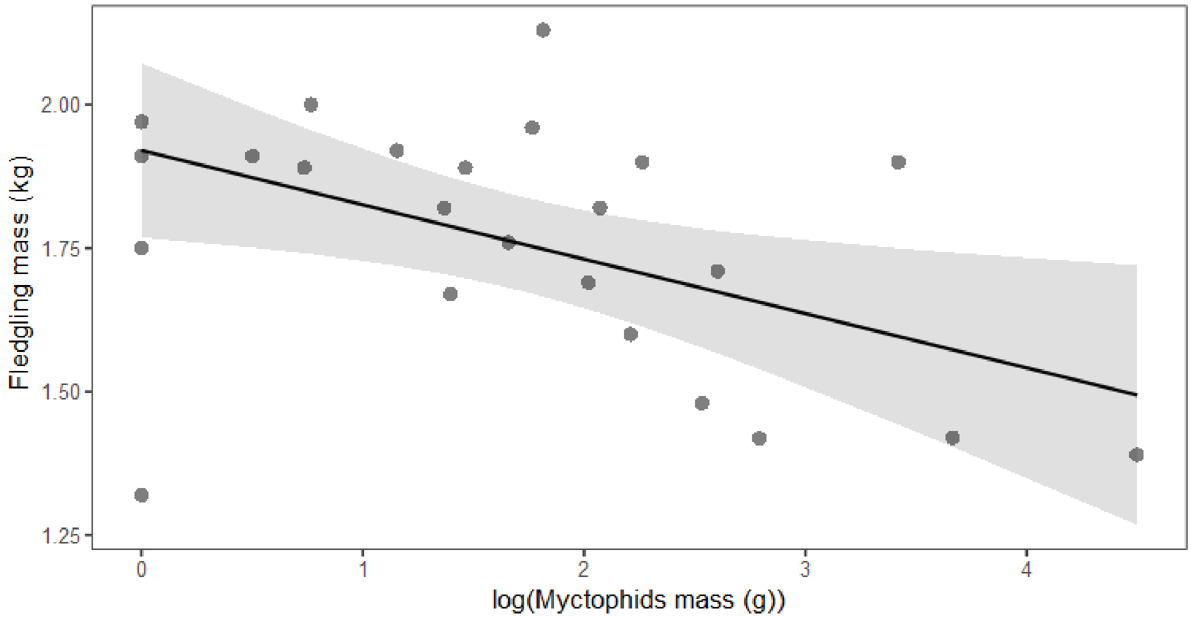


Figure 4.4: The relationship between the mean mass of myctophids in the diet of Eastern Rockhopper Penguins at Marion Island and fledgling mass from 1994 to 2019.

Link between reproductive performance and oceanographic variability

Four of the environmental variates (SOI, SAM, SST and SLA) had no influence on all reproductive performance variables (breeding success, fledgling mass, male and female) of both Macaroni and Rockhoppers Penguins over the study period (Table 4.4). However, sea surface height influenced fledgling mass of both Macaroni and Rockhopper Penguins and male arrival mass of Rockhopper Penguins (Table 4.4).

Macaroni Penguins tended to fledge heavier chicks at low sea surface height (General additive model: F = 3.10, Dev explained = 29%, p = 0.06, Table 4.4, Fig. 4.5) while Rockhopper Penguins fledged heavier chicks at higher sea surface height (General additive model: F = 3.5, Dev explained = 13%, p = 0.07, Table 4, Fig. 4.5), however this result was not statistically significant.

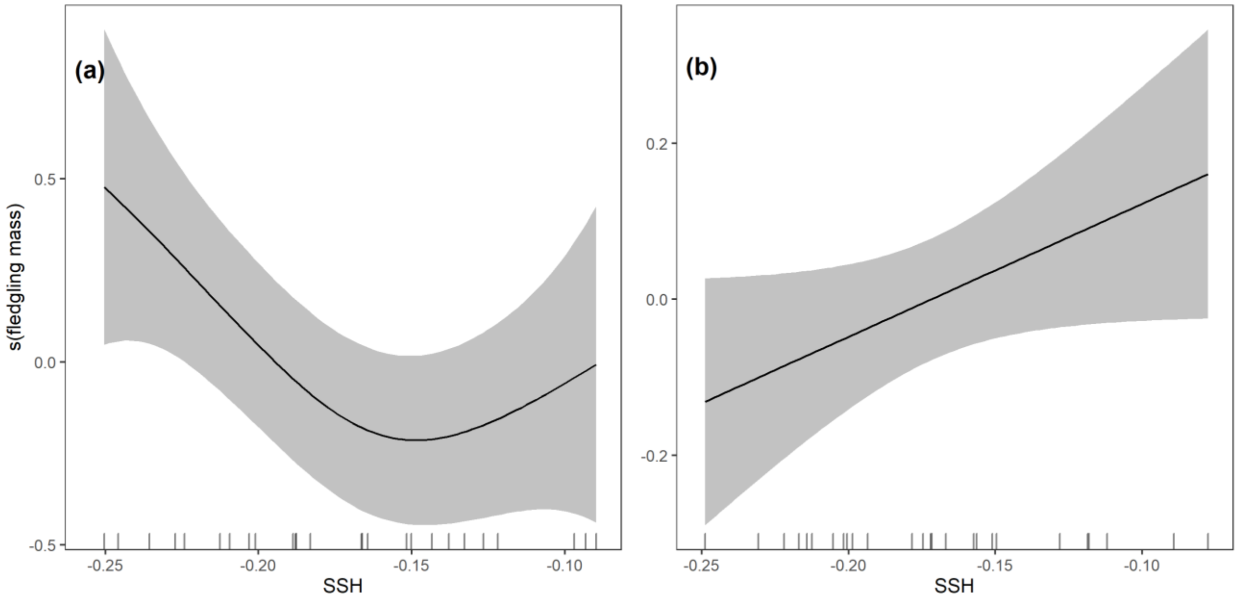


Figure 4.5: The relationship between the fledgling mass of Macaroni Penguins (a) and Eastern Rockhopper Penguins (b) and sea surface heigh at Marion Island 1994 to 2019.

Sea surface height had an influence on arrival mass of male Rockhopper Penguins. Their body mass increased with increasing sea surface height up to a certain level and plateaued (General additive model: F = 3.28, Dev explained = 34%, p = 0.04, Table 4.4, Fig. 4.6).

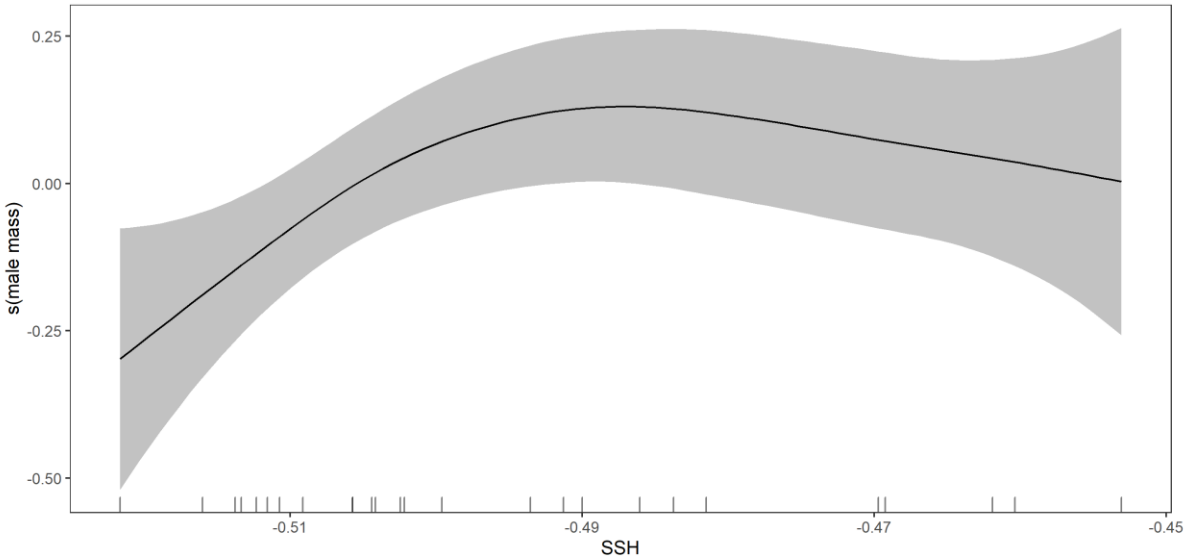


Figure 4.6: The relationship between the male arrival mass of Eastern Rockhopper Penguin and sea surface height at Marion Island 1994 to 2019.

Table 4.4: The influence of oceanographic variables on breeding success, fledgling mass and male female adult arrival mass of Macaroni and Eastern Rockhopper Penguins.

Model	Term	Macaroni				Eastern Rockhopper			
		Edf	F	Dev expl%	p-value	Edf	F	Dev expl%	p-value
Breeding success	SOI	1	0.1	0.44	0.75	1	0.41	1.7	0.53
	SAM	1.59	1.83	14.25	0.22	1	0.69	2.81	0.41
	SST	1	0.17	0.72	0.68	1.04	0.4	1.88	0.57
	SSH	1	0.1	0.42	0.75	1	0.04	0.17	0.84
	SLA	1.68	1.06	11.27	0.35	1.85	1.38	14.38	0.31
Fledgling mass	SOI	1	0.01	0.03	0.939	1.6	0.32	6.44	0.71
	SAM	1	1.05	4.19	0.316	1.48	0.26	5.13	0.72
	SST	1.54	0.36	5.89	0.664	3.4	1.89	34.02	0.13
	SSH	2.19	3.10	28.82	0.061	1	3.5	12.74	0.07
	SLA	1	0.3	1.23	0.589	1.64	0.42	6.99	0.64
Male arrival mass	SOI	2.17	1.53	0.23	19.64	1	0.37	1.51	0.55
	SAM	3.23	1.82	0.2	29.57	1	0.29	1.18	0.6
	SST	1.31	1.02	0.47	6.67	1.04	1.74	7.17	0.21
	SSH	1	0.19	0.67	0.79	2.49	3.28	34.32	0.04
	SLA	1	0.06	0.82	0.23	1	0.03	0.12	0.87
Female arrival mass	SOI	1	0.19	0.79	0.67	1	0.99	3.94	0.33
	SAM	1.59	1.15	12.48	0.29	1	0.05	0.2	0.83
	SST	1.31	0.49	4.21	0.7	1	0.67	2.72	0.42
	SSH	1	0.17	0.71	0.68	1.68	1.94	17.18	0.18
	SLA	1	0.45	1.82	0.51	1	0.21	0.86	0.65

Link between diet and oceanographic variability

There was an annual variability in the diet of Macaroni and Rockhopper Penguins with their diets dominated by crustaceans (*T. vicina* and *E. vallentini*), however Macaroni Penguins contained more myctophids (*K. anderssoni P. tenisoni*) in their diet than Rockhopper Penguins (Chapter 3).

Over the study period the position of the M-SAF moved gradually closer to the island from an average latitude of -43.55 ± 0.33 (± SD) in December 1994 to -45.10 ± 1.12 in December 2018 (Fig. 4.7). For Macaroni Penguins, there was a significant positive relationship between the latitudinal position of middle M-APF and the contribution of *T. vicina* in the diet of Macaroni Penguins (beta regression, z = 1.96, p = 0.049, Pseudo R^2 = 0.13, Fig. 4.9a). The euphausiids *T. vicina* was more prevalent in the diet of Macaroni Penguins when M-APF was close to the island (2017, 2008 and 1999) than when it was farther away (2006 and 1995; Figs 4.7 and 4.9).

In contrast there was a decrease in the frequency of *P. tenisoni* when M-APF (beta regression, z = -2.49, p = 0.013, pseudo R^2 = 0.28, Fig. 4.9b) and N-APF (beta regression, z = -3.37, $p<0.01$, pseudo R^2 = 0.30, Fig 4.8 and 4.9c) were relatively closer to the island. The highest amount of *K. anderssoni* in the diet of Macaroni Penguins occurred when S-SAF was extremely far south of Marion Island in 2015 (Fig. 4.7 and 4.9d). However, if the 2015 outlier is removed, the relationship becomes non-significant (beta regression, z = -3.35, p = 0.73, pseudo R^2 = 0.003).

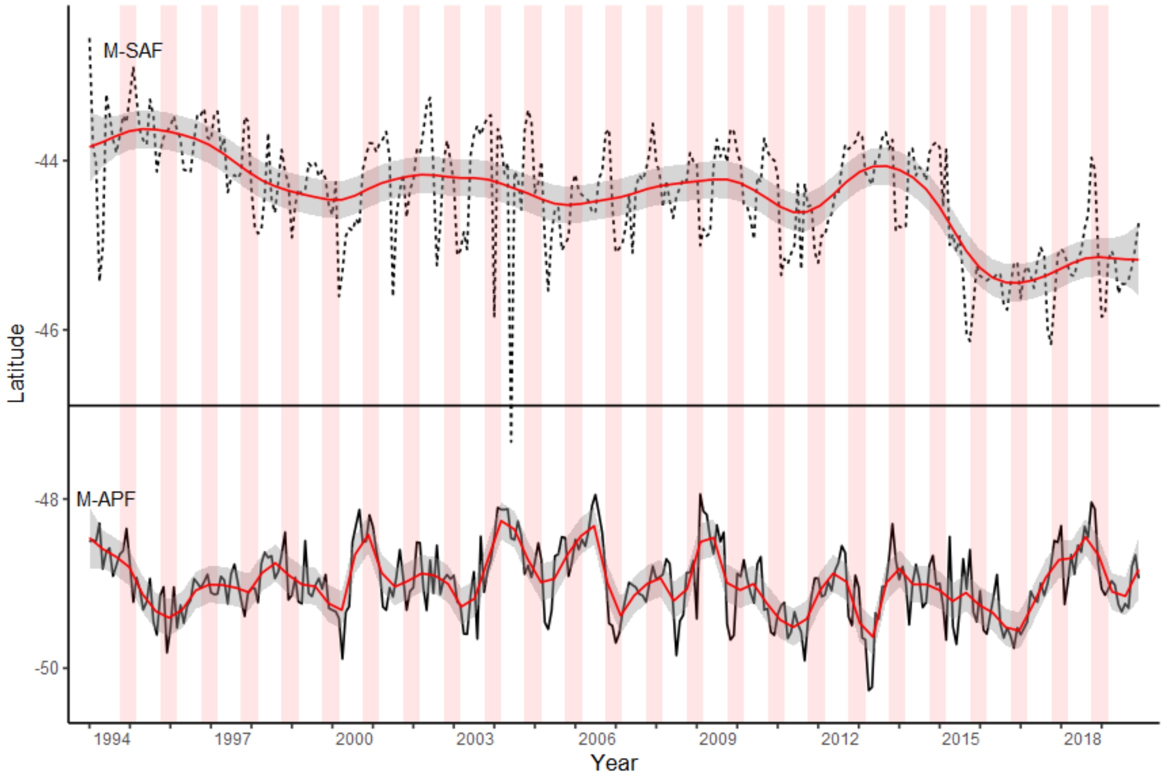


Figure 4.7: Mean monthly latitudinal positions of the middle Sub-Antarctic Front (M-SAF) and middle Antarctic Polar Front (M-APF) between 35–40 °E. The black line indicates position of Marion Island, ticks show 1 January each year, red line shows spline trend of position of fronts and red bars show Macaroni and Eastern Rockhopper Penguin breeding seasons at Marion Island.

For Rockhopper Penguins, there was a significant positive relationship between the position of the M-APF (beta regression, z = 3.019, p = 0.003, pseudo R^2 = 0.16, Fig. 4.7 and 4.10d) and N-APF (beta regression, z = 2.08, p = 0.04, pseudo R^2 = 0.28) with the contribution of *T. gaudichaudii* in their diet (Fig. 4.7 and 4.10f). *T. gaudichaudii* became more important in the diet of Rockhopper Penguins when N-APF and M-APF was relatively closer to the island (2002 and 2005, Fig. 4.10 d, f) and when M-SAF was relatively further away from the island (beta regression, z = 2.27, p = 0.02, pseudo R^2 = 0.30, Fig. 10b) in 2002 and 2005.

P. tenisoni was more dominant in the diet of Rockhopper Penguins when M-SAF was relatively further away from the island in 1994 and 2005 (beta regression, z = 2.06, p = 0.04, pseudo R^2 = 0.14, Fig. 10a). *T. vicina* was more important in the diet of Rockhopper Penguins when M-SAF was closer to the Island (beta regression, z = -2.46, p-value = 0.01, Pseudo R^2 =0.17, Figs 4.7 and 10c). There was more *E. carlsbergi* in the diet of Rockhopper Penguins when N-

APF was relatively closer to the island in 2004, 2000 and 1994 (beta regression, z = 1.99, p = 0.046, pseudo R^2 = 0.18, Fig. 4.8 and 10e).

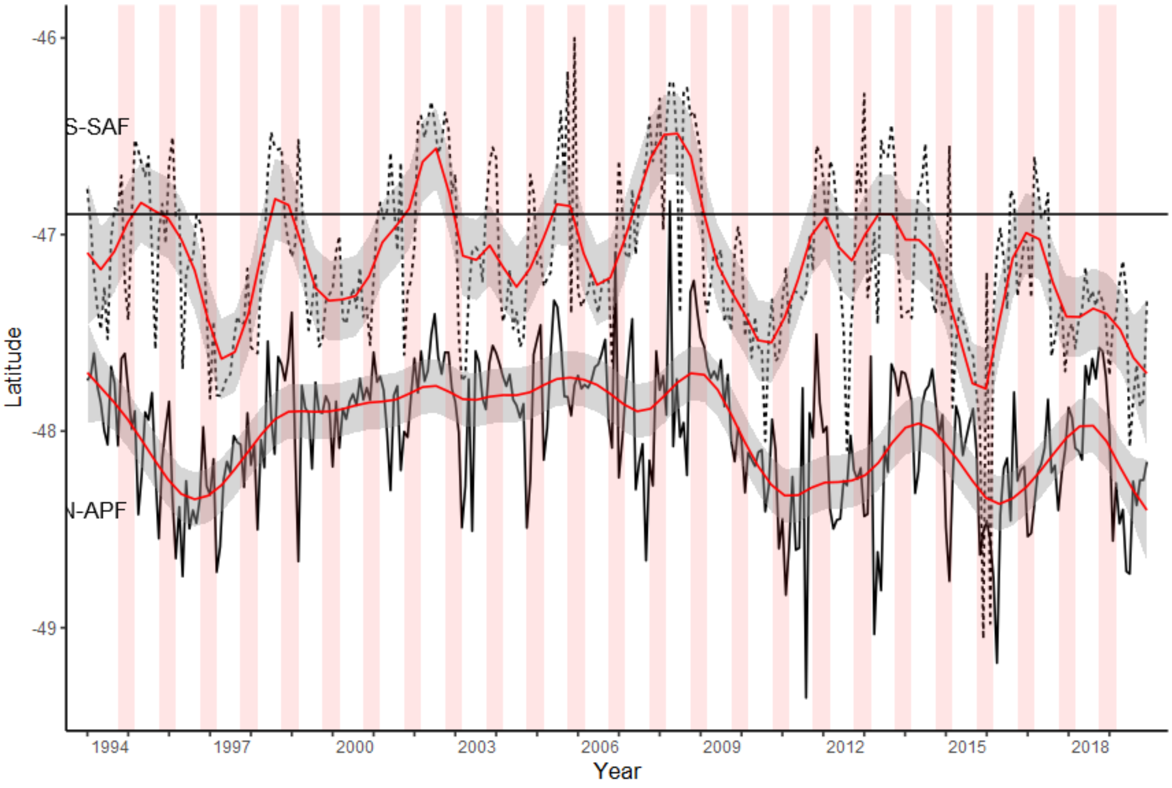


Figure 4.8: Mean monthly latitudinal positions of southern sub-Antarctic front (S-SAF) and northern Antarctic Polar Front (N-APF) between 35–40°E, black line indicates position of Marion Island and ticks show beginning and ending of a year, red line shows spline trend of position of fronts and red bars show annual breeding period of Macaroni and Eastern Rockhopper Penguins at Marion Island.

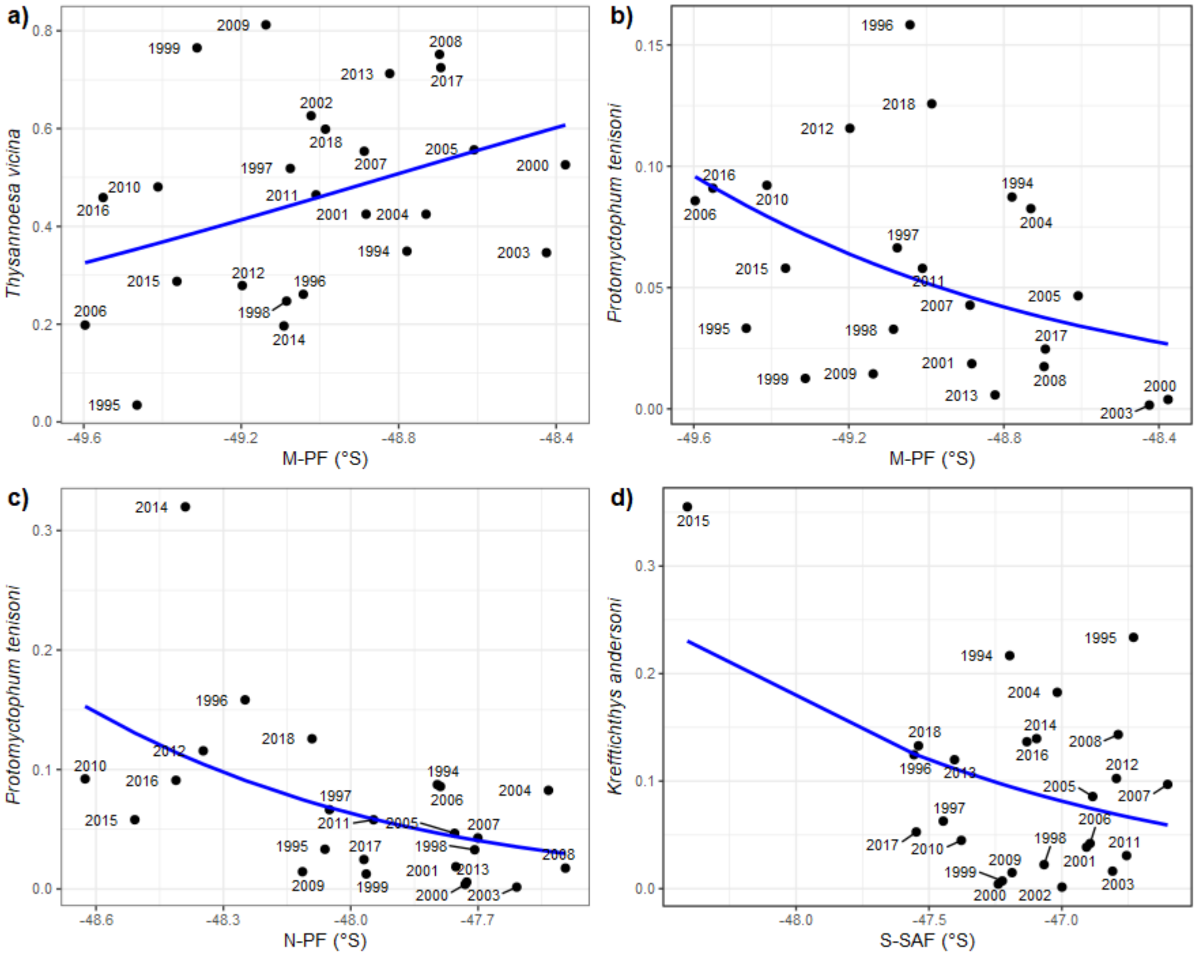


Figure 4.9: Beta regression models of the relationship between prey in the diet of Macaroni Penguins and the southern boundary of the Sub-Antarctic Front (S-SAF), the northern boundary of the Antarctic Polar Front (N-APF) and the middle Antarctic Polar Front (M-APF).

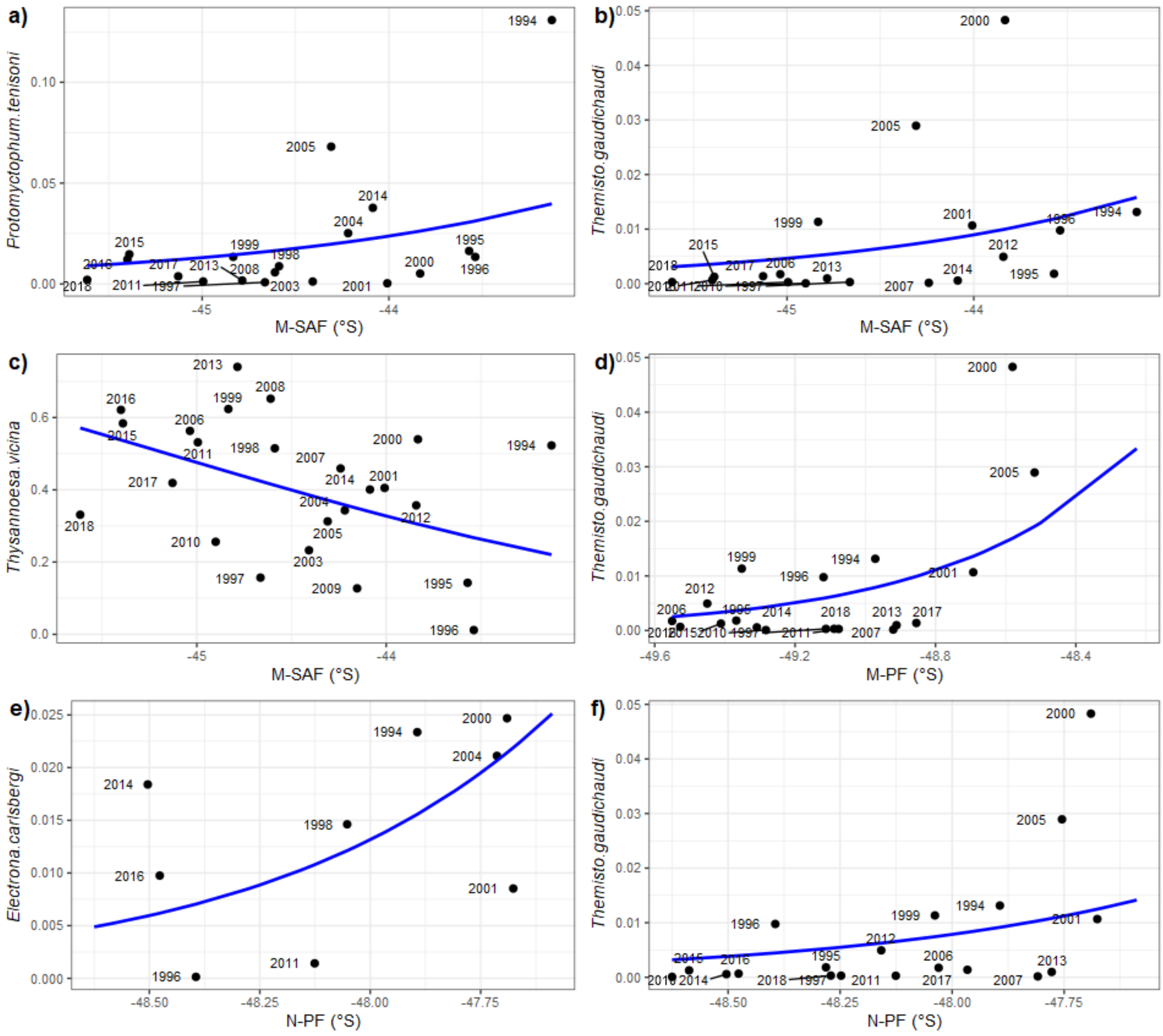


Figure 4.10: Beta regression model of the relationship between prey in the diet of Eastern Rockhopper Penguins and the middle Sub- Antarctic Front (M-SAF), the northern boundary of the Antarctic Polar Front (N-APF) and the middle Antarctic Polar Front (M-APF).

Discussion

Diet versus reproductive performance

In this study I use the diet of two *Eudyptes* penguins as proxies of prey availability to reflect their influence on reproductive performance. The breeding success of Macaroni Penguins was positively related to the proportions of myctophids in their diet. The results also show that Macaroni Penguins fledgling mass was positively related to fish prey in their diet, but it did not yield a significant relationship with diet, in contrast Rockhopper Penguins fledged lighter chicks when they fed on myctophid prey. Foraging theory predicts that individuals should optimise their foraging strategy balancing between energy expenditure and intake especially during breeding for the survival of their young (MacArthur and Pianka 1966, Jeffries et al. 2021). Fish are upper trophic level prey with high energy value compared to macro-zooplanktonic crustaceans like krill and cephalopods. It would be expected that penguins would provision their chick prey with high quality prey to improve their reproductive performance (Frederiksen et al. 2006, Morrison et al. 2014). The high energy content of fish prey could compensate the cost of foraging and locating prey. Penguins like Magellanic *Spheniscus magellanicus* and Adélie Penguins have been shown to provision their chicks with prey of upper trophic level during breeding when their foraging is constrained and have to as a foraging strategy to balance their energy intake and expenditure of their rapidly growing chicks (Forero et al. 2002, Cherel 2008). This is evident with Macaroni Penguins at Marion Island and in agreement with Crawford et al (2003) where Macaroni Penguins at Marion Island had an increase in reproductive performance with the increase of fish in their diet.

Rockhopper Penguin reproductive performance was less sensitive to fish prey in their diet, and this could be explained by the foraging strategy between these two *Eudyptes* penguins at Marion Island during breeding. Both Macaroni and Rockhopper Penguins primarily feed on euphausiids (*T. vicina* and *E. vallentini*), but both species prey on fish and cephalopods as but Macaroni Penguins feed on more fish compared to Rockhopper Penguins (Brown and Klages 1987) (Chapter 3). Whitehead (2017) shows that Macaroni Penguins are more efficient in reaching deep myctophids prey than Rockhopper Penguins by performing longer deep dives (143± SD 14 s vs 113± SD 16 s, respectively), spend more time feeding at the bottom (70 ± SD 14 s vs 42 ± 10 s) and have a higher bottom feeding efficiency (0.38 ± SD 0.08 s vs 0.28 ± SD 0.06). Macaroni Penguins have larger bill and body size compared to Rockhopper Penguins and hence can exploit larger reproductively mature prey with higher energy density (Chapter 3). Feeding on myctophids for Rockhopper Penguins would potentially be more energy consuming and likely increase competition for resources with their advantaged sympatric counterpart. This is reflected by the negative response of Rockhopper Penguins fledgling mass to myctophids in their diet. In years of low krill supply at Marion Island Rockhopper Penguins breeding performance would likely be affected more than that of Macaroni Penguins.

Similar to Marion Island, using stable isotopes it was shown that Rockhopper Penguins at Campbell Island between 2011–2012 fledged heavier chicks when they were provisioned with low trophic level macro zooplankton prey. Conversely, Rockhopper Penguins fledged lighter chicks when they were provisioned with upper trophic prey like fish and/or cephalopods (Morrison et al. 2014). They specialised their foraging strategy by preying more on the abundant pelagic zooplankton and performed shorter foraging trips closer to the island and provisioned their chicks more frequently and consequently fledged heavier chicks. In contrast when they fed on more fish they performed longer trips and provisioned their chicks less frequently and consequently fledged lighter chicks; frequently provisioned chicks are likely to survive (Morrison et al. 2014, 2016). The scenario at Campbell Island could also be what is happening at Marion Island as Macaroni Penguins have been shown to perform longer trips on average (49 ± SD 22 km vs 37 ± 21 km) and spend more time at sea (29 ± SD 17 hours vs 27 ± 15 hours compared to Rockhopper Penguins respectively (Whitehead 2017). Contrary to Marion Island, the reproductive performance of Macaroni Penguins at South Georgia was high when they fed on macro zooplanktonic euphausiid prey and their fledgling mass was strongly related to the energy content of all euphausiids and particularly *Euphausia superba* (Waluda et al. 2012). This shows the site-specific response of penguins to available and abundance prey around their colonies when breeding and the energy cost associated with foraging and provisioning their chicks with specific prey. This predator prey relationship could be exacerbated by the effect of climatic variables on prey availability and distribution within the marine ecosystem.

Diet versus oceanographic conditions

Here I show that the fluctuating latitudinal position of Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF) relative to Marion Island to some extent explained the inter-annual variability in the dietary composition of Macaroni and Rockhopper Penguins. This shows the influence oceanographic conditions have on prey availability and the importance of penguins as indicators of ecosystem change. Macaroni Penguins preyed more on euphausiid *Thysanoessa vicina* when Antarctic Polar Front (APF) was relatively closer to the island and conversely preyed more on *Protomyctophum tenisoni*. when the APF were relatively further away from the Island. Likewise, Rockhopper Penguins preyed more on *euphausiids T. vicina* and amphipod *T. gaudichaudii* when SAF and APF was closer to the island and conversely *P. tenisoni* when SAF was further away from the island.

The latitudinal position of SAF and APF have been shown to influence changes in the physical condition, macro- zooplanktonic and phytoplankton species diversity and abundance through altering the flow dynamics and propagating highly productive eddies around Prince Edward Archipelago (Hunt et al. 2001, Hunt and Pakhomov 2003, Ansorge et al. 2009). The Prince Edward Island lies directly in the path of the Antarctic Circumpolar Current (ACC) and is sandwiched between two fronts in a transition zone called the Antarctic Polar Frontal Zone (APFZ) (Lutjeharms and Ansorge 2008, Ansorge et al. 2012).

When the SAF is further north from the island there is reduced flow rate of the ACC and water retention within the inter-island shelf of the Prince Edward Archipelago near the island

(Pakhomov et al. 2000, Durgadoo et al. 2010). There is a weak interaction of the ACC with the Islands which promotes the formation of eddies around the islands (Perissinotto et al. 2000, Durgadoo et al. 2010). The retention of water encourages the formation and accumulation of phytoplankton bloom, this attracts Antarctic species around the island. The eddies influence changes in physical conditions by promoting the intrusion of Antarctic surface waters typical of the Antarctic species and benthic communities close to the islands (Pakhomov and Froneman 1999, Pakhomov and Chown 2003). This is likely reflected by the increase in importance of fish *P. tenisoni* in the diets of the two penguins which has been advected by the eddies increasing its availability. In contrast when the fronts are closer to the island there is an increase flow rate of the ACC creating advective force preventing the formation of phytoplankton bloom and eddies (Perissinotto et al. 2000). The proximity of the fronts near the island promotes the intrusion of warm sub-tropical and sub-Antarctic waters in the vicinity of the island which carry sub-Antarctic euphausiid species like *T. vicina* and *E. vallentini* (Hunt et al. 2001, Hunt and Pakhomov 2003).

The findings of this studies are also in agreement with the foraging behaviour of Macaroni and Rockhopper Penguins in relation to the latitudinal position of the fronts during breeding. When the SAF is closer to the Island the two penguin species were shown to consistently make shallower dives between 40-60 m. When the front was further away from the Island both penguins performed more frequent deeper dives associated with the pursuit of fish (Whitehead 2017). During breeding when the two *Eudyptes* penguins undertook long trips, they tended to forage further south and target the Antarctic Polar Front (Whitehead 2017).

Hunt et al. (2001) shows that the average position of SAF has been moving southward and in this study the average position of the SAF was closer to the island by the end of the study in 2019 compared to 1994. The consequences of the southward shift of the front means the intrusion of warmer sub-tropical and sub-Antarctic waters and abundance of euphausiid prey around the Island. There was an observed increase in the importance of *E. vallentini* in the diet of Gentoo Penguins with the southward movement of SAF at Marion Island (Carpenter-Kling et al. 2019). Ansorge et al (2009) suggest that the southward shift in SAF will result in the increase in zooplanktonic sub-tropical prey and reduction in Antarctic species around the Prince Edward Islands. Macaroni and Rockhopper Penguins feed on more fish and cephalopods as they go further into their breeding season however, Rockhopper Penguins switch back to a crustacean dominated diet while Macaroni Penguins continue to feed their chicks with fish (Brown and Klages 1987). The shift in SAF could potentially benefit Rockhopper Penguins more than Macaroni Penguins although I did not find a significant link between the diet of these *Eudyptes* penguins and euphausiids in their diet. To determine the consequences of the southward movement of the SAF there is need for more research linking the position of the fronts with the foraging behaviour and diet of these two *Eudyptes* penguins at Marion Island.

Reproductive performance versus oceanographic conditions

Large scale climatic variables (ENSO, SAM, SOI) and localised ocean climate variables (SST, SLA) could not significantly explain the variation in the reproductive performance (fledgling mass, breeding success) during breeding and body condition (mass on arrival) prior to breeding for both penguins. This shows the complexities in interpreting interaction between seabird population dynamics and marine ecosystems. The relationship between *Eudyptes* penguins population process (breeding success, fledgling mass, survival rates) could be masked by other factors such as competition between the two sympatric penguins or top down factors like predation or competition for resources with other top predators on the Island like Antarctic and sub-Antarctic Fur Seals (Reisinger et al. 2018). Further research is required linking penguin population dynamics with improved climatic variables.

There was a contrast in the relationship between fledgling mass and sea surface height (SSH) between the two *Eudyptes* species. Macaroni Penguins tended to fledge heavier chicks in years of low SSH values, while Rockhopper Penguins fledged heavier chicks in years of high SSH. This reflects the different responses two species can have to ocean climate variables. Low SSH values are associated with colder waters, low heat content and more upwelling while higher SSH values are associated with warmer waters, greater heat content and less upwelling. (Wolf et al. 2009). Both species responded to negative SSH values which indicate offshore water movement but comparatively the different responses to SSH between Macaroni and Rockhopper Penguins reflect segregation in foraging behaviour and at sea distribution during breeding. In the context of competitive exclusion, spatially and temporally, the more efficient species could exclude the less efficient species in areas of high productivity (Hardin 1960). This could explain why Macaroni Penguins thrived in comparatively colder and more productive waters compared to Rockhopper Penguins potentially trying to reduce competition for resources during breeding.

Whitehead (2017) shows that Macaroni Penguins during winter foraged in colder waters compared to Rockhopper Penguins. Postulating that due to larger body mass of Macaroni Penguins they are energetically capable of thermoregulating their body in cooler waters compared to Rockhoppers, hence Rockhopper Penguins are energetically more constrained to forage in warmer waters. This difference in foraging grounds could potentially be carried over during breeding, but due to the constraints of breeding on foraging area there is potential overlap between species foraging grounds.

Sea surface height also explained variation in the mass on arrival of Rockhopper Penguins. Similar to fledgling mass, the mass on arrival was more in years of higher sea surface height, but the relationship was non-linear plateauing as SSH increased. Non-linear relationship relationships highlight levels of foraging plasticity, hence Rockhopper Penguins could potentially adapt to changes in environmental conditions (Baylis et al. 2012, Gilmour et al. 2018). During winter Rockhopper Penguins were shown to move to comparatively cooler waters in the last month preceding their arrival on Marion Island, likely a response to the absence of Macaroni Penguins which would have started arriving to the Island (Whitehead et al. 2016, 2017). Rockhopper Penguins presented with foraging plasticity behaviour however longer dataset linking foraging behaviour, climate and population dynamics are required to elucidate on these relationships.

During winter Macaroni Penguins prefer cooler waters while Rockhopper Penguins have been shown to forage in both cooler waters and warmer waters further north associated with the sub-Antarctic Front (Enticott 1986, Whitehead 2017). This preference is likely carried out well into the breeding season, this is explained by Rockhopper Penguins diet responding to both APF and SAF showing foraging plasticity during breeding to consolidate competition for resource with Macaroni Penguins (Thiebot et al. 2013).

Little research has been done on the foraging behaviour of these two species at Marion Island (Brown 1987, Whitehead 2017). A long-term study is required to elucidate the response of these species to the changing marine environments. Satellite derived climate variables generalise oceanographic conditions over a large area which potentially reduces the power of any statistical test to find a significant relationship between climatic variables and population dynamics of penguins. This is also affected by the foraging behaviour of Macaroni and Rockhopper Penguins which are offshore foragers and cover a very large area during breeding. However, tracking data shows the oceanographic conditions experienced by the two penguin species during foraging, and can elucidate on the climate conditions within their preferred habitat. This also gives more information of the responses of penguins to changing environments, coupled with prey stocks data, this can show the response of penguins to changes in prey species availability exacerbated by ocean climate variables. The ocean around the Prince Edward Island has been warming by 1.4 degrees from 1949–2003 and possibly has continued increasing, the SAF has been shown to be moving southwards (Mélice et al. 2003, Ansorge et al. 2012). This will all have consequences on the marine ecosystem around the Island. Future research should focus on the long-term foraging behaviour of these species linked to ocean climatic variables and how this could explain the variation in population dynamics of top marine predators Macaroni and Rockhopper Penguins at Marion Island.

This study shows that Macaroni and Rockhopper Penguins could be good indicators of changes in marine ecosystems. The diet affects the breeding performance of both penguins showing that population dynamics of the penguins varies in response to prey availability. The contrast in breeding performance response to diet between the two penguins, shows levels of segregation in response to specific prey availability. To reduce competition and facilitate co-existence of the two closely related penguin species on the same Island. The diet of the two penguins responded to the latitudinal position of which shows the effect of changes in oceanographic conditions around Marion Island to prey abundance and availability. This shows that the relationship between diet and reproductive performance are probably driven by oceanographic conditions. This is further shown by the response of the two penguins to changes in sea surface height. The contrast in response to sea surface height further shows the segregation in foraging behaviour between these two species round Marion Island before and during breeding.

Chapter 5: Synthesis and Conclusions

The aim of this study was to investigate the long-term trends in the demographic processes and diet during breeding, to possibly explain the decline of the two *Eudyptes* penguin species at Marion Island over the past 26 years (Crawford and Dyer 2008, Chapter 2). Macaroni and Rockhopper Penguins are listed as Vulnerable, having been observed to decline across their distribution around the Southern Ocean (IUCN 2021). The two species are top marine predators and their dependence on both marine and terrestrial ecosystem to breed makes them good indicators of changes in marine ecosystem health (Boersma 2008). They are large consumers of marine resources and their wide distribution across space and time makes then good ecosystem sentinels integrating information from bottom to top of the food web (Hazen et al. 2019). I linked their population trends, breeding biology and diet to environmental and oceanographic conditions, to assess the impact of climate change on marine populations and communities.

Chapter 2 reported on the long-term population trend of Macaroni and Rockhopper Penguins and used the annual variability in pre-breeding condition and breeding performance to explain trends in the populations. Numbers of Macaroni Penguins have been reducing steadily over the past 26 years while Rockhopper Penguin numbers declined more rapidly between 1994–2001 but stabilised from 2001 to the end of the study. The mass on arrival of Rockhopper Penguins had a similar trend as their population number however the increasing trend started in 2006. The breeding success of Rockhopper Penguins had a positive increasing trend at all the monitored colonies. Both these variables could explain the stabilisation in population of Rockhopper Penguins at Marion Island.

Arrival dates were negatively related to breeding success for Macaroni Penguins. Similarly, arrival dates were negatively related with mass on arrival for Rockhopper Penguins. This reflects the positive effect of early arrival on the breeding performance of penguins, which likely leads penguins to commence egg laying early and potentially shows increased prey availability in years of early arrival before the onset of breeding (Williams and Croxall 1991). Mass on arrival was positively correlated to fledgling weights in both penguins but this was only significant in Macaroni Penguin males. This suggests that chicks respond to good parental body condition, which likely resulted in improved parental expenditure and provision rate to growing chicks. Macaroni Penguins fledged heavier chicks when the males arrived in good condition. This shows the effect of added biparental investment in feeding chicks during breeding when the males join the females. Breeding success was positively related to mass on arrival for both Macaroni and Rockhopper Penguins. *Eudyptes* penguins undergo long fasting periods during breeding, especially the males, hence heavier birds in good condition at the start of the breeding season are likely to have improved breeding performance. The link between pre-breeding parameters (arrival date and mass on arrival) and breeding performance (breeding success and fledgling weights) shows the influence of wintering conditions experienced by both penguins on their breeding performance. Breeding performance might not only be influenced by local environmental conditions and prey availability during breeding because of foraging constraints but the influence might be on a broader scale outside the breeding season. There was a positive relationship between breeding success and fledgling mass for Macaroni Penguins. Heavier chicks have a higher probability of survival than lighter chicks (Horswill et al. 2014). There was high inter-annual variability in pre-breeding and breeding parameters of Macaroni and Rockhopper Penguins. This shows high variability in prey availability across different breeding seasons around Marion Island, despite the improved breeding success of Macaroni and Rockhopper Penguins compared to the early 2000s and 1990s. Guinard et al. (1998) suggests their breeding success is still too small for the population to be in equilibrium, but information on the survival rate of the two penguins has not yet been studied at Marion Island.

In Chapter 3 I used long-term data on the diet of Macaroni and Rockhopper Penguins to attempt to explain trends in their population decline over the past 25 years. There was substantial overlap in the diet between the two species over the past 25 years. The two *Eudyptes* penguins primarily feed on euphausiids *T. vicina* and *E. vallentini*, but Macaroni Penguins fed on more and larger myctophid prey *K. anderssoni* and *P. tenisoni*. Macaroni Penguins had a more diverse diet than Rockhopper Penguins, also feeding on more *T. gaudichaudi* and *E. carlsbergi*. This is explained by the differences in foraging behaviour between the two penguin species. Macaroni Penguins are bigger and have larger lung capacity and bill size compared to Rockhopper Penguins hence they can feed on larger myctophid prey (Williams 1980, Whitehead et al. 2016, 2017). Macaroni Penguins make more frequent deep dives, dive for longer, spend more time feeding at the bottom compared to their sympatric counterpart hence they are better able to exploit deep diel migratory myctophid prey (Whitehead 2017). Despite considerable inter-annual variability in the diet composition, there was no long-term change in the two penguins' diets over the past 25 years. Both penguins maintained a diet dominated mostly by euphausiids *T. vicina* and *E. vallentini*. Surprisingly in 1996 and 1997 Rockhopper Penguins fed on substantial amounts of Horsefish *Z. spinifer*, which likely shows Rockhopper Penguins exhibit a level of plasticity in their diet outside of euphausiid prey. Macaroni Penguins arrive 3-5 weeks earlier than Rockhopper Penguins, reducing spatio-temporal overlap of foraging effort. If their foraging range overlap during breeding there might be considerable competition for resources, this could be exacerbated by the constraints of central foraging. In years of low krill availability during breeding the high incidence of fish in the diet of Macaroni Penguins suggests that they could outperform their sympatric counterpart, and this could explain why Macaroni Penguins are found in larger numbers than Rockhopper Penguins at Marion Island.

In Chapter 4 I compared the above variables, breeding performance vs diet, breeding performance vs climatic variables and diet vs latitudinal position of oceanographic fronts around Marion Island. In Chapter 3, I established that Macaroni Penguins fed on more myctophid prey than Rockhopper Penguins. Macaroni Penguins had a higher breeding success when they preyed on fish. In contrast, Rockhopper Penguins fledged lighter chicks when they preyed on fish. Fish are higher trophic level prey and have a high energy content compared to lower trophic level prey like zooplanktonic crustaceans (Frederiksen et al. 2006). Both penguins feed on more fish as they go further into the breeding season, potentially to balance the expenditure of foraging and increased provisioning rate of their rapidly growing chicks. Rockhopper Penguins feed on less fish at the end of the breeding season while Macaroni Penguins continue to feed on more fish (Brown and Klages 1987). Macaroni Penguins are more efficient at foraging for deep fish prey particularly myctophids like *K. anderssoni* and *P. tenisoni* compared to Rockhopper Penguins (Brown 1987, Whitehead et al. 2016, 2017).

There was no relationship between the breeding performance of Macaroni and Rockhopper Penguins with large-scale or local-scale environmental variables over the study period. Marine ecosystems are dynamic across space and time, which makes monitoring and finding a connection between these species' demographic processes and climate variables very complex (Hazen et al. 2019, Reisinger et al. 2021). Macaroni Penguins tended to fledge heavier chicks in years of low Sea Surface Height (SSH) values associated with cooler waters while Rockhopper Penguins fledged heavier chick in years of higher SSH associated with warmer waters (Wolf et al. 2009). Similarly male Rockhopper Penguins arrived in better conditions in years of higher SSH. This indicates some segregation in preferred habitats between the two species around Marion Island. During winter, Macaroni Penguins forage further in cooler waters near the Antarctic Polar Front (APF) while Rockhopper Penguins forage in warmer waters associated with the Sub-Antarctic Front (SAF) (Enticott 1986, Whitehead 2017). The contrasting preferences in habitats maybe associated with difference in body size between the two *Eudyptes* species. The larger bodied Macaroni Penguins are better able to inhabit cooler waters compared to Rockhopper Penguins, because larger body size is better able to cope with the cold. They have a lower rate of heat loss related to smaller surface area to volume ratio and can produce more internal heat than smaller body sizes (Lustick 1984, Stahel 1984). The contrasting preference could also be the two penguins trying to minimise spatial overlap in foraging grounds to reduce competition or resources.

Annual variation in the diet of Macaroni and Rockhopper Penguins was related to the latitudinal position of the SAF and the APF. When the APF was closer to the island Macaroni Penguins fed on more *T. vicina*. In contrast when SAF and APF where farther away from the island they fed more on myctophids *P. tenisoni*. Rockhopper Penguins also responded to SAF in a similar way feeding on crustacean prey *T. vicina* when the front was closer to the Island and fish prey *P. tenisoni* when the front was farther away from the island. Oceanographic settings and marine organism assemblages around Marion Island are affected by the latitudinal variability of the fronts. The movement of the fronts farther away from the Island causes a reduction in the flow rate of the Antarctic circumpolar front. This results in retention of water within the inter-island shelf of the Prince Edward Archipelago and reduced geostrophic flow. These conditions promote the formation and advection of eddies towards the island which carry Antarctic species like *P. tenisoni* and increase in phytoplankton stocks which increase productivity (Hunt et al. 2001, Ansorge and Lutjeharms 2003, Hunt and Pakhomov 2003). Under these oceanographic settings Macaroni and Rockhopper Penguins were observed to perform deeper dives and presented more fish in their diet (Whitehead 2017). When the fronts are closer to the island there is increased flow of the ACC which prevents the formation of eddies and reduction in phytoplankton stocks. There is intrusion of sub-tropical and sub-Antarctic waters dominated by zooplankton prey like euphausiids *T. vicina* and *E. vallentini* in the vicinity of Marion Island (Pakhomov and Froneman 1999, Ansorge et al. 2009).

Rockhopper Penguin diet responded to both SAF and APF while Macaroni Penguins only responded to APF, further showing the segregation in foraging ground preferences between these two species during breeding in order to reduce competition for resources when foraging is constrained (Enticott 1986, Whitehead 2017). The SAF has been moving southward, closer to Marion Island, resulting in changes in species composition of zooplankton around the island, increasing subtropical species and reducing Antarctic species (Ansorge et al. 2009). This will potentially have drastic consequences for Macaroni Penguins whose breeding success responded positively to fish in their diet and thus Rockhopper Penguins are likely to be better adapted to the southward movement of the SAF than Macaroni Penguins. Further investigation is needed to determine the effect of the southward shift of the SAF.

Recommendations for future research

The study has identified several areas for further research. Penguin population growth is highly sensitive to adult and juvenile survival (Dehnhard et al. 2013b, Horswill et al. 2014, Morrison et al. 2015). There is high inter-annual variability in breeding performance of the two penguin species at Marion Island showing variability in prey availability and oceanographic conditions around the island. Breeding performance data should continue to be collected but survival estimates of adults and juveniles are necessary to understand their population dynamics. Body condition of adults and fledgling mass are positively related to reproductive success and chick survival, and they are in turn related to post fledgling survival and recruitment into the breeding population (Dehnhard et al. 2014). The survival rates at Marion Island should be investigated, as they could elucidate the population trends of the two penguins and their drivers at Marion Island.

Since the early 1980s, stomach content analysis (SCA) has been used to determine the diet composition of the two *Eudyptes* penguin species breeding at Marion Island (Brown and Klages 1987). This method is time sensitive due to digestion of stomach content by the time they arrive at the Island, especially when penguins make long foraging trips. There is potential for under representation of diet composition, especially for soft-bodied prey like fish (Polito et al. 2011). Given the shortcomings of SCA, it is important to integrate this method with stable isotope analysis (SIA) and DNA diet analysis on *Eudyptes* penguins on Marion Island. This can give a more detailed diet composition of the species with insight into trophic relationships and foraging ecology (Bond and Jones 2009).

More tracking data of Macaroni and Rockhopper Penguins during winter and breeding are required to show their distribution in relation to changes in climatic variables, frontal positions and how they reduce overlap in foraging grounds to avoid competition for resources. In this study I used climatic variables summarised over a large area of their foraging distribution, given that Macaroni and Rockhopper Penguins are offshore foragers. This has the drawback of reducing the power of any statistical test. Tracking data give insights into the environmental conditions experienced by the species and hence their habitat preferences, which better indicate how these species respond to different climatic condition in this rapidly changing environment. Tracking data tends to represent a small subset of individuals, this method can be integrated with other approaches like trip duration from birds tagged with transponders. This approach also allows for the estimation of survival rates which is a missing data that needs to be address when understanding population dynamics of the two penguins at Marion Island.

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