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The Impact of Climate on the Breeding and Foraging Success of the King Penguin *Aptenodytes patagonicus*

Emile Brisson-Curadeau

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ÉCOLE DOCTORALE

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THÈSE

présentée par :

Émile BRISSON-CURADEAU

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pour l'obtention du grade de Docteur de La Rochelle Université

Discipline : Biologie

**The Impact of Climate on the Breeding and Foraging Success of the King
Penguin *Aptenodytes patagonicus***

JURY :

William MONTEVECCHI	Professeur, Memorial University of Newfoundland, Président du jury
Jennifer SUNDAY	Directeur de recherche CNRS, Université McGill, Rapporteur
Brigitte McDONALD	Professeur, San José State University, Rapporteur
Andrew TRITES	Professeur, Southern Illinois University
Jim LOVVORN	Professeur Université, University of British Columbia
Elliott Kyle	Professeur, Université McGill, codirecteur de thèse
Charles-André BOST	Professeur, La Rochelle Université, codirecteur de thèse

The Impact of Climate on the Breeding and Foraging Success of the King Penguin *Aptenodytes patagonicus*

Émile Brisson-Curadeau



Department of Natural Resource Sciences
Macdonald Campus of McGill University, Montréal

And



Centre d'Études Biologiques de Chizé



Université de La Rochelle

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A thesis submitted to McGill University and La Rochelle University in partial fulfilment of the requirements of the
degree of DOCTOR OF PHILOSOPHY

Contact: emile.brissoncuradeau@mail.mcgill.ca

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Supervisors

Kyle Elliott
McGill University
kyle.elliott@mcgill.ca

Charles-André Bost
Centre d'Études Biologiques de Chizé
Charly.bost@cebc.cnrs.fr

Internal examiner

Jennifer Sunday
McGill University

External examiner

Birgitte MacDonald
San Jose State University

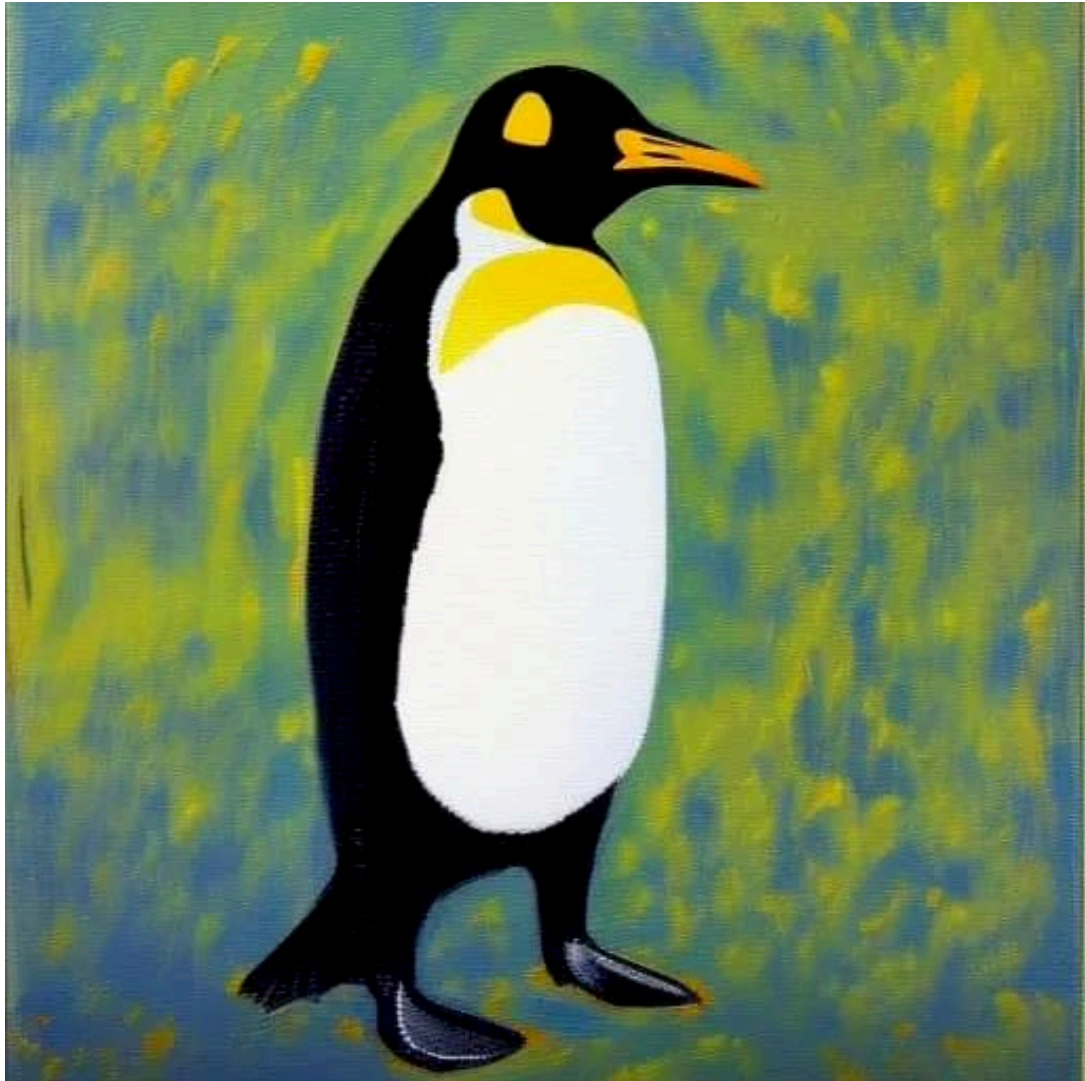


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List of abbreviations

AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected for small sample size
ENSO	El Niño Southern Oscillation
ML	Machine Learning
MSE	Mean Square Error
SAM	Southern Annular Mode
SOI	Southern Oscillation Index
SSH	Sea Surface Height
SST	Sea Surface Temperature

Abstract

The Southern Ocean is among the most productive marine ecosystems in the world, with complex circumpolar currents sustaining a rich trophic chain. It is unclear how climate change might affect the food webs in this region, where oceanographic sampling in lower trophic chains is difficult to conduct. Alternatively, top predators could be used as reliable indicators of the changes occurring in the food web. In this thesis, I look at the effects of climate on the foraging and breeding success of a marine predator, the king penguin *Aptenodytes patagonicus*, at Kerguelen Island and use the results to understand the state of the food web. In Chapter 1 and 2, I introduce key concepts for the thesis, such as the marine dynamics around Kerguelen and the complex breeding biology of king penguins. In the Chapter 3, I test a technique to remotely detect prey captures in king penguin dives using accelerometry, a method that would be useful to estimate foraging success in two other Chapters. Accelerometry assessed prey capture rate with far better accuracy than traditional techniques. In Chapter 4, I examine seven years of foraging success and isotope data to understand whether king penguins change their diet when faced with poor foraging conditions – such as those that might arise in the context of a changing world. King penguins had a homogenous diet despite the conditions encountered and are unlikely to switch prey with climate change, but might rather adjust foraging effort. In Chapter 5, I study habitat choice in wintering king penguins. Populations had different strategies for selecting wintering habitat based on the biogeographic aspects surrounding their colony. In Chapter 6, I conduct a case study on the catastrophic breeding failures of 2009 and 2010 occurring at Kerguelen. The winter period was likely where penguins experienced poor at-sea conditions – eventually leading to the observed

breeding failures – highlighting the importance of this period for the food web of the Southern Ocean. Finally, in Chapter 7, I examine links between the climate, the foraging success and the breeding success of penguins during the chick-rearing season using 25 years of data. Prey abundance likely depended on sea surface temperature, seemingly increasing with warmer weather. This benefited the foraging and breeding success of king penguins in the last, warmer decade. My thesis shows how the state of the king penguins and their prey varied with climate change, allowing predictions for how they might change going forward, and provided new tools to aid the ongoing monitoring of this species with regards to the ecosystem.

Résumé

L'Océan Austral est parmi les écosystèmes marins les plus productifs de la planète, mais aussi un des plus vastes. L'effet des changements climatiques sur la faune de cet océan est toutefois meconnu, car le suivi à long terme est difficile à réaliser dans cette région éloignée. En contre partie, l'étude en mer de prédateurs marins pourrait servir d'indicateur des changements affectant la chaîne trophique de cet environnement. Dans cette thèse, je me suis intéressé à l'effet du climat sur le succès de reproduction et d'alimentation du manchot royal *Aptenodytes patagonicus* – un prédateur marin – se reproduisant sur l'archipel Kerguelen, dans l'Océan Indien sud. J'utilise ensuite mes résultats pour mieux comprendre la dynamique avec les maillons inférieurs des réseaux trophiques. Dans les deux premiers chapitres, j'ai introduit les concepts clés de ma thèse, comme la dynamique des courants autour de Kerguelen et l'écologie de reproduction des manchots royaux. Dans le troisième chapitre, j'ai testé une technique pour détecter à distance les captures de proie des manchots en utilisant l'accélérométrie, une méthode qui me sera utile dans les chapitres suivants. L'accélérométrie s'est avérée bien plus précise pour estimer le taux de capture que les techniques traditionnelles. Dans le quatrième chapitre, j'ai utilisé sept ans de données isotopique pour vérifier si les manchots sont susceptibles de modifier leur alimentation en cas de périodes difficiles, comme celles pouvant avoir lieu avec les changements climatiques. Les manchots se sont avérés avoir un régime alimentaire très stable, quelque soit les conditions rencontrées en mer, mais peuvent, en contrepartie, ajuster leur comportement et effort d'alimentation. Dans le chapitre cinq, j'ai analysé les premières données de distribution hivernale pour la colonie de Kerguelen, et comparé la sélection d'habitat avec la colonie de Crozet. Dans le chapitre six, j'ai produit une étude de cas sur l'échec de reproduction

catastrophique des manchots royaux de la colonie en 2009 et 2010. Je découvre que ces deux échecs se sont probablement produits à cause de conditions peu favorables rencontrées durant l'hiver, soulignant l'importance de cette période pour l'écosystème de l'Océan Austral. Finalement, j'ai examiné dans le chapitre sept les liens entre le climat, le succès d'alimentation et le succès reproducteur des manchots durant l'élevage des poussins en utilisant 25 ans de données. L'abondance des proies semble dépendre de la température, avec paradoxalement une augmentation de la productivité lors des années légèrement plus chaudes que la normale. Cela fut bénéfique pour le succès reproducteur des manchots dans les dernières années, plus chaudes en moyenne. Ma thèse fournit des éléments concrets pour aider à prédire le statut des manchots royaux et de leurs proies et propose de nouveaux outils pour améliorer le suivi de cette espèce en fonction de la dynamique écosystémique.

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First and foremost, I want to thank my two supervisors, Kyle Elliott and Charly Bost. They both gave me the support I needed throughout these 4 years, while still trusting me when I needed to shift on the “life” side of the “work-life” balance. Charly, thanks for enduring my “go-getter” way of working. I am grateful to my committee members, Akiko Kato and Melissa McKinney, for providing useful feedback.

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weird disco bedroom...), Jade Legros, Elena Tranze-Drabinia, Rose Lacombe (thanks for your isotope help!) and Eli Mira. I counted sixteen! Finally, I want to thank Wren Wagenbach for her crucial help with the isotope analysis and Alexandra Nalivaev for her help with the Lagrangian analysis.

I want to thank my family, who initiated my love for nature and science. By being proud of every step in my academic life, you made me value education. I would not be where I am without you. That goes for the parents, but also the step-parents! Thank you Jamie for your support, your sweet company, and of course your constant help proof-reading my poor English.

Finally, one cannot ignore the fact that money makes the world go round and that research is not possible without funding. I want to thank Vanier Canada Graduate Scholarships for meeting my needs, as well as the generous funding from the John and Pat Warham Scholarship by the British Ornithological Union, which allowed me to conduct research without constantly thinking about making funding applications. As for the fieldwork, it would have been impossible without the logistics of the Institut Polaire Français. A big thanks also to the American Ornithological Society for helping me cover the cost for travelling to their wonderful conference in Puerto Rico.

I am extremely grateful to have had the opportunity to study penguins. Not everyone has the chance to combine hobby and profession. I could not think of a more exciting job than the one I have, visiting majestic remote islands and working with both majestic species and wonderful people!

Contribution to science

It is clear that climate change is not a subject that will fade away anytime soon: some journals almost exclusively focusing on climate change are still among the most cited journals in science, such as *Nature Climate Change* or *Global Change Biology*. In wildlife ecology, the progress of new monitoring technologies (e.g. GPS, camera-loggers, etc.) have permitted only recently a thoughtful assessment of how the behavior and foraging of animals will change with climate. Unfortunately, because these technologies have only been available recently, few datasets go back in time far enough to allow for a good understanding of the long-term effects of climate on wildlife. I was lucky enough to have access to 25 years of data on the foraging and breeding of a key marine predator, the king penguin. This is one of the oldest dataset of such kind, which I helped expand during three years of fieldwork. This allowed me to not only answer several questions regarding the response of this indicator species to climate change, but also make inferences about the fate of the ecosystem in which the penguin lives.

In Chapter 3, I provided **the first validated methodology to determine the prey capture rate of the king penguin using accelerometers**. A recurrent theme in this thesis is that king penguins are good indicators of the southern marine ecosystem resources. King penguins are also among the most studied birds on the planet. For these reasons, I believe the method described in this paper will be useful for future research. Indeed, foraging success is an important aspect of an animal's fitness and is also usually the first facet affected by changes in the environment. To better understand how foraging success varies both spatially and temporally in this indicator

species, as well as to better understand habitat selection, an accurate method to estimate prey-capture rate at the scale of each individual dive is crucial.

This chapter is also one of the first-ever validation of accelerometry-based foraging success estimation in any deep-diving species, which is particularly important as they are difficult to observe when diving to hundreds of meters. Furthermore, I used a machine learning algorithm to translate acceleration into prey capture. As machine learning is a powerful tool, I hope that my study can serve as an example for using such an approach.

In Chapter 4, I provide **the first study looking at diet flexibility of king penguins in relation to the foraging conditions**. King penguins had a very steady diet, even when poor foraging conditions were encountered. This is particularly relevant to predict the effect of climate change on this species, as predators that are more flexible in their selected prey usually respond differently to ecosystem changes than strict specialists. The isotope data in this chapter also spreads over seven years, a very respectable timeframe to study diet change in seabirds (similar studies only rarely go over three years). I hope that my results can provide a case study showing how some marine predators are very tightly linked to their main prey, with a reciprocal fate regarding future ecosystem changes.

In Chapter 5, I compare the distribution of king penguins in winter between the Crozet and the Kerguelen population. This **is the most complete study on king penguin wintering distribution and first multi-colony dataset on that topic**. I intend to provide biological explanations on the clear dichotomy between the two colonies. This is also the first ever

published data for the Kerguelen population. These results will also be used to better understand the variables that can potentially affect king penguins in the winter (notably in Chapter 6).

In Chapter 6, I attempted to provide explanations for the two consecutive breeding failures that occurred in 2009 and 2010 at the king penguin colony of Kerguelen. **This is the first description of these unprecedented catastrophic breeding seasons in the literature.** I show that carry-over effects likely had an important role in at least one of these two breeding failures. Particularly, the delay in the timing of egg-laying was a major driver for the 2010 breeding failure.

I have also confirmed that the winter period can be crucial for the king penguin, and that resource then can likely be limiting at times. Very few studies have investigated the winter period at all for any penguin species, while none have suggested strong carry-over effects originating from this season. This tendency to overlook the winter period goes well beyond this taxa: the dynamics of the whole ecosystem in the Southern Ocean has been under-studied in winter compared to the summer.

Finally, Chapter 7 looks at the link between the climate, the foraging success of the king penguins and the resulting breeding success, with a particular emphasis on the chick-rearing period. This particular type of study has already been conducted on another colony. However, **I show that the dynamics at Kerguelen is extremely different from its neighboring colony, resulting in a contrasting fate regarding the impact of climate change on these two populations.** This emphasizes once again that the ecosystem dynamics in the Southern Ocean is quite complex, and that population trends from one region cannot necessarily be applied to another.

In Chapter 7, I also find that **air temperature can have a beneficial long-term effect on chick survival in the winter**. While most studies focus on ocean warming, no studies have looked at long-term effect of air-temperature on chick survival. Chapter 7 is also uses fully the 25 years of foraging behavior data and breeding success, a never-published dataset. This is one of the most complete dataset ever used in seabird research.

In summary, my thesis not only investigates the effect of climate change on the king penguin, but also provides a framework on how we can use this species to better understand changes in the lower trophic levels.

Contribution of authors

This is a manuscript-based thesis containing an introduction chapter, five data chapters that were published or submitted to a peer-reviewed journal, as well as a discussion chapter. Supervised and guided by my two co-supervisors, Charles-André Bost and Kyle Elliott, **I conceptualized the projects, conducted the analysis and led the writing of all chapters.** While I helped expand the dataset used in most of these chapters, most of the data was not collected by me. Several other collaborators were crucial to the completion of certain chapters. The contribution of coauthors for each chapter is detailed below.

Chapter 3 was published in *Marine Biology*

Brisson-Curadeau, É., Handrich, Y., Elliott, K. H., & Bost, C. A. (2021). Accelerometry predicts prey-capture rates in the deep-diving king penguin *Aptenodytes patagonicus*. *Marine Biology*, 168, 1-10.

In this chapter, I was lucky to inherit a dataset collected by Yves Handrich, a collaborator from the Strasbourg University (France) and CA Bost. This dataset consisted of combined accelerometry data and beak-opening data on wild king penguins. Y. Handrich also helped with early ideas for the analysis.

Chapter 4 was published in *Ibis*

Brisson-Curadeau, É., Bost, C. A., Cherel, Y., & Elliott, K. (2023). King Penguins adjust foraging effort rather than diet when faced with poor foraging conditions. *Ibis*.

I helped collect three years of data for this chapter, while the other four years of the dataset was provided by the long-term monitoring program led by CA Bost. Furthermore, Yves Cherel provided valuable comments on the early versions of the manuscript.

Chapter 5 was submitted in Polar Biology

Brisson-Curadeau, É., Nalivaev, A., d'Ovidio, F., Delord, K., Elliott, K., Bost, C-A. (submitted 2024). Wintering distribution of two king penguin populations of the Southern Indian Ocean. Submitted to Polar Biology.

The data for this chapter was collected by a team of field assistants and I (financial support from CA Bost and K. Elliott). Alexandra Nalivaev (supervised by Francesco d'Ovidio) helped with the Lagrangian analysis, while Karine Delord helped with the GLS analysis. All coauthors read and commented on early versions of the manuscript.

Chapter 6 was published in Scientific Reports

Brisson-Curadeau, É., Scheffer, A., Trathan, P., Roquet, F., Cotté, C., Delord, K., ... & Bost, C. A. (2023). Investigating two consecutive catastrophic breeding seasons in a large king penguin colony. *Scientific Reports*, 13(1), 12967.

The data collected for this chapter originates from many sources. The 2009 and 2010 data, during the reproductive failure, was collected by the long-term monitoring program led by CA Bost, as well as by his student, Annette Scheffer. Co-supervised by Phil Trathan at the time, A. Scheffer also provided the first tentative explanation of the 2010 breeding failure, although the

explanation in Chapter 5 greatly diverged from her early explanation. Cédric Cotté and Fabien Roquet helped with the interpretation of the climate data, while Christophe Barbraud and K. Delord provided colony count data. The rest of the data originated from the long-term dataset (CA Bost), with the last three years being collected by me. All coauthors read and commented on early versions of the manuscript.

Chapter 7 was published in *Global Change Biology*

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All data in this chapter originated from the long-term dataset (CA Bost), with the last three years being collected by me. As in other chapters, I conceptualized the projects, conducted the analysis, and led the writing, while CA Bost and K. Elliott provided crucial guidance.

Chapter 1: Introduction

In this thesis, I will study how climate impacts the foraging and breeding success of a marine top-predator, the king penguin. The objective is to understand and predict the future of the stronghold population at Kerguelen archipelago (South Indian Ocean) by considering the interactions between the environment, the trophic chain and the penguins. While the focus of the study is the king penguin, I hope that my thesis will provide new insights on the dynamics of the marine environment in the Southern Ocean, as well as expected interactions with climate change.

To better understand how climate has affected and will affect the king penguin at Kerguelen, there are many questions that I will try to answer throughout the thesis:

- 1) What tools are available to conduct long-term monitoring of the foraging behavior of penguins?
- 2) Can climate change influence the diet of penguins?
- 3) Can climate change influence the foraging behavior of penguins?
- 4) What is the link between foraging success and breeding success?
- 5) What is the effect of climate on the breeding success of penguins?

The five data chapters of the thesis will help answer these questions. In Chapter Three, I will develop a method that will allow accurate estimation of prey capture rates of king penguins, an important metric of foraging success. In Chapter Four, I will observe the diet flexibility of the

king penguin in relation to the foraging conditions, providing insights on the expected behavioral adjustment of king penguins with global warming. In Chapter Five, I will record the wintering distribution of two populations of king penguins. In Chapter Six, I will try to unveil the mystery behind the two catastrophic breeding failures of 2009 and 2010. Finally, in Chapter Seven, I will investigate the link between the climate, the foraging success and the breeding success of king penguins, with a focus on the chick-rearing period.

Chapter 2: Literature Review

Literature Review

In this literature review, I will first explain the ocean and climate dynamics of the Southern Ocean in the context of climate change. I will describe the main currents and water masses of the region, and how they can be affected by climate. I will also explain the role of the oscillation systems (e.g. El Nino), which not only originate from this region, but also have strong impact on the Southern Ocean. I will then focus on the marine environment surrounding the Kerguelen Archipelago. This region is a major hotspot of marine diversity sustained by complex bathymetric features, as well as by an important circumpolar current passing nearby.

I will then review the use of the king penguin (*Aptenodytes patagonicus*) to better monitor how climate change affects the Southern Ocean. The king penguin has distinctive life history traits that facilitates its use as an indicator species for the Southern Ocean. The review will put particular attention on one particular trait: their long and complicated breeding cycle, as well as their distant foraging trips in deep waters. Understanding of king penguin foraging and reproduction is indeed crucial to better interpret research on the species. I will also discuss their foraging behavior, another crucial aspect for such indicator species. I will then proceed by describing the research that has been done on king penguins breeding at Kerguelen, and identify the research needs for this population. Finally, I will explore the use of biologgers to help fill the research gaps for using penguins as sentinels of the marine environment.

1- The effects of climate on wildlife

The awareness that large climatic forces can severely impact wildlife predates the “climate change” era. For example, the increased occurrence of drought and its effect on wildlife was already discussed in the 1970’s, and probably before that (Smith 1970, Hillman & Hillman 1977). However, studies on the climatic effects on animals have really flourished in the past two decades, with the realisation that all aspects of climate (temperature, rain, wind, etc.) have been rapidly changing over the last century and will continue to do so (Root & Schneider 2002). These large-scale anthropomorphic changes have been identified as threats for 10 900 species worldwide (IUCN 2022). The examples are countless, but the Polar Regions have been affected more dramatically than the other regions (Post et al. 2019). Among the most impressive examples are the increasing reports of starving polar bears (*Ursus maritimus*) having to feed on birds in the summer due to the shorter ice season (Smith et al. 2010, Iverson et al. 2014, Obbard et al. 2022). Ice-associated Arctic seabirds have also been affected by climate change, with their behavior and diet having changed in the past decade in synchrony with rising temperatures (McKinney et al. 2022, Amélineau et al. 2019, Divoky et al. 2021).

While the southern pole has been given slightly less attention than its northern counterpart, many studies have nonetheless looked at how climate change might affect wildlife in the southern regions. Before we take a look at these studies in section 3, the following section will introduce the Southern Ocean – which produces almost all of the marine biomass of the southern

hemisphere – as well as the Sub-Antarctic region, the biodiversity hotspot of the region and focus area of the thesis.

2- The Southern Ocean and the Sub-Antarctic regions

In the Southern Ocean, most of the oceanic currents can circle around the globe without coming across any continental masses, a unique feature in the world. This creates a series of circumpolar currents and fronts, which define distinct biogeographical regions. The northernmost of these currents is called the Subtropical Front. It is the northern limit of the Southern Ocean and is formed by the meeting of the warm tropical waters with the colder Sub-Antarctic waters (Talley 2011). Another front occurs farther south, called the Sub-Antarctic Front. This front separates the sub-Antarctic waters north with the Polar Frontal waters south (Orsi et al. 1995, Giglio & Johnson 2016). Yet again, another front called the Polar Front separates the Polar Frontal waters with the Antarctic waters (Taylor et al. 1978, Park et al. 2014). The region including these fronts, from the Sub-Tropical Front to the Polar Front, is called the Sub-Antarctic region (Orsi et al. 1995, Belkin & Gordon 1996). Below the Sub-Antarctic region is the Antarctic oceanic region, up until the Antarctic continent, which combined with the Sub-Antarctic region forms the Southern Ocean (See Figure 2.1).

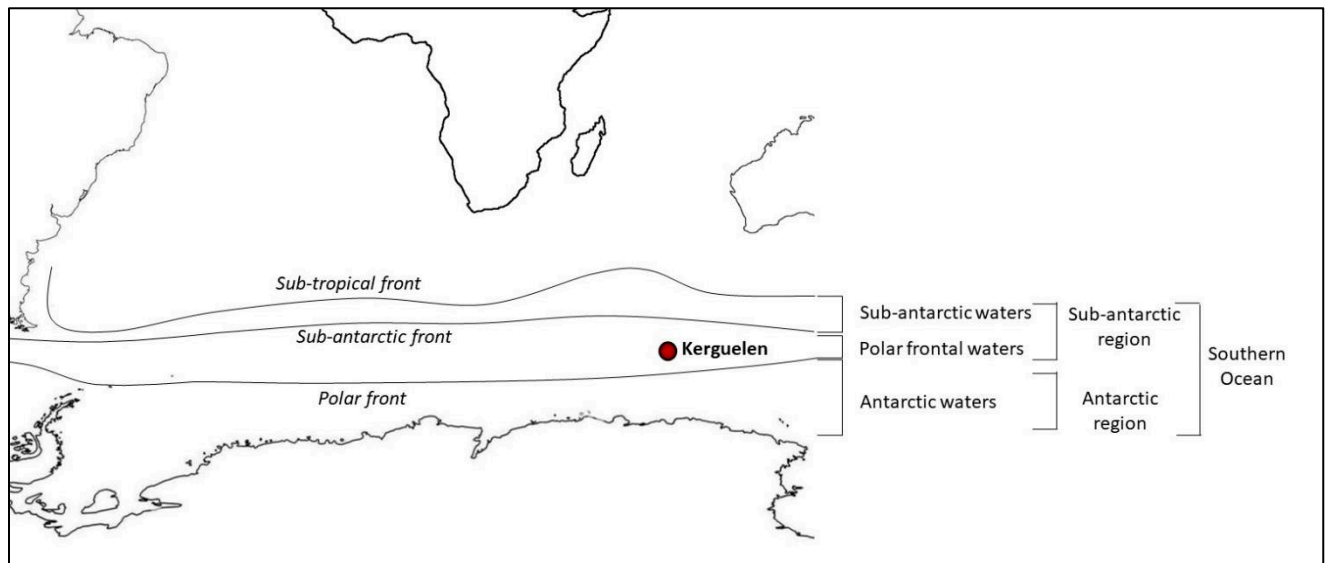


Figure 2.1: Delimitations and definitions of the fronts, waters and regions contained in the Southern Ocean

The Sub-Antarctic region – the region of interest of the thesis – is a breeding hotspot in the Southern Ocean, especially in the large offshore islands of the region including Kerguelen and Crozet archipelagos, South Georgia, Macquarie, Marion, Prince Edward, and many more. These islands are the main favorable land available for birds and non-cetacean mammals to breed in a region otherwise composed mainly of water (Woehler & Croxall 1997). Moreover, the bathymetric features around these islands, combined with the circumpolar currents named above, create highly productive areas (Pakhomov & McQuaid 1996, Bost et al. 2009, Chapman et al. 2020). As a result, more than 90% of the seabird and mammal species of the Southern Ocean live in the Sub-Antarctic region (Shirihai 2019).

Out of the fronts comprised in the Sub-Antarctic region, the Polar Front is among the most used by marine predators (Rodhouse et al. 1996, Guinet et al. 2001, Bost et al. 2009, Thiebot et al. 2011). Its main advantage to predators is the extensive upwelling occurring at the front, as the

two water masses – the Polar Frontal waters north and the Antarctic waters south – diverge from one another (Sokolov & Rintoul 2007). This upwelling makes nutrients available for the primary producers and eventually to the top predators foraging on this food chain (Charrassin et al. 2002, Scheffer et al. 2016). The Polar Front is often the closest source of upwelling from the Sub-Antarctic islands (e.g. in Kerguelen and South Georgia), so that it is the most convenient to use for marine animals breeding on land (Rodhouse et al. 1996, Guinet et al. 2001, Bost et al. 2009, Thiebot et al. 2011).

The other two fronts of the Sub-Antarctic region – the Sub-Tropical Front and the Sub-Antarctic Front – can also be associated with foraging birds and mammals, although they are usually located farther from the main breeding islands. Therefore, they tend to be less used by central foragers with limited feeding range during the reproduction season (e.g. Scheffer et al. 2010, Thiebot et al. 2011). However, these currents are still productive, and attract considerable numbers of non-breeding seabirds (Abrams 1985). On the rare islands that reside close to these fronts, such as Gough Island, the Sub-Tropical Front dictates the abundance of plankton, creating high carbon input for seabirds (Abraham 1985, Miller 1985).

3 - Climatic effects in the Southern Ocean

The Southern Ocean's climate is particularly affected by oscillating climatic phenomena. These cyclic climatic events, including the El Nino, originate from differences in pressure in very large sections of oceans and have large-scale influences on the weather (Rasmusson & Wallace 1983, Allan et al. 1991). They affect the Southern Ocean especially because they mostly originate

from the southern hemisphere, and so affect first the southern oceanic regions (Yuan et al. 2004, Stammerjohn et al. 2008).

The El Niño–Southern Oscillation (or ENSO), is the most important of these oscillating systems. ENSO is created by an irregular air pressure difference between the oceanic region in the Pacific (historically recorded near Tahiti) with the marine area off Darwin, in Australia (Allan et al. 1991). This difference in pressure is expressed with an index, called the Southern Oscillation Index (or SOI). In average SOI year, there is lower pressure over Darwin and higher pressure over Tahiti, leading to an east-to-west circulation of the air (Cane 2005). This circulation ensures that the heat from the warm western Pacific circulates west and transforms into precipitation in Australia. When the pressure diminishes in Tahiti (low SOI values), this east-to-west wind dies down, and the heat disperses all around the globe (Allan et al. 1991, Cane 2005). These low SOI years, also called El Niño years, have dramatic impacts on the weather and wildlife throughout the planet (Zhang et al. 1996, Magaña et al. 2003, Brönnimann 2007).

In the Southern Ocean, a close neighbour to this cyclic system, the effects are numerous. Firstly, warmer weather can be observed during El Niño years, as is the case in most parts of the world's oceans (Stammerjohn et al. 2008, Fogt et al. 2011). Secondly, the circumpolar currents are less strong during El Niño (Yuan et al. 2004). This can be problematic, as these currents typically form a barrier against the warmer tropical water, keeping the Sub-Antarctic region cold (Stammerjohn et al. 2008). Therefore, the attenuation of these currents increases even more the temperature, through higher teleconnection of the heat at lower latitudes (Yuan et al. 2004). Unsurprisingly, the temperature changes during El Niño also affect the sea ice cover observed

near Antarctica (Simmonds & Jacka 1995, Stammerjohn et al. 2008). Finally, the ENSO being one of the strongest oscillating system on Earth, it also usually triggers other smaller cyclic climate systems, such as the Southern Annular Mode (or SAM) in the Southern Ocean (Fogt et al. 2011 - see below).

SAM is another large-scale cyclic system, this one taking place directly in the Southern Ocean. It is the main non-tropical dipole of the southern hemisphere and is defined as the pressure difference between the 40° south latitude line and the 65° south latitude line (Marshall 2003). In years of positive SAM, the westerly winds are stronger, reinforcing the circumpolar currents (Gillett et al. 2006, Fogt & Marshall 2020). The change in oceanic circulation around the Southern Ocean also affects sea ice distribution. For example, in positive SAM, there is less sea ice around the Antarctic Peninsula, but more around the Ross Sea (Levbre & Goose 2005, Stammerjohn et al. 2008).

With climate change, extreme events associated with these large-scale climatic systems are expected to occur more regularly (Fogt & Marshall 2020). This might have repercussions on wildlife. For example, ENSO was negatively correlated with various Blue Petrel *Halobaena caerulea* demographic variables (Guinet et al. 1998), while both ENSO and SAM was correlated with the long-term population dynamics of the Adelie penguin *Pygoscelis adeliae* (Zheng et al. 2022). Even more dramatic, a massive die-off of rockhopper penguins in 1986 at the Falkland Islands were suspected to be due to a strong El Nino event that year (Boersma 1987). The effects are not the same for all species, however, as the number of breeding pairs of gentoo penguin

Pygoscelis papua, again in the Falkland Islands, correlated positively with ENSO events (Baylis et al. 2012).

Climate change might also directly affect the sea surface temperature of the Southern Ocean, with expected impacts on wildlife (Pendlebury & Barnes-Keoghan 2007). For example, a major population crash of southern rockhopper penguins occurring on Campbell Island is suspected to be driven by a warming of the nearby waters, impacting prey availability (Morrison et al. 2015). Similarly, high sea surface temperatures was correlated with the foraging success of gray-headed albatross *Thalassarche chrysostoma* and wandering albatross *Diomedea exulans* (Xavier et al. 2003). Generally speaking, all species sensitive to ocean temperatures in the Southern Ocean should face fluctuations in their foraging success, as the surface temperature is expected to increase by 0.3 to 1.6°C by 2100 (Eyring et al. 2016, Tonelli et al. 2021).

4 - The Kerguelen marine ecosystem

Kerguelen is among the most prolific wildlife archipelagos in the Sub-Antarctic region. Located in the Southern Ocean, at the junction with the southern Indian Ocean (49.5° S, 69.5° E). At over 7000km², it is the second largest archipelago in the Southern Ocean, after the Falkland Islands. It holds major populations for many key Sub-Antarctic species, such as the king penguin *Aptenodytes patagonicus* (~10% of the world population – Bost et al. 2013, Barbraud et al. 2020), the macaroni penguin *Eudyptes chrysolophus* (29% of the total breeding population – Weimerskirch et al. 1989, Crossin et al. 2013) and the gentoo penguins (12% of the total population – Bost & Jouventin 1990, Lynch & Larue 2014). It also holds endemic and near-

endemic species, such as the Kerguelen shag *Leucocarbo verrucosus* and the Eaton's pintail *Anas eatoni*, and is a major breeding site for two species of marine mammals: the elephant seal *Mirounga leonina* and the Antarctic fur-seal *Arctocephalus gazella* (Bester & Roux 1971, Young et al. 1996, Guinet et al. 1999).

There are many oceanographic features around Kerguelen that help sustain the rich marine ecosystem in the vicinity of the islands (Charrassin et al. 2002, Hindell et al. 2011). The first one is the proximity of the Polar Front, located around 70km south (Park et al. 2014 – Figure 2.2). As mentioned earlier, this front produces upwelling that sustains the trophic levels, and its proximity to Kerguelen is convenient for central place foragers, such as the black-browed albatross *Thalassarche melanophris* and the king penguin (Cherel & Weimerskirch 1995, Scheffer et al. 2016). The interaction between the front and the plateau of Kerguelen also favours the forming of eddies east of the archipelago (Dragon et al. 2010, Gille et al. 2014). Eddies are large-scale circular movements of water, creating both upwelling and downwelling depending on the direction of rotation (Robinson 2012). Eddies are used by wildlife around the Sub-Antarctic region, such as macaroni penguins and Antarctic fur seal (Bon et al. 2015, Ream et al. 2005). At Kerguelen, elephant seals use these eddies east of Kerguelen for foraging (Dragon et al. 2010).

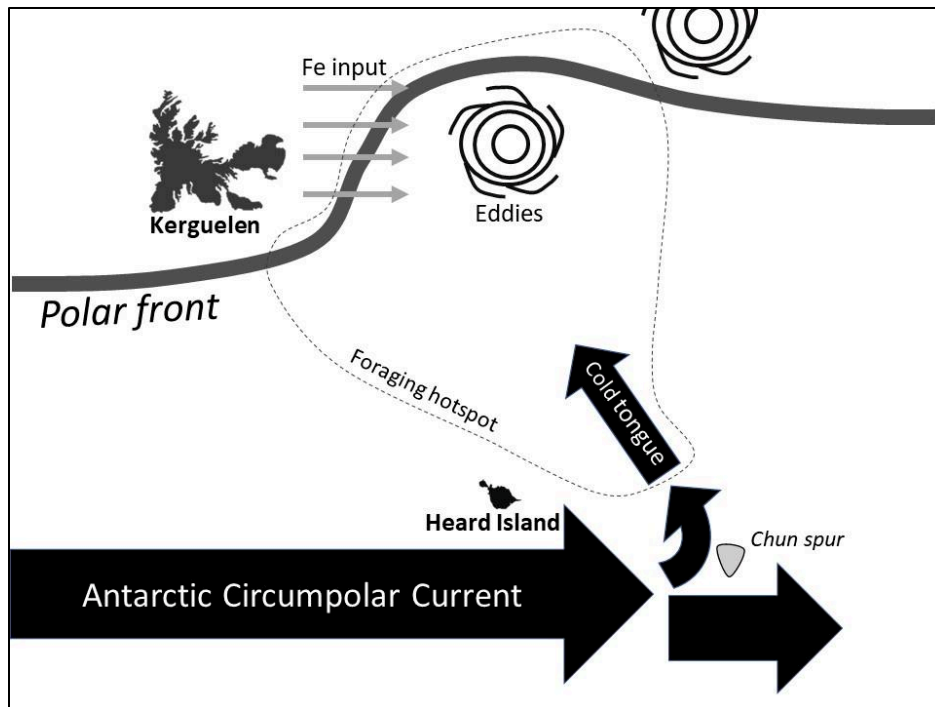


Figure 2.2: Main oceanic features around the Kerguelen archipelago. Westerly winds transport iron east of Kerguelen. Meanwhile, the Polar Front create eddies in the same region. Southeast of Kerguelen, the Chun spur, an underwater peak, deviates part of the Antarctic circulation towards the islands and closer to the surface. The whole area is a wildlife foraging hotspot for top predators.

Another interesting feature is the enrichment of iron coming from the islands and creating a high-productivity area east of the Islands (Blain et al. 2001, Uitz et al. 2019). Iron is often the limiting factor for marine productivity (Martin 1992). The strong westerlies near Kerguelen blow iron from the islands in the form of dust into the ocean, east of the islands (Uitz et al. 2019). The tidal currents around Kerguelen further favors mixing of the nutrients and create productive waters for prey and their predators (Charrassin et al. 2002). This productive area is used by marine predators breeding on the islands, such as the Antarctic fur seal and the king penguin (Bost et al. 2009, Hindell et al. 2011).

A final oceanic feature near Kerguelen used by wildlife is the cold subsurface tongue of water located south-east of the islands. Cold water originating from the ice melting in Antarctica (also called “winter water”) usually sinks well below the surface, out of reach for diving predators (Park et al. 1998). Located at about 500km from the islands, an underwater rocky peak called the Chun spur deviates some of that deep winter water towards Kerguelen (Park et al. 2008). As it is deviated, the cold tongue rises near the surface to about 100m, making it available for deep-diving predators, such as king penguins (Charrassin et al. 2002, van Wijk et al. 2010, Scheffer et al. 2016). The change of density between this cold layer and the warmer surface temperature above traps nutrients between the two layers (Park et al. 2014, Scheffer et al. 2016). It is therefore a hotspot for plankton-eating fish, as well as predators that eat those fish (Hindell et al. 2011).

As in other parts of the Southern Ocean, the waters near Kerguelen are expected to be warming with climate change (Turner et al. 2006). Some population declines, such as those observed for the Kerguelen population of gentoo penguin, are already suspected to be partly caused by a warming of the ocean near the islands, affecting prey availability (Lescroël & Bost 2006). Furthermore, the marine system around the archipelago is sensitive to variations in the SAM index, as well as strong El Nino events (Guinet et al. 1998, Favier et al. 2016, Pohl et al. 2021). A higher occurrence of those events with climate change could affect the marine ecosystem around Kerguelen. Air temperature on the islands has also risen considerably since 1960, with suspected impacts on wildlife (Weimerskirch et al. 2003). Overall, little is known on how global warming will impact the different trophic levels, particularly since different species respond very differently to such changes (Cohen et al. 2018). As Kerguelen is a major breeding ground for many

Sub-Antarctic animals, surrounded by productive waters, there is an urgent need to better understand how the fauna will be affected by climate change in this region.

5 - King penguins as indicator species

The effects of climate can be very different throughout the different taxa of the ecosystem, making it difficult to obtain a global picture of the situation with the limited resources available for polar research (e.g. Rockwell & Gormezano 2009). A solution to this problem is to use indicator species that could provide information about the whole ecosystem without extensive sampling (Piatt et al. 2007a).

An indicator species is defined as a species that can provide information about the environment that is otherwise too difficult, inconvenient, or expensive to measure directly (Rolstad et al. 2002). Traditionally, these are species with very specific habitat requirements, such that their presence/absence in an environment is revealing of that habitat. For example, the absence of certain invertebrate species in a river can be used to assess the degree of pollution in a river (Hawkes 1979), while the presence of wood thrush *Hylocichla mustelina* in a forest can be used to evaluate its degree of fragmentation (Drapeau & Allard 2022). Yet, the definition of an indicator species can be broadened, with applications that go well beyond the presence/absence in an environment. For example, the foraging behavior of seabirds can be used to assess prey availability (Piatt et al. 2007a, Bost et al. 2008, Brisson-Curadeau et al. 2017).

In the Southern Ocean, marine top-predators can reliably be used as indicator species to assess changes in the food chain occurring with climate change (Trivelpiece et al. 1990, Ainley 2002, Trathan et al. 2007, Bost et al. 2015). Indeed, predators integrate many aspects of the lower trophic levels through their demography, breeding success, diet and foraging behavior (Cairns 1988). Studying these aspects in a single species could provide information on the whole food web of the region, such as changes in species composition and prey availability. In the Sub-Antarctic, the king penguin could be a valuable choice of indicator species (Bost et al. 2015, Cristofari et al. 2018).

King penguins are consumers of mesopelagic fish and thus at a relatively high trophic position (Cherel et al. 1993). They usually dive 150-200m to forage on myctophids (or lanternfish), their main prey, but also consume other prey, such as squids (Charrassin & Bost 2001, Bost et al. 2002, Hindell 1988, Moore et al. 1998). Their strong preference for myctophids, the most abundant deep-water fish in the Southern Ocean, make them a potential indicator species for the entire Sub-Antarctic Polar Region (Kozlov 1995, Catul 2011). Indeed, the king penguin has a circumpolar distribution and so can be used to assess the impact of climate on the ecosystem around the Sub-Antarctic region. For example, the foraging distance from the colony was used to assess prey availability at the Crozet archipelago, which holds one of the largest populations of this seabird. In warm years, such as those triggered by large-scale anomalies (e.g. El Niño and Subtropical Dipole), penguins were constrained to forage much farther from their colony, likely reflecting poor conditions for myctophids (Bost et al. 2015).

The length of the foraging trips that king penguins undergo during reproduction is another important feature that increases the relevance of using king penguins to monitor the ecosystem. Indeed, king penguins typically travel several hundreds of kilometers during foraging trips, during both incubation and chick-rearing (Bost et al. 1997, Pütz 2002, Bost et al. 2015). Consequently, information directly or indirectly inferred from its foraging behavior or diet can be applied to a large-scale area. King penguins travel approximately 200 – 600 km from their colony to forage during both the incubation and chick-rearing period (depending on the colony – Bost et al. 1997, Pütz 2002, Bost et al. 2015). These long foraging trips across the breeding stages cover the most area compared to any other species of deep-diving seabird in the world. In comparison, other sympatric penguin species forage much closer to the coast (gentoo penguins *Pygoscelis papua*: <100km – Lescroël & Bost 2005; macaroni penguins *eudyptes chrysolophus*: typically <100km – Deagle et al. 2008; southern rockhopper penguins *Eudyptes chrysocome*: <300km – Pütz et al. 2018). The smaller foraging range of these species is thus less helpful to assess large-scale ecosystem changes.

The breeding cycle of king penguins is another interesting feature concerning their use as an indicator species. The species takes over a year to fledge a single chick, the longest breeding cycle in birds (Olsson 1996). The breeding period is typically the period of interest for the use of seabirds as indicators, as they are easily sampled at that time and energy demand is higher then, making their foraging choices crucial and revealing food availability (Cairns 1988). Breeding success at this period can also be assessed, again as a proxy of the foraging conditions encountered (Piatt et al. 2007b). Moreover, the central-place constraints of seabirds at this

period make them easier to study. Considering these points, the long and complex breeding cycle of penguins provides an ideal opportunity to assess marine conditions year-long using this species. A complete examination of the breeding cycle of king penguins will be discussed in the next section.

Despite the king penguin being a promising candidate as a circumpolar indicator species, it has not been used as such throughout the Sub-Antarctic region. Indeed, some regions, like the vicinity of Kerguelen, have few if no studies looking at the effect of climate on the different life stages of the king penguin. On the other hand, other colonies such as those locating in the Crozet archipelago, have received more attention on the subject (Péron et al. 2012 , Bost et al. 2015) partly due to the presence of a permanent research station inside the colony. Studies conducted in wildlife hotspots apart from Crozet are needed.

6 - The breeding cycle of king penguins

King penguins are truly marine birds, returning to land only for moulting and breeding. Moulting typically starts in late September and early October and lasts around 3-4 weeks (Gauthier-Clerc et al. 2002a). Because birds are constrained to fast when on land, and because moulting is an energetic process, birds lose ~44% of their mass by the end of the moult (Cherel et al. 1994, Gauthier-Clerc et al. 2002a). Before starting to breed in early summer (November in the southern hemisphere), birds must then return to sea for three weeks to regain mass (Charrassin & Bost 2001, Gauthier-Clerc et al. 2002a).

When returning to the colony, adults pair with a partner. An individual typically pairs with a different partner every year, as the inter-annual divorce rate is extremely high in king penguins compared to other Sphenicidae. Indeed, only about 25% of king penguins retain the same partner in consecutive breeding attempts (Barrat 1976, Olsson 1998). This rate is typically much higher in other penguins, such as in the macaroni penguin (around 75% - Williams & Rodwell 1992), the rockhopper penguin (around 80% - Croxall & Davis 1999), and the gentoo penguin (>90% - Croxall & Davis 1999). The main reason for this contrast is that the arrival of king penguins for mating is rather asynchronous compared to other species; while the peak is in November in most colonies, individuals keep arriving for breeding until January (Weimerskirch 1992). The benefits of pairing with a known partner with known breeding performance are thus well offset by the costs of using fat reserve while waiting on land for the partner (Bried et al. 1999).

King penguins lay one egg, usually from November to December (Weimerskirch et al. 1992, Bost et al. 2013), and incubation lasts 53 days (Handrich 1989). Relaying occurs only if egg loss happened during the week following laying. Parents take incubation shifts ranging between 10 to 20 days, during which time the partner will be at sea (Charrassin et al. 1998). Egg predation is relatively rare, but does occur from brown skua *Stercorarius antarcticus* and black-faced sheathbill *Chionis minor* (Descamps et al. 2005). After the chicks start to hatch, the period is called the brooding period. For four weeks, the parents take turns incubating the small chick while the parent is at sea foraging (Weimerskirch et al. 1992, Bost et al. 2013). Each foraging trip lasts around 4-10 days, after which the adult will relieve the partner and feed the chick progressively

by regurgitation (Charrassin et al. 1998, Gauthier-Clerc et al. 2002b). Chicks grow to about 2 kg during this period (de Margerie et al. 2006).

In early March, when the chick has gained sufficient weight, both parents forage simultaneously while the chick remains unsupervised at the colony, forming creches with other chicks to avoid predation and facilitate thermoregulation (Duchamps et al. 2002, Le Bohec et al. 2005). By April, chicks will have a mass comparable to adults, if not heavier, averaging 12.5kg (Cherel & Le Maho 1985). In early May, winter starts in the southern hemisphere, and prey availability is typically very low in the Sub-Antarctic region (Koslov et al. 1991). Adults must then migrate south toward the ice edge and leave their chick fasting at the colony for up to five months, a unique feature among birds (Cherel et al. 1987, Bost et al. 2004). Chick mortality is high during this period (Stier et al. 2014). Many die of starvation or hypothermia, while predation by the northern giant-petrel *Macronectes halli* is at its highest (Cherel et al. 1987, Descamps et al. 2005). By the end of the winter, chicks will have lost nearly 50% of their mass (Cherel et al. 1987, Stier et al. 2014).

The wintering area of adults during the chick fasting has been poorly studied, due to obvious logistic constraints. In the Falkland Islands, king penguins seem to winter north of the colony (Baylis et al. 2015), but those in Crozet head south (Bost et al. 2004), although these studies usually have low sample size. The wintering location of adults in some colonies are completely unknown, such as in Kerguelen.

Parents eventually return to the colony in September and resume provisioning at a high rate (Weimerskirch et al. 1992). Chick will then acquire progressively their waterproof plumage and fledge by December (Corbel et al. 2008).

The complexity of the king penguin breeding cycle is a direct result of its very long chick rearing period. Because it takes over a year to fledge a chick, adults cannot breed two years in a row following the normal “phenology” described above. Indeed, birds that successfully fledge a chick at a given year can skip breeding during the following year or attempt a second breeding attempt with a delayed phenology (Olsson 1996). Around 50-94% of birds opt for the second option (hereafter “late-breeders”), despite a very low chance of success (Weimerskirch et al. 1992, Olsson 1996).

Late-breeders typically start moulting up to 13 weeks later than earlier breeders, but accelerate the moulting process, so that they typically start laying with a 10-11 week delay compared with the regular phenology (Olsson 1996, Gauthier-Clerc et al. 2002a). Still, because adults have less time to feed their chick before the onset of winter, most offspring will die before the end of the winter (Stir et al. 2014). Overall, for late-breeders, the chances of successfully fledging their offspring is between 0-8%, compared to 41% on average (but quite variable) for early-breeders (Weimerskirch et al. 1992, Heezik et al. 1994, Olsson 1996).

The high number of birds attempting two consecutive breeding seasons despite the low chances of success in the second season can seem at first odd in terms of strategy and fitness. Indeed, breeding usually involves high costs in animals, and long-lived species such as the king penguin typically do not breed when chances of success are low (e.g. Jenouvrier et al. 2008).

However, the survival rate of the king penguins does not seem to be affected when breeding: both breeders and non-breeders have the same survival rate in a given year, the highest among penguins (Weimerskirch et al. 1992, Le Bohec et al. 2007). It is therefore advantageous for adults to attempt breeding, even when the phenology is delayed, as even low chances of success could increase the fitness of individuals (Le Bohec et al. 2007).

7 - King penguins at Kerguelen

The Kerguelen colonies have been relatively poorly studied compared to other locations such as Crozet archipelago and South Georgia Island. This is mainly because the colony is located more than 25 km from the scientific base, and accessible only by foot. In comparison, the Crozet archipelago colony of La Grande Manchotière is located less than a kilometer away from the scientific base.

Early research on king penguins at this location recognized the significance of the species as a major top predator: king penguins, along with three other species, consume over half of the prey eaten by the entire community of the islands (Guinet et al. 1996). Indeed, king penguins were quite numerous even at the time (around 170 000 to 200 000 in the late 20th century – Weimerskirch et al. 1989), when they were still recovering from the commercial exploitation for oil ongoing up until the early 20th century (Bost et al. 2013). More recently, the total population at Kerguelen has continued increasing, with around 300 000 breeding pairs (Barbraud et al. 2020). There are six colonies present at Kerguelen, with the two largest being Ratmanoff colony and

Doigt-de-Sainte-Anne colony, together accounting for half of the total population (Barbraud et al. 2020).

Although they belong to the same subspecies *A. patagonicus halli*, the Kerguelen population seems different from the nearest neighbour Crozet's population in its genes, morphology and phenology. Indeed, genetic studies have shown that the two population have a considerably different genome, although the difference has not been enough to designate Kerguelen as its own subspecies (Viot 1987). The phenology of the Kerguelen population is also slightly earlier than the population at Crozet, with egg laying typically starting in late November, compared to early December for the latter (Weimerskirch et al. 1989, Weimerskirch et al. 1992). The individuals at Kerguelen are also smaller on average than their oceanic neighbour (Weimerskirch et al. 1989).

One of the most significant contributions to king penguin research at Kerguelen was conducted by Bost et al. (2002), focusing on the diet, prey selection and vertical habitat selection of this population. They compared stomach content of penguins with fish trawl composition sampled in the foraging area of the species. They found that this population feeds primarily on myctophids *Krefftichtys andersonii* (a common prey for other king penguin populations - Cherel et al. 1993, Olsson 1997), but also on eel-cod *Muraenoleptis marmotus*. These prey items were present only during the day at the depth targeted by the penguins, suggesting that king penguins do not forage at night near Kerguelen. Some other prey, like myctophids of the genus *Protomyctophum*, were underrepresented in the penguin diet, despite being the most abundant prey in the foraging habitat of the bird.

Another important work for which this thesis is built upon is the study from Charassin et al. 2002 and Scheffer et al. (2016) on king penguin foraging strategies in relation to oceanographic features. They found that king penguins at Kerguelen use a cold tongue of winter water deviated by the Chun spur to forage during incubation. They also use the thermocline, as prey may accumulate between the two layers of water with different densities. Finally, brooding penguins rather used the Polar Front to capture prey for their chick. Scheffer et al. (2016) complemented two earlier studies showing that king penguins at Kerguelen target water associated with the Polar Front (i.e. low sea surface temperature and sea surface height), as well as regions with high bathymetric gradients (Charrassin et al. 2002, Bost et al. 2011).

Considerable effort was made to assess the use of king penguins as a monitoring species of the ocean temperature (Koudil et al. 2000, Charrassin et al. 2002, Charrassin et al. 2004). Birds were equipped with temperature-loggers on several occasions to examine how the species could be used to remotely record water temperature at different depth. The species has also been considered to assess mercury contamination in the region (Carravieri et al. 2013). No studies yet looked at using this species to monitor the effect of climate on the ecosystem at Kerguelen, rather than the physical components of the ocean only.

8 - Biologging as a tool for penguin monitoring

Foraging of the king penguin is hard to observe, occurring far at-sea and at depths greater than 200m (Charrassin & Bost 2001). Yet, many aspects of the foraging, such as energy intake or number of prey captures, are necessary to better understand the effect of climate on this top

predator and on the ecosystem. For example, prey intake can drop in years of extreme weather, while a migration of the prey in the water column can constraint birds to capture their prey at deeper depth, affecting their foraging success (Carscadden et al. 2002, Hedd et al. 2002). Detecting these changes is impossible without the use of biologgers (Wilson et al. 1994).

There are several technologies available to monitor the foraging of seabirds while underwater. Camera-loggers provide the most information among loggers, as they are able to detect, when, where, and which prey was consumed during a given dive (Kokobun et al. 2011, Watanabe and Takahashi 2013, Watanabe et al. 2014, Volpov et al. 2015). Unfortunately, this technology becomes unreliable for species, such as thick-billed murre *Uria lomvia*, that can dive at depth of >90m with low light-levels, where filming is difficult (Brisson-Curadeau et al. 2018). Consequently, camera loggers are not used to monitor the foraging of king penguins, which dive much deeper to regions in perpetual darkness. While some camera loggers are equipped with a light, this presumably disrupts the very foraging behaviour they are designed to capture.

Other technologies such as esophageal sensors and beak-opening sensors can also provide accurate information on the number of prey captured. Esophageal sensors detect drops of temperature in the esophagus, corresponding to a prey ingestion (Charrassin et al. 2001, Horsburgh et al. 2008), while beak-opening is also a strong proxy of prey capture (Hanuise et al. 2010). Unfortunately, both of these methods are invasive for birds, as esophageal sensors need to be ingested and Hall sensors require surgery to be installed on the bird (Charrassin et al. 2001, Horsburgh et al. 2008, Hanuise et al. 2010). For this reason, none of these two loggers make good solutions for the long-term monitoring of foraging in penguins in the context of climate change.

Tracking loggers provide useful information on the foraging behavior of animals and have been extensively used over the last decade, including on the king penguin (e.g. Bost et al. 2011, Scheffer et al. 2012). These loggers can be used to assess foraging area, time allocation while at sea, as well as trip length (e.g. Trathan et al. 2008, Zimmer et al. 2008). Some studies have used this technology on the king penguins of Kerguelen (e.g. Scheffer et al. 2016). Unfortunately, many aspects of foraging cannot be assessed using GPS, such as the number of prey captured and energy intake.

An attempt to assess these “missing” aspects of foraging that cannot be estimated using GPS was made using depth-loggers. Indeed, some species display quick up and down motions in the water column when capturing a prey. These movements can be detected by depth-loggers, providing an estimation of the prey captures (Schreer & Testa 1996, Halsey et al. 2007). This technique has been used in whales, little penguins, but also king penguins (Hanuise et al. 2010, Doniol-Valcroze et al. 2011, Zimmer et al. 2011). A downside of this technique is that its accuracy is rather poor, with high percentages of both false positives and false negatives (Hanuise et al. 2010).

Accelerometers have been widely considered as being the best alternative to assess prey intake in deep-diving species (Kokobun et al. 2011, Viviant et al. 2014, Volpov et al. 2015). As in depth-loggers, accelerometers can detect motions associated with prey captures. However, they can detect much more subtle movements (i.e. those that do not necessarily results in a changes in depth), and in three dimensions (Viviant et al. 2014, Del Caño et al. 2021). As a result, their accuracy is much greater than that of depth-loggers and prey type can even be determined at

times (Del Caño et al. 2021). This technique does need validation prior for being used on a species, as the movements detected by the accelerometer cannot be interpreted without prior experiments. This validation is often done using either camera-loggers or by filming feeding captive animals equipped with accelerometer (e.g. Watanabe & Takahashi 2013, Viviant et al. 2014). Because such validation is difficult to achieve in king penguins for the reasons previously mentioned, accelerometers have never been used in this species to assess prey capture. There is an unexploited potential of this technology on king penguins.

9 - Conclusion

In conclusion, many ecosystem aspects of the Sub-Antarctic region are expected to be affected by climate change. The main islands of the region, such as Kerguelen, are of particular interest for monitoring, as they host most of the breeding activities for top predators. The king penguin could be used as an indicator species to help monitor the changes occurring in these islands and their surrounding waters. Indeed, this species is a top predator distributed throughout the region and with a very long breeding cycle, which are interesting aspects when considering the species as indicator of the environment. Biologging could help refine the use of king penguins as an indicator species.

Chapter 3: Accelerometry predicts prey-capture rates in the deep-diving king penguin *Aptenodytes patagonicus*

AUTHORS

Émile Brisson-Curadeau^{1,2}, Yves Handrich³, Kyle H. Elliott¹ & Charles-André Bost²

AFFILIATIONS

1 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

2 : Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, Villiers-en-Bois, France

3 : CNRS, IPHC UMR 7178, Université de Strasbourg, 67000, Strasbourg, France

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Abstract

Remotely estimating prey-capture rates in wild animals is key to assess foraging success. In diving animals, accelerometers have been particularly useful to remotely detect prey captures and have been shown to be more precise than traditional estimates relying on depth-derived measures (e.g., wiggles). However, validations of the accelerometry technique using a gold standard (i.e., with supervision) have been mostly restricted to shallow diving species, which can be equipped with camera-loggers for visual validation of prey-capture events. In species diving near the euphotic limit (150–200 m), accelerometers remain mostly untested due to the difficulty of validating such methods in darkness at extreme depth in the wild. In addition, prey-pursuits in low-light conditions might not result in intense and long-duration acceleration signatures, as predator–prey perception likely occurs at close-range in the dark (i.e., the “visual-interactions hypothesis”). We combined accelerometers with beak-opening sensors (for validation) and depth recorders on a wild deep-diving seabird, the king penguin *Aptenodytes patagonicus*, to describe prey captures at depth and create predictive models using accelerometers. Surprisingly, prey pursuits and captures were similar in duration (3.9 ± 3.5 s) and intensity (0.78 ± 0.31 g) as shallow-diving species reported by similar studies. As accelerometry signatures were distinct, accelerometry-derived variables were almost twice as accurate (Mean-squared error = 8.6) at predicting prey-capture events as depth-derived variables (“wiggles”, Mean-squared error = 16.0). As in the shallow-diving species, accelerometry outperforms traditional depth-derived models at measuring the foraging intake in deep-diving animals, highlighting the usefulness of accelerometers for measuring animal behavior.

Introduction

Knowing where and when animals forage is an important aspect in ecology and conservation (Grémillet et al. 2004; Pichegru et al. 2010; Scheffer et al. 2010, Hays 2016). In deep-diving species, the identification of foraging hotspots has been mainly facilitated by the analysis of horizontal movements obtained from satellite or GPS technology (e.g., Trathan et al. 2008; Zimmer et al. 2008). Analytical techniques applied to horizontal movements employ animal's speed, tortuosity, and step length to define Area Restricted Searches (ARS) and determine whether the animal is travelling or foraging (Fauchald and Tveraa 2003; Langrock et al. 2012).

As recent bio-logging devices record much more information than just the location of an animal, several devices, such as camera loggers, mouth opening sensors, temperature loggers inserted in the digestive track, depth loggers and accelerometers, have been used to remotely assess foraging success (e.g., prey capture rate) in diving animals (Kokobun et al. 2011; Viviant et al. 2014; Volpov et al. 2015). In addition, some species-specific methods have been used, such as buoyancy change in seals (Adachi et al. 2021), echolocation clicks in whales (Miller et al. 2004) and visceral warming in tunas (Bestley et al. 2008). While most of these approaches are in theory widely applicable across taxa, their use has been limited, because their deployment on wild animals can be challenging. For instance, mouth opening sensors use a magnet on one part of the mouth and a Hall sensor on the opposing part to detect whenever the animal opens its mouth or beak, and are typically a precise and powerful tool to detect prey captures (Wilson et al., 2002; Hanuise et al. 2010; Viviant et al. 2014). However, the equipping of these loggers can require invasive surgical procedures to conceal beneath the skin the electrical lead between the Hall

sensor and data logger. Temperature loggers detect drops in temperature in the oesophageal track due to the ingestion of prey. While these loggers provide very good estimates of prey-capture rates, they are again quite invasive for the animal (Charrassin et al. 2001; Horsburgh et al. 2008). Furthermore, only a small proportion of Hall sensors or temperature loggers deployed provide useful information, due to difficulties with wiring or retrieval (Charrassin et al. 2001; Wilson et al. 2002).

Camera loggers attached to the back or head of the animal have been used more recently, with high-quality miniature cameras now available on the market (Kokobun et al. 2011; Watanabe and Takahashi 2013; Watanabe et al. 2014; Volpov et al. 2015). However, success of this method on deep-diving animals is mixed, as prey captures are not systematically detected at low-light depths, despite the use of external LEDs (Naito et al. 2013, Brisson-Curadeau et al. 2019). For this reason, camera-loggers equipped on deep-diving animals have been mostly used to evaluate the diet of an animal—which requires only a few “good” pictures/footage to be assessed—rather than systematically quantifying prey capture (Naito et al. 2013, Naito et al. 2017, Adachi et al. 2021, Yoshino et al. 2020; but see Watanabe et al. 2020).

As most of the previously described approaches are difficult to apply in the field, the use of depth profiles has been historically one of the most widely used methods to estimate prey capture in deep-diving animals (e.g., Kirkwood and Robertson 1997; Zimmer et al. 2011; Hanuise et al. 2013; Scheffer et al. 2016). Depth loggers are generally easy to deploy and can provide information on foraging behavior. In particular, many derived variables (descent angle, maximum

depth, dive shape, etc.) are indicative of foraging dives (Schreer et al. 1996; Halsey et al. 2007, 2010). The presence of short up-and-down motions (called “wiggles”, see Figure 3.1) has been particularly used in the literature to estimate the number of prey captures in a dive (e.g., Charrassin et al. 2001; Bost et al. 2007; Zimmer et al. 2011; Scheffer et al. 2016; Tessier & Bost 2020). Other commonly used depth-derived variables include maximum depth, dive duration and dive shape, where deeper dives with proportionally longer bottom time are indicative of increased feeding activity (Ropert-Coudert et al. 2000; Mori et al. 2002; Elliott et al. 2008). While these variables are easy to collect and compute, their accuracy to quantify prey capture can be rather low, at least in some species (Bost et al. 2007; Hanuise et al. 2010; Carroll et al. 2014).

Accelerometers, such as depth loggers, are small and easily deployable, with few effects on the fitness of the equipped animal (Chivers et al. 2016). They can detect movement in three dimensions (x,y and z axis) and at a higher resolution than depth loggers, therefore, providing more information on the behavior of the animals. Moreover, recent studies have shown accelerometers to be more accurate at estimating prey capture than the traditional use of wiggles (e.g., Del Caño et al. 2021). Consequently, their use to quantify prey capture has been increasing in the past few years (Gallon et al. 2013; Carroll et al. 2018; Yoshino et al. 2020). Yet, testing the accuracy of accelerometry at predicting foraging events in the wild has been mainly limited to animals diving above 100 m depth (hereafter referred as “shallow-diving species”), mostly feeding on plankton and crustaceans, with validation on camera loggers (Kokobun et al. 2011, Watanabe and Takahashi 2013; Watanabe et al. 2014; Sato et al. 2015; Volpov et al. 2015). While

acceleration has been used on deep-diving animals to compute prey-capture rates (Yoshino et al. 2020; Adachi et al. 2021), true validation at deeper depths is rare in the literature, because low-

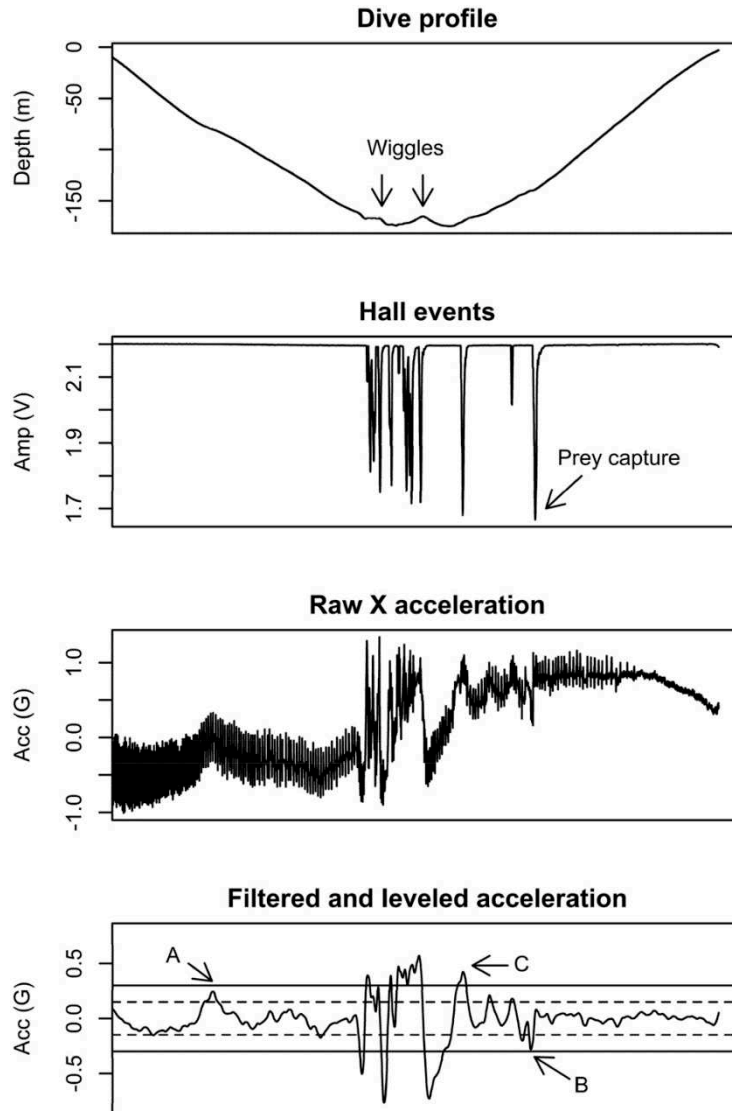


Figure 3.1: Depth-profile, Hall events, raw acceleration and filtered acceleration of a representative king penguin dive. Point A represents a false positive under the 0.15 g threshold, but a true negative under the 0.3 g threshold. Point B represents a true positive under the 0.15 g threshold, but a false negative under the 0.3 g threshold. Point C represents a true positive under both thresholds

light conditions limit the potential of camera loggers for validation (but see Watanabe et al. 2020). In addition, it is possible that prey-pursuits near or below the limit of the euphotic zone are shorter in duration and amplitude, as predator–prey perception occurs at closer range. The “visual-interaction hypothesis” states that since the escape behavior is less efficient at depth due to reduced detection distance by both prey and predator, deep ectothermic fish are less reactive and have a low metabolism (Childress et al. 1990; Drazen and Seibel 2007). This could potentially reduce the detectability of prey-capture attempts in the acceleration signal, as predators do not need dynamic chases to capture prey.

The objective of this study is to validate the use of accelerometry as a reliable tool to estimate prey-capture rate in a deep-diving bird. We first aim to describe the typical prey-capture acceleration signature at depth, and evaluate whether the “visual-interaction hypothesis” complicates detection of prey capture as depth increases. We predict that deeper captures will generate acceleration peaks with a lower amplitude and duration than shallower captures. Second, we aim to build a model predicting prey capture using accelerometry data as inputs. We chose machine learning algorithms to compute our model, as their outputs are typically more accurate than those of linear models—especially when fed with a high data volume like that of accelerometry data—and hence have been increasingly used to convert accelerometry signals into behavioral classification (Brewster et al. 2018; Pucci et al. 2020; Sutton et al. 2020). The validation of such algorithms requires a gold standard, which can be done in deep-diving seabirds using either beak-opening sensors or esophageal temperature sensors. We use a unique data set that combines a beak-opening sensor and a 1D-accelerometer on the wild king penguins

(*Aptenodites patagonicus*), and compare our results with the traditional methods using wiggles and other depth-derived variables.

Methods

The data set was collected in February and March 2006 on Possession Island, Crozet (46.4°S, 51.8°E), and was used by Hanuise et al. (2010) to compare wiggles and a combination of two sensors measuring esophageal temperature and beak-opening amplitude to detect prey captures. While acceleration data was also collected, it was unused in Hanuise et al. (2010) study. The ethics committee of the Institut polaire français Paul-Émile Victor approved all field procedures. All analysis were conducted using R version 4.0.3 (R Core Team 2020).

Two brooding king penguins (named E1 and H1) were equipped with one SMAD data logger (DEPE-IPHC, France) attached externally to their back. The SMAD is a TDR equipped with a single axis accelerometer (capturing the surge or x axis) and a long and single connector, buried under the skin from the back to the corner of the beak. From this position, one temperature probe was inserted 10 cm depth inside the esophagus, while a Hall sensor was glued on the orange tip of the mandible, just in front of a miniaturized magnet, glued on the maxilla. Depth and esophageal temperature were continuously recorded at 2 Hz, while beak-opening amplitude and acceleration were recorded at 16 Hz during two daily periods of 1 h starting at 7 AM and 4 PM. Only dives with a maximal depth deeper than 40 m were considered in our analysis, as shallower dives in king penguins are travelling or exploratory dives not associated with foraging and only anecdotally contain prey captures. King penguins prey are quasi absent in the 0–70 m

depth range during the day (Bost et al. 2002). For this reason, shallow dives in this species are often removed from foraging analysis (e.g., Hasley et al. 2010; Le Vaillant et al. 2013; Scheffer et al. 2016; Tessier and Bost 2020). Indeed, only 0.39% of all prey captures in our data set occurred above 40 m.

Because Hall sensors were determined to be the most accurate method to detect prey capture in the earlier study (Hanuise et al. 2010), we ignore esophageal sensors in this study and used prey-capture events recorded by the Hall sensors as the gold standard. In any cases, both esophageal sensor and Hall sensor provide similar estimations of prey capture (Hanuise et al. 2010).

Accelerometry data

Raw acceleration profiles for each dive were filtered twice with two different Local Polynomial Regressions using the “loess” function available in R. Loess is a nonparametric method using locally weighted polynomial regressions to fit a smooth curve through datapoints (Cleveland et al. 1992). The smoothness of the curve is decided by the alpha parameters, which controls the size of the sliding widow that locally fits the regressions. Alpha = 1.0 means that the sliding widow is as wide as the data (smoother curves), while alpha = 0.0 means that the window includes only one point at a time (coarser curve).

The first filter was used to remove the pitch signal from the 1-D accelerometry data. We, therefore, ran the first Loess with a running window of 120 s (alpha \approx 0.4), determined empirically to capture general trends in acceleration due to changes in main directional pitch during the dive. We ran a second Local Regression with a running window of 6 s (alpha \approx 0.02) to remove wing

beat noise, leaving only the pitch variation plus medium-scale peaks, assumed to be mostly associated with prey captures. The final output was obtained by subtracting the 6 s-window regression (pitch plus prey-capture acceleration) from the 120 s-window regression (pitch only), leaving solely the acceleration peaks that we hypothesized were mostly associated with prey capture (see Figure S3.1 for a graphical representation of the two-filter method).

Once we filtered the acceleration profile, we visually scanned a sample of all prey-capture events to determine which parameters could be used by the machine learning (ML) algorithm to automatically detect prey captures. We determined that feeding events caused acceleration peaks, either of positive or negative force, of at least ± 0.15 g, with varying maximal intensity but rarely over ± 1.2 g. By counting peaks above/below ± 0.15 g, we, therefore, concluded that the ML algorithm would detect nearly all capture events. However, preliminary analyses also showed that some acceleration peaks above/below ± 0.15 g were not related to feeding events, potentially leading to false positive errors by the algorithm. Fortunately, these peaks were rarely above/below ± 0.35 g. We, therefore, used two distinct values to feed the algorithm: a conservative threshold, a high value that would reduce the amount of false positive but omit true positives, and a liberal threshold, that would potentially include all true positives but allow false positives as well. To determine the best values for these two thresholds, we ran the ML algorithm with all combinations of values between ± 0.15 g and ± 0.40 g in incrementation of 0.05 g and determined which combination gave the best results. The threshold duo of ± 0.15 g and ± 0.30 g were thereby determined to be the best combination (see Figure 3.1).

Diving data and Hall events

Wiggles are defined as an increase in the depth, followed by a decrease and another increase, creating a bump in the profile (Schreer et al. 1996; Halsey et al. 2007). We used the method for king penguins described in Bost et al. (2007) to automatically detect wiggles in our data set, with a minimal threshold of 2 m in vertical deviation for depth deviations to be considered wiggles. We also calculated the proportion of the dive occurring in the bottom phase, which is an index of dive shape (Halsey et al. 2007). The bottom of the dive was defined as the dive portion occurring below 90% of the maximum depth (Bost et al. 2007).

Hall events from beak-opening sensors were classified as type A and B using Hanuise et al. (2010). Type A Hall events are very short beak opening of less than a second of duration and are associated with non-feeding beak opening (i.e., unsuccessful attempts). Type B are longer (> 1 s) beak opening events associated with prey capture and handling, as validated with esophageal temperature sensors (Hanuise et al. 2010). Only type B events were considered for analysis and will refer to the gold standard of a feeding event, i.e., successful feeding attempts.

Machine learning algorithm and linear models

Four neural networks were designed to evaluate the accuracy of accelerometry-derived data compared with depth-derived data to predict the number of prey capture per dive. All neural networks consisted of one layer and ten nodes, with Hall events used as gold standard. The first neural network (named “NN1”) used the two accelerometry variables (number of peaks above/below ± 0.15 g and ± 0.3 g per dive) as inputs. First, 65% of the data set (both birds combined) was used to train the algorithm. Then, the algorithm was tested on the remaining 35% of the data set. Because our sample size of different birds is small ($n = 2$), we also made a different

neural network with accelerometry data (NN2) which we trained on one bird and tested on the other, so that we could further assess inter-individual variability. The third and fourth neural networks (NN3 and NN4) used two of the most common depth-derived variables as predictors of prey captures: number of wiggles and dive-shape per dives. As with the accelerometer-derived variables, one model used 65% to predict the remaining 35% (NN3), while the other used one bird as training to predict the other (NN4). Package neuralnet was used to create neural network models (Günther and Fritsch 2010).

We made a fifth model, a linear model labelled “LM1”, which only used wiggles as predictors. The linear model using wiggles is, to our knowledge, the most widely used method in the literature to directly estimate prey capture in penguins (e.g., Bost et al. 2007; Zimmer et al. 2011; Hanuise et al. 2013; Scheffer et al. 2016; Tessier and Bost 2020). The linear model served as the “traditional” method and was directly compared with our neural network models using standardized metrics (see the next section).

Model validation and statistics

To test whether the “visual-interaction hypothesis” influenced the acceleration signatures, we compared acceleration peaks associated with prey captures below or near the euphotic limit (> 150 m) with those in shallower water (< 150 m). We used a Student’s t test to assess the difference in peak amplitudes (absolute value) and durations between those two groups.

To compare capture-rate prediction models, we calculated the Mean Square Error (hereafter “MSE”) of all five models. We also modeled the predicted outputs of the five models

over the observed values (Hall sensor data) using linear models and compared those outputs with the 1:1 regression. Finally, we calculated the R² of each regression to evaluate dispersion of the predictions (as done in Bost et al. 2007 and Hanuise et al. 2010). Direct comparison with two other studies using wiggles as predictors on king penguins were possible using the slope, origin and R² of the regressions of the predicted over observed values (Bost et al. 2007; Hanuise et al. 2010).

Results

The loggers recorded 206 dives deeper than 40 m. The bird labelled E1 recorded 127 dives over 8 days of foraging, while H1 recorded 79 dives over 8 days. Mean maximal dive depth was 113 ± 34 m (range: 40–219 m). The average number of Hall events B in a dive was 3.70 ± 6.92 (range: 0–46), while the average number of wiggles was 0.95 ± 1.23 (range: 0–7). Acceleration peaks associated with prey captures were on average 0.78 ± 0.31 g in maximum amplitude and 3.9 ± 3.5 s in total duration. There was no significant difference between the maximum intensity of peaks occurring below 150 m and those occurring above 150 m ($t_{176} = -0.33$, $p = 0.74$), but acceleration peaks occurring above 150 m were shorter in duration compared to deeper peaks (above: $3.8 \text{ s} \pm 3.4$, below: $4.8 \text{ s} \pm 4.2$, $t_{170} = -2.96$, $p = 0.004$).

Using the ± 0.3 g or the ± 0.15 g threshold, the number of accelerometry peaks in a dive was highly correlated with the number of Hall events-B (Figure 3.2). As expected, the number of peaks beyond ± 0.3 g slightly underestimated the number of Hall events, while the ± 0.15 g threshold slightly overestimated the number of Hall events.

Models with accelerometry-derived variables (NN1 and NN2) scored significantly better than those with depth-derived variables (NN3 and NN4) in all metrics (Table 3.1, Figure 3.3). For models NN2 and NN4, bird H1 was used as the training data set, as the number of dives performed was comparable to the sample size of the training data set for model NN1 and NN3 (127 dives for NN2/NN4, 132 for NN1/NN3). The two models which used accelerometry-derived data had similar accuracy ($\Delta 4.5$ in MSE, $\Delta 0.12$ in R²). In contrast, the difference between depth-derived

Model	Variable	Training dataset	Validation dataset	Slope	Intercept	R ²	Mean Square error	Graph
Neural Network 1	Accelerometry derived	65% of dataset (n = 132)	35% of dataset (n = 72)	0.88 ± 0.12	0.6 ± 0.8	0.79	8.6	Figure 3.2
Neural Network 2	Accelerometry derived	Bird E1 (n = 127 dives)	Bird H1 (n = 79 dives)	0.96 ± 0.15	1.0 ± 1.0	0.67	13.1	Figure 3.3a
Neural Network 3	Depth-derived	65% of dataset (n = 132)	35% of dataset (n = 72)	0.51 ± 0.11	1.8 ± 0.8	0.52	16.0	Figure 3.2b
Neural Network 4	Depth-derived	Bird E1 (n = 127 dives)	35% of dataset (n = 79 dives)	0.75 ± 0.24	3.6 ± 1.5	0.28	41.4	Figure 3.3b
Linear Model 1	Wiggle	Whole dataset	Whole dataset	This study: 0.32 ± 0.6 Bost et al. 2007 :0.45 Hanuise et al. 2010 : 0.8	This study: 2.5 ± 0.5 Bost et al. 2007 :1.77 Hanuise et al. 2010 : 1.82	This study: 0.32 Bost et al. 2007 :0.26 Hanuise et al. 2010 : 0.39	32.3	Figure 3.4

models NN3 and NN4 was much greater ($\Delta 25.4$ in MSE, $\Delta 0.24$ in R²).

Table 3.1: Model outputs predicting prey captures (Hall sensor data) using either acceleration-derived or depth-derived data

The traditional approach, with a linear model using only the number of wiggles as predictor, did poorly compared to most neural network models (MSE = 32.4, slope = 0.32 ± 0.06 , intercept = 2.5 ± 0.50 , $R^2 = 0.32$, see Figure 3.4). Nonetheless, the R^2 (0.32) was similar to other studies that used similar methods (Bost et al. 2007: 0.26, Hanuise et al. 2010: 0.39).

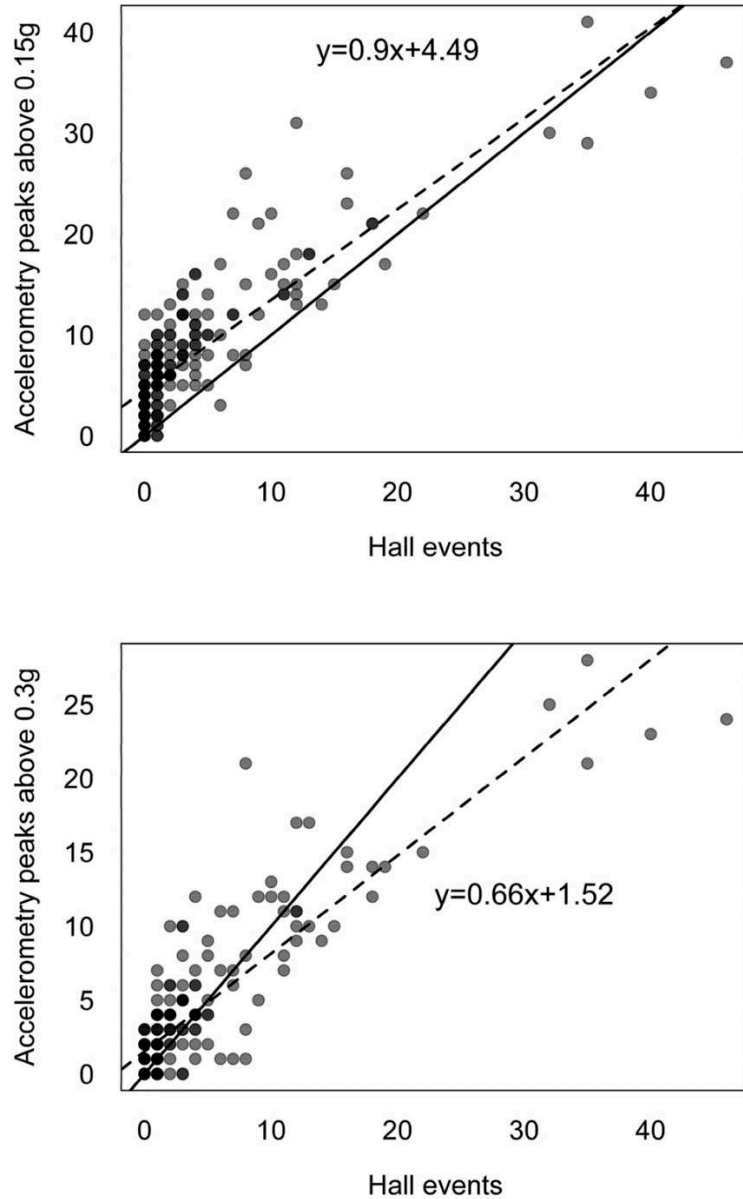


Figure 3.2: Number of acceleration peaks in a king penguin dive relative to the number of Hall events (dotted line) compared to the 1:1 line (solid line). The 0.15 g threshold (top panel) slightly

overestimates the number of captures, while the 0.3 g threshold (bottom panel) underestimates the number of captures over most of the regression. Darker data points show overlapping values.

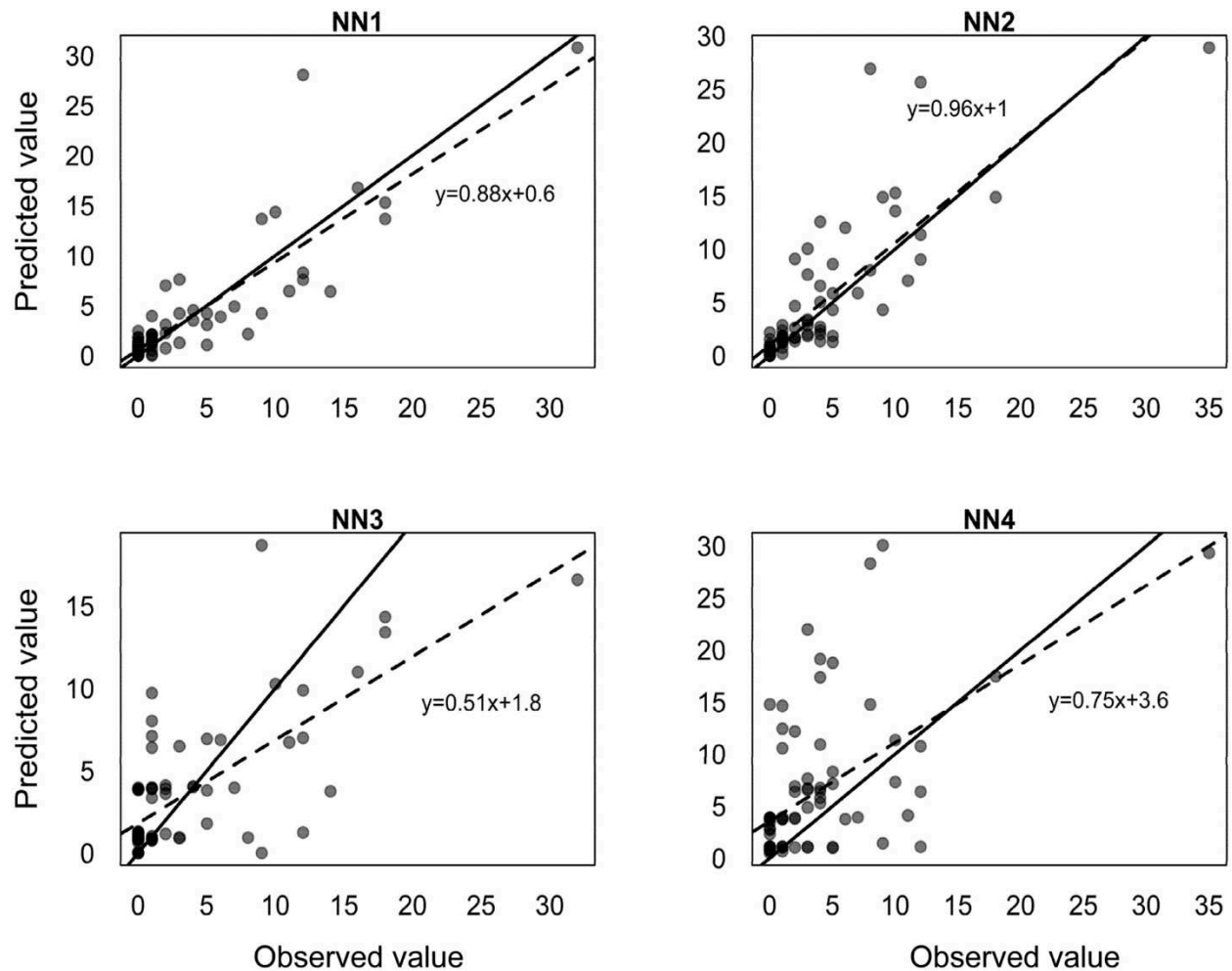


Figure 3.3: Predicted relative to observed prey-capture rates for king penguins from all four neural network models (dotted lines) compared to the 1:1 line (solid lines). Models NN1 and NN2 used accelerometry derived variables as predictors, while models NN3 and NN4 used depth-derived variables. Models NN1 and NN3 were trained and validated with data from both birds combined, while models NN2 and NN4 trained with one bird and validated with another. Darker data points show overlapping values.

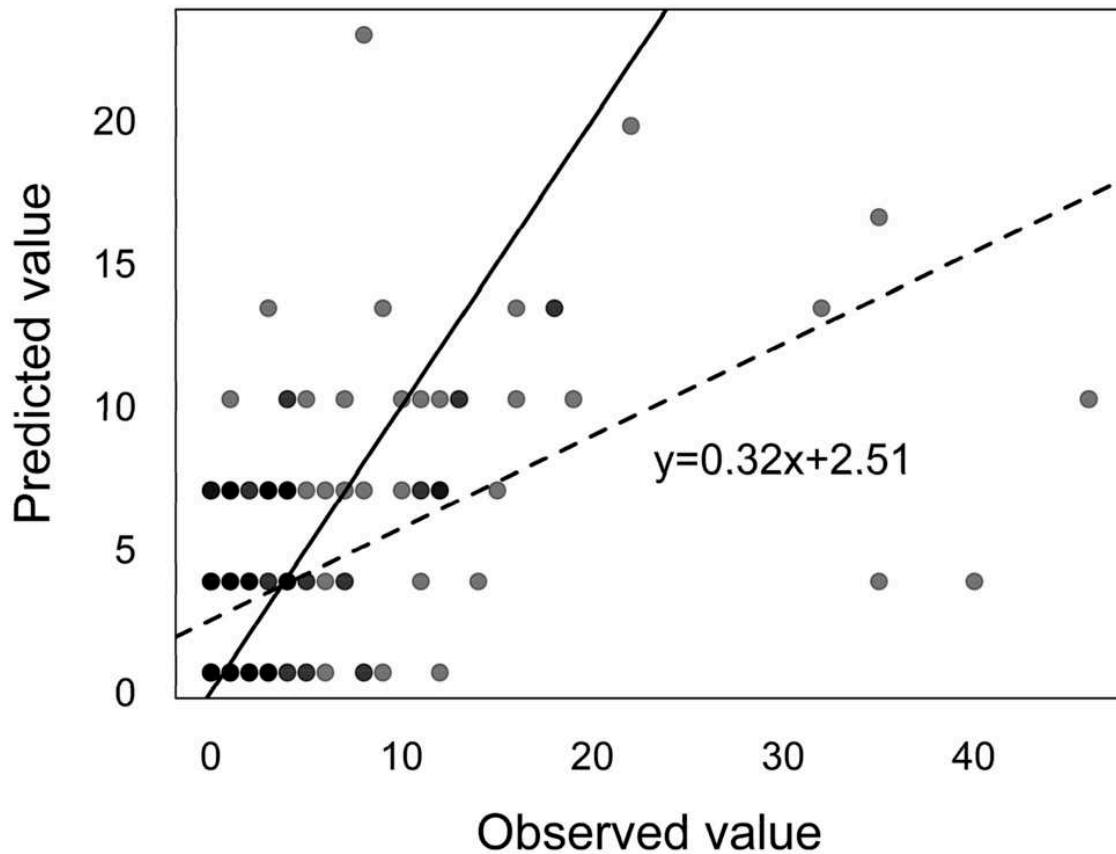


Figure 3.4: Predicted relative to observed prey-capture rates for king penguins (dotted line) compared to the 1:1 line (solid line) for the traditional linear model using the number of wiggles in a dive as the explanatory variable. Darker data points show overlapping values

Discussion

Prey captures at depth in the king penguin produced discernable acceleration signatures of considerable intensity and length. Furthermore, neural networks using acceleration inputs accurately predicted the number of prey-capture events in a dive. These results add to the growing number of studies showing the benefits of using accelerometry to predict prey capture (e.g., Gallon et al. 2013, Kokobun et al. 2011, Watanabe and Takahashi 2013, Watanabe et al. 2014, Sato et al. 2015, Volpov et al. 2015, Carroll et al. 2018, Yoshino et al. 2020, Adachi et al.

2021), and provides one of the first validations for deep-diving species. Our models were significantly more accurate than the previous studies using depth-derived variables on king penguins.

Acceleration signature of prey captures

The “visual-interaction hypothesis” stipulates that, at depth, the escape behavior of fish is less effective, as predator–prey detection occurs so close that evasion is futile (Childress et al. 1990; Drazen and Seibel 2007). This, combined with a lower water temperature at depth, leads fish such as myctophids to reduce their metabolism when in deeper, dark waters (Drazen and Seibel 2007; Catul et al. 2011). In contrast, fish well above the euphotic zone have high metabolism to accommodate a more explosive escape response. King penguins feed on mesopelagic myctophids near or below the euphotic zone and exclusively use vision to detect their prey (Martin 1999; Bost et al. 2002; Cherel et al. 2007). It was, therefore, expected that the acceleration needed to pursue and capture prey would not contrast well with the acceleration noise of regular underwater movements. This was not the case, as the filtered acceleration peaks associated with prey capture was discernable (0.78 g in average) and total pursuit and capture time lasted several seconds (3.9 s in average). This is comparable to similar-size seabirds diving closer to the surface: the surge acceleration of Magellanic penguins *Spheniscus magellanicus* when capturing schooling fish averaged 0.31–0.64 g in maximum amplitude, while the optimal tri-axial acceleration thresholds for detecting fish captures in Adelie penguins *Pygoscelis adeliae* were 0.25–0.45 g, similar to our 0.15 g and 0.30 g thresholds for surge acceleration (Watanabe and Takahashi 2013; Del caño et al. 2021). Both of these penguins feed on fish in shallow waters

above 50 m. Similarly, prey chase and capture in the little penguin *Eudyptula minor* averages 2.9 ± 3.3 s, which is quite similar to our results (Ropert-Coudert et al. 2006). Obviously, the prey-capture acceleration signature associated with different predator species depends on much more than solely the depths at which they forage. Predator and prey size, diving speed and foraging tactics are all factors that could influence the prey-capture signatures. Further study is needed to assess whether, with a larger species sample size, deeper species will tend to display fainter acceleration signatures compared to shallow-diving species.

Another unexpected result was the significant difference between the duration of prey captures occurring above and below 150 m, with shallower captures taking less time than deeper captures. The opposite result was anticipated by the visual-interaction hypothesis assuming that darkness reduces chasing initiation distance. However, king penguins may opportunistically feed on smaller fish larvae and/or plankton when diving in shallow water. These prey types, which are more abundant near the surface, might not require great acceleration to be captured. On the other hand, larger fish near the euphotic zone targeted by the penguin might be more mobile, especially considering that these fish initiate vertical migration at night. Even in poor light conditions, the prey might require considerable acceleration to be captured compared to fish larvae and plankton in shallow waters. Further study is needed to validate this idea.

Advantage of accelerometry data to estimate feeding activity

Accelerometers provide one of the most convenient and accurate methods to estimate prey capture (Watanabe & Takahashi 2013; Volpov et al. 2015; Del Caño et al. 2021). They are small and can be deployed with relative ease, while their low power consumption allows for

extensive data recording. However, validation of accelerometry requires a gold standard, which is often easier obtained using camera-loggers. Hence, most validations of accelerometry on wild animals have been conducted on shallow divers feeding in the euphotic zone (e.g., pygoscelid penguins: Watanabe et al. 2014, fur seals: Volpov et al. 2015, Del magellanic penguin: Caño et al. 2021).

While deep-divers feeding on mesopelagic fish are a crucial key to understand food-chain mechanisms in the open-ocean, the use of accelerometry to quantify foraging success is recent in these species (Watanabe et al. 2020; Yoshino et al. 2020; Adachi et al. 2021). Furthermore, true validation with a gold-standard is very rare: Watanabe et al. (2020) showed that the number of accelerometry peaks was highly correlated with the number of video-confirmed feeding events in a deep-diving pinniped. Yet again, the heavy camera-loggers used in their study would exceed 3% of body mass ethical guidelines to equip on deep-diving birds, such as *Uria* alcids and *Aptenodytes* penguins. For this reason, foraging activity and success on these species have been almost exclusively determined using depth-derived variables (Kirkwood and Robertson 1997; Zimmer et al. 2011; Hanuise et al. 2013; Scheffer et al. 2016; Orgeret et al. 2019; Tessier and Bost 2020). Accelerometry provides a more accurate alternative: our results show that accelerometry greatly outperforms wiggles in quantifying foraging success. Even foraging activity cannot be determined accurately with depth-derived variables, as many deep-dives—some even containing wiggles—were not associated with prey captures in our study (see Figure 3.4). Therefore, identification of foraging dives cannot be made reliably with depth-derived variables, such as wiggles. By combining a conservative acceleration threshold at ± 0.3 g with a more liberal one

at ± 0.15 g, we were able to obtain accurate machine-learning models for the king penguin that surpassed the wiggle method.

Limitations and next step

While neural networks are superior than linear models at making accurate predictions, they are usually more so with very large sample sizes and many input variables (Bonaccorso 2017). Our sample size was moderate in size and only two variables were used as inputs. Ideally, a larger sample size would likely increase the accuracy of the algorithm, fully taking advantage of the ML method. Data on more individuals is necessary for better testing of the inter-individual variability.

One limitation of our method is the pre-determination of the acceleration thresholds to identify acceleration peaks. These thresholds likely differ from one species to another. Repeating the experiment for each species would provide accurate estimates of prey-capture rate, but would be unrealistic considering the difficulty of obtaining gold standard data. Depth-derived variables also suffer from the same flaws and need species-specific validations; the minimum deviation for a change in the depth profile to be considered a wiggle is species-specific (Hasley et al. 2007). Nonetheless, these values are often easy to determine without validation by simply looking at trends in the depth-profile data (e.g., Zimmer et al. 2011; Crossin et al. 2012). The same logic can be used with accelerometry data without validation to speculate on which accelerometry signatures are associated with feeding events (e.g., Naito et al. 2010). Still, we encourage similar methods to be tested on more deep-diving species, avian or not, to assess variation among taxa.

Conclusion

Despite a small sample size, this study confirmed the potential of accelerometry as an input to neural network models to predict prey-capture rates in a deep-diving seabird, using Hall sensor data as validation. We concur with other studies on shallow-diving species that accelerometry outperforms depth-derived variables at detecting and quantifying prey capture, and provide one of the very few validation on a deep-diving animal.

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Linking statement

In Chapter 3, I developed a methodology to assess the foraging success of king penguins while at sea using accelerometers. This methodology will be used in two chapters: Chapter 7, where I will discuss the links between climate, foraging success and breeding success of king penguins during the chick-rearing period, and in the following chapter, Chapter 4. The latter chapter will look at the links between the foraging success of the king penguin and its diet. More specifically, I will try to understand whether king penguins adjust their diet whenever they encounter unfavorable conditions. This is crucial to predict whether future changes in the environment will affect the diet of the king penguin, its foraging behavior, or both. Understanding the flexibility (or inflexibility) of the king penguin regarding its diet and prey choice will also help interpret the results of the later chapters.



A myctophid, the king penguin's main prey

Chapter 4: King Penguins (*Aptenodytes patagonicus*) adjust foraging effort rather than diet when faced with poor foraging conditions

AUTHORS

Émile Brisson-Curadeau^{1,2}, Charles-André Bost¹, Yves Cherel¹, Kyle Elliott²

AFFILIATIONS

1 : Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, Villiers-en-Bois, France

2 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

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Abstract

The links between foraging success, foraging effort and diet in a myctophid specialist seabird, the King Penguin *Aptenodytes patagonicus*, were investigated during seven breeding seasons using tracking and isotopic data. Despite the variable foraging conditions encountered by the birds, isotopic signature (a proxy for diet) were invariable throughout the study. On the other hand, penguins stayed longer at sea when the foraging success indices (i.e. prey capture attempts per day and mass gained per day) were low. While King Penguins can compensate for low prey capture rates by increasing foraging effort, their specialist diet during reproduction makes the species particularly sensitive to prey availability, with its conservation tightly linked to its main prey.

Introduction

There are multiple strategies available to birds to cope with periods of low prey availability. For example, dietary-specialist species can increase foraging effort to compensate for low prey capture rates (e.g. Abrams 1991, Cox et al. 2019, Fromant et al. 2021). Alternatively, generalists can switch to feeding on other still-available prey (e.g. Scopel et al. 2019, Milchev & Georgiev 2020). The strategy chosen is highly species-dependent, with both specialist and generalist displaying variable flexibility in both foraging effort and diet.

In the marine environment, species composition is changing drastically, as environmental disturbances such as overfishing or recurrent marine heat waves might induce periods of low prey availability (Jones et al. 2018, Osborne et al 2020, Sydeman et al 2021). While generalist species that switch prey will likely better tolerate these ecosystemic changes, specialists might be impacted as the foraging effort increases to compensate for poor conditions (Gilman et al. 2010). Such is the case for species including the Little Auk *Alle alle* or the African Penguin *Spheniscus demersus*, two specialist species that increased time spent foraging in response to reduced availability of their main prey (Jakubas et al. 2007, Pichegru et al. 2012). Yet, even species regarded as specialists can sometimes shift their diet in critical periods, so that a certain level of flexibility might help these species cope with a changing environment (e.g. Ludynia et al. 2010, Ancona et al. 2012).

Here, we investigate the links between foraging success, foraging effort, and diet in a specialist deep-diving seabird, the King Penguin *Aptenodytes patagonicus*. This species feeds mainly on small mesopelagic myctophids, often dominated by *Krefflichthys anderssoni*, for which the

availability to the top predators may change across the polar region, mainly due to climatic anomalies (Bost et al. 2002, 2015, Le Bohec et al. 2008, Péron et al. 2012). Yet, King Penguins can also forage opportunistically on other prey such as squids and other myctophids (Adams & Klages 1997, Bost et al. 2002, Cherel et al. 2007). Consequently, the species could theoretically diversify its diet in periods of low prey availability.

We test whether King Penguins would become more opportunistic when foraging success is low by comparing isotopic values (a proxy of diet) of foraging breeding adults over seven years. We predicted that, if King Penguins compensated for low prey availability by switching diet, we would find different isotopic values in individuals experiencing dissimilar foraging success. On the other hand, if King Penguins did not seek different prey despite low prey availability, we expected a compensating increased foraging effort (e.g. longer foraging trips, deeper dives) as foraging success decreases, while isotopic values would remain constant.

Methods

All data were collected in February on chick-rearing King Penguins at Ratmanoff's colony (around 85 000 pairs, Barbraud et al. 2020) in the Kerguelen archipelago ($-49^{\circ} 14' 33''$, $70^{\circ} 33' 40''$) situated in the southern Indian Ocean. Data were obtained during the chick-rearing period in all years from 2015 to 2022 except 2019 (i.e. seven years total). The ethics committee of the Institut polaire français Paul-Émile Victor approved all field procedures.

King Penguins of this colony feed mostly on a small myctophid, *Krefflichthys anderssoni*, and opportunistically (up to 25% of their diet) on other prey such as other fish species and squids (Bost et al. 2002, Cherel et al. 2010, Cherel et al. 2011). During the chick-rearing period, parents make trips at sea lasting about 4 to 10 days. While prey availability estimates are not known during the study period, the years 2015 and 2016 were possibly less favorable for King Penguins at Kerguelen, as inferred from the lower chick mass observed (Brisson-Curadeau et al. 2023).

Isotopic analysis

Stable isotopes of nitrogen ($\delta^{15}\text{N}$) are considered to be indicative to the trophic position of consumers, thus reflecting its diet, while $\delta^{13}\text{C}$ is a proxy of the consumers' foraging habitat (Hobson et al. 1994, Quillfeldt et al. 2005, Cherel & Hobson 2007). The resulting isotopic niche described by these two isotopes can be thus used as a proxy of the consumers' trophic niche.

Between 2015 and 2022, a total of 83 chick-rearing King Penguins were captured using a long poles and blood sampled (2 ml) after their return from a foraging trip. The blood was freeze-dried and about 0.7mg was weighed into tin capsules. The capsules were analysed for bulk stable isotopes ratio of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) at the Ján Veizer Stable Isotope Laboratory (Ottawa, Ontario, Canada). Isotopic composition was measured by combustion on an Elementar VarioEL Cube Elemental Analyser followed by "trap and purge" separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope ratio mass spectrometer coupled with a ConFlo III interface. The isotope concentration determination used the following conventional equation:

$$\delta = ([R_{\text{sample}}/R_{\text{standard}}]-1) * 1000$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotope in the sample and standard, respectively. The standards used were air for nitrogen, and Pee Dee Belemnite for carbon. Replicate measurements of internal laboratory standards indicate measurement errors of 0.35‰ and <0.1‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

All alternate prey types of King Penguins have a higher $\delta^{15}\text{N}$ value than *K. anderssoni* (Bost et al. 2002, Cherel et al. 2010). We therefore expected individuals with a more diverse diet to have a higher $\delta^{15}\text{N}$ value. The full list of potential prey and their respective $\delta^{15}\text{N}$ value around Kerguelen can be found in Table S4.1.

Foraging effort

Foraging effort during the foraging trip was determined using biologgers from various brands recording GPS location and/or depth. Some of these loggers also recorded 3D acceleration (starting in 2020) as well as water temperature. Over the seven years, 52 birds were equipped with one or two of these devices (see Table S4.2-S4.3 for exact sample size by year). Loggers were retrieved after a single foraging trip. King Penguins were weighed before and after each foraging trip. The weight of the loggers varied with models, but never exceeded 2% of the bird's mass.

For analysis, only dives >50m were considered, as shallower dives are not associated with foraging activity (Charrassin et al. 2002). Depth was used to compute two foraging effort metrics for each individual: mean diving depth and total vertical distance travelled during a foraging trip, calculated as the sum of the maximum depths of all dives (Charrassin et al. 2002). Using location

data, we computed the mean distance to the colony of all foraging dives, as well as the mean latitude and longitude for correlation with isotopic variables. A final metric of foraging effort was calculated as the total number of days spent at sea during the foraging trip.

Due to logistical reasons, not all blood sampled King Penguins were assessed for foraging effort. Reasons explaining this mismatch include logger failures and logger detachment.

Conditions encountered and foraging success

King Penguins target the depth just below the thermocline to capture prey (Charrassin & Bost 2001, Scheffer et al. 2016). Consequently, shallower thermoclines are more accessible and therefore provide better conditions for foraging King Penguins. To assess the conditions encountered, we therefore combined depth data and temperature data to calculate the depth of the thermocline for each dive. We defined the thermocline as the depth where the change in temperature was the greatest (see Charrassin & Bost 2001). We then calculated the average thermocline depth among all dives for each individual.

We computed two metrics of foraging success. First, we calculated the mass gained per day of foraging at sea. A second metric was computed using the accelerometry data: the number of Prey Capture Attempts (PCAs) in each dive was estimated with the algorithm from Brisson-Curadeau et al. (2021) using the number of acceleration peaks in the dive. The number of PCAs per day has been shown to closely correlate with the number of daily prey captured and so we used this to indicate foraging success.

Statistics

We tested how blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were influenced by the following variables: mean diving depth, total vertical distance travelled, mean thermocline depth, mean distance from the colony, mean latitude, mean longitude, trip duration, mass gained per day and PCAs per day. We also tested the influence of the foraging effort variables (mean diving depth, total vertical distance travelled, trip duration, mean distance from colony) on the two foraging success metrics. All these tests were conducted by creating several linear models with mixed effects, each with one of these variables and “year” as a random effect. Only one fixed effect was used per model to avoid overfitting and correlation between explanatory variables.

Because most of these variables had a different number of observations, and because models with different number of observations are not directly comparable, we created a corresponding null model (with only the random effect) for each model using only the observations available. We then scored the models using the Akaike Information Criterion (AIC) and compared the score with its associated null model. Only models that had a $\Delta\text{AIC} > 2$ with their corresponding null model were considered.

We also tested if there were differences among years for all variables (isotopes, foraging effort, and foraging success) using ANOVAs. In such a case, we used Tukey’s tests to identify the pairs of years that differed.

All analysis were conducted in R version 4.1 (R Core Team 2023). Package lme4 was used to build the mixed-effect models (Bates et al. 2015). Validation of assumptions were conducted on all models (see also table S4.4). We tested for heteroskedasticity of residuals using the Breusch Pagan test in the lmtest package (Breusch 1978, Zeileis & Horton 2002). Pearson correlation tests were conducted between residuals and the independent variables, while the autocorrelation in the residuals was assessed by extracting the autocorrelation coefficient (Venables & Ripley 2002).

Results

Foraging behaviour

Most foraging effort indices varied greatly among individuals (Figure 4.1), as shown by the standard deviation (σ) and mean (μ) of total vertical distance travelled ($\mu = 123$ km, $\sigma = 62$ km, $n = 48$), trip duration ($\mu = 8.5$ days, $\sigma = 3.1$ days, $n = 53$) and mean distance from the colony ($\mu = 251$ km, $\sigma = 102$ km, $n = 36$). To a lesser degree, mean diving depth also differed among individuals ($\mu = 141$ m, $\sigma = 16$ m, $n = 48$). Two foraging success variables, mass gained per day ($\mu = 0.28$ kg/day, $\sigma = 0.15$ kg/day, $n = 31$) and PCAs per day ($\mu = 406$ PCAs/day, $\sigma = 185$ PCAs/day, $n = 52$) also varied greatly from one individual to another. When testing for among-year differences, only mean depth, trip duration and total vertical distance showed significance (Figure 4.1, Table S4.5).

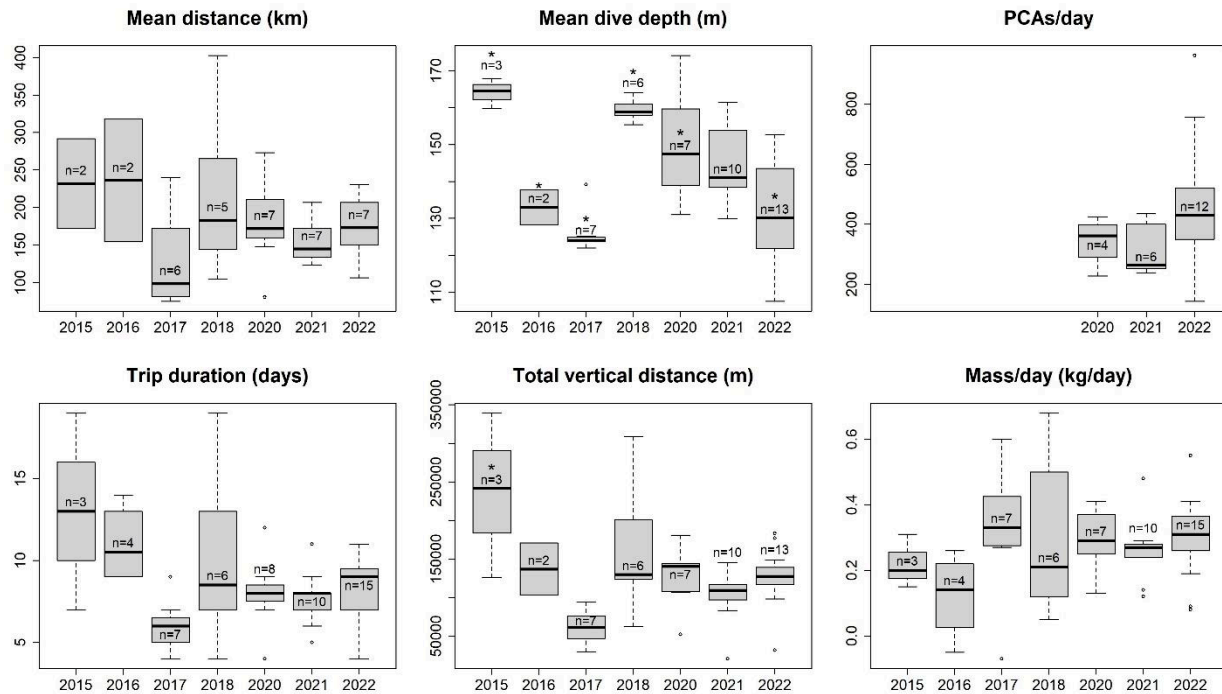


Figure 4.1: Annual variation of foraging effort variables (middle and left graphs) as well as foraging success variables (right graphs) among sampled King Penguins breeding at Kerguelen Island. Numbers in the boxes indicate the number of King Penguins sampled. Stars indicate years that were significantly different from at least two other years when conducting Tukey's tests. The black lines represent the median.

Stable isotopes

Blood $\delta^{13}\text{C}$ ($-22.0 \pm 0.4\text{‰}$, $n = 83$) varied with mean longitude, as the model containing this variable was the only model which scored higher than its associated null model (Table 4.1). There was a strong tendency for $\delta^{13}\text{C}$ to decrease as King Penguins foraged farther east, off the Kerguelen shelf (Figure 4.2). Furthermore, $\delta^{13}\text{C}$ varied significantly among years as shown by ANOVA analysis (Figure 4.3, Table S4.5).

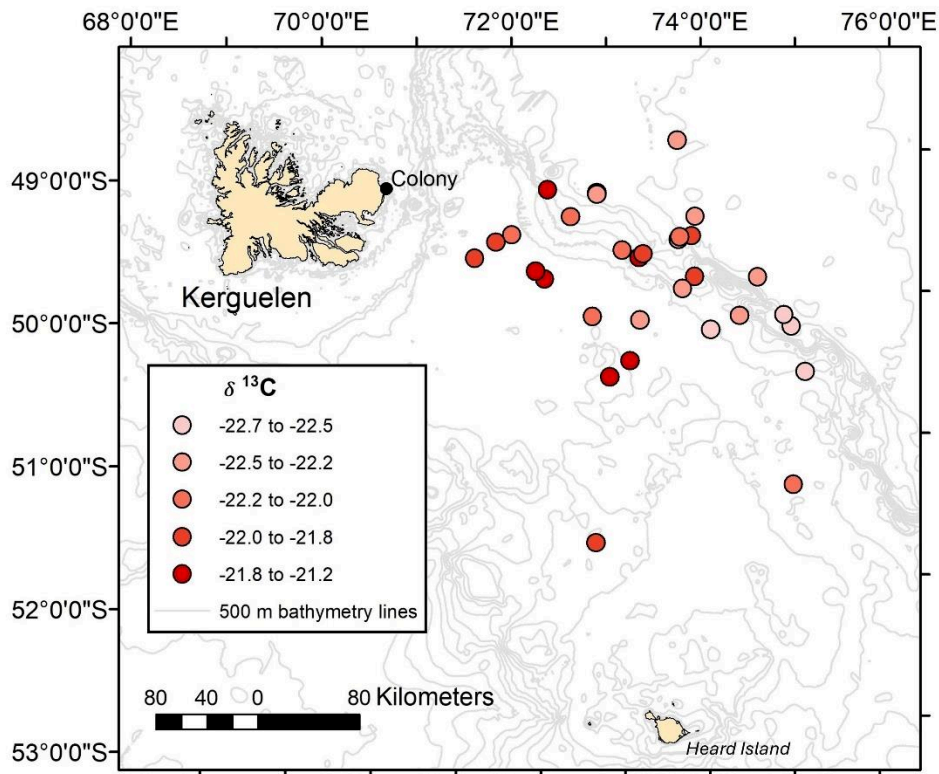


Figure 4.2: Mean diving position of foraging King Penguins during breeding. Each point represents a King Penguin's trip. Colors represent blood $\delta^{13}\text{C}$ of the King Penguin at the end of the foraging trip, after returning to the colony. Notice the strong East-West gradient, with blood $\delta^{13}\text{C}$ values decreasing when King Penguins forage farther off the island's shelf.

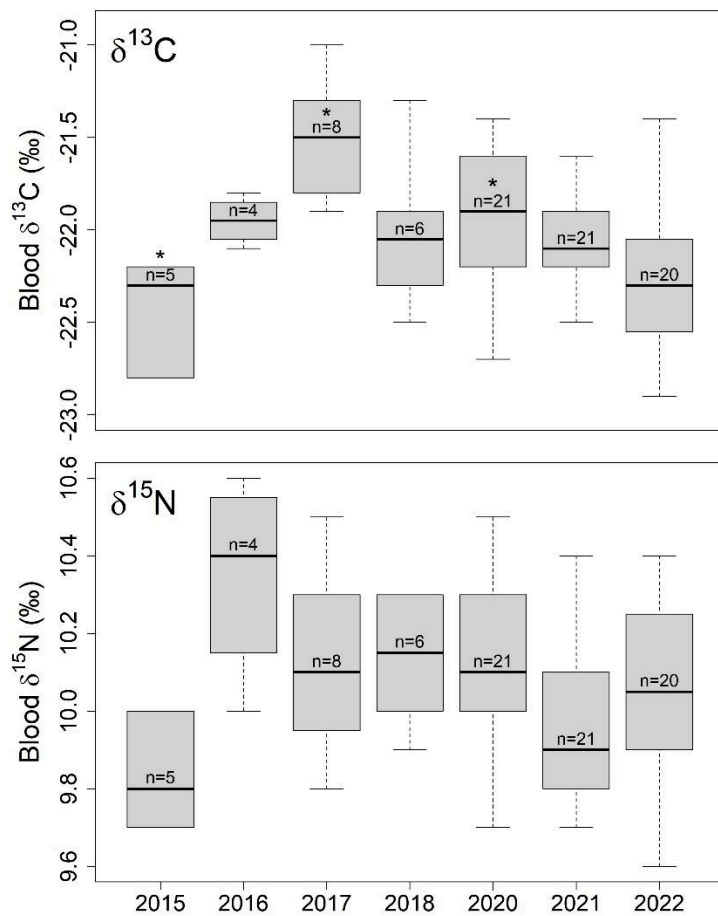


Figure 4.3: Annual variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for blood samples among King Penguins breeding at Kerguelen Island. Numbers in the boxes indicate the number of King Penguins sampled. Stars indicate years which were significantly different than at least two other years when conducting Tukey's tests. The black lines represent the median.

Similarly, blood $\delta^{15}\text{N}$ (10.1 ± 0.2 ‰, $n = 83$) varied among years (Figure 4.3, Table S4.5). However, the inter-year variation in $\delta^{15}\text{N}$ was less pronounced than with $\delta^{13}\text{C}$ and only two years (2016 and 2021) were significantly different from each other according to the Tukey's tests ($P = 0.02$).

Overall, there was little variation in $\delta^{15}\text{N}$ among individuals ($\delta^{15}\text{N}$ range: 9.6 – 10.6 ‰). As for the models predicting $\delta^{15}\text{N}$ using foraging effort and success variables, none scored higher than their corresponding null model, despite high variability detected in all these explanatory variables (Table 4.1).

Table 4.1: Best ranked models explaining $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, mass gained per day and PCAs per day

Best ranked models	Number of observations in the models	AIC	ΔAICc with null model	equation
Blood $\delta^{13}\text{C}$ as the response variable				
$\delta^{13}\text{C} \sim$ Mean longitude of foraging dives (°)	n = 34	31.5	$\Delta -8.06$	$-0.33x + 2.61$
Blood $\delta^{15}\text{N}$ as the response variable				
No models outranked the null model	-	-	-	-
Mass gained per day of foraging (kg/day) as the response variable				
Mass \sim Foraging trip duration (days)	n = 51	-55.5	$\Delta -8.39$	$-0.02x + 0.50$
PCAs per day as the response variable				
PCA \sim Foraging trip duration (days)	n = 28	294.2	$\Delta -2.54$	$-7.72x + 419.6$

Foraging success

When considering mass gained per day as a response variable, only the model with foraging trip duration as a fixed effect scored better than its respective null model. Similarly, when values of PCAs per day were considered as the response within models, the only model that scored better

than its respective null counterpart was the one containing the fixed effect of foraging trip duration (Table 4.1). In both models, the response variable decreased with increasing foraging trip duration.

Discussion

Seabird species include taxa labelled as both diet generalists and specialists. Yet, almost all seabird species can display a certain level of flexibility, as even specialist species can feed opportunistically on prey outside of their main diet (e.g. Ancona et al. 2012). This flexibility might be of particular utility when certain prey types become temporarily scarce. Yet, we found that the King Penguin, a myctophid specialist, does not greatly vary its diet in terms of trophic position ($\delta^{15}\text{N}$), even when encountering highly variable foraging conditions. Instead, the species relies more on increasing foraging effort to compensate for low prey capture rates. Our research emphasizes the tight link existing between some marine predators and their prey, with the conservation of the former being strongly dependent on the latter.

Isotopic landscape

A first observation that can be made from our results is that there is a strong longitudinal gradient of $\delta^{13}\text{C}$ in the environment near Kerguelen. In the Southern Ocean, most reported gradients for this isotope are usually latitudinal, not longitudinal (Cherel & Hobson 2007, Espinasse et al. 2019). However, the North-South gradient is evident at a larger scale, while at a smaller scale $\delta^{13}\text{C}$ is





influenced by habitat, with ^{13}C depleted in offshore habitats relative to coastal habitats (Cherel & Hobson 2007). As the Kerguelen Plateau extends south of the island to Heard Island (Figure 4.2), King Penguins foraging south will remain in the same shelf habitat. On the other hand, King Penguins foraging east will quickly encounter deeper bathymetry, likely explaining the gradient in $\delta^{13}\text{C}$ as habitat changes with longitude.

Diet specialisation

The use of $\delta^{15}\text{N}$ as a proxy of diet has been controversial when used at a large scale, as spatial gradients of the isotope exist regardless of trophic position due to variation in baseline $\delta^{15}\text{N}$ (Seminoff et al. 2012). However, we did not detect spatial gradients influencing $\delta^{15}\text{N}$ at a local scale near Kerguelen. It is therefore a fair assumption that $\delta^{15}\text{N}$ could be used in this study to assess trophic position of King Penguins, as in similar studies conducted in the Southern Ocean (Cherel & Hobson 2007, Cherel et al. 2010, Polito et al. 2015). Consequently, we expected $\delta^{15}\text{N}$ to vary with foraging success in our study. Indeed, low food availability sometimes causes even specialist species to become more opportunistic in their diet (e.g. Ancona et al. 2012, Buren et al. 2012). As all alternative prey of King Penguins on Kerguelen islands have a higher $\delta^{15}\text{N}$ value than their main prey *Krefftichthys anderssoni*, we expected $\delta^{15}\text{N}$ value of King Penguin to be higher in low foraging success individuals (Bost et al. 2002, Cherel et al. 2010). Items sometimes consumed by King Penguins at Kerguelen that have a higher $\delta^{15}\text{N}$ value include the squid *Gonatus antarcticus* and almost all alternate myctophids prey (see Table S4.1). Yet, blood $\delta^{15}\text{N}$ value of foraging King Penguins did not increase (or decrease) significantly with the substantially different foraging

effort, foraging success and marine conditions encountered by the King Penguins. In fact, the $\delta^{15}\text{N}$ range of Kerguelen’s King Penguins was very narrow across individuals and across years - even when compared to other seabirds regarded as specialists - suggesting little variation in the diet (see Table 4.2). However, the use of $\delta^{15}\text{N}$ to estimate diet composition does have limitations, as more subtle prey switch could go undetected in the isotopic signature. Indeed, while all alternate prey have higher $\delta^{15}\text{N}$ values than the main prey, some have relatively close values (Table S4.1), so that some degree of dietary switch might remain unnoticed using the isotopic method.

Table 4.2: Comparison of among-year and among-individuals variations in $\delta^{15}\text{N}$ between the king penguin at Kerguelen and three other specialist seabird populations (chinstrap penguin, Peruvian booby and guanay cormorant). King penguins showed the least variation from year to year, and an average variation between individuals in a given year.

	 King Penguin (Kerguelen Island) This study	 Chinstrap Penguin (Livingston Island) Polito et al. 2015	 Peruvian Booby (Peru) Renedo et al. 2021	 Guanay Cormorant (Peru) Renedo et al. 2021
<i>Total individuals sampled</i>	n = 83	n = 110	n = 116	n = 122
<i>Number of years sampled</i>	n = 7	n = 5	n = 7	n = 6
Maximum difference between $\delta^{15}\text{N}$ yearly means	$\Delta 0.45\text{‰}$	$\Delta 0.7\text{‰}$	$\Delta 2.65\text{‰}$	$\Delta 2.55\text{‰}$
Maximum $\delta^{15}\text{N}$ yearly standard deviation	$\pm 0.26\text{‰}$	$\pm 0.3\text{‰}$	$\pm 0.23\text{‰}$	$\pm 0.19\text{‰}$

We confirmed that King Penguins are very restrictive in their foraging strategy and targeted prey. Whatever the oceanic area used, they likely seek myctophid schools near frontal currents and have little flexibility in their foraging tactics (Bost et al. 2009). During the breeding season, marginal prey items such as squid might only be opportunistically captured by the King Penguins when preying on mesopelagic schools of *K. anderssoni*, rather than being the result of a switch in strategy as in some generalist seabirds (e.g. Brisson-Curadeau et al. 2019). Consequently, unsuccessful individuals prolonged their stay at sea to compensate for low prey availability rather than changing their foraging strategy and diet. Indeed, both foraging success indices were negatively correlated to trip duration, suggesting that individuals encountering few prey stayed longer at sea.

In conclusion, our study shows an example of a strict specialists that seldom adjusts its diet despite the different conditions encountered, but rather stayed at sea for a longer period to compensate for lower foraging success. We highly suspect population parameters of such species to be tightly linked to the availability of its main prey. Indeed, foraging effort cannot increase indefinitely to compensate for low prey availability, meaning strict specialists might face breeding failures and/or at-sea mortality if prey composition started shifting in the future, especially in the growing context of climatic changes (e.g. Cury et al. 2011). Ongoing population monitoring efforts are particularly valuable for specialist species, as population trends might be particularly sensitive

to climate change. Long-term prey surveys are also important to detect such shifts and predict future bottom-up effects affecting seabirds.

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Linking statement

Like Chapter 4, Chapter 5 looks at more basic yet less studied aspects of the biology and life history of king penguins that will later come in two plays in the following Chapters. Here, I will present new data on the wintering location of both Crozet and Kerguelen populations, and compare both distributions. It is noteworthy that wintering location of the Kerguelen was largely unknown prior to the study. The results of this chapter will serve as reference for the following chapter, which will look, inter alia, at the at-sea conditions of king penguins.



King penguins spend the winter at sea, where they are difficult to observe.

Chapter 5: Wintering distribution of two king penguin populations of the Southern Indian Ocean

AUTHORS

Émile Brisson-Curadeau^{1,2}, Alexandra Nalivaev³, Francesco d'Ovidio³, Karine Delord², , Kyle Elliott¹,
Charles-André Bost²

AFFILIATIONS

1 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

2 : UMR 7372-CNRS, Centre d'Études Biologiques de Chizé, La Rochelle University, Villiers-en-Bois, France

3 : Laboratoire d'Océanographie et du Climat : Expérimentations et Approches Numériques (LOCEAN),
UMR 7159 de Sorbonne Université, Paris, France

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Abstract

The king penguin (*Aptenodytes patagonicus*) is a top predator of the Southern Ocean which has been heavily studied for its key importance in the ecosystem. While there is extensive movement-ecology research focusing on the summer period, when chick-provisioning first occurs, little information is available for the winter period, when breeding adults leave the colony for months before returning to resume chick-provisioning. Here, we equipped with tracking devices 13 individuals from two neighboring populations, the Kerguelen Archipelago and the Crozet Archipelago, and used remote sensing data to better understand wintering water selection. We found that both populations head in significantly different directions, i.e. east for Kerguelen and south for Crozet. At Kerguelen, phytoplankton blooms originating from the rich waters around the islands were pushed east by the circumpolar currents, creating a seemingly prolific environment for king penguins in the winter. At Crozet, the bathymetry and marine flux dynamic are not favorable for such phytoplankton blooms and king penguins rather head south to feed near the ice limit, likely to benefit from the shallower thermocline. Our results highlight two different strategies from two neighboring populations, constrained by the geobiological conditions surrounding their breeding sites.

Introduction

Assessing the habitat and distribution of a species is often one of the first steps for establishing conservation plans (Crossman et al. 2012, Gauthier et al. 2013). For species that are easily observed, this can be done without extensive resources. However, some species are either very cryptic, or use remote habitat, such that direct observation alone cannot be used to assess the distribution and movement patterns (e.g. Roper & Boss 1982).

Seabirds are among these species that are often difficult to observe, as at-sea surveys are very costly to conduct. Diving-specialists are further challenging to detect, as they spend an extensive amount of time underwater, only separated by resting periods on the water where the bird is often concealed between the waves. Yet, understanding the distribution and movement of diving seabirds is crucial for many implications such as the implementation of no-fishing zones (Pichegru et al. 2012), the predictions of future habitat use with climate change (Péron et al. 2012), or the assessment of contamination hotspots for seabirds (Fort et al. 2014). Fortunately, the advancement of biologging and tracking technologies in the past decades, as well as their increased accessibility for researchers, have provided an easy solution to assess movement in seabirds and facilitate such implications (Yoda 2019).

The king penguin (*Aptenodytes patagonicus*) is a diving-specialist of the Southern Ocean. During the breeding season, it is strongly associated with the Polar Front, where it feeds on small myctophids (Scheffer et al. 2016). As a circumpolar top predator, it is often used to assess the lower trophic levels of the sub-Antarctic waters (Bost et al. 2002, Proud et al. 2021, Brisson-Curadeau et al. 2023a). While its distribution during the summer has been extensively studied

(e.g. Trathan et al. 2008, Scheffer et al. 2016, Brisson-Curadeau et al. 2023b), only a few studies have looked at its wintering movements, which occur entirely at sea (Charrassin et Bost 2001, Bost et al. 2004, Pistorius et al. 2017). Part of the challenge for equipping birds in winter is retrieving the biologgers – usually glued to the feathers – as some adults molt immediately after they return to land (Weimerskirch et al. 1992). Yet, understanding of the wintering distribution of king penguins is important, as this period might have an impact on the breeding success in the following seasons (Brisson-Curadeau et al. 2023c).

Using two different types of biologging technologies, we provide the wintering distribution for two of the largest king penguin colonies: the Crozet Archipelago, where wintering data of breeding king penguin is scarce (Charrassin et Bost 2001, Bost et al. 2004), and the Kerguelen Archipelago, where wintering data is inexistant. We then describe the biogeographic characteristics of the wintering waters using available remote sensing data. Our aim is to help identify wintering zones in the king penguin, as well as understanding the major oceanographic features driving the species' choice of wintering water.

Methods

Study site

The study took place in two king penguin colonies located in two neighboring islands of the southern Indian Ocean. The first colony, called La Manchotière (46°25'S, 51°51'E) is located on the Crozet Archipelago and hosts around 24 000 breeding pairs (Barbraud et al. 2020). The second colony, called Ratmanoff (49°14' S, 70°33' E), is located in the Kerguelen Archipelago and hosts around 87 000 breeding pairs (Barbraud et al. 2020). Together, Crozet and Kerguelen host among

the largest king penguin population in the world and contain over 45% of the total population (Bost et al. 2013, Barbraud et al. 2020).

Biologging equipment

Biologging equipment took place during the wintering seasons of 2021 and 2022, at Crozet and Kerguelen respectively. King penguins provision their chick frequently in the austral summer (February – April) but leave their chick at the colony in the winter (May – August) and spend most of their time foraging at sea, returning only occasionally – if at all – to feed their chick (Saraux et al. 2012). Chick provisioning resumes in spring (September) and fledging occurs in November. We thus equipped adults in April, before their winter departure, and retrieved the loggers in spring, when they returned to the colony.

Penguins were captured using a pole and equipped by gluing the biologger to the back feathers using Loctite glue. Two types of loggers were used in the study. The first type was SPLASH-283 tags (99g) from Wildlife Computer (Redmond, USA). These tags transmit data daily via the ARGOS satellite network, and penguins do not need to be recaptured for the retrieval of the data. Eight penguins were equipped with these loggers at Crozet, four at Kerguelen. The second type of logger was Intigeo C330 light-recorder from Migrate Technology Ltd (Cambridge, UK). These loggers are GLS units that collect light intensity data every 60s and maximum light value every 5 min period, which can in turn be transformed into location data (see next section). These tags need to be retrieved for the download of the data. Yet, penguins can go undetected when they return to the colony in spring, even when feeding their chick, and can molt their feathers on land before we retrieve the biologgers. To avoid losing the logger during molting, we glued these tags

with V2G 154C VHF tags (42g) from Lotek (Havelock North, New Zealand) that emitted radio frequencies detectable with VHF antennas. This system not only increased the likelihood of detections of adults when returning to the colony, but also greatly facilitated the search for loggers that fell on the ground during molting. Fifteen penguins were equipped with these GLS/VHF loggers, all at Kerguelen.

Data processing

Only datapoints from June and July were retained in the analysis, as May and August typically include long inward/outward trips to the colony.

For GLS data, thresholds in the light curves were used to determine sunrise and sunset. An internal clock in GLS enabled estimation of latitude based on day length and longitude based on the timing of local mid-day with respect to Universal Time (Afanasyev 2004). GLS light data were analyzed using IntiProc v1.03 (Migrate Technology 2015), which uses the threshold method and BASTrak software (Locator, British Antarctic Survey 2009) to estimate two positions per day, with an average accuracy of ~200 km (Phillips et al. 2004).

Physical and biogeochemical variables

Averages of Sea ice and SST over the two winters were extracted E.U. Copernicus Marine Environment Monitoring Service (CMEMS) at a 0.083° resolution (<https://doi.org/10.48670/moi-00016>). The position of the Polar Front was extracted from Pauthenet et al. 2018.

No data exist on prey abundance in the Southern Ocean for the winter 2021 and 2022. To indirectly assess prey abundance, we instead used an index based on remote sensing data of

chlorophyll, a proxy of phytoplankton production. In the Southern Ocean, most of the low-trophic-level biomass relies on phytoplankton blooms occurring in spring (Sullivan et al. 1993, Rohr et al. 2017). Using the Numerical Lagrangian methods (Griffa et al 2012), a backward-in-time advection experiment was computed to estimate where waters sustaining the spring phytoplankton blooms would be located during the following winter of interest. The Lagrangian perspective consists in using current velocity fields to extrapolate the position of a drifting object that doesn't have a significant inherent motion (Lehahn et al 2018), here phytoplankton and by extension zooplankton. We calculated a “bloom index”, where the index value of a parcel at time t (here winter) is defined as the chlorophyll concentration where the water of the parcel was located at time $t-1$ (here spring).

Monthly surface chlorophyll concentration during the spring bloom period (November to January) was extracted from CMEMS at 16 km² resolution (<https://doi.org/10.48670/moi-00283>) to calculate the bloom index. The position shift of the water from spring to winter was computed using a Lagrangian Manifolds and Trajectories Analysis (LAMTA - Rousselet et al 2024 in prep). Surface geostrophic velocity fields data at 0.25° resolution from CMEMS (<https://doi.org/10.48670/moi-00145>) was used to model water particle movement in the LAMTA.

Analysis

The kernels for the winter foraging locations of both colonies were calculated using a 90% quartic kernel function (Silverman, 2018). The differences in latitude and SST between the zones targeted by the two colonies were assessed using mixed effect models, with colony as the fixed effect,

individual as the random effect, and the two environmental variables successively as the response variable.

To test whether penguins from each colony would target zones of higher bloom index, we built a pseudo-absence model and compared the bloom index between the king penguin locations (presence) and random points outside the foraging range (pseudo-absence). These points were taken within the available habitat, defined as the ice-free area within the maximum foraging distance and south of the 45° latitude line, i.e. approximate location of the sub-Antarctic front (Kostianoy et al. 2004) and theoretical northern limit of the king penguin range. The comparison was used by building a binomial Generalized Linear Model, with presence/pseudo-absence as the response variable and the bloom index as the explanatory variable.

The position of the kernels relative to the Polar Front and the sea ice limit was assessed visually. All analyses were conducted in R (R Core Team, 2021). Maps were created using ArcGIS Pro 3.1 (Environmental Systems Research Institute 2010).

Results

Three of the twelve ARGOS tags stopped emitting data before June and therefore couldn't be used for analysis. Of the fifteen GLS deployed, only four were retrieved the next spring. The total sample size was thus of seven birds at Crozet (all with ARGOS tags) and six at Kerguelen (two equipped with ARGOS tags and four equipped with GLS).

All seven birds at Crozet headed south or south-west of the Island, while five birds headed east at Kerguelen and only one headed south (Fig. 4.1). Resulting was a clear dichotomy in the wintering water of the two colonies (Fig. 4.2).

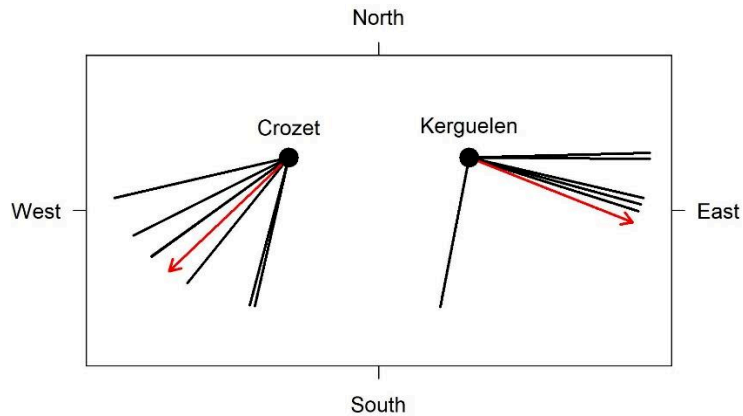


Figure 5.1: Average direction of the wintering location for each king penguin, from the colonies' perspective. The Red arrow represents the average direction across all penguins from a given colony.

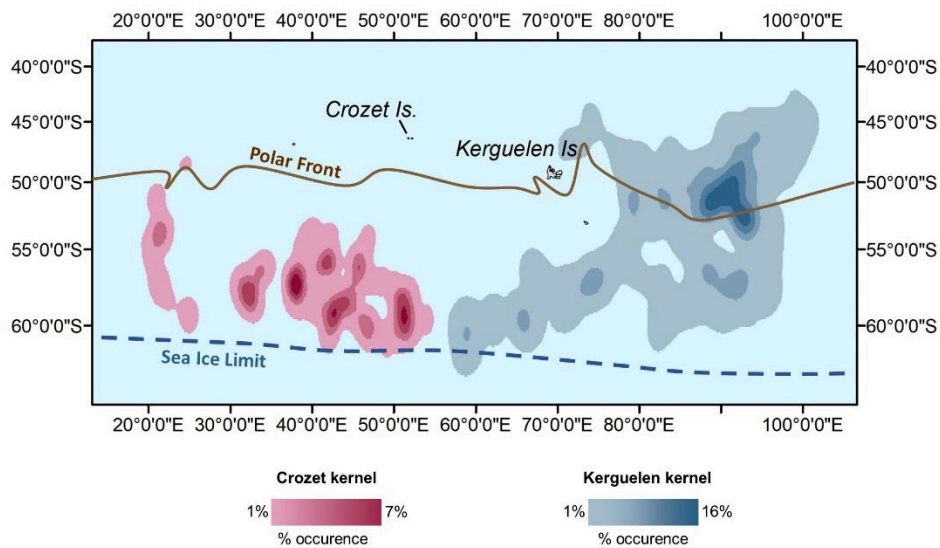


Figure 5.2: Kernel densities of the wintering location of Crozet (red) and Kerguelen (blue). Locations from all equipped penguins in a colony are pooled. The average Polar Front position and sea ice limit are displayed with a solid and a dashed line respectively.

The strong southern component of the Crozet's bird resulted in a lower average latitude ($-55.5 \pm 2.6^\circ$, $n = 7$) than the Kerguelen's bird ($-53.3 \pm 3.2^\circ$, $n = 6$). This difference was significant in the linear model with mixed effect (p -value < 0.0001). Consequently, the average SST experienced by the birds was lower for Crozet ($0.7 \pm 0.9^\circ\text{C}$, $n = 7$) than Kerguelen ($3.1 \pm 2.5^\circ\text{C}$, $n = 6$), although this difference was less significant according to the model (p -value = 0.02).

All birds at Crozet foraged well below the Polar Front, close to the sea ice limit (Fig. 2), in waters of low bloom index compared to average of the available habitat ($\beta = 1.19$, p -value < 0.0001 , Fig. 4.3a). At Kerguelen, most birds foraged at or above the Polar Front (Fig. 4.2), in zones where the bloom index was higher than the average of the available habitat ($\beta = 0.16$, p -value < 0.0001 , Fig. 3b).

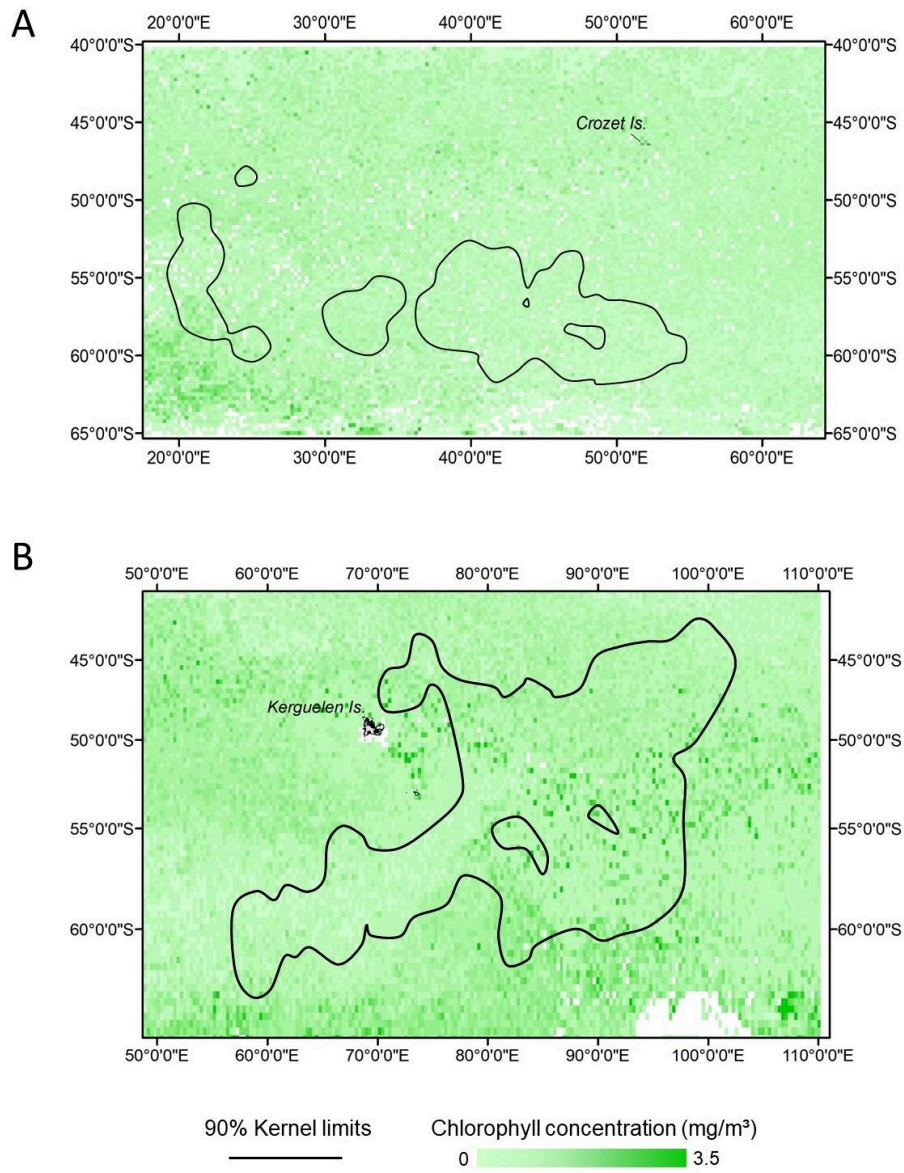


Figure 5.3: Bloom index (in chlorophyll concentration) of the waters surrounding (A) Crozet and (B) Kerguelen. The kernel polygons from Fig. 4.2 are displayed with a black solid line.

Discussion

Until now, wintering locations of king penguins of the Southern Indian Ocean were only known from a handful of studies from Crozet (Charrassin & Bost 2001, Bost et al. 2004). Our data confirms the findings from these studies that king penguins at Crozet head south in winter. However, our first published data on Kerguelen shows that this population mostly heads east in the winter, at similar latitudes than their breeding site. These two distinct directions taken by these populations in winter might indicate different strategies shaped by the biogeographic features surrounding the two archipelagos.

At Kerguelen, the polar front interacts with the extensive archipelago's plateau and enhances circulation of minerals such as iron (Mongin et al. 2008). These nutrients enhance the primary production and favor phytoplankton blooms around the island in spring, when light and temperature is optimal. This bloom typically also sustains a higher biomass of zooplankton, the main consumer of phytoplankton (Razouls et al. 1998). The bloom's aftermath, composed of zooplankton as well as the remaining phytoplankton, is then moved east by the westerly flow of the Polar Front and is – by the next winter – sparsely located east and southeast of the island (see Fig. 4.3b). It is possible that these post-bloom waters sustain high abundance of myctophids, which feed on zooplankton (Pakhomov et al. 1996), explaining why penguins at Kerguelen targeted the southeast of the island.

At Crozet, there is no extensive plateau as in Kerguelen. Furthermore, the Polar Front flows hundreds of kilometers south, in deep oceanic waters, and so does not strongly interact with shoals to enhance primary production. The result is a much more homogenic chlorophyll

landscape around the island (see Fig. 4.3a). Instead of targeting specific post-bloom waters, king penguins at Crozet seem to rather travel to areas near the sea ice limit, where a shallow thermocline could facilitate foraging (see Bost et al. 2004). There is thus a difference in strategies that seem to occur between the two colonies.

Naturally, there is potentially much plasticity within islands, and the observed tendencies might not reflect strategies for all individuals. At Crozet, non-breeding individuals have been shown to target other areas in the winter than breeders, with tracks heading west rather than south (Orgeret et al. 2019). Non-breeders might be much less time constrained compared to breeders, as the latter must return early in spring to resume chick provisioning. It is possible that this freedom allows non-breeding individuals to target prolific areas located outside the reach of breeding individuals. At Kerguelen, tracking data of non-breeders is absent from the literature. However, we did observe some plasticity among breeders, with one individual heading south and feeding in low-productive zones near the ice limit, similarly to Crozet's population. More research is needed to understand wintering plasticity in these two populations.

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Linking statement

Chapter 4 shed light onto the very restrictive diet of the king penguin, with no adjustment in prey sought even when encountering poor foraging conditions, while Chapter 5 presented new data on the wintering distribution of adults. Both chapters are crucial to interpret future responses of the species to climate change. The last two chapters will rather look at the past decades to understand the links between the environment and the breeding success of the king penguin. Chapter 6 will focus on the importance of the conditions during the winter period for the breeding of king penguins. More specifically, I will examine a case study: the consecutive catastrophic breeding failures of 2009 and 2010 at Kerguelen. I will link these events with the winter period, highlighting the importance of this season for king penguins.

Note: The results of Chapter 5 were supposed to have been published before Chapter 6, as the latter uses the wintering location to verify the wintering conditions that adult penguins might have encountered prior to the catastrophic breeding failure. However, recaptures of equipped penguins in spring were problematic, and we had to wait a whole year to adopt a new strategy for logger deployment. While penguins were at sea, I started to work on Chapter 6 using two complete ARGOS tracks that were transmitting in real time as reference. Chapter 6 was eventually published before I even received all the wintering data to work on Chapter 5, and analysis showed that the actual distribution was not quite representative of the two ARGOS tracks. Nonetheless, analysis done post-publications showed that results in Chapter 6 were similar when adjusted with the “true” distribution found in Chapter 5 (see Figure S5.0).

Chapter 6: Investigating two consecutive catastrophic breeding seasons in a large king penguin colony

AUTHORS

Émile Brisson-Curadeau^{1,2}, Annette Scheffer³, Phil Trathan⁴, Fabien Roquet⁵, Cédric Cotté⁶,
Karine¹ Delord, Christophe Barbraud¹, Kyle Elliott², Charles-André Bost¹

AFFILIATIONS

1 : UMR 7372-CNRS, Centre d'Études Biologiques de Chizé, La Rochelle University, Villiers-en-Bois, France

2 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

3 : OKEANOS Centre, University of the Azores, 9901-862 Horta, Portugal

4 : British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK; National Oceanography Centre, Waterfront Campus European Way, Southampton SO14 3ZH, UK

5 : Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

6 : Sorbonne Université, CNRS, IRD, MNHN, Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques (LOCEAN-IPSL), Paris, France

CITATION

Brisson-Curadeau, É., Scheffer, A., Trathan, P., Roquet, F., Cotté, C., Delord, K., ... & Bost, C. A. (2023). Investigating two consecutive catastrophic breeding seasons in a large king penguin colony. *Scientific Reports*, 13(1), 12967.

Abstract

Large-scale breeding failures, such as offspring die-offs, can disproportionately impact wildlife populations that are characterized by a few large colonies. However, breeding monitoring – and thus investigations of such die-offs – is especially challenging in species with long reproductive cycles. We investigate two unresolved dramatic breeding failures that occurred in consecutive years (2009 and 2010) in a large king penguin *Aptenodytes patagonicus* colony, a long-lived species with a breeding cycle lasting over a year. Here we found that a single period, winter 2009, was likely responsible for the occurrence of breeding anomalies during both breeding seasons, suggesting that adults experienced poor foraging conditions at sea at that time. Following that unfavorable winter, the 2009 breeding cohort – who were entering the late stage of chick-rearing – immediately experienced high chick mortality. Meanwhile, the 2010 breeding cohort greatly delayed their arrival and egg laying, which would have otherwise started not long after the winter. The 2010 breeding season continued to display anomalies during the incubation and chick-rearing period, such as high abandonment rate, long foraging trips and eventually the death of all chicks in winter 2010. These anomalies could have resulted from either a domino-effect caused by the delayed laying, the continuation of poor foraging conditions, or both. This study provides an example of a large-scale catastrophic breeding failure and highlights the importance of the winter period on phenology and reproduction success for wildlife that breed in few large colonies.

Introduction

Animals face extreme challenges during reproduction, such as poor foraging conditions, unfavorable weather, or diseases (Stokke et al. 2005, Romano et al. 2020). Occasionally, these challenges are simultaneously experienced by most individuals of a population, resulting in a large-scale breeding failure.

Perhaps the most impressive manifestations of breeding failures occur when massive die-offs of offspring are observed in colonial species. For example, heavy precipitation and extreme sea-ice conditions in 2014 led to all chicks dying at a 34 000 pair Adélie penguin *Pygoscelis adeliae* colony located in Antarctica (Barbraud et al. 2015, Ropert-Coudert et al. 2015). Yet, the cause of such die-offs is not always readily identified, particularly in species breeding over long periods; monitoring throughout the full reproductive cycle is generally costly and logistically challenging.

The king penguin *Aptenodytes patagonicus* is one seabird species that has an unusually long breeding season: pairs take approximately 13-14 months to fledge a chick, one of the longest breeding cycles among birds (Weimerskirch et al. 1992). Chick-rearing starts in the summer, but parents leave the colony for the winter, while the chick fasts unsupervised on land. In spring, adults come back to the colony to resume chick provisioning, while the next breeding wave has already started incubation. This long breeding cycle prevents most of the birds to lay annually, creating overlap between cohorts and complicating the understanding about large-scale breeding failures. In fact, this species has also suffered from large-scale chick die-offs in the past at several localities, some resulting from prey depletion, climate anomalies or even tsunamis (Olsson 1997, Viera et al. 2006, Bost et al. 2015). Yet, some colony breeding failures remain unresolved, as the

initial causes are particularly hard to determine over such a long breeding cycle (Weimerskirch et al. 1992).

Here, we report and investigate two of the most catastrophic breeding failures in king penguins, which occurred in a 100 000 breeding-pair colony on Kerguelen Island. During the consecutive breeding seasons of 2009 and 2010, two seemingly unrelated massive die-offs occurred among the chicks. We use the available tracking and diving data, chick monitoring and colony counts from the two breeding seasons for comparison with similar data from the long-term monitoring program at the colony available between 1998-2022. This allowed us to provide a complete description of the catastrophic failure with regards to the “normal” years and establish the chain of events that led to the breeding failures. Finally, we explore the possible triggers of the failures. Because there is negligible interaction between king penguins and fisheries in this region, we expected the failures to be driven by extreme environmental conditions affecting prey availability. We therefore explored the environmental variables that are known to affect foraging conditions and that could have affected each reproduction season.

Methodology

All data was collected at Ratmanoff’s colony in the Kerguelen archipelago ($-49^{\circ} 14' 33''$, $70^{\circ} 33' 40''$), situated in the southern Indian Ocean. The colony hosts nearly 100 000 breeding pairs of king penguins (Barbraud et al. 2020).

King penguins have an extended breeding cycle. Egg laying starts in the austral spring (late November), and hatching occurs 54-57 days later, in early summer, with a peak in late January (Weimerskirch et al. 1992, Bost et al. 2013). Adults then start provisioning their offspring until the onset of winter, in mid-April, when they then leave the colony for up to five months, returning only occasionally to feed their offspring. Throughout winter, chicks fast and primarily survive on the fat reserves accumulated during the summer (Cherel et al. 1987). When adults return in spring (early September), they resume chick provisioning until December, when chicks finally fledge. At that point, the subsequent breeding season has already started. This extended chick rearing period implies that penguins can only successfully breed every other year (Jiguet et Jouventin 1999, Le Bohec et al. 2007).

For simplicity, breeding seasons are named using the calendar year during which most of the reproduction cycle takes place. For example, birds of the “2010 breeding season” started incubation in November-december 2009, but provisioned their chicks throughout the summer 2010 (February to April), with a chick fasting period in winter 2010 (April to September), followed by another chick-provisioning period and fledging in spring 2010 (September to December).

The foraging range of the Kerguelen population during incubation and chick-rearing encompasses an area of 235,000 km² immediately to the southeast of the colony (between 49°S and 53°S and 70°E and 78°E degrees – Scheffer et al 2016, Brisson-Curadeau et al. 2022). In winter, adults migrate south to the northern limit of the seasonal sea ice (from -55.7° to -61.5° South and 57.6 to 79.8° East – Brisson-Curadeau & Bost, unpublished at that time, see Figure S6.1).

Colony counts during incubation

The colony was photographed with aerial images (either by helicopter or camera-fitted kites - Delord et al. 2015) in mid-December during five years between 1998 and 2009. This period corresponds to the middle of the incubation stage, so that a photo taken in December 2009 will be associated with the 2010 breeding season. To estimate the number of breeding pairs, the images were stitched together and incubating penguins were counted by hand based on the typical incubation posture (Delord et al. 2015).

Foraging behavior during incubation

For the 2010 season, foraging data were obtained only during incubation, as high abandonment rates of tracked adults prevented the recovery of their data logger. It was then also decided to stop any telemetry of chick-rearing birds, given the breeding failure rates. Consequently, only foraging data during incubation were used to compare the 2010 breeding season with other years.

During nine years between 1999 and 2022, 44 individuals (including 7 in 2010) were equipped during incubation (December-February) with GPS or ARGOS tags from various manufacturers. From this data, the maximum foraging distance was calculated and used as a measure of foraging effort. During the same period, 37 individuals (two in 2010) were equipped with depth-loggers either from Wildlife Computer (Redmond, United States) or Technosmart (Colleverde, Italy). The number of foraging dives per day was calculated from this data and served as a metric of foraging effort. A foraging dive was defined as a dive with maximum depth >50m (Pütz et al. 1998, Charrassin et al. 2002). We also calculated the average number of undulations or wiggles in the dive per day as a measure of foraging success. Wiggles are short up-and-down motions in the

depth-profile of a dive and are associated with prey capture attempts in king penguins (Charrassin et al. 2001, Bost et al. 2007, Brisson-Curadeau et al. 2021). Here, they are defined as an increase in the depth, followed by a decrease and another increase, with a minimum of 2 m in vertical deviation (Bost et al. 2007).

All loggers were retrieved after the individuals had returned from their first trip to sea (typically lasting around 17 days). Birds were weighed before and after the foraging trip to determine the mass gained per day at sea as another metric of foraging success, and trip duration was recorded as a measure of foraging effort. The breeding status of all equipped individuals were monitored during their foraging trip. If the incubating partner deserted the egg while the equipped individual was at sea, we considered the breeding status as failed. In the 2010 breeding season, when a high abandonment rate was apparent, an additional 37 breeding pairs from non-equipped individuals were monitored to better quantify incubation failure. In a similar fashion, 36 additional breeding pairs were monitored in 2011 for comparison.

The exact sample size for all years is reported in the supplementary material (table S4.1), as well as in the results. No data could be collected during incubation for the 2009 season. It is also noteworthy that egg abandon rate, trip length and mass gained per day can all have sample sizes slightly differing from the number of equipped individuals. Reasons explaining these occasional discordances are listed in the supplementary material (table S4.2).

Foraging behavior during chick-rearing

Foraging data in 2009 were only collected during the chick-rearing period (February 2009). Four individuals were equipped with an ARGOS tag, while thirteen were equipped with a depth-logger.

Maximum distance from the colony, number of dives per day, and number of wiggles per day were calculated during this breeding period as well as for all others between 1998 and 2022, except for 2010 (i.e. 24 years, with a total of 161 GPS/ARGOS-equipped birds, 173 depth-logger-equipped birds). Mass gained per day (n=380 individuals) and trip length (n=583 individuals) were also recorded for those individuals as well as for additional non-equipped birds. The total sample size of equipped individuals for all years during chick-rearing is reported in the supplementary material (table S4.3).

Chick mass and survival

Chick mass and survival were assessed annually between 2002 and 2022, apart from 2007 (i.e. 20 study years). Randomly selected chicks were weighed and marked with fish tags (FloyTags, Seattle, USA) in April before the winter fast. The number of chicks marked varied between years, ranging from 28 to 55, with most years (15) having n=40 chicks. The colony was visited in spring (October-November) to assess post-winter mortality of marked chicks. For 14 years, including the 2009 and 2010 cohort, mortality was also assessed earlier in July, corresponding to the mid-winter mortality.

Environmental variables

To investigate if a climatic variable was responsible for the 2009 and 2010 breeding failures, we looked at variables known to affect the foraging and breeding of king penguins. At Kerguelen, the sea surface temperature in April with a one year lag (hereafter “SST_{april-1 year}”) has been shown to be related to the breeding success of king penguins, and so was a plausible physical driver of these failures (Brisson-Curadeau et al. 2022). Four other probable drivers – chlorophyll

concentration, thermocline depth, SST (no lag) and sea ice cover (in winter only) – have also been shown to relate to king penguins foraging at other colonies, and thus were also considered in our analyses (Charrassin & Bost 2001, Cotté et al. 2007, Peron et al. 2012, Bost et al. 2015). The Southern Annular Mode (SAM) and Southern Oscillation Index (SOI), influence multiple components of ocean dynamics in both the wintering and breeding areas used for foraging, and so could potentially affect breeding success (Stammerjohn et al. 2008, Forcada & Trathan 2009). Furthermore, carbon concentration is an indicator of ocean productivity, and so was added as an additional plausible correlate. Finally, we looked at air temperature at the colony during the winter chick fast (June to August), as low temperatures been shown to negatively impact chick survival (Brisson-Curadeau et al. 2022).

Monthly multi-depth ocean temperatures, chlorophyll concentrations, carbon concentrations and Sea Ice Coverages (SIC) were obtained for the 2007-2022 period through the E.U. Copernicus Marine Environment Monitoring Service (CMEMS) at 0.25 geographic degree resolution (Copernicus 2020). Using the Global Ocean Reanalysis product, temperatures were retrieved from the 0-266m range depth (28 depth points total), from which thermocline depth was calculated as the depth where temperature changes are maximal (Fiedler 2010, Ferry et al. 2016). Monthly SAM (from Marshall 2003) and monthly SOI (retrieved from NCEI 2016) were obtained for the 1998 to 2022 period. Air temperature anomalies at the colony were obtained through the National Centers for Environmental Information (NOAA 2021).

Statistical analysis

We compared the across-year mean of each variables by building linear models with the variable year as the explanatory variable and the variable of interest (either foraging distance, trip durations, dives per day, etc.) as the response variable. When the response variables was binomial (e.g. chick survival), we instead modeled a generalised linear model with a binomial error distribution. In all cases, we then performed Tukey's Tests to compare the years 2009 and/or 2010 individually with all other years. Tukey's test allow pairwise group comparison while reducing type-1 errors caused by repeated tests (Williams & Abdi 2010).

The number of incubating pairs in mid-December, the air temperature in winter, as well as the climatic variables in February (when foraging data collection occurred), were inspected visually for anomalies (i.e. extreme values). Any other period that seemed post-hoc to be of importance to the 2009 or 2010 breeding seasons were investigated for climatic anomalies.

Results

Breeding season 2009

Available data from 2009 included tracking and diving data during the chick-rearing period, as well as chick mass and survival monitoring.

During the early chick-rearing period (i.e. February, summer) of 2009, foraging effort appeared to be normal, as foraging trip distance, trip duration, and dives per day were not statistically different from the other years (Figure S6.2). Similarly, the foraging success metrics (dive wiggles per day –

a proxy for prey pursuit – and mass gained per day) were not statistically different than other years (Figure S6.2).

Chick mass before winter (i.e. April) in 2009 was lower than average, but still within the range of the observed variations: it was even significantly higher than 3 other years (Figure 6.1). Similarly, chick survival in mid-winter (i.e. July) was 78%, which was below average but not exceptionally low, as it was only significantly lower than three of the twelve years with similar data (Figure 6.2). In contrast, chick survival decreased drastically between mid-winter and the following spring (i.e. October), as survival decreased to 6%, which was lower than all other 17 years (not accounting for 2010) and significantly so for 14 of the 17 years (Figure 6.2). The low yet not unprecedented breeding success of the three other years was due to low ocean productivity during the chick-rearing period and was explained in Brisson-Curadeau et al. (2022).

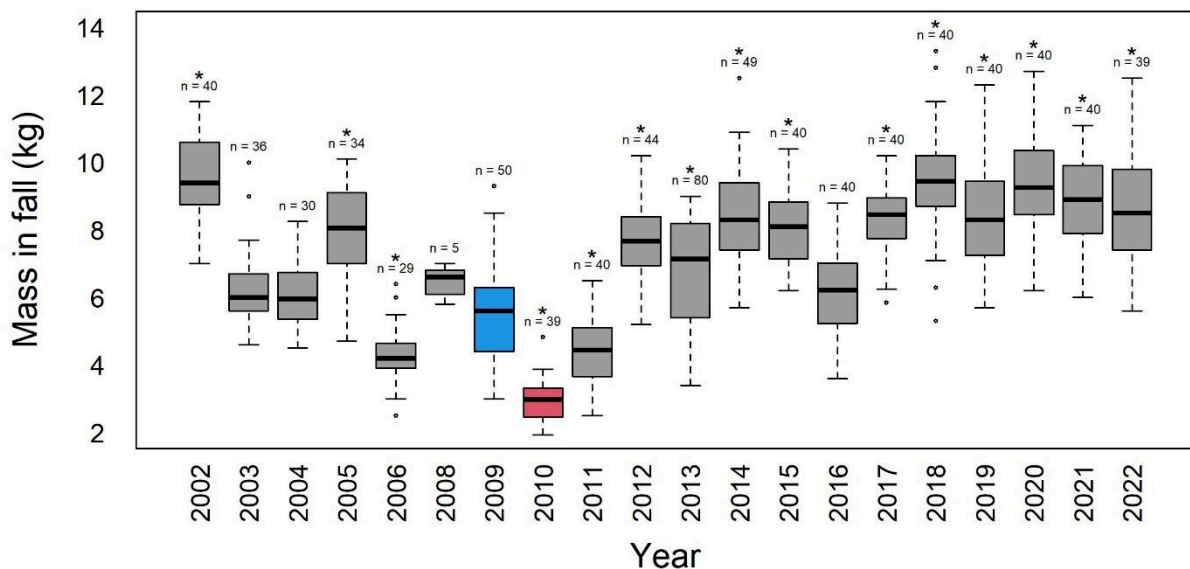


Figure 6.1: Chick mass in fall, before the winter fast. The 2009 breeding season is in blue and the 2010 breeding season is in red. Masses in all years are significantly different from 2010 (Tukey's Test). Asterisks are displayed above years that are significantly different from 2009.

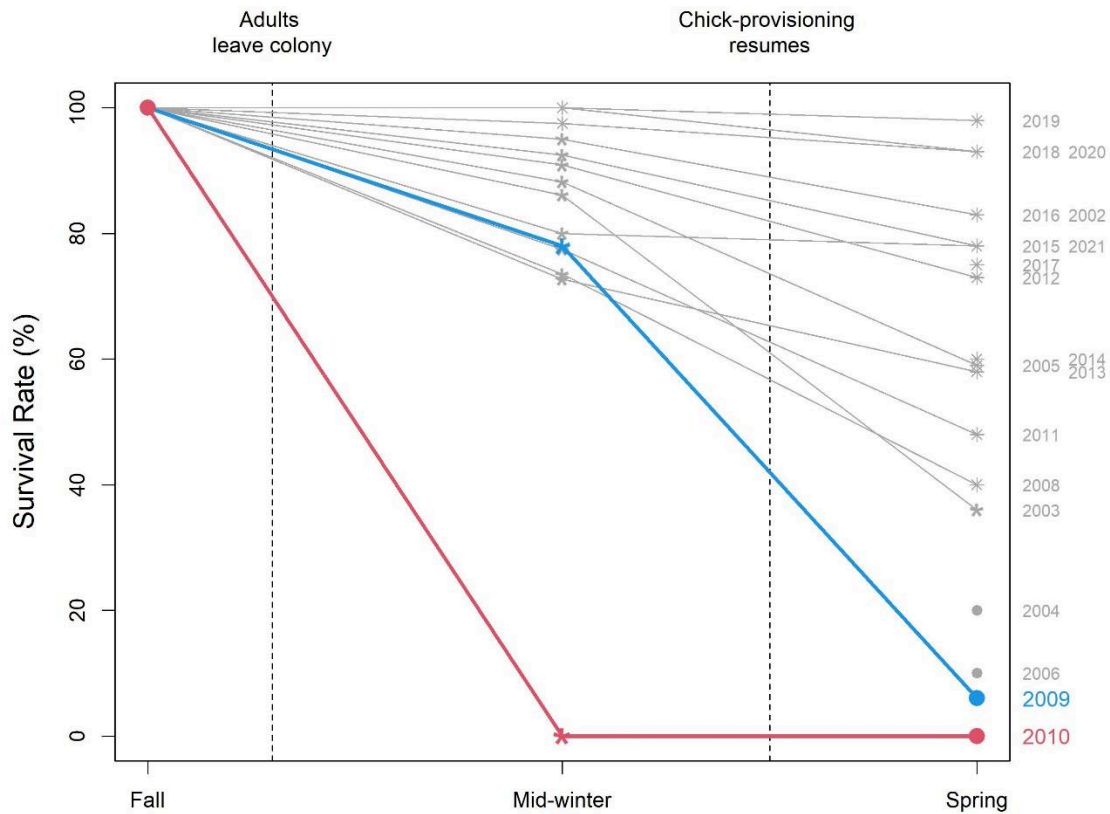


Figure 6.2: Chick survival throughout the winter. Results for the 2009 breeding season is in blue and results for the 2010 breeding season is in red. For a given period, survival rates that are significantly different than either 2009 or 2010 are represented with an asterisk (*), those that are significantly different than both years are represented with an eight-spoke star (*)

Breeding season 2010

Available data from 2010 included colony counts, tracking and diving data during the incubation period, as well as chick mass and survival monitoring (see methods for further details).

A marked delay in adult arrival was apparent during the 2010 breeding seasons. On December 14th 2009 (i.e. austral spring), when the 2010 parents were expected to have already laid their egg three weeks earlier, only 30 incubating pairs were counted in the entire colony. In comparison,

the numbers were in the tens of thousands for similar dates in previous years (Table 6.1). While no official counts of incubating birds have been conducted since 2009, yearly visits at the colony in December from 2011-2022 have also showed estimates in the tens of thousands (pers. obs.).

Table 6.1: Number of king penguin incubating pairs during each breeding season at Ratmanoff colony, Kerguelen. Note that incubation starts in the calendar year prior to the rest of the reproduction cycle.

Breeding season	Date of count	Number of incubating pairs
1999	18-12-1998	106583
2005	16-12-2004	105490
2006	22-12-2005	98042
2008	16-12-2007	52671
2010	14-12-2009	30

Adults eventually arrived and by February 2010 (i.e. austral summer) there was seemingly normal numbers in the colony, but due to logistic constraints, an exact breeding count could not be undertaken.

Egg abandonment rate during the incubation period was exceptionally high in 2010, with 93.8% of the 48 monitored pairs abandoning their egg. In contrast, none of the 85 monitored pairs over the eight other years with similar incubation data abandoned their egg (all years significantly different from 2010). Trip duration and foraging distance were longer in 2010 than all other nine

years with available incubation telemetry data (Figure 6.3-6.4). Dives per day and dive wiggles per day were both lower than all other years (Figure 6.3), albeit with a very small sample size in 2010 because of a high desertion rate of tagged birds. Adult mass gained per foraging day was lower than average but not significantly different from six of the other eight years with similar data (Figure 6.3).

The average chick mass before winter was much lower in 2010 (3.0 ± 0.6 kg) than the average (7.5 ± 2.0 kg), resulting in a significant difference when tested individually with all other years, including the 2009 cohort (Figure 6.1). All monitored chicks died in the winter by July. The final chick survival rate of 0% was the lowest ever observed at this colony (Figure 6.2) and in any large king penguin colony.

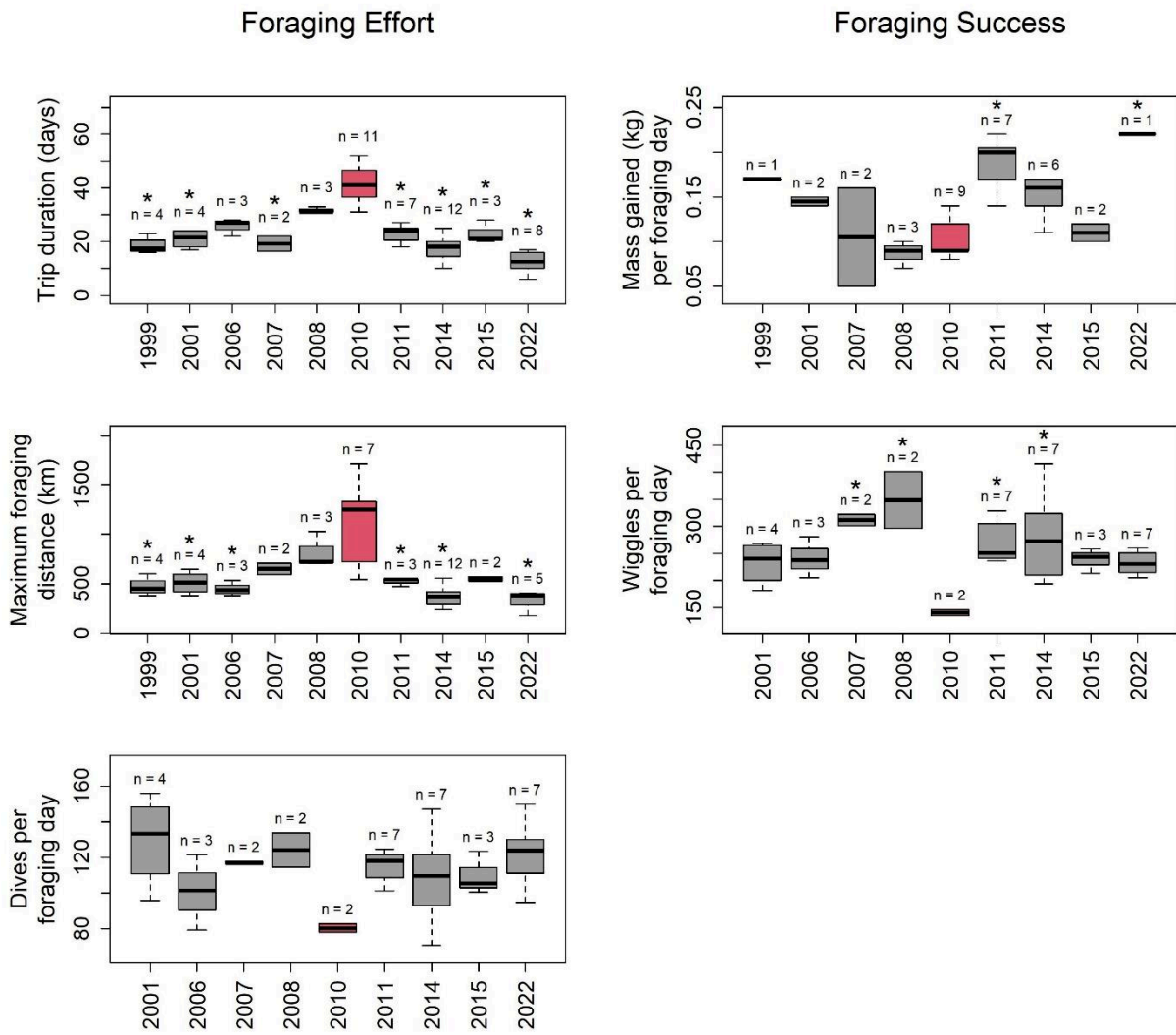


Figure 6.3: Foraging effort (left) and foraging success (right) variables during incubation. The year 2010 is highlighted in red. Asterisks are displayed above years that are significantly different from 2009 (Tukey's Test).

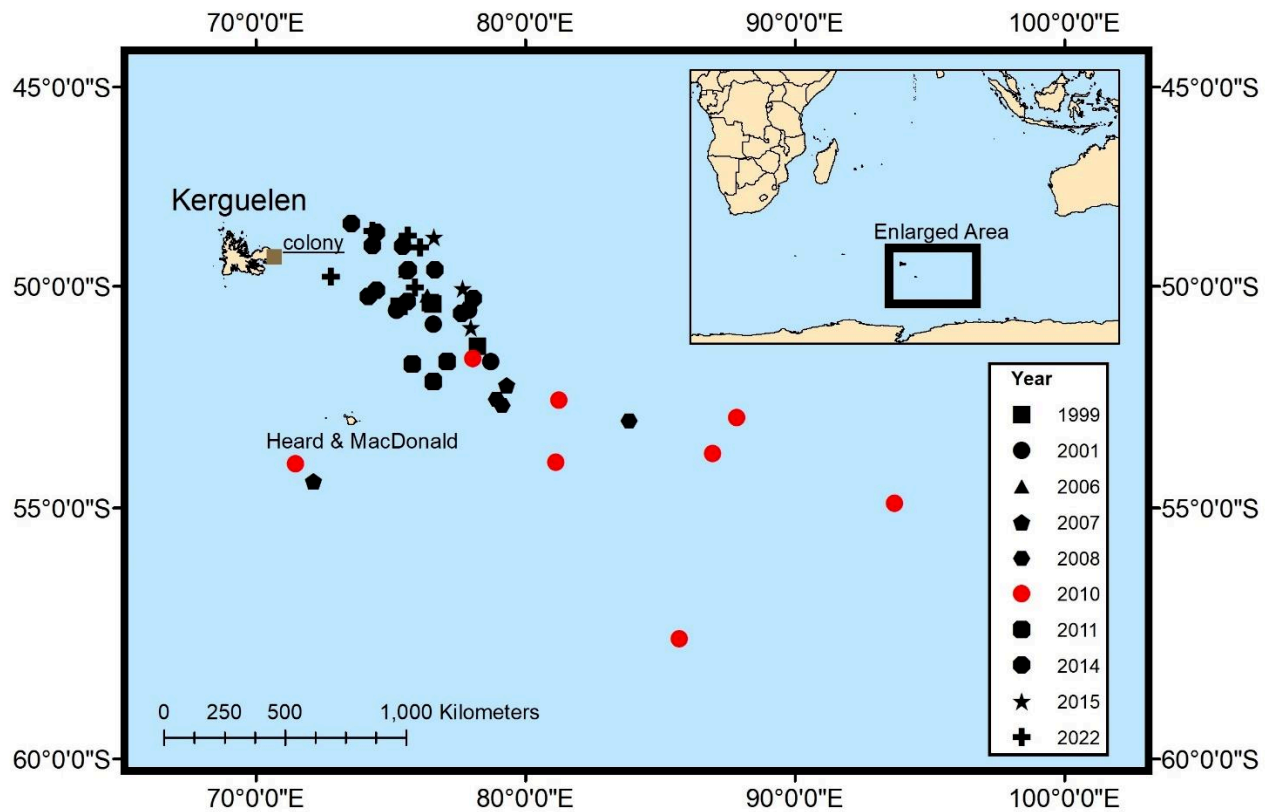


Figure 6.4: Furthest foraging location detected for each equipped penguin during incubation, sorted by year. In 2010, the foraging trips were significantly further from the other years. Map created using ArcGIS Pro 3.1. Country contour lines downloaded from <http://tapiquen-sig.jimdo.com> (Carlos Efraín Porto Tapiquén. Orogénesis Soluciones Geográficas. Porlamar, Venezuela 2015. Based on shapes from Enviromental Systems Research Institute. Free Distribution).

Climate

From the results above, we postulated that the winter of 2009 led to the failures for both the 2009 and 2010 cohorts. Consequently, we explored whether any environmental variables showed extreme values during that period (average of July-August 2009). Sea ice coverage was extensive during that winter, but did not show the highest value of the dataset (Figure 6.5). All other environmental variables showed approximately average values during the winter period.

Finally, it is noteworthy that all variables were average in February during both years, when foraging behavior was assessed (Figure S6.3). Air temperatures at the colony during the winters 2009 and 2010 were also slightly below average (2009 = -0.22°C below average, 2010 = -0.04°C below average), but not extremely so compared to other years, such as 2005 (-0.41°C below average) and 2007 (-0.37°C below average).

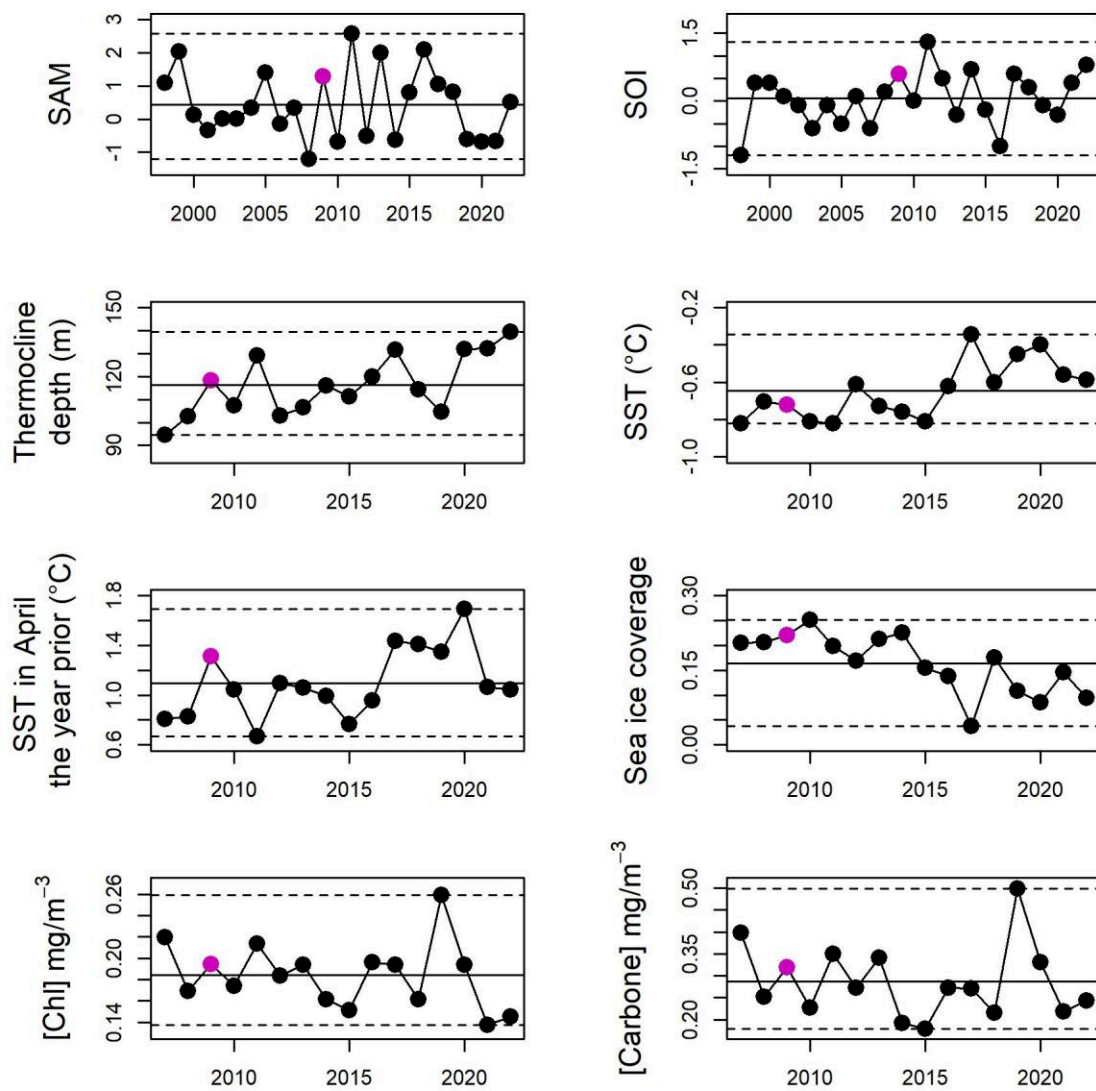


Figure 6.5: Climatic variables in winter (Jul-Aug averaged). The winter 2009 – identified as the key period that triggered the breeding failure for both the 2009 and 2010 breeding seasons – does not show extreme values on any variables. Maximum and minimum values are represented by a dotted line.

Discussion

We reported two catastrophic breeding failures occurring in a large colony of seabirds. During the years 2009 and 2010, we recorded the highest chick mortality documented for a large king penguin colony (Bost et al. 2013). We suspect the winter 2009 to have been problematic for both breeding seasons, with adults likely encountering poor feeding conditions at sea, affecting chick provisioning during spring for the 2009 breeders and delaying egg laying for the 2010 breeders (see Figure 6.6). For the 2010 breeders, it is unclear whether the problems encountered further in the reproductive season (egg abandonment, chick mortality, etc.) were caused by the continuation of these poor conditions, or by cascading effects resulting from delayed laying. Further questions around the 2009-2010 breeding failure at Kerguelen remain, as no environmental variables showed extreme values during the winter of 2009, leaving few clues as to what exactly could have caused the poor foraging conditions.

The 2009 breeding season

The 2009 breeding season appeared unlikely to be catastrophic until the very end. Foraging success metrics during the chick-rearing stage were only slightly below average and well within the observed inter-annual variation. Similarly, chick mass before winter – a crucial determinant of chick survival over winter (Brisson-Curadeau et al. 2022) – was low, but not unprecedented. Consequently, the survival of chicks in the middle of the winter was within the normal range.

However, almost all chicks had died by November, suggesting an important reversal by spring. When winter ends, adults usually come back to the colony and start feeding their chicks. For king penguins, the timing of the return of the adults in spring is critical, and any delay is thought to be fatal for the chick, which by the end of winter has low fat reserves (Cherel et al. 1987). We suggest that adults experienced very poor foraging conditions in winter (e.g. reduced prey availability), affecting their timing of return to the colony, with catastrophic consequences. Reports indeed suggest very low colony attendance as early as August (Chevalier, El Ksabi & Planade, pers. com.). This would confirm the delayed arrival of adults in early spring. Further continuation of poor foraging conditions into late spring could have also affected chick-provisioning rates.

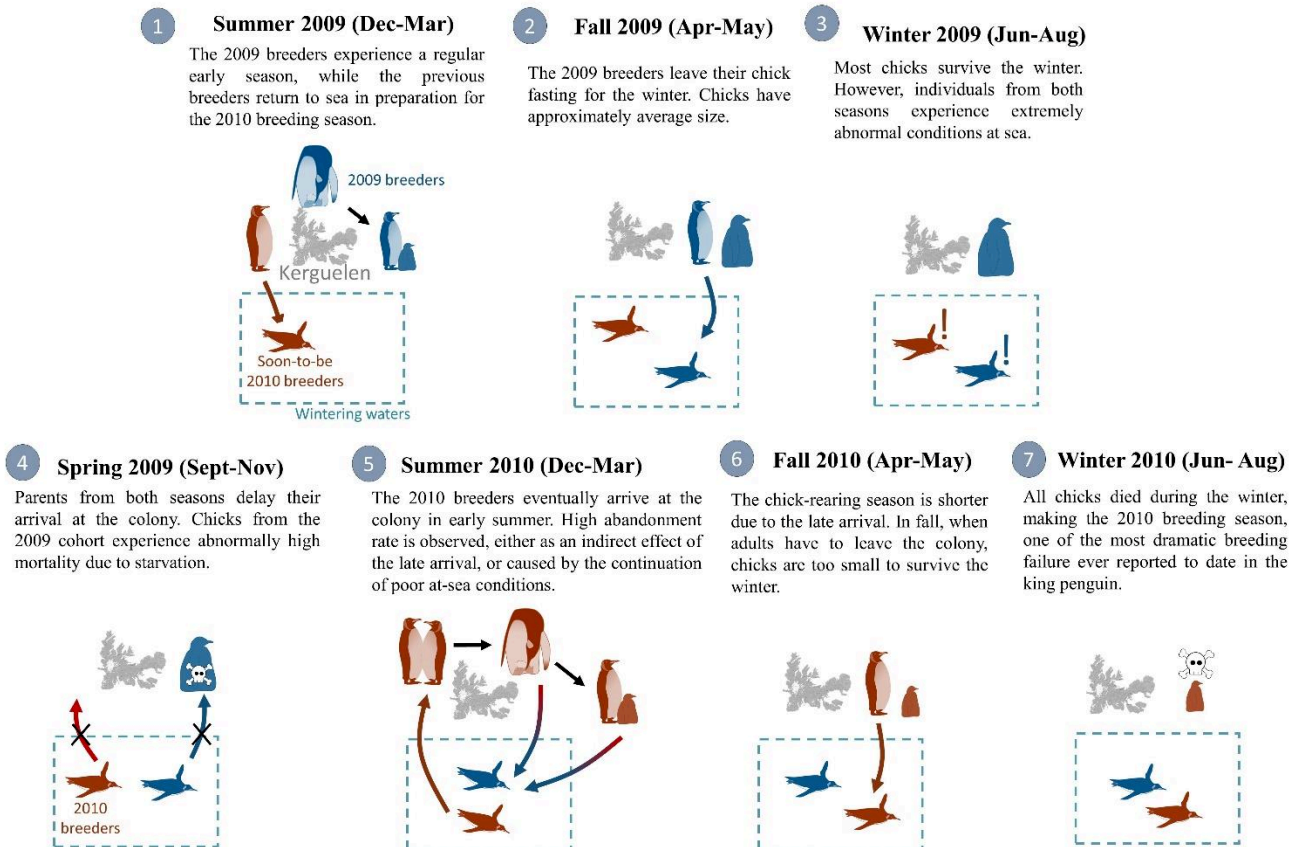


Figure 6.6: Proposed hypothesis retracing the events leading to the breeding failure in 2009 and 2010. The exact conditions during the winter 2009 that might have influenced the two reproductive seasons are still unknown.

The 2010 breeding season

The 2009 low breeding success is second only to the 2010 breeding season, the most dramatic breeding failure recorded for king penguins. The first anomaly observed in this breeding seasons was the colony-wise >3 week delay in egg laying. It is likely that this delay in arrival of adults was caused by the same factors which triggered the 2009 breeding failure. Indeed, during the winter 2009 – when the 2009 breeders presumably started experiencing poor conditions at sea – the 2010 breeders were also at sea, accumulating reserves for the upcoming breeding season (see Figure 6.6). In the following spring, both the 2009 and 2010 breeders experienced breeding anomalies: a chick-rearing failure for the 2009 breeders and a marked delay in egg-laying for the 2010 breeders. Therefore these two breeding seasons seem to have been affected by the same event, i.e. poor at-sea conditions in winter and/or early spring.

The breeding anomalies in 2010 never ceased and were recorded in other breeding stages; including unusually long trips at sea and high abandonment rates during the incubation period, as well as extremely low mass of chicks before the winter, and finally the death of all chicks in the winter.

We see two possible non-exclusive explanations for these breeding anomalies. Firstly, all these observations during the 2010 breeding season could ultimately be consequences from the delayed laying, passing on from one breeding stage to the other through cascading effects. Timing of life-history events is critical at the beginning of the season for king penguins, because time is limited for the chicks to gain sufficient mass to survive the winter fasting period (Stier et al. 2014). For this reason, late arriving individuals may be less invested in their reproduction attempt, as the

chances of success are low (Weimerskirch et al. 1992, Groscolas et al. 2008). This might be what occurred in 2010, as the colony-wide delay in phenology led most birds to abandon their egg before it hatched. Parents that did not abandon their egg were less invested when foraging during incubation: they undertook long and distant foraging trips, while reducing diving effort. Indeed, individuals experiencing lower drive for breeding are not constrained by the need to return quickly to the colony, and so can undergo longer foraging trips (Charrassin et al. 1998). Furthermore, they do not need to increase diving effort to sustain long fasting incubation shifts, contrary to birds more invested in breeding. By the onset of the winter, chick mass was less than half that of the long-term average, and by far the lowest ever recorded at that colony. This was likely caused by the short period available for penguins that year to provision their chick. The consequence was a massive winter die-off of chicks, unprecedented in a large king penguin colony.

Secondly, the poor conditions suspected to have taken place in winter 2009 could have continued during the following spring and perhaps summer. This also leads to a reduced parental investment and high abandonment rate. Furthermore, poor foraging conditions could partially explain the low mass of chicks before the winter, in addition to the delayed laying/hatching. Unfortunately, data on the foraging success during chick-rearing of 2010 are scarce because of the very low of successful tracked birds.

Limitations and future directions

Examining causes behind anomalous events will always remain a difficult task because these events occur only rarely by definition, offering few replicates for investigation. The main unsolved issue around the 2009 and 2010 extreme breeding failures is the exact nature of the presumed poor conditions occurring in winter 2009. We did not find any relevant climatic variables that could explain a large-scale prey depletion during that period. Prey data (myctophid fish) is scarce in this region of the world, and foraging conditions for king penguin adults have usually been deduced indirectly from environmental variables, with a focus on the chick-rearing period (e.g. Bost et al. 1997, Guinet et al. 1997, Scheffer et al. 2016). More research is needed to fill the gap between climate, prey, and marine predators such as penguins, especially in winter. There is also a need to monitor the foraging success during all the breeding stages for pelagic foragers such as king penguins that are present year-round in the same oceanic region.

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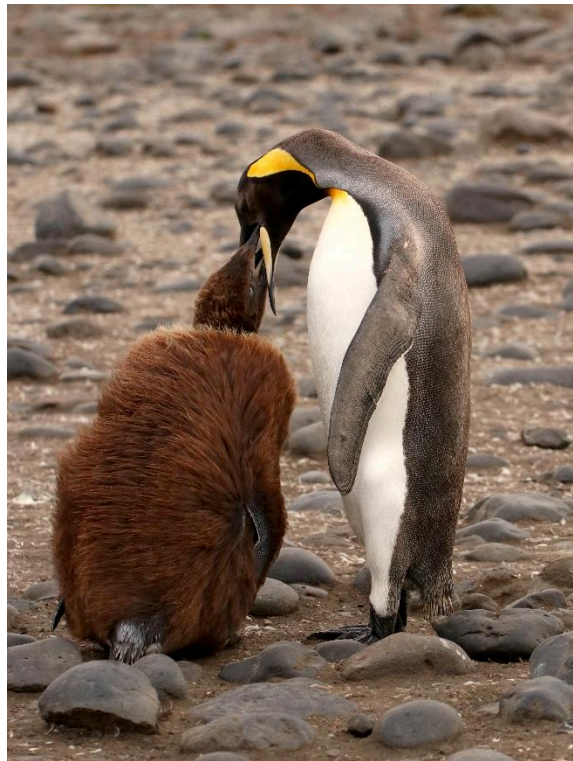
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Linking statement

Chapter 6 showed that events preceding the laying periods can affect the whole breeding cycle of the king penguin, as carry-over effects can create delayed consequences on the breeding success. In Chapter 7, I will rather focus on the chick-rearing period. I will examine how the conditions at sea during this period influence the chick-provisioning. I will also study how the chick conditions and climate will ultimately influence their survival. Finally, I will make a comparison with the nearby population of king penguin (Crozet Archipelago) and compare the effect of the climate on these two populations.



An adult feeding a chick. This photo made the cover of Global Change Biology.

Chapter 7: Contrasting bottom-up effects of warming ocean on two king penguin populations

AUTHORS

Émile Brisson-Curadeau ^{1,2}, Kyle H. Elliott¹ & Charles-André Bost²

AFFILIATIONS

1 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

2 : Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, Villiers-en-Bois, France

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Abstract

Breeding success is often correlated with climate, but the underlying bottom-up mechanisms remain elusive—particularly in marine environments. Consequently, conservation plans of many species often consider climate change as a unilateral threat, ignoring that even nearby populations can show contradicting trends with climate. Better understanding the relationship between climate and environment at different scales can help us interpret local differences in population trends, ultimately providing better tools to evaluate the global response of a species to threats such as global warming. We studied a growing king penguin population nesting at Kerguelen island (Southern Indian Ocean), hosting one of the largest colonies in the world. We used a unique dataset of foraging, breeding success, and climate data spanning over 25 years to examine the links between climate, marine environment, and breeding success at this colony. The results were then compared to the neighboring population of Crozet, which experienced the steepest decline for this species over the past few decades. At Crozet, penguins experienced lower breeding success in warmer years due to productive currents shifting away from the colony, affecting foraging behavior during chick rearing. At Kerguelen, while chick mass and survival experienced extreme variation from year to year, the annual variation was not associated with the position of the currents, which varied very little compared to the situation in Crozet. Rather than being affected by prey distribution shifts, we found evidence that chick provisioning in Kerguelen might be influenced by prey abundance, which seem to rather increase in warmer conditions. Furthermore, warmer air temperature in winter increased chick survival rate, likely

due to reduced thermoregulation cost. Investigating the mechanisms between climate and fitness allowed us to predict two different fates for these populations regarding ongoing global warming.

Introduction

Events of abnormally high ocean temperature have been reported in all oceans to affect the dynamic of currents, creating a cascading effect on the trophic chain (Frölicher & Laufkötter, 2018; Piatt et al., 2020). Increased occurrence of these warm events might be particularly devastating in the Southern Ocean, as it hosts around a quarter of the total fish biomass of the world (Dornan et al., 2022; Irigoien et al., 2014). This abundance of prey is mostly supported by unique circumpolar currents creating complex water mass interactions and distinctive surface and sub-surface dynamics, all of which are sensitive to ocean warming (Bost et al., 2009; Chapman et al., 2020). Yet, predicting the effect of climate change on this ecosystem is a difficult task, as complex currents result in complex interactions with wildlife.

The Polar Front is one of these important currents widely used by prey and top predators all around the Southern Ocean (Bost et al., 2009; Rayner et al., 2017; Scheffer et al., 2016; van Franeker et al., 2002). It is formed by the divergence of the cold $<2^{\circ}\text{C}$ Antarctic water (also called Winter Water) with the warmer Sub-Antarctic water, creating strong upwelling bringing prey such as myctophid (lantern fish) closer to the surface (Catul et al., 2011; Cotté et al., 2007; Marshall & Speer, 2012). However, the Polar Front is expected to contract towards the Antarctic continent with ocean warming (Fogt & Marshall, 2020; Péron et al., 2012). These spatial shifts may create a prey–predator mismatch for those central-place foragers, such as birds and pinnipeds breeding on islands, leading to population decline. At Crozet for example, located in the Southern Indian

Ocean, three of the four species of breeding penguins, as well as some species of albatross, have experienced decline (Barbraud et al., 2020). While the causes of these declines are not always known, the Polar Front shifting southward and further away from the island has raised concern about the future of some species (Bost et al., 2015; Péron et al., 2012). For this reason, climatic models predicts that some of these front-associated species may soon face serious population threats in that region (Charrassin & Bost, 2001; Le Bohec et al., 2008; Péron et al., 2012). The main concern is that the Polar Front might migrate a critical distance away from the island—where food provisioning is no longer sustainable—leading to a strong decrease in chick feeding frequency and eventually high chick mortality (Péron et al., 2012).

Yet, even population trends of neighboring islands can be quite contrasting, showing that observed effects of climate change at a given site cannot be extrapolated without taking into account the location-dependant specifics. For example, most of the penguin species and albatrosses declining at Crozet have been stable or increasing at Kerguelen Island—its ocean neighbor located 1400 km to the east (Barbraud et al., 2020). Some of these species also feed on the Polar Front there, but too few studies have linked global warming with the marine environment at Kerguelen to predict future population trends, or even explain why past trends differed from Crozet's. The Polar Front near Kerguelen is also more constrained by strong bathymetric features, with less movement associated with warming temperature compared to Crozet (Pauthenet et al., 2018). Yet, no studies have looked at how this particularity might influence the life history of marine predators. In this context, comparative long-term studies are valuable to not only understand how two neighboring populations might show diverging

responses to global warming, but also how these responses can be extrapolated to other populations.

As a circumpolar breeder, the king penguin *Aptenodytes patagonicus* is an ideal model species to study location-dependant effects of climate. It is a central-place forager feeding almost exclusively on myctophids and foraging mainly on the Southern edge of the Polar Front, where a wide zone of the Winter Water upwelling occurs (Bost et al., 2009; Charrassin & Bost, 2001). Furthermore, adult king penguins provision their chicks throughout the austral summer but leave them fasting at the colony throughout winter for up to 4 months, a unique behavior among birds. During this fasting period, chick mortality is at its highest, as they must survive on the fat reserve they have built throughout the summer (Cherel & Le Maho, 1985). Temperature changes in winter might therefore potentially impact their survival rate, providing an opportunity to also investigate direct climatic effects on this population. At Crozet, ambient temperatures outside of the -1 to 9°C range have been shown to affect chick metabolism, but no studies have looked at long-term climatic trends on the survival of chicks (Barré, 1976).

We used 25 years of unpublished data to understand the effects of climate on the foraging and breeding success of a seldom studied population of king penguins at Kerguelen Island. We used accelerometers to assess at-sea foraging success in relation to the Polar Front, while chick mass after the chick-provisioning period—or before the winter fast—will serve as a metric to assess the overall summer foraging success of adults. As pairs raise only one chick, and as most of the energy intake by the chick is invested in building fat reserves for the winter (rather than

structural development; de Margerie et al., 2004), the pre-winter mass is likely a good indicator of the foraging success of adults in this species. We also test if summer air temperature at the colony affected the final pre-winter chick mass by increasing thermoregulation costs. Finally, we investigated the effect of winter air temperature on chick survival during the fasting period. We then compare our results with a decreasing king penguin population at Crozet, where bottom-up climatic-effects on their life history are well known.

Methods

All data was collected at Ratmanoff's colony in the Kerguelen archipelago ($-49^{\circ} 14' 33''$, $70^{\circ} 33' 40''$), which hosts approximately 80,000–90,000 breeding pairs of king penguins (Barbraud et al., 2020). During the chick rearing period, king penguins forage southeast of the island, between -49° S and -53° S and 70° E and 78° E, hereafter “foraging zone” (Bost et al., 2002; Scheffer et al., 2016).

Chick mass and survival

Chick mass and survival was assessed yearly from 2002 to 2021, apart from 2007, 2009 and 2010 (i.e. 17 studied years). Randomly selected chicks were weighed and marked with fish tags (FloyTags) in April before the winter fast, except for 2008, where weighing occurred in May due to fieldwork constraints. The number of chicks marked annually varied from 28 to 55, with most years (11) having $n = 40$ chicks. The colony was again visited in October–December to relocate the marked chicks and assess winter mortality.

Foraging behavior

A total of 148 foraging penguins were equipped during the brooding period (February–March) between 1998 and 2022 with GPS or ARGOS tags from various brands, except for 2010 and 2012 which contained no equipped penguins (23 years). For ARGOS tags, locations with a precision class of 0, A or B (i.e. with >1500 m precision) were removed. When the animal speed between two consecutive GPS or Argos locations was >10 km/h, we removed the second point, which was also likely imprecise.

From these GPS/ARGOS-equipped penguins, 60 penguins were also equipped with depth-loggers from either Wildlife Computer or Technosmart. The maximum distance of the foraging trip from the colony was computed for all individuals, while kernel densities of foraging dives (see Section *Foraging habitat selection at Kerguelen* of the statistical analysis) were processed for individuals equipped with both GPS and Depth-loggers. A foraging dive was defined as a dive with maximum depth >50 m (Charrassin et al., 2002; Pütz et al., 1998).

During 2019–2022, 16 of the GPS-Depth-logger equipped individuals were also equipped with accelerometers (Technosmart). Acceleration data in each dive was then converted into prey capture attempts—a measure of foraging success—throughout the foraging trips using a machine-learning algorithm tested on wild penguins equipped with beak-opening sensors (Brisson-Curadeau et al., 2021).

We retrieved all biologging equipment after the individuals had returned from their foraging trip at sea, which typically lasted 4–12 days.

Environmental data

Monthly air temperature data at the colony during the winter chick-fast (April–August) and summer brooding period (February–March) was extracted from the NOAA National Centers for Environmental Information (2021). The wind chill effect was then added using wind data retrieved from NOAA Physical Sciences Laboratory (Kalnay et al., 1996).

Daily sea-surface height (SSH) and multi-depth ocean temperatures during the brooding period were obtained through the E.U. Copernicus Marine Environment Monitoring Service (CMEMS) at a 0.083° resolution (<https://doi.org/10.48670/moi-00016>, <https://doi.org/10.48670/moi-00021>). Temperatures were retrieved from the 0–266 m depth range (28 depth points total) from 2007 onward, as significantly different methodologies were used pre-2007 by CMEMS to extrapolate temperature data, making across-year comparisons impossible. From this dataset, the Polar Front position was calculated as the northernmost extent of surface/subsurface water temperatures <2°C (Park et al., 2014). We also calculated the depth of the Winter Water layer throughout the foraging zone and the thermocline depth, the latter being defined as the depth where temperature changes are maximal (Fiedler, 2010).

Statistical analysis

Foraging habitat selection at Kerguelen

To understand which zones near the colony are the most prolific for penguins, we made several linear mixed models predicting the average number of prey capture attempts in a dive

(using the 2019–2022 accelerometry data). Explanatory variables were: thermocline depth, SSH, upper depth limit of the Winter Water, and sea surface temperature (SST) at the dive location (Péron et al., 2012; Scheffer et al., 2016). Distance of the dive from the colony was also added as a variable to detect any effect of prey depletion (“Ashmole's halo”, Birt et al., 1987). The individual was used as a random factor.

We also plotted the kernel density of foraging dives and polar front positions near Kerguelen for the whole period and compared it with the foraging maps at Crozet. The kernels for both locations were calculated using a 90% quartic kernel function (Silverman, 2018). The kernel foraging range near Crozet was made possible using metadata from the Bost et al. (2015) study, with permission from coauthors, while the kernel density near Kerguelen was calculated using the data described in Section *Foraging behavior* of the methods. Only foraging data post-2007 were used to create both kernel maps (i.e. 2007–2010 for Crozet, 2007–2022 for Kerguelen), as this was the earliest year with accurate Polar Front data (see section *Environmental data* of the methods). While the yearly range and total sample size at Crozet (n = 8 individuals equipped with both GPS and depth loggers) was smaller than at Kerguelen (n = 60 individuals), it still provided an interesting visual contrast in the foraging range at the two locations, with regards to the Polar Front.

Finally, to assess whether there was a temporal trend at Kerguelen in the mean foraging distance, we built a linear model with the variable “year” as the explanatory variable and compared it to a null model.

Effects on chick growth

We made several linear regressions predicting annual chick mass before winter to assess which climatic variables influence inter-annual chick growth variations at Kerguelen (n = 12 years). These variables were: mean air temperature at the colony (accounting wind chill), average SST in the foraging zone, and distance of the Polar Front from the colony. All these variables were computed for the February–March period, which is when chick-provisioning and hence chick-growth occurs. SST in the foraging zone with a time lag was also added as a variable to assess whether climatic events preceding the breeding period could influence prey abundance during chick-rearing and consequently affect chick-provisioning itself. Our preliminary results showed that SST with a lag of 1 year (i.e. in April the year before) showed greatest correlation with chick mass, and so SST-1 year was introduced in the model selection.

Effects on chick survival

A beta-regression model selection was conducted to assess which factors influenced annual chick survival rate in the winter (n = 17 years). The three explanatory variables of interest to build these models were mean wind chill at the colony in winter (April–August), average chick mass before winter (April), and year (to detect temporal trends). We chose beta-regression to account for the response variable (annual chick survival rate) being a ratio, and not a continuous value.

The Akaike information criterion corrected for small sample size (AICc) was used to rank models in all model selections. Only models with $<2\Delta$ AICc were considered (Hu, 2007). All analyses were conducted in R (R Core Team, 2021).

Results

General climatic trends at Kerguelen

Wind chill in winter was consistently higher in the last decade (2012–2021) compared to the first decade of the study (2002–2011), and a positive linear trend was significant throughout the study period (slope = $0.04 \pm 0.01^{\circ}\text{C}/\text{year}$, p value = .005, $R^2 = .038$). No such trend was detected in the summer, during the brooding period, where air temperature did not show any significant trend (slope = $0.04 \pm 0.03^{\circ}\text{C}/\text{year}$, p value = .13).

Similarly, the SST of the foraging zone during chick provisioning did not show any significant linear trends throughout the dataset (slope = $0.03 \pm 0.02^{\circ}\text{C}/\text{year}$, p value = 0.27). However, the last 5 years of the study (2017–2021) did show higher SST on average compared to the other years and included the three warmest years of the whole dataset (Figure 7.1). The position of the Polar Front varied little from year to year (range: 63–107 km from colony, n = 16 years, see Table 7.1 and Figure 7.2).

Effects of climate on foraging and breeding success

Foraging habitat selection at Kerguelen

From 1998 to 2022, penguins foraged on average 266 ± 98 km from the colony (n = 148 penguins). From year to year, the average foraging distance varied from 172 to 379 km (n = 23 years, see Table 7.1). The average southernmost latitude reached by penguins varied from -49.9° to -51.3° among years. There were no temporal trends in the foraging distance of penguins

at Kerguelen (Table S7.1). The kernel density maps of foraging dives showed that penguins travelled south-east to where the Polar Front came the closest to the colony and started foraging at and beyond the front (Figure 7.2).

A final assessment of habitat selection was made using the 2019–2022 accelerometry data and model selection to determine which foraging zones are profitable to penguins. The model selection showed that SST and upper depth limit of the Winter Water layer were the two most important variables predicting prey capture attempts in a dive ($R^2 = 0.11$, Table S7.2). Both variables had a negative effect, with more productive dives occurring in cold SST water and where the Winter Water upper-limit is shallower. When accounting for distance to the colony, only SST was present in the best ranked model ($R^2 = 0.12$, Table S7.3). Equipped penguins attempted 367 ± 112 captures on average per day at sea.

Effects on mass before winter

The model with SST-1 year as a unique explanatory variable scored the lowest AICc ($R^2 = 0.56$, Table S7.4). The effect of SST-1 year was positive on chick mass, with higher SST-1 year increasing chick mass (Figure 7.3).

Effects on chick survival

Both average chick mass before winter and winter air temperature explained chick survival ($R^2 = 0.76$, Table S7.5). Both variables had a positive effect, with higher temperature and higher average chick mass increasing chick survival (Figures 7.4 and 7.5). Regardless of the year, individual chicks above 7 kg had high probabilities (>60%) of surviving the winter (Figure 7.4).

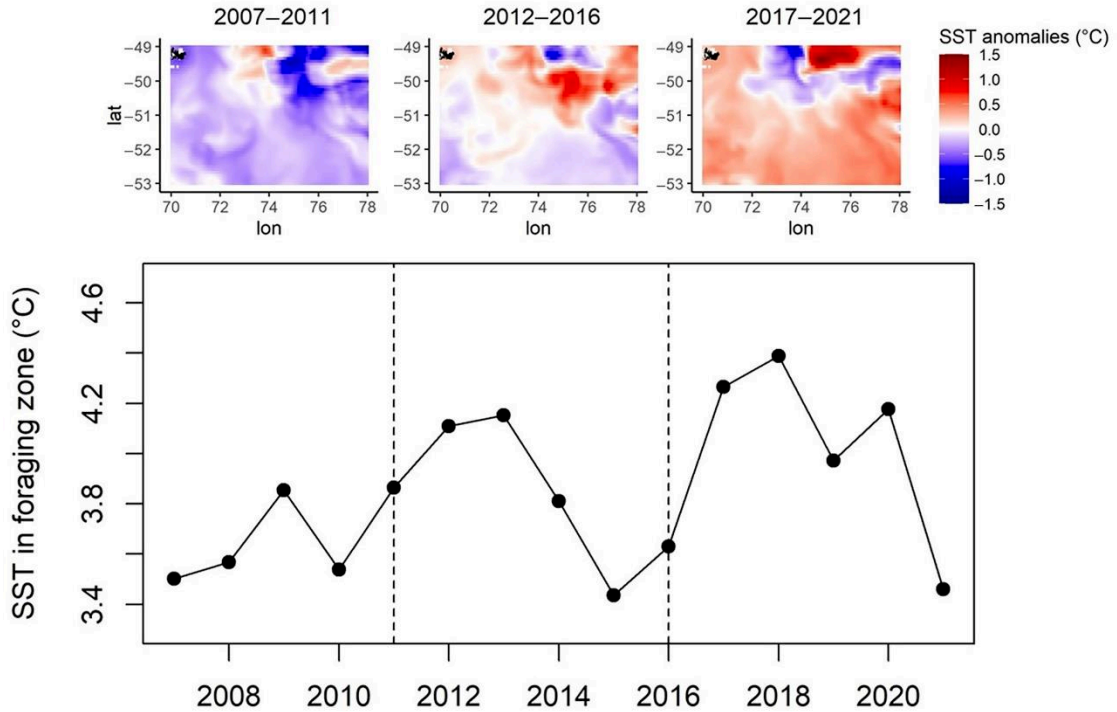
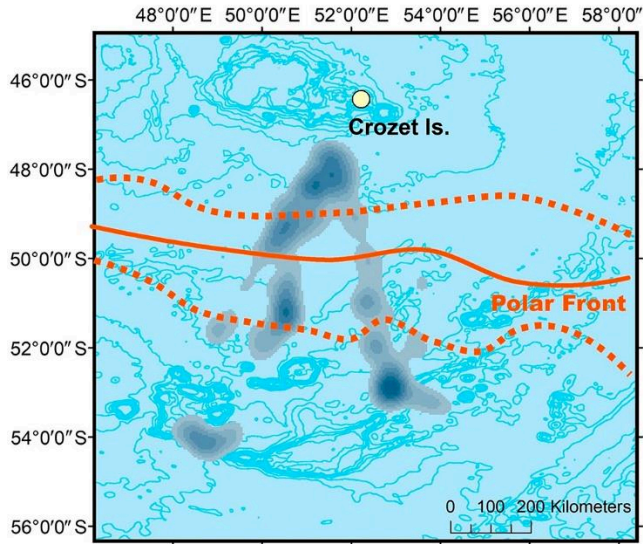


Figure 7.1: Sea surface temperature anomalies in the full extent of the foraging zone, with Kerguelen Island in the top left corner. Anomalies were calculated based on the 2007–2021 time series. Despite no significant trends, the last five years (2017–2021) were warmer on average compared to previous years of the study.

Table 7.1: Comparison of Polar Front position and king penguin foraging distance between the Kerguelen archipelago (this study) and Crozet archipelago (Bost et al., 2015)

Variables compared	Kerguelen archipelago (this study)	Crozet archipelago (Bost et al., 2015)
<i>Inter-annual range in Polar Front distance from colony</i>	63–107 km ($n = 16$ years between 2007 and 2022)	217–642 km ($n = 16$ years between 1992 and 2010)
<i>Inter-annual range in foraging distance</i>	117–387 km ($n = 23$ years between 1998 and 2022)	290–580 km ($n = 16$ years between 1992 and 2010)
<i>Inter-annual range in Southernmost latitude reached by foraging penguins</i>	–49.9° to –51.3° ($n = 23$ years between 1998 and 2022)	–48.8° to –51.9° ($n = 16$ years between 1992 and 2010)

Crozet Is.



Kerguelen Is.

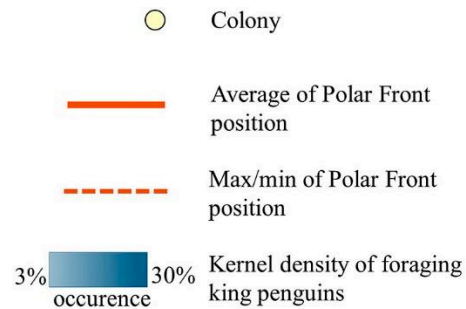
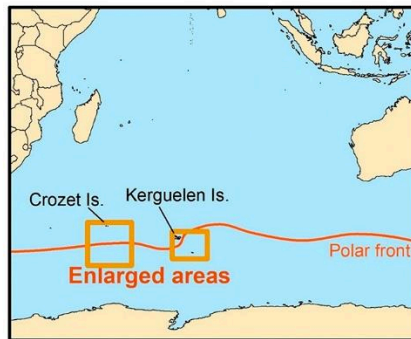
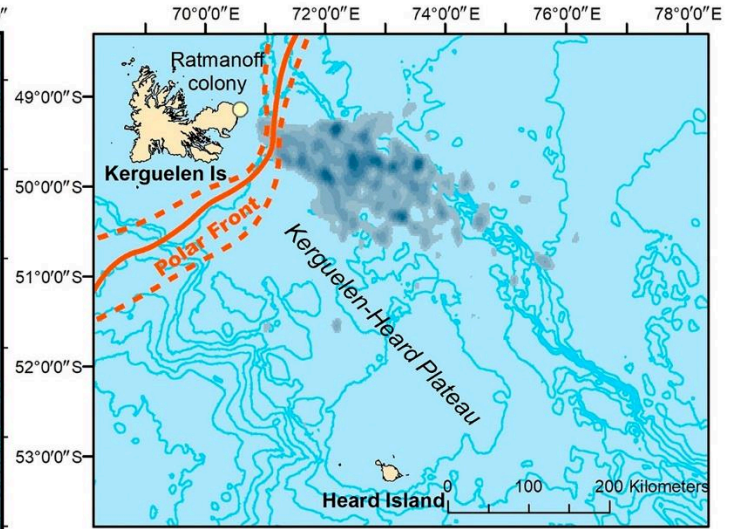


Figure 7.2: Between-location comparison of the polar front position and kernel density of king penguin foraging dives, for the 2007–2022 period. The base map is a 500 m contour bathymetry. Notice how the Polar Front systematically passes close to Kerguelen—at the bathymetric frontier between the island and the Kerguelen-Heard Plateau—while it is much freer to move in the deep oceanic waters far off Crozet. This impacts the foraging distance of penguins, which is typically much further at Crozet (notice the different scale of the two maps). Polar Front position for both locations was calculated as the northernmost extent of the subsurface $<2^{\circ}\text{C}$ layer using E.U. Copernicus Marine Environment Monitoring Service data (spanning 2007–2022). Kernel density maps from Kerguelen were calculated using GPS and depth-logger data ($n = 60$ individuals, spanning 2007–2022), while kernels from Crozet were calculated using the Bost et al. (2015) foraging metadata, with authorization from coauthors ($n = 8$ individuals, spanning 2007–2010).

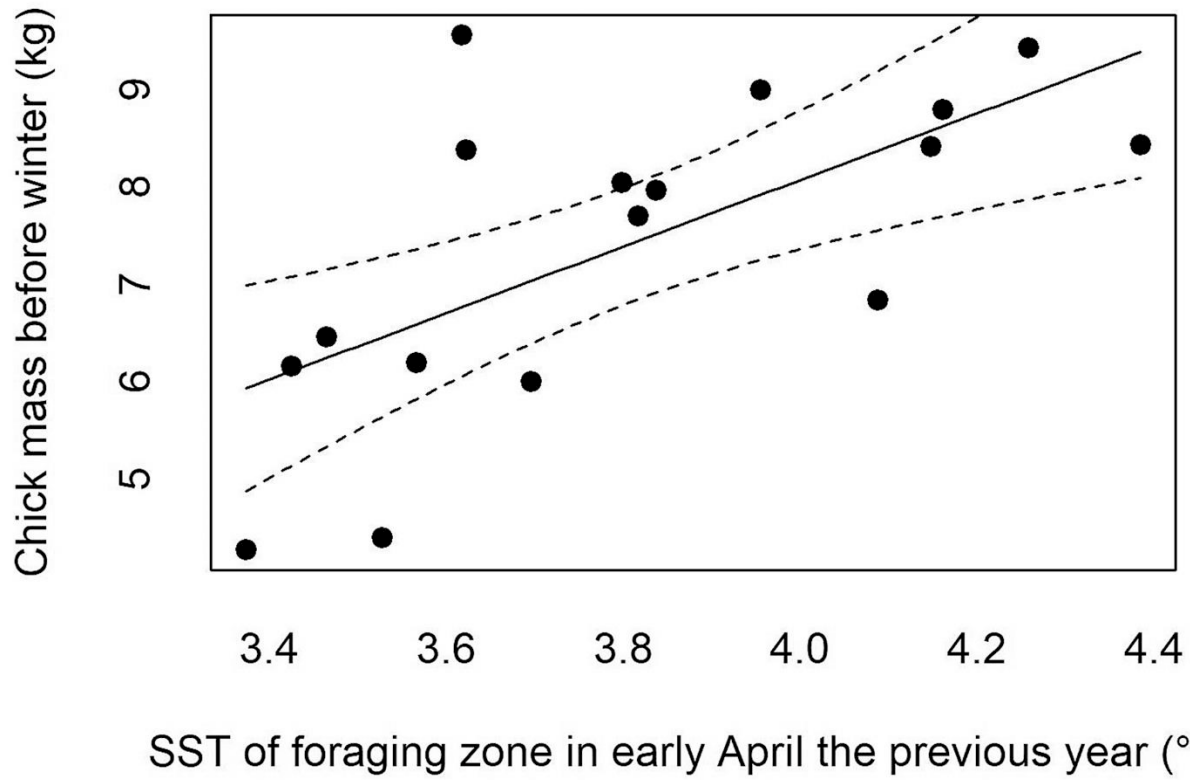


Figure 7.3: Relationship between average annual chick mass before winter (April) and SST-1 year. The solid line represents a linear regression ($\text{Chick mass} = 3.4 \times \text{SST} - 5.6$, $p = .004$, $\text{adj. } R^2 = .39$). The dashed lines represent the 95% confidence intervals. SST, sea surface temperature.

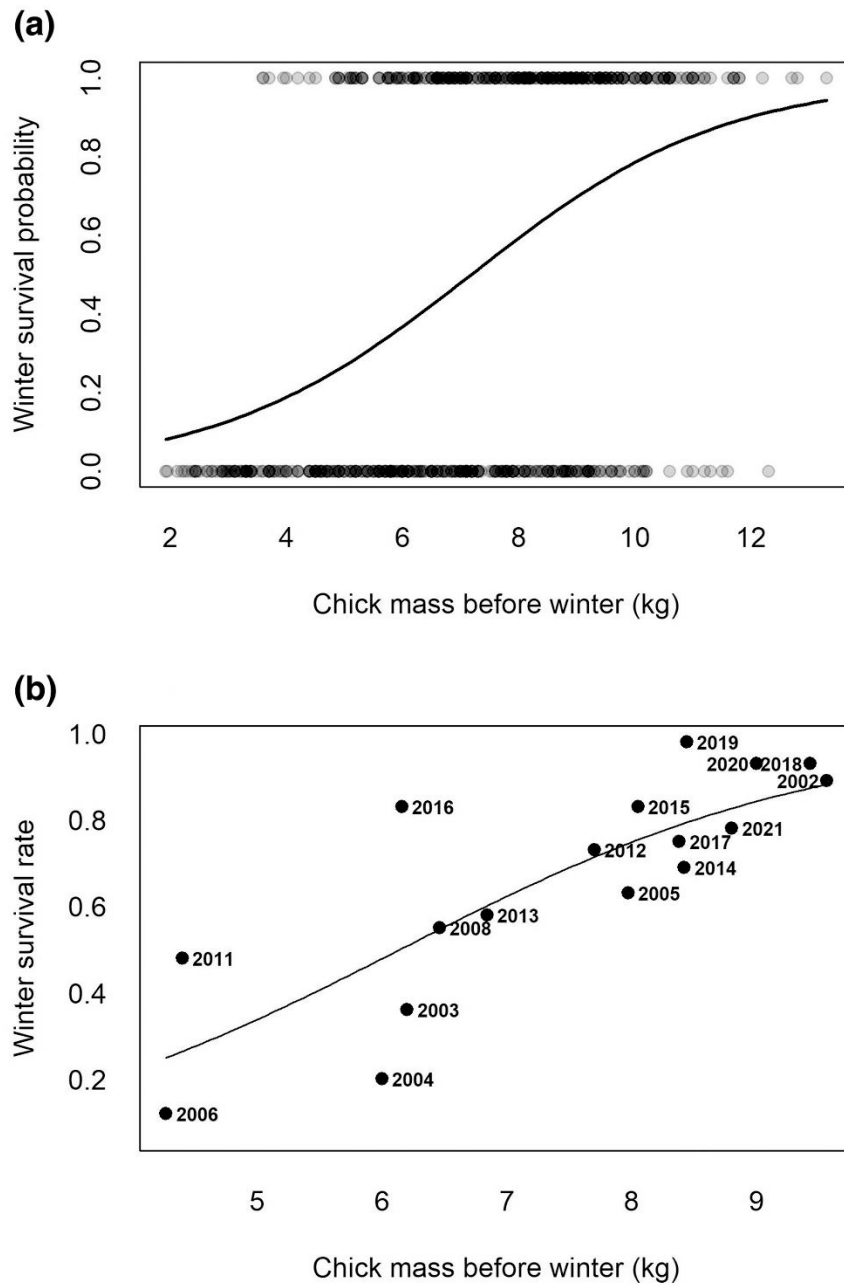


Figure 7.4: Effect of chick mass before winter on survival (a) at the individual level, where the solid line represents a logistic regression (survival probability = $1/[1 - e^{-(0.65 \times \text{chick mass} - 4.1)}]$), p value < .001) and (b) across years, where the solid line represents a beta regression ($\mu = 0.6$, $\Phi = 8.1$, p value < .001)

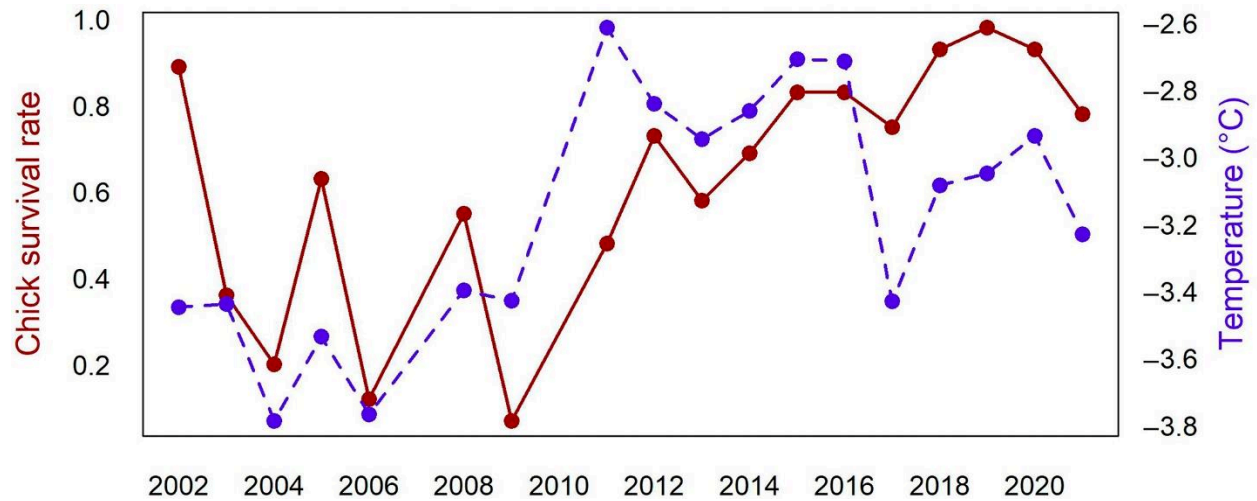


Figure 7.5: Temporal trends in the chick survival rate (in dark red) and the average winter temperature (accounting for wind chill, blue dashed line).

Discussion

Global warming and the increased occurrence of extreme warm ocean events is expected to have a strong impact on the marine ecosystem, with cascading effects reaching top predators (Frölicher et al., 2018; Frölicher & Laufkötter, 2018). However, the mechanisms of these effects are often elusive, as long-term marine studies remain scarce. We used a unique dataset spanning over 25 years and looked at the interaction between the physical climatic variables and the fitness of a circumpolar predator and link these interactions with possible cascading effects in the food webs.

Our results show that the breeding success of a marine predator, the king penguin, varied dramatically from year to year, mostly due to differences in climate. However, the climatic variables influencing breeding success in Kerguelen were not the same as in Crozet, its closest

neighbor. For instance, chick mass and survival were not influenced by shifts in the Polar Front position during warmer years, which was the case at Crozet. While chick-rearing king penguins at Kerguelen do feed at and beyond the Polar Front, the front displays inter-year position variation that is too small to affect chick-provisioning. Rather, we suggest that warmer climate might positively affect chick-provisioning penguins at Kerguelen by increasing prey abundance and/or growth. Winter wind chill at the colony also directly affected chick survival, with warmer conditions increasing survival rates. A graphical visualization of the air-temperature and ocean-temperature effects on the different stages of the king penguin reproduction cycle can be found in Figure 7.6. Our results help understand the mechanisms between climate and the fitness of a marine predator, as well as highlighting how these interactions can vary locally, creating distinct responses from different populations.

Foraging habitat selection

Previous studies suggested that low SST and cold subsurface layers (Winter Water) originating from Antarctica, found around the Southern Ocean at and south of the Polar Front, is an important feature for the foraging of king penguins (Charrassin & Bost, 2001; Scheffer et al., 2016). Our results support this, as shallower 2°C layers and colder SST were associated with more productive dives.

Because there is an abrupt change in density between the deeper Winter Water and the warmer surface water, nutrients and plankton are thought to accumulate at the frontier of these two layers, creating favourable conditions for penguins' prey, that is myctophids (G. Duhamel, unpublished; Park et al., 2014; Scheffer et al., 2010, 2016). When these layers are particularly

shallow, it might benefit the foraging success of the king penguins by bringing prey closer to the surface. Such is the case in the area South of the Polar Front—where an upwelling effect brings the Winter Water closer to the surface—and south-east of Kerguelen, past the Polar Front, where an offshore shoal deflects the Winter Water upward (Charrassin et al., 2002; Park et al., 2008). These two areas, the southern Polar Front boundary and the area to the south-east, were both targeted in all years by the foraging king penguins. Elsewhere around the sub-Antarctic region, king penguins also closely associated with these shallow cold layers upwelled by the Polar Front, as in South Georgia, Prince Edward Islands and Crozet archipelago (Bost et al., 2009; Pistorius et al., 2017; Pütz, 2002).

Comparison with Crozet

At Crozet, the Polar Front position ranged from 217 to 642 km away from the colony in 16 years (Bost et al., 2015, Table 7.1). This variation ($\Delta 425$ km) is almost a 10-fold difference compared the one observed at Kerguelen in our study ($\Delta 44$ km) using the 16-year CMEMS dataset, and surely a significant difference for a species that can theoretically only travel ~ 170 km a day. The stability of the Polar Front near Kerguelen is likely caused by the strong bathymetric features occurring there: the front passes in a narrow trench, with Kerguelen's island forming the northern boundary preventing the front from shifting Northward, and the Kerguelen-Heard plateau forming the equivalent southern boundary (Park et al., 2014, also see Figure 7.3). No such bathymetric features are present at Crozet, and so the front can more freely move with annual sea temperatures there (Pauthenet et al., 2018). In addition, the Polar Front passed 3–6 times closer to Kerguelen than Crozet in all years of the study. The proximity and stability of the Polar

Front at Kerguelen might explain why king penguins there do not have to travel as far as those at Crozet to reach the productive Winter Water zones during the brooding season (Table 7.1, also see

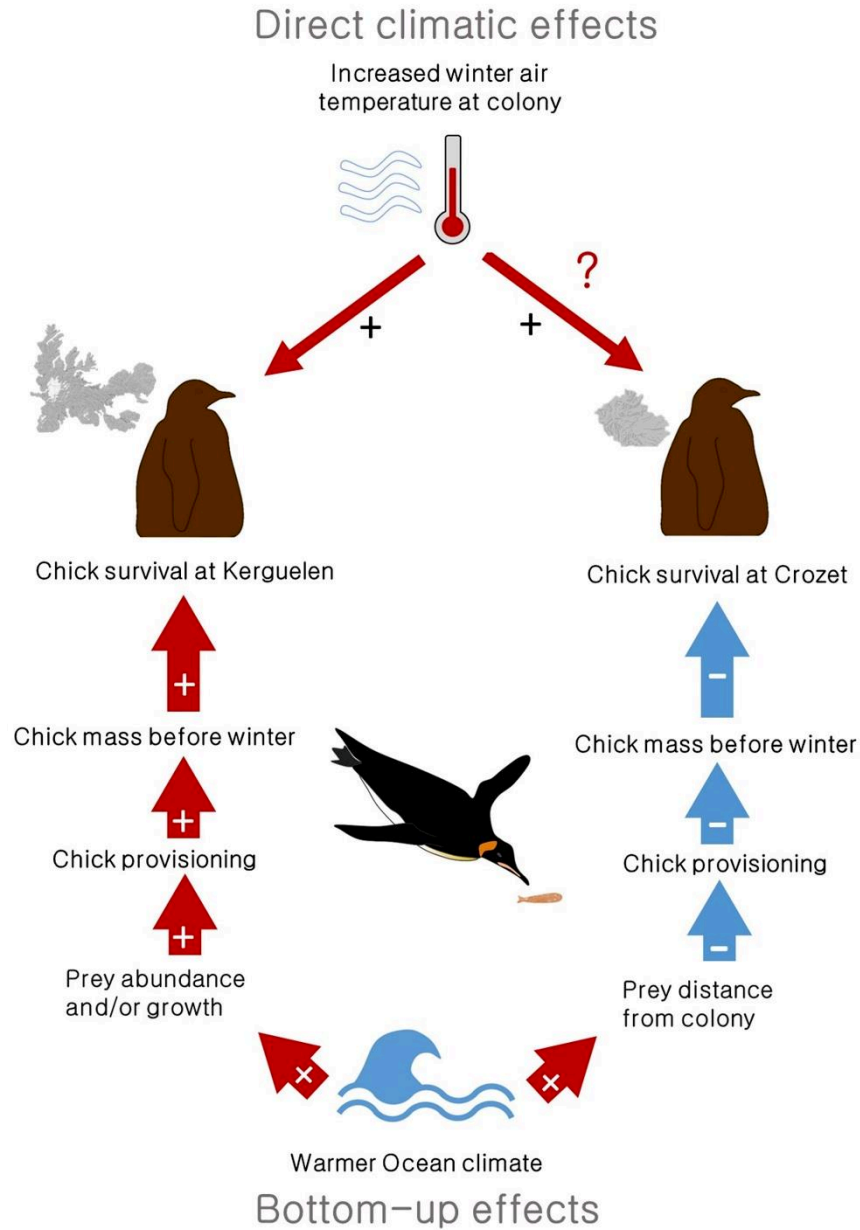


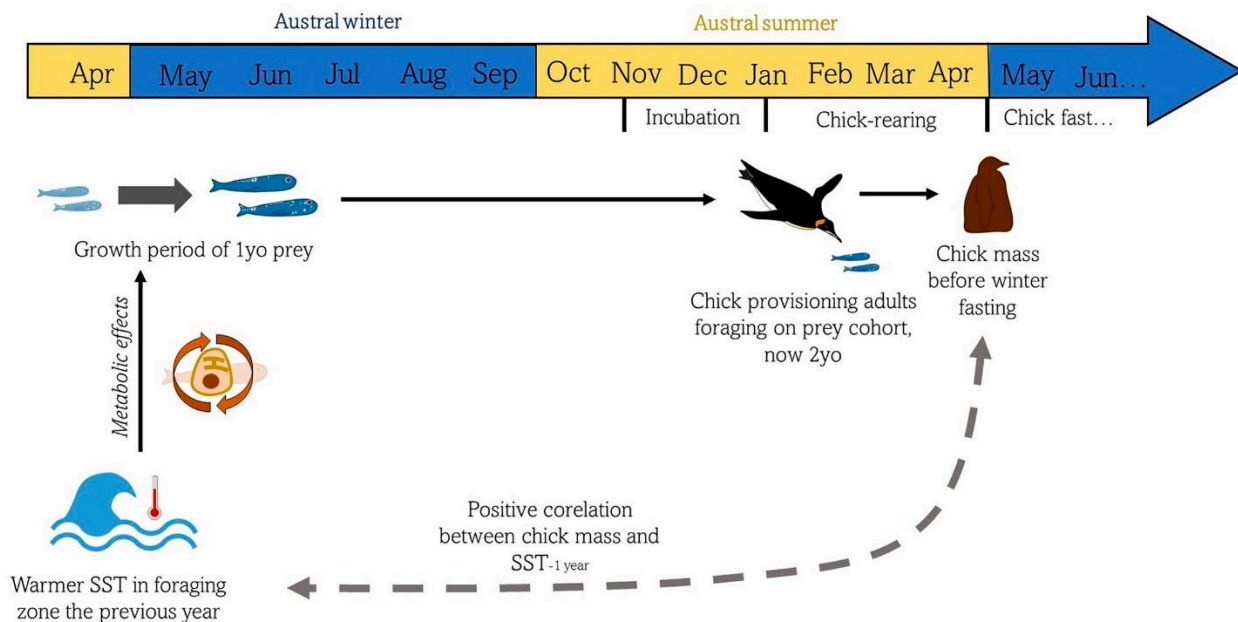
Figure 7.6: Conceptual diagram of the results at Kerguelen in contrast with the system at Crozet, with positive effects in red and negative effects in pale blue. Strong bottom-up effects dictate most of the variation of king penguin foraging and breeding success in both locations, but with opposite relationships to ocean warming. Top-down effects were also present at Kerguelen especially in winter, with warmer air temperature increasing chick survival. Although top-down effects on the

long-term breeding success of penguins were never investigated at Crozet, the ambient temperature optimum for winter chick metabolism is higher than the current air temperature, suggesting that warmer temperatures would likely generate similar benefits as in Kerguelen. However, these effects would likely be offset by the negative bottom-up effects of ocean warming on chick survival.

Duhamel et al., 2019; Duhamel & Welsford, 2011). As the foraging hotspots are consistently accessible to penguins in Kerguelen, prey distribution shifts caused by warmer climate are not likely to be a limiting factor like at Crozet.

Yet, there is still considerable annual differences in chick growth at Kerguelen, with the average mass before winter ranging from 4.4 ± 0.9 kg in 2006 to 9.6 ± 1.3 kg in 2002 (Figures 7.4 and 7.5). Such extreme differences suggest that adults can experience significantly different foraging conditions from year to year, despite what is shown by their foraging tracks. A possible explanation would be that, rather than being limited by prey distribution, the foraging success of brooding penguins at Kerguelen is dependent on prey abundance at the foraging location. Brooding penguins at Kerguelen primarily feed on 2-year-old myctophids *Krefftichthys anderssoni* measuring between 40 and 55 mm (Bost et al., 2002; Cherel & Ridoux, 1992; Lourenço et al., 2017; Saunders et al., 2020). The 2-year-old *K. anderssoni* cohort of a given year exited the larval stage and entered its maximum growth period in April the year prior (Saunders et al., 2020). This is also the period when SST was correlated with chick growth the following year. We propose that higher SST in April the year before positively might influences the 1-year-old cohort growth and/or survival of *K. anderssoni*, increasing foraging and breeding success of penguins the following year. It is not yet clear how exactly the mechanism of this correlation could operate, but

a possible explanation is through the metabolic enhancement of fish. Growth of many cold water fish has been shown to increase with temperature (Brander, 1995; Imsland et al., 2006; Nytrø et al., 2014). In the North Atlantic, Atlantic cod *Gadus morhua* were larger following warmer temperatures, especially for younger cohorts (Brander, 1995). Similarly, warmer conditions in Kerguelen could produce a larger 1-year-old *K. andersonni* cohort. The larger fish might also benefit from a better survival rate, and hence more food would be available for brooding penguins the following year when that same cohort is then 2 years old (Figure 7.7). This interpretation is further strengthened by the fact that the average size and abundance of *K. andersonni* can vary considerably between years (G. Duhamel, unpublished). It is also noteworthy that the maximum growth period of *K. andersonni* actually extends beyond April, and also occurs in May–July. While the correlation with chick mass was the highest with SST in April the year prior (when prey maximal growth starts), it was also significant in May and June, reinforcing this interpretation (Saunders et al., 2020). Further research using long-term prey data is needed to confirm this hypothesis.



*Figure 7.7: Proposed interpretation of the link between chick mass before winter and SST 1 year. High SST in April the year before could directly increase metabolism and positively influence the growth period of 1 year old prey (myctophid *Krefftichthys anderssoni*) during late fall to mid-winter (Saunders et al., 2020). By the following February, brooding foraging king penguins—which feed on 2-year-old prey (Bost et al., 2002; Cherel & Ridoux, 1992)—will benefit from a more abundant prey cohort, positively influencing chick provisioning and ultimately chick mass. SST, sea surface temperature.*

Population trend predictions

Many regions within the Southern Ocean have experienced warming in the last two decades (Bulgin et al., 2020). While the sea around both Crozet and Kerguelen have been spared from a steady temperature increase, the warmer episodes have been more dramatic in recent years. Worldwide, events of abnormally high ocean temperature have become more common, but little is known about how these extreme climatic events influence the ecosystem (Frölicher & Laufkötter, 2018).

In the eastern Southern Ocean, these high temperatures might have, to a certain degree, a positive effect on myctophid growth and/or survival. However, for top predators breeding in archipelagos such as Crozet's, the distance of the Polar Front is expected to double in the next century, ultimately creating poor foraging conditions (Péron et al., 2012). With climate change, it is therefore expected that marine predators at Crozet and other northern localities (e.g. Marion-Prince Edward islands) will experience a decrease in foraging and breeding success. This trend might already be visible: king penguin colonies at Crozet have experienced some of the strongest population declines for this species in the last decades (Barbraud et al., 2020; Delord et al., 2004; Le Bohec et al., 2008; Weimerskirch, Le Bouard, et al., 2018).

In contrast, chick survival and total population at Kerguelen have increased in the last decades, in synchrony with both ocean and air temperature warming (Barbraud et al., 2020). We have shown that warmer air temperature in winter could benefit the survival of penguin chicks during these crucial months. The same effect is also expected to be present at Crozet, as the average wind-chill temperature in winter there (-3°C) is lower than the ambient optimum for metabolism of winter-acclimated chicks (between -1°C and 9°C , Barré, 1976). Yet, the strong bottom-up effects at Crozet might outweigh any positive effects of air-temperature, so that the predicted lower breeding success of its king penguin population still holds (e.g. Le Bohec et al., 2008; Péron et al., 2012). This is especially true for the summer dynamic, when no significant direct effects of air temperature were detected—in contrast with other species (e.g. Adelie Penguin *Pygoscelis adeliae*) that experience colder summers—so that bottom-up effects are dominating during this period (Salihoglu et al., 2001).

The Crozet archipelago and Kerguelen Island hold the two largest populations of king penguins in the eastern hemisphere (Barbraud et al., 2020). Before 1980, Crozet held the largest population of king penguins in the world, but has since inexplicably reduced by more than half (Delord et al., 2004; Weimerskirch, Le Bouard, et al., 2018). Further warming of the foraging zone might apply additional pressure to this population. We predict that Kerguelen Island will replace the Crozet Archipelago as the stronghold for king penguins in the eastern hemisphere, as its high chick survival rates and foraging zone stability will create good conditions for further population increase. Other marine predators associated with the Polar Front have experienced similar trends—that is, a decrease in Crozet but an increase in Kerguelen—like the black-browed

albatross, but the exact reasons of the population trends are yet to be determined (Weimerskirch, Delord, et al., 2018).

For king penguin colonies located south of the Polar Front, as in South Georgia, we predict that populations will also increase. These colonies are not expected to be negatively affected by prey distribution shifts, as these shifts will occur towards the colonies rather than away as in Crozet. For this reason, colonies in South Georgia might benefit from the warming weather (increased chick winter survival, etc.) without the disadvantages, at least in the short term. Similar to Kerguelen, the king penguin population in South Georgia has experienced strong increase in the last decade (Foley et al., 2018).

Nonetheless, further monitoring at all colonies needs to be conducted, as the potential “beneficial” effects of warming might eventually be reduced, if not disappear completely, past a certain warming threshold. This is especially true for the ocean, where a certain degree of warming might approach the optimal conditions for prey, but further warming might bring the temperature away from that optimum. This might already be apparent in the Kerguelen area, where the correlation between SST-1 year and chick mass seems to have stabilised in the last 7–8 years (Figure 7.4). Air temperature warming could also eventually become detrimental for penguin chicks (e.g. Holt & Boersma, 2022). Maintaining the monitoring program in penguin colonies is needed to better assess any future non-linear association between marine predators of the Southern Ocean and climate change.

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Chapter 8: General discussion

Climate change has had strong influences on countless aspects of the ecosystems from the phenology of species to their foraging and breeding success. Yet, the effects of climate change can be very different from a species to another, making it complicated to predict trends at the ecosystem scale. This thesis provides a case study on the king penguin, reporting the direct and indirect effects of climate on this species. The advantage of this seabird as an indicator species is therefore assessed contingent on how we can interpret these effects regarding ecosystem changes. The use of biologgers was crucial to achieve these goals, and a novel application of accelerometers to assess foraging success was also described in the thesis. This work emphasizes the complexity of the interactions between climate, prey and predators.

Biologging : a tool to study climatic effects on diving seabirds

Biologgers are a must when it comes to studying foraging seabirds, especially deep-diving species (Watanabe & Papastamatiou 2023). All five data chapters were highly dependant on biologger data, such as GPS, accelerometers and depth-loggers. Understanding the effects of climate on the foraging of king penguins cannot be achieved without these technologies. Similarly, the use of king penguins as an indicator species is only possible with the help of biologgers. Yet, there are still many aspects of the king penguin's foraging that are seldom recorded, despite technologies capable of doing so. Often, the limitation of using biologgers is

that the link between what is recorded by the biollogger and the behavior of the animal is not always easy to interpret and often require complex experiments prior to application.

Accelerometers are among these unexploited technologies in king penguin studies. This thesis aimed to provide better interpretation for the use of this technology to assess prey capture rate, a key aspect of predators used in many studies (e.g. Thaxter et al. 2013, Ortega et al. 2020). In fact, the algorithm created in Chapter 3 was used in Chapter 7 to confirm the importance of the Polar Front for king penguins at Kerguelen. I hope that this new methodology will further improve research on the species, as well as providing a framework for developing similar methods on other diving species. While there are other species for which the link between accelerometry and behavior has been explored (e.g. Little blue penguins – Roper-Coudert et al. 2006, Steller sea lions – Viviant et al. 2010), the use of accelerometers remains vastly under-exploited in marine species.

Many other features of the foraging of king penguins were efficiently assessed in this thesis using different types of biologgers (GPS to reveal foraging distance, depth-loggers to reveal diving effort, etc.). Yet, there are still many aspects that could not be sampled in this thesis and that could benefit from the use of biologgers. For example, pioneer studies at Kerguelen have used stomach pumping, an accurate but invasive technique (Bost et al. 2002). Any long term effect of climate on the diet of king penguins would have to be conducted using camera-loggers. Models with powerful LEDs have recently been used on the much larger deep-diver, the elephant seal (Adachi et al. 2021). Smaller models would be promising for seabirds diving below the euphotic

zone. The use of sonars to detect prey captures (e.g. Goulet et al. 2019) is yet another avenue that will likely be possible on smaller avian species.

Indirect effects of climate

I found direct and indirect effects of climate on both the breeding and foraging success of king penguins. Direct effects have immediate impacts the animals, such as when a heatwave weakens or even kills individuals of a species (e.g. Holt & Boersma 2022). Indirect effects impact other organisms interacting with the animal, ultimately affecting the subject by altering these interactions. For example, warming events affected the food availability of common murrelets, influencing its foraging success (Piatt et al. 2020). In a potential indicator species, such as the king penguins and other marine predators, indirect effects are particularly of importance. Indeed, these effects reflect the cascading consequences of climate on the trophic levels below, rather than those only occurring on the species itself (see Cairns 1988). We can therefore assess information on the whole trophic web by looking at a single species, hence the “indicator” species.

In my thesis, the most apparent indirect effects I recorded were those of Chapter 7, where I showed that ocean temperature affects the foraging and breeding success of king penguins with a lag of one year. The underlying mechanism assumed behind this correlation was that higher temperatures increased the productivity in the area, benefiting the prey who would then be consumed by the breeding penguins the year after. This suggests that prey such as myctophids are not necessarily experiencing negative effects of climate change, at least for the moment. After

a given threshold, it might be expected to observe an opposite trend, with further warming negatively impacting the food web at Kerguelen. This is one of the main reasons to continue the monitoring of the foraging and breeding success of king penguins at Kerguelen, as any effects at lower trophic levels will be detected by the marine predators.

The delay in the arrival at the colony for the 2009 and 2010 breeding penguins reported in Chapter 6 might be another example of indirect effects of climate. It is suspected that winter 2009 was the period where king penguins started experiencing extremely poor conditions. At that time of the year, most penguins mainly forage for their own maintenance (Jouventin et al. 1994). Any problem occurring then must therefore come from the prey (e.g. reduced prey availability), which could subsequently affect the penguins. While the location of foraging waters was unveiled in Chapter 5, it is still unclear what could have affected the prey of that region. A climatic phenomenon is usually at cause in large prey depletions, along with fisheries interactions (e.g. Barbeaux et al. 2020, Piatt et al. 2020). Because the fishing industry of myctophids is currently marginal, a climatic anomaly becomes the top suspect. Unfortunately, I could not find any anomalies in the climate based on the available remote-sensing variables. Furthermore, the large-scale climatic index (El Nino and SAM) were average during that period. The link between the environment and their prey is sometimes complex, and Chapter 6 showed the limits of an indicator species: while the probable period of low prey availability was detected in winter 2009, the causes of this low prey availability remain cryptic with the available data.

The diet of an animal is another aspect that can change indirectly due to climate change. For example, reduced ice cover since the mid-1990s in Northeast Canadian waters caused the

thick-billed murre *Uria lomvia* to shift their prey from Arctic cod *Boreogadus saida*, a cold water species, to capelin *Mallotus villosus*, a species adapted to warmer climate (McKinney et al. 2023). In my thesis, I showed that king penguins have an invariable diet and feeding strategy, whatever the conditions encountered. They showed almost no plasticity in their isotopic nitrogen signature during the seven years with available data, indicating that they foraged on the same prey (or at least the same trophic position) over the years. The high energetic value of myctophid might explain the need for king penguin to maintain such specialized diet. It is unlikely that climate change will affect their diet, as king penguins might be more prone to increase their foraging effort (foraging distance, etc.) rather than targeting different, less energetically profitable, species. This might be problematic for populations such as Crozet, where myctophid schools vary greatly in their locations, following the annual position of the Polar Front (Bost et al. 2015). This population is indeed expected to increase their foraging range with climate change, to a point where their breeding success could be severely affected (Peron et al. 2012). In theory, a more generalist diet could prevent these breeding king penguins from travelling too far and experiencing low breeding success in warm years. As a general rule, generalist species tend to do better than specialists with climate change, as they can adapt their targeted prey depending on the available species, rather than being constrained with a narrow trophic niche (e.g. Terraube et al. 2011). Fortunately, the king penguins at Kerguelen are not expected to be as affected by climate change as those at Crozet, despite their narrow diet (as per Chapter 7).

Direct effects

Direct effects were detected in Chapter 7, where air temperature influenced the survival of chicks in winter. Direct effects are less of an interest for the use of an indicator species, because they do not provide information on the rest of the food web. However, they do provide insight on the response of the studied species to climate change and help us predict population trends.

At Kerguelen, higher air temperature increased chick survival in winter. This was at first surprising, because other warming events in penguins have caused die-offs in some cases, such as in the Megellanic penguin (Holt & Boersma 2022). However, these warming events occurred in summer and at higher latitude, where conditions are already quite warm. King penguins are the only species of penguins for which chicks are present at the colony throughout the winter, where temperatures drop below zero at this latitude. It is therefore compelling that chicks during this period are rather limited by the cold, especially since they fast throughout the period, with few opportunities to replenish any insolation lost through fat burning. Any slightly warmer temperatures and/or reduced wind speed during this period are thus likely to aid the chicks survive the winter, as I found. It is unclear however if further warming could cause a reversal of this trend, eventually leading to die-offs as in other species.

King penguins as an indicator species

My thesis helped understand the potential uses of a mesopelagic marine predator, the king penguin, as an indicator species. The contrast in the response to ocean warming between

the Crozet population and the Kerguelen population (Chapter 7) is extremely revealing on how the behavior and breeding success of this species can be used to compare different ecosystems. Indeed, indicator species are expected to mirror their environment through the different aspects of their life history (Rolstad et al. 2002). There is no doubt that long-term studies looking at the response of king penguins to climate – like those presented in this study or conducted at Crozet (Bost et al. 2015) – could provide useful information on the dynamics of the ecosystem in other regions, such as South Georgia, Falklands or Macquarie Islands. I will discuss in this section the different life history aspects that should be of interest for such use of the king penguin as an indicator species, considering the thesis' results.

Foraging distance: Foraging distance has been used an index of the foraging conditions: in years of bad conditions, king penguins are expected to forage further, as at Crozet (Bost et al. 2015). However, this metric is only valid if the foraging distance is a limiting factor for a given population. At Kerguelen, the foraging location did not seem to vary from year to year, so that the small variations of foraging distance observed were not necessarily a good proxy of the foraging conditions (see table S8.1, containing information initially included in Chapter 7 but removed in the review process). I therefore advise that an assessment of the variations of the foraging distance be made prior to any interpretation: if the year-to-year variations in foraging distances are quite small in a population (such as Kerguelen), the foraging distance likely does not necessarily reflect well the conditions. If, on the contrary, the year-to-year variations are considerable (such as Crozet), it is likely that the foraging distance is a limiting factor and can therefore be used to estimate foraging conditions.

Diet: The king penguin is a myctophid specialist (Olsson 1997, Bost et al. 2002). Furthermore, the population at Kerguelen does not vary greatly its targeted prey trophic levels depending on the conditions encountered. While some seabird species shift their diet following a change in the species composition due to climate change (e.g. thick-billed murre – Gaston et al. 2003; McKinney et al. 2023), the king penguin is unlikely to do so. The species' diet is therefore not a good indicator of the marine prey composition. However, because king penguins are absolute specialists, they compensate important changes in food stock through their foraging behavior. The foraging effort can therefore be used in certain conditions to assess myctophid availability in the ocean (see point above “Foraging distance”).

Phenology: The results of Chapter 6 showed that, following bad winters, king penguins can display significant delays in their arrival at the colony and laying date in spring. This could prove useful to detect changes in the environment occurring in the winter, a period when the marine habitat is otherwise extremely hard to sample. Mean egg laying date should be estimated yearly in all large king penguins colonies to provide more information on the previous winter conditions. This is still not done systematically, even at Kerguelen, where a more precise estimation of laying date has only recently been considered as an addition to the yearly monitoring program of king penguins.

Chick survival: Chick survival is often used in seabirds to assess the conditions at sea for a given year. Indeed, chick survival is often correlated with prey abundance in seabirds, especially in species with low offspring predation rates (Cairns 1988). This is also true for the king penguin, but many caveats need to be considered. Chapter 7 showed that there might be a lag of over a

year between the conditions at sea, the prey availability, and the chick response. This is an important consideration when interpreting years of low reproduction success. Furthermore, other factors not related to at-sea conditions can greatly influence penguin chick mortality, such as air temperature at the colony (also in Chapter 7). Finally, a delay in phenology (see previous section) can cause high chick mortality rates, but then the period when poor conditions are encountered by the foraging penguin (i.e. winter) is not the same as when chick mortality results from poor chick provisioning in the summer. Once more, it is advisable to record laying date as well as air temperature at the colony to better interpret chick mortality in king penguins and pinpoint which period is responsible for any low breeding success observed.

Number of prey captured: The number of prey captures in a dive can be used as a proxy for foraging success. This is especially true in a specialist such as the king penguin where the number of prey captured is expected to be highly correlated with energy intake. Foraging success can in turn be used to understand how foraging is affected by the different climatic variables. I suggest using accelerometry as a highly efficient tool to assess foraging success in the king penguin, which in turn can be used as an indicator for marine ecosystem health—or at least the abundance of myctophid fish, a key forage fish in the region.

Climatic effects at Kerguelen

As I advocated in the previous section and throughout the thesis, king penguins can be useful to understand the effects of climate on the marine environment around the sub-Antarctic. This also means that, in the light of my results, I can come up with predictions on how we can

expect the Kerguelen environment to respond to climate change. Indeed, both air and ocean warming are expected at Kerguelen, as well as an increase in positive El Niño and SAM events, which can transmit further heat in the surrounding marine system (Fogt & Marshall 2020). Based on the past response of king penguins to climatic variability, here are projections on certain aspects of the environment.

As seen in Chapter 7, the strong bathymetric features around Kerguelen provide a buffer for the effects of climate change on the currents and water masses. Not only has the Polar Front's position not varied much over the last decade because of this, but the prey availability has likely increased recently, as shown by an improved foraging and breeding success of the Kerguelen population. This is despite high sea surface temperature values recorded, strong El Niño events (such as in 2015-2016) and increasingly high SAM index. There is nothing to suggest yet that the marine community around myctophids will suffer in the short term from a further increase of these variables, but caution must remain as "threshold" values can rapidly turn trends around (Newbold et al. 2020). Ongoing monitoring of the king penguins at Kerguelen is crucial to continue assessing the ecosystem's health.

Projections regarding the area further offshore from the Kerguelen Plateau, such as the marine area visited by the king penguin in winter, are a bit more uncertain. Results of Chapter 6 showed that, while large-scale depletions are likely to sporadically occur, there are few explanations on the cause of these phenomena. Neither SAM nor El Niño seemed to have been the cause of the mysterious winter 2009 anomaly, but unknown climate and/or oceanographic features could have nonetheless triggered a prey depletion in some way. Because the climate

variables responsible are not known, it is impossible to assess whether climate change will increase or decrease the likeliness of such events. As far as we know, no such anomaly has occurred since 2010. Further monitoring is fundamental to better understand the dynamics of this region and to better predict future trends. These trends might, in turn, depend how humanity manages (or not) to reduce carbon emissions and limit global warming (e.g. the Paris Agreement's Long Term Temperature Goal of 1.5°C).

Limitations and future directions

Using a long-term, 25-year dataset (which started when I was a toddler!) provided a unique opportunity for me to understand the links between the climate, the prey, and the marine predators such as the king penguin. This dataset covered a large spectrum of the life history of penguins, using GPS data, diving data, chick mass data and chick survival data. However, there are still additional aspects that could be incorporated into the long-term data collection program to further understand the missing links between the behavior of the penguin and the environment.

Laying date: As established in Chapter 6, laying date can provide useful information about the at-sea conditions. Precise lay date estimates are not part of the long-term monitoring program at Kerguelen. For Chapter 6, only a qualitative description was provided using colony counts. While this is enough to detect extreme delays in the phenology, such as in 2010, it is not precise enough to detect small or even medium delays in laying date. Having better laying date estimates using the existing methods (e.g. Hinke et al. 2018) is also needed to understand the link between

the climate and the phenology of king penguins, which I did not manage to uncover in this thesis. This could be accomplished by time-lapse photography, with a camera setup to take a photo every few hours for the entire season, or possibly via satellite imagery. These types of information might go a long way towards filling gaps throughout the year at a colony where frequent visits are unlikely to ever be possible.

Prey capture rate: Using accelerometry to detect long-term trends in prey capture rate could prove beneficial to understanding how climate affects the foraging behavior of king penguins. It could also prove useful to detecting shifts of the productive foraging area. Accelerometers have been deployed on king penguins since 2019, which is too early yet to detect long-term trends, or make associations with climatic variables. In this thesis, accelerometry was only used to assess general preferences of the king penguins in relation to the Polar Front, but no inter-year comparisons could be obtained in relation to the climate. It is planned that accelerometry data collection be permanently implemented in the program. I am strongly in favor of this decision.

Prey data: It is often difficult to assess the relationship between the climate and the different aspects of king penguins without collecting data on the missing link: prey availability. Fish-trawling data is often collected by the Marion Dufresne ship near Kerguelen, leading to collaborations such as in the Bost et al. (2002) study. Multi-year prey data would be useful to confirm, or refute, certain assumptions used in this thesis, such as those in Chapter 6 and Chapter 7 (and similar research – e.g. Scheffer et al. 2016).

Another thing to consider is that, even in a study using 25 years of data, the “abnormal” years are, by definition, very few. It is therefore crucial to collect as much as data as possible when these years do occur. It is usually discouraging to conduct fieldwork during these years, with high logger losses, high chick mortality, etc. In 2010, biollogger equipping was stopped to avoid further logger losses. Yet, the data collected from these years are of high scientific value and help us understand the mechanisms behind these anomalies. When resources allow, I advocate to increase sampling effort in colonies during abnormal years.

While the correlations that I observed are relevant in the timeframe of the dataset, one should remember that penguin behavior and population dynamics have been greatly fluctuating on a larger temporal scale. For instance, had this research been conducted over a century ago, when king penguins were heavily hunted, the correlations between penguin life history and the different factors of interest in my thesis (i.e. climate) would have probably been much different. My results are thus solely relevant in the present context, with a changing climate, but no hunting and no competition from fisheries.

Finally, I strongly advocate to monitor the different life-history aspects of the king penguin (as described in this thesis) on other colonies around the Sub-Antarctic region. Doing so would allow a global portrait of the changes occurring in the Southern Ocean. While some colonies are already thoroughly monitored, such as at Crozet, other colonies could probably benefit from increased research effort (e.g. South Georgia and Macquarie). I believe the resources invested in such programs would prove profitable in the long run.

Final conclusion

Using a long-term dataset, this thesis illuminated the effect of climate on king penguins breeding at a key locality, the Kerguelen archipelago, predicted population trends of the population, and provided tools to better use the species as an indicator species of the changes in the Sub-Antarctic region.

The thesis identified several aspects of the life history of king penguins that should be continued to be monitored in Kerguelen, or that should be implemented in the long-term monitoring program of other colonies around the Southern Ocean. These aspects are: diet (Chapter 4), phenology and pre-laying life history (Chapter 5 and Chapter 6), as well as foraging behavior and offspring survival during chick-rearing (Chapter 7). These aspects will help understand how climate affects the different regions of the Southern Ocean. We also provided a tool using accelerometry to better quantify the foraging success of penguins at-sea (Chapter 3), which could prove useful to such monitoring programs.

In the end, if there is one thing that I wish the reader should remember after reading this thesis, it is that the marine ecosystem is complex, and that long-term monitoring programs of key predators are not only valuable when conducted on single populations, but also across the species range. Indeed, different regions, species or even populations might react quite differently to climate change, and understanding these differences could help conservation and awareness efforts. Indicator species might facilitate the understand of these geographic variations, helping our understanding of the interactions between climate change and a fast changing environment.



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Supplementary material

Supplementary tables

Table S4.1: $\delta^{15}\text{N}$ values of alternate prey items of king penguins at Kerguelen, in comparison with the main prey, *Krefftichthys anderssoni*

Prey item	$\delta^{15}\text{N}$ (‰)	Source
<i>Krefftichthys anderssoni</i>	7.6 ± 0.2	Cherel et al. 2010
<i>Protomyctophum bolini</i>	9.2 ± 0.4	Cherel et al. 2010
<i>Electrona carlsbergi</i>	9.5 ± 0.2	Cherel et al. 2010
<i>Protomyctophum tenisoni</i>	8.1 ± 0.3	Cherel et al. 2010
<i>Protomyctophum andriashevi</i>	8.7 ± 0.4	Cherel et al. 2010
<i>Electrona antarctica</i>	8.9 ± 0.3	Cherel et al. 2010
<i>Martialia hyadesi</i>	7.7 ± 0.6	Cherel et al. 2011, Hobson & Cherel (2006)
<i>Gonatus antarcticus</i>	13.3 ± 0.5	Cherel et al. 2011, Hobson & Cherel (2006)

Table S4.2: Loggers used from 2015-2022

Model name	Company	Company location	Information recorded by logger			
			GPS	Depth	3D acceleration	Temperature
FastLoc	SirTrack Ltd	Havelock North, NZ	x			
PTT Kiwisat	SirTrack Ltd	Havelock North, NZ	x			
MK9	Wildlife Computer	Redmond, US		x		x
Axy-Trek	Technosmart	Colleverde, It	x	x	x	x
Axy 4 XS	Technosmart	Colleverde, It			x	

Table S4.3: deployment by year

Year	Deployment
2015	3 birds equipped with both FastLoc and Mk9
2016	2 birds equipped with both FastLoc and Mk9 2 bird equipped with FastLoc only
2017	7 birds equipped with both FastLoc and Mk9
2018	6 birds equipped with both FastLoc and Mk9
2020	3 birds equipped with both PTT Kiwisat and Mk9 4 birds equipped with Axy-Trek
2021	7 birds equipped with Axy-trek 3 birds equipped with MK9
2022	8 birds equipped with Axy-trek 7 birds equipped with both Axy 4XS and MK9

Table S4.4: Test for linear model assumptions for models reported in the study

Model	Mean of residuals	Pearson correlation test between residuals and independent variable	Autocorrelation coefficient of the residuals	Breush Pagan Test (Homoskedasticity of residuals)
$\delta^{13}\text{C} \sim$ Mean longitude of foraging dives ($^{\circ}$)	<0.0001	t = 3.873e-11 df = 32 p-value = 1	0.14	BP = 2.3353 df = 1 p-value = 0.1265
Mass \sim Foraging trip duration (days)	<0.0001	t = -1.167e-14 df = 48 p-value = 1	-0.13	BP = 1.1619 df = 1 p-value = 0.2811
PCA \sim Foraging trip duration (days)	<0.0001	t = 4.652 e-15 df = 26 p-value = 1	-0.31	BP = 0.55567 df = 1 p-value = 0.456

Table S4.5: ANOVA results to compare differences among years for isotopic signatures, foraging effort indices and foraging success indices

Variable	Degrees of freedom	F value	p-value
$\delta^{13}\text{C}$	6	7.375	<0.001
$\delta^{15}\text{N}$	6	2.971	0.01
Mean distance to colony	6	1.406	0.25
Trip duration	6	3.294	0.009
Mean depth	6	9.769	<0.001
Total vertical distance	6	5.196	<0.001
PCAs per day	2	2.088	0.15
Mass gained per day	6	1.049	0.41

Table S6.1: Sample size of loggers deployed during incubation

Year	Number of GPS/ARGOS equipped	Number of depth-loggers equipped
1998	4	0
1999	0	0
2000	0	0
2001	4	4
2002	0	0
2003	0	0
2004	0	0
2005	0	0
2006	3	3
2007	2	2
2008	3	2
2009	0	0
2010	8	2
2011	0	7
2012	0	0
2013	0	0
2014	12	7
2015	2	3
2016	0	0
2017	0	0
2018	0	0
2019	0	0
2020	0	0
2021	0	0
2022	5	7

Table S6.2. Reasons for differences between sample size of the different metrics and number of equipped individuals

Scenario	Reason
<i>Egg abandon rate sample size being higher than the number of equipped individuals</i>	<ul style="list-style-type: none"> - The nests of non-equipped individuals were monitored in 2010 and 2011 (see methods) - The nests of individuals equipped with loggers not used in this study (e.g. camera-loggers) were monitored and included in the study
<i>Egg abandon rate sample size being lower than the number of equipped individuals</i>	<ul style="list-style-type: none"> - Nest failure was sometimes unreported
<i>Trip length sample size being higher than the number of equipped individuals</i>	<ul style="list-style-type: none"> - The trip lengths of individuals equipped with loggers not used in this study (e.g. camera-loggers) were monitored and included in the study
<i>Mass gained/day sample size being lower than the number of equipped individuals</i>	<ul style="list-style-type: none"> - To weigh returning equipped penguins, the individuals had to be captured before their arrival at the nest. If penguins returned to the nest unnoticed, the logger was retrieved quickly while the bird was still incubating, to avoid disturbance at the nest. Hence, the mass could not be taken in that case.

Table S6.3: Sample size of loggers deployed during chick-rearing

Year	Number of GPS/ARGOS equipped	Number of depth-loggers equipped
1998	17	9
1999	6	4
2000	8	9
2001	3	4
2002	9	8
2003	8	6
2004	8	7
2005	4	5
2006	7	6
2007	4	5
2008	2	2
2009	4	13
2010	0	0
2011	6	1
2012	0	5
2013	6	6
2014	6	1
2015	3	4
2016	11	8
2017	7	9
2018	6	10
2019	4	6
2020	8	10
2021	11	16
2022	13	19

Table S7.1: Model selection explaining yearly individual-averaged maximum foraging distance

Model variables	AICc	ΔAICc
NULL	43.6	0.0
Year	47.2	3.6

Table S7.2: Model selection explaining the number of prey captures in a dive

Model variables	AICc	ΔAICc
SST + 2°C layer depth	-3414.2	0.0
SST + Thermocline depth	-3407.0	7.2
2°C layer depth	-3406.7	7.5
Thermocline depth + 2°C layer depth	-3399.4	14.8
SSH	-3375.9	38.3
NULL	-3343.9	70.3
Thermocline depth	-3336.4	77.8

Table S7.3: Model selection explaining the number of prey captures in a dive, with prey depletion effect taken into account

Model variables	AICc	ΔAICc
SST + Distance colony	-3450.0	0.0
2°C layer depth + Distance colony	-3444.2	5.8
SST + Thermocline depth + Distance colony	-3443.8	6.2
Thermocline depth + Distance colony	-3442.5	7.5
SSH + Distance colony	-3441.8	8.2
SST + 2°C layer depth + Distance to colony	-3441.0	9.0
NULL	-3343.9	106.1

Table S7.4: Model selection explaining chick mass before winter

Model variables	AICc	ΔAICc
SST _{-1 year}	43.6	0.0
NULL	47.2	3.6
Foraging distance	48.4	4.8
SST	50.7	7.1
Air temperature	50.9	7.3
Distance of Polar Front	50.9	7.3

Table S7.5: Model selection explaining chick survival in winter

Model variables	AICc	ΔAICc
Winter air temperature + Chick mass before winter	-23.7	0.0
Chick mass before winter + year	-19.1	4.6
Chick mass before winter	-14.0	9.7
Air temperature	1.7	25.4
Year	-3.0	20.7
Winter air temperature	-0.8	22.9
Year + Winter air temperature	-0.6	23.1
NULL	1.7	25.4

Table S8.1: Summary of linear models explaining foraging success across years using foraging distance as the explanatory variable

Response variable	Explanatory variable	p-value of explanatory variable	R² of model
Mass of chicks in fall	Maximum foraging distance	0.99	<0.01
Wiggles per day	Maximum foraging distance	0.30	0.05

Supplementary figures

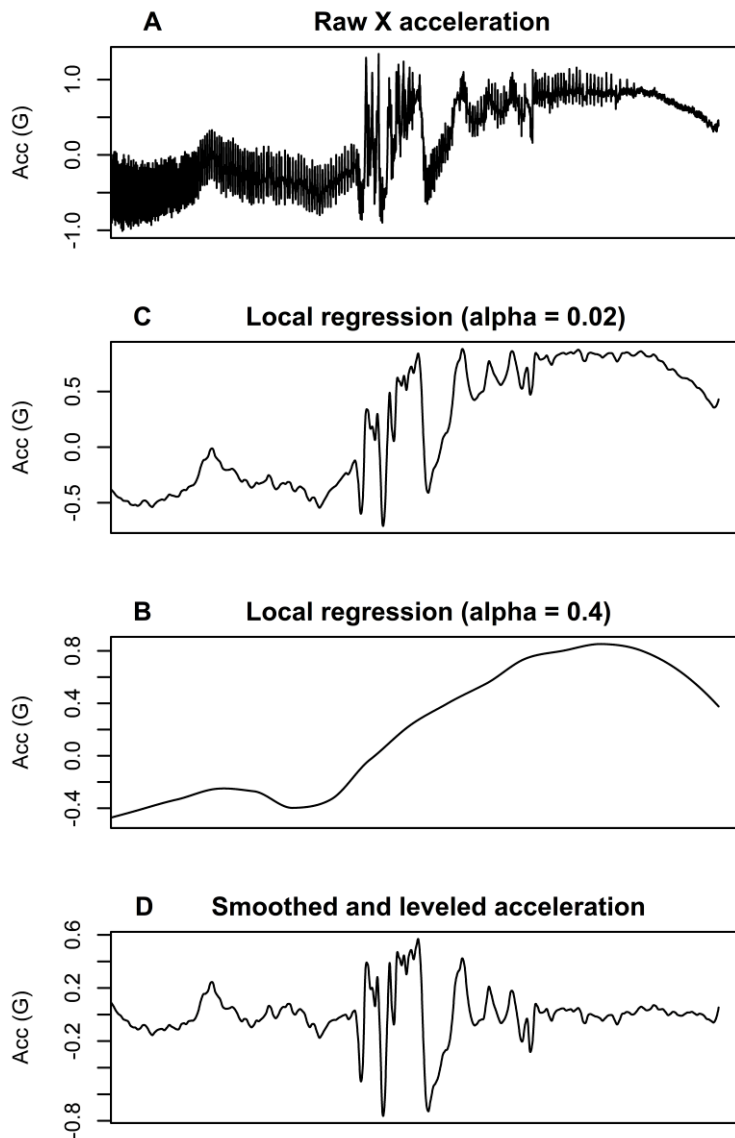


Figure S3.1: Filtering process of the X-axis acceleration. Raw acceleration (A) is first finely smoothed with a local regression ($\alpha=0.02$) to remove the wing beat noise (B). In parallel, a coarser local regression ($\alpha=0.4$) to obtain general trends in acceleration due to pitch changes is also applied (C). The final output is obtained by subtracting the B graph with the C graph, thus removing pitch effect and wing beat effect, and leaving only acceleration presumably associated with prey capture (D)

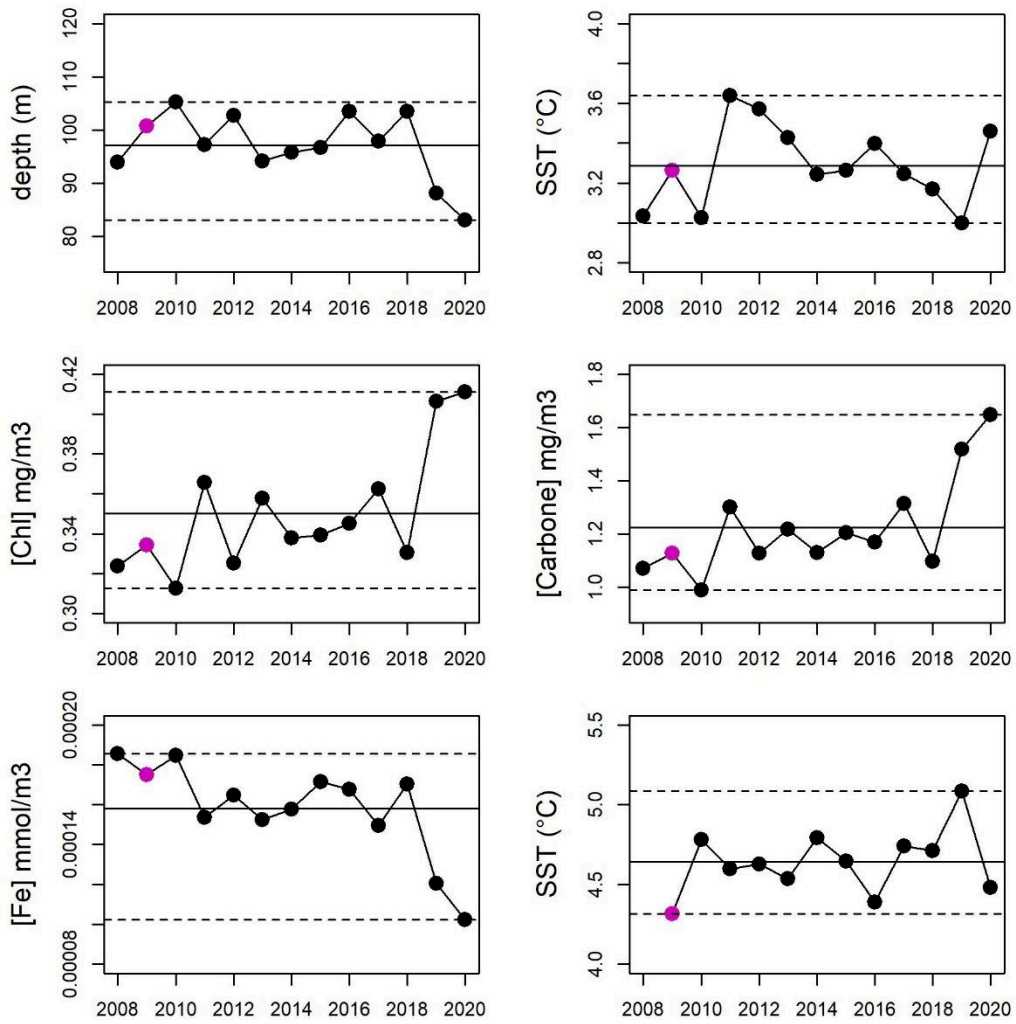


Figure S5.0: This is the updated figure 5.5 from Chapter 6, looking at winter environmental variables east of the island instead of south (based on the results of Chapter 5). The rest of Chapter 6 is exactly as published.

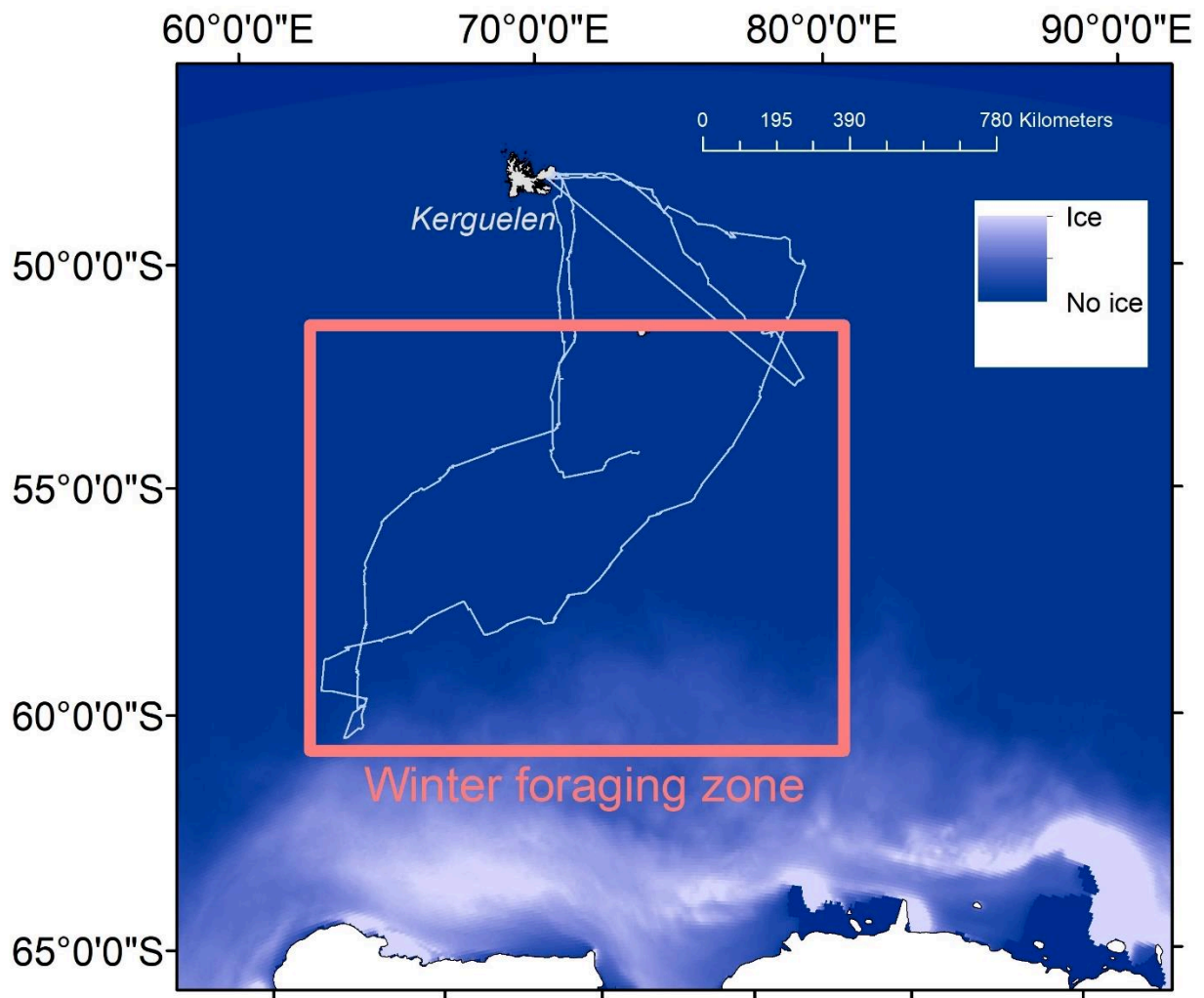


Figure S6.1: Winter foraging location based on three king penguins equipped with ARGOS Splash tags from Wildlife Computers (Redmont, US). These results are expected to be published in a separate paper in 2024. Map created using ArcGIS Pro 3.1. Country contour lines downloaded from <http://tapiquen-sig.jimdo.com> (Carlos Efraín Porto Tapiquén. Orogénesis Soluciones Geográficas. Porlamar, Venezuela 2015. Based on shapes from Environmental Systems Research Institute. Free Distribution).

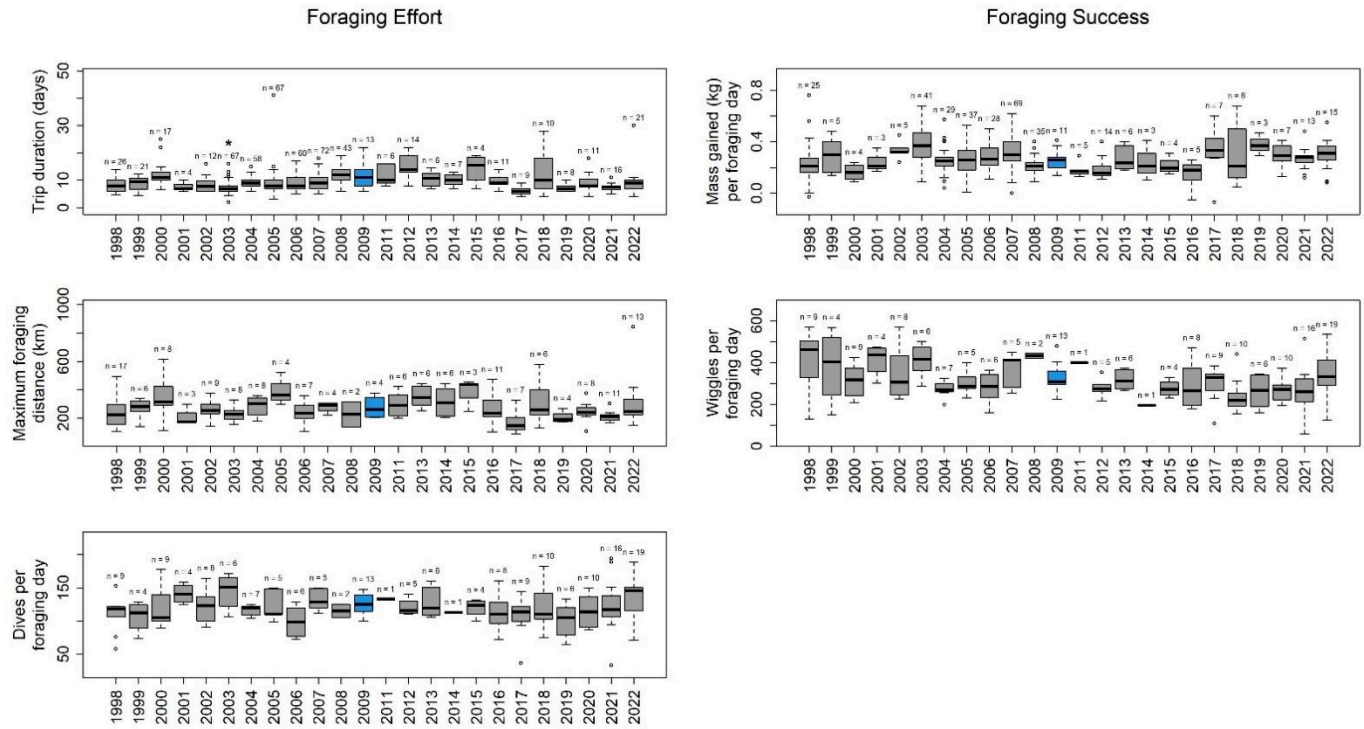


Figure S6.2: Foraging effort (left) and foraging success (right) variables during chick-rearing. The year 2009 is highlighted in red. Asterisks are displayed above years that are significantly different from 2009 (Tukey's Test).

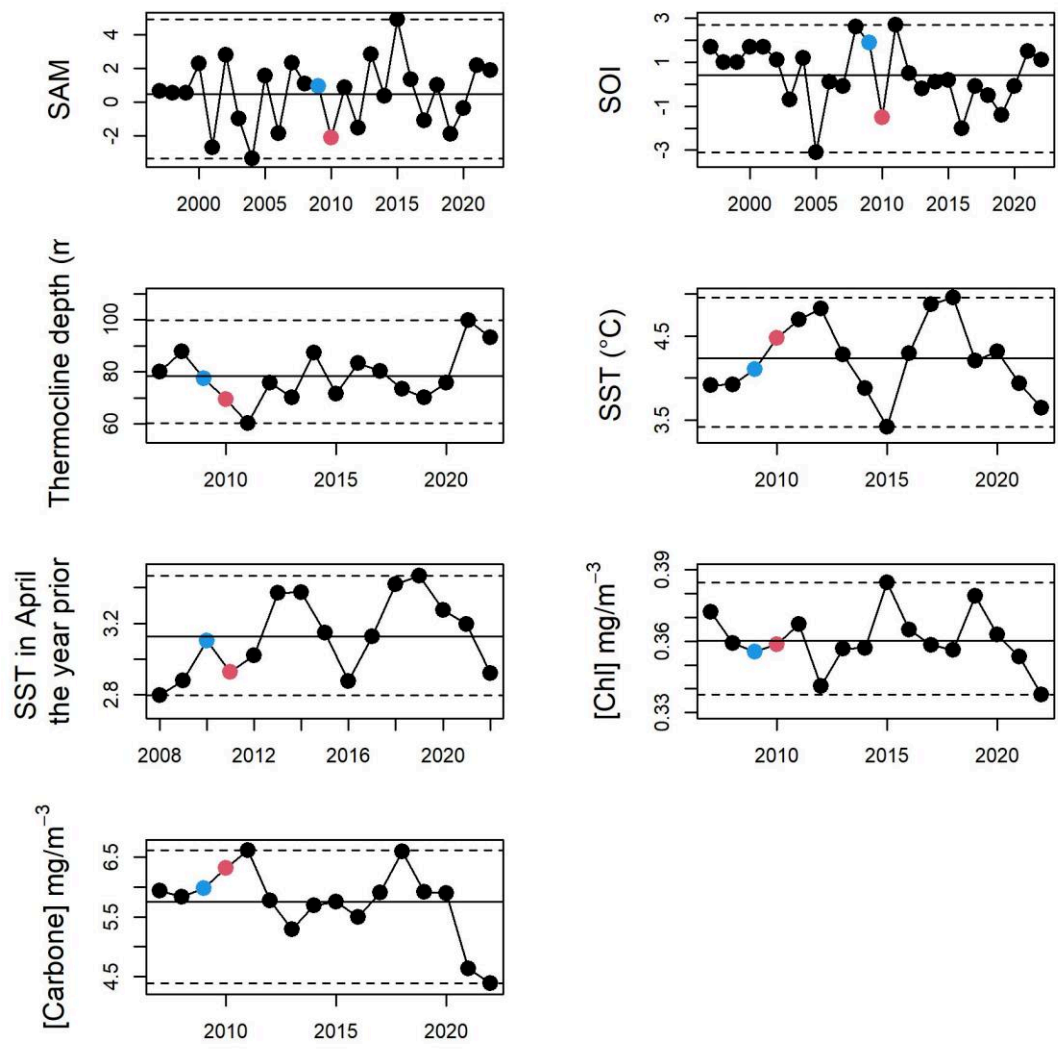


Fig S5.3: Environmental variables in the foraging zone during February 2009 (blue) and 2010 (red) in comparison with other years from the dataset (black). Maximum and minimum values are represented by a dotted line. Sea ice was not shown, as it is absent from the foraging zone in summer.

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