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Aymeric Fromant. The ecology and niche segregation of diving petrels. Agricultural sciences. Université de La Rochelle; Deakin university (Geelong, Australie), 2022. English. NNT : 2022LAROS017 . tel-03959129

HAL Id: tel-03959129

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LA ROCHELLE UNIVERSITE

ÉCOLE DOCTORALE

-
618

Laboratoire CEBC

THÈSE

présentée par :

Aymeric FROMANT

soutenue le 28 mars 2022
pour l'obtention du grade de Docteur de La Rochelle Université en co-tutelle avec
l'Université de Deakin, Australie

Discipline : Biologie de l'environnement, des populations, écologie

L'écologie et la ségrégation de niche chez les pétrels plongeurs

JURY :

Christel LEFRANCOIS	Professeure, La Rochelle Université, Présidente du jury
Matt RAYNER	Curator of Terrestrial Mammals, Université d'Auckland, Rapporteur
Brendon DUNPHY	Senior Lecturer, Université d'Auckland, Rapporteur
Nicholas CARLILE	Senior Scientist, Office of Heritage and Environment, Rapporteur
Charles-André BOST	Directeur de recherche CNRS, La Rochelle Université, Directeur de thèse
John ARNOULD	Professeur, Université de Deakin, Directeur de thèse
Pierrick BOCHER	Maître de conférences, La Rochelle Université
Vincent RIDOUX	Professeur, La Rochelle Université

The ecology and niche segregation of diving petrels

by

Aymeric Fromant

BSc (Ecology) and MSc (Marine Science)

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University (Australia),

in cotutelle with Université de La Rochelle (France) école doctorale Euclide.

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Preface

The ethical procedures were conducted in accordance with the guidelines, and approval, of the Deakin University Animal Ethics Committee (B16-2017) and conducted under Wildlife Research Permits (100084552) of the Department of Environment, Land, Water and Planning (Victoria). Fieldwork conducted at Kerguelen Islands was authorised by the Comité d’Ethique Polaire (CEP 13/6/2017). This work was included in the research programm “Oiseaux Plongeurs” Prog. No.394, funded and logistically supported by IPEV (Institut Polaire Français Paul Emile Victor).

This project was supported financially by research grants provided by BirdLife Australia, Sea World Research and Rescue Foundation Inc., the Centre for Integrative Ecology at Deakin University, the Museum of New Zealand Te Papa Tongarewa, the Institut Polaire Français Paul Emile Victor, and the Terres Australes et Antarctiques Françaises.

The present thesis opens with a general introduction to the work in Chapter 1. The core chapters (Chapters 2-5) are data-chapters published (Chapters 2, 3 and 4), or submitted (Chapter 5) for publication in peer-reviewed journals. Lastly, Chapter 6 forms the General Discussion of the main findings of the study.

I am the primary contributor to all aspects of the work presented in this study, and John P.Y Arnould and Charles A. Bost (supervisors) are co-authors on the resulting publications for providing guidance and assistance in all aspects of this PhD. Karine Delord provided helpful advices and assistance with GPS and GLS data analysis in Chapters 3, 4 and/or 5. Yves Cherel, Paco Bustamante, Alice Carravieri and Maud Brault-Favrou contributed to the stable isotopes analysis presented in Chapters 3, 4 and/or 5. Jonathan A. Botha contributed to the habitat modelling analysis in Chapter 4. Akiko Kato and Grace Sutton contributed to the dive and accelerometry data analysis in Chapter 5. Finally, Yonina H, Eizenberg, Colin M. Miskelly,

Arnaud Lec'hvien and Brett R. Gardner helped for the fieldwork and manuscript editing in Chapters 2, 3, 4 and/or 5.

Publications arising from this body of work:

- **Fromant A**, Miskelly CM, Arnould JP, Bost CA (2020) Artificial burrows as a tool for long-term studies of diving petrels. *Polar Biology* 43(5):435-442. (**Chapter 2**) (see Annex 1 – Authorship Statement). <https://doi.org/10.1007/s00300-020-02645-y>
- **Fromant A**, Bost CA, Bustamante P, Carravieri A, Cherel Y, Delord K, Eizenberg YH, Miskelly CM, Arnould JP (2020) Temporal and spatial differences in the post-breeding behaviour of a ubiquitous Southern Hemisphere seabird, the common diving petrel. *Royal Society open science* 7(11):200670. (**Chapter 3**) (see Annex 1 – Authorship Statement). <https://doi.org/10.1098/rsos.200670>
- **Fromant A**, Delord K, Bost C-A, Eizenberg YH, Botha JA, Cherel Y, Bustamante P, Gardner BR, Brault-Favrou M, Lec'hvien A, Arnould JPY (2021) Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird. *Progress in Oceanography* 198:102676. (**Chapter 4**) (see Annex 1 – Authorship Statement). <https://doi.org/10.1016/j.pocean.2021.102676>
- **Fromant A**, Arnould JPY, Delord K, Sutton GJ, Carravieri A, Bustamante P, Miskelly CM, Kato A, Brault-Favrou M, Cherel Y, Bost C-A (2022) Stage-dependent niche segregation: insights from a multi-dimensional approach of two sympatric seabirds. *Oecologia* 199:537-548. (**Chapter 5**) (see Annex 1 – Authorship Statement). <https://doi.org/10.1007/s00442-022-05181-0>
- **Fromant A**, Schumann N, Dann P, Cherel Y, Arnould JPY (2020) Trophic niches of a seabird assemblage in Bass Strait, south-eastern Australia. *PeerJ* 8,e8700. <https://doi.org/10.7717/peerj.8700>

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- Beal M, [...], **Fromant A** et al. Quantifying annual spatial consistency in breeding seabirds: is one year of tracking data sufficient for identifying important sites for conservation? Under review in Biological Conservation
- **Fromant A**, Eizenberg YH, T Poupart, Bustamante P, Arnould JPY (2022) Year-round at-sea movements of fairy prions from south-eastern Australia. Royal Society Open Science 9(5):220134. <https://doi.org/10.1098/rsos.220134>

Acknowledgments / Remerciements

During this PhD, part of the fieldwork was conducted on Wamoon country, and I would like to acknowledge the Boon Wurrung, Bunurong and Gunaikurnai people who are the Traditional Custodians of this land. I would also like to pay respect to the Elders past, present and emerging.

Ngāti Toa have mana whenua over Mana Island, and are acknowledged for their ongoing support for seabird conservation and research there.

I would like to express my gratitude to my supervisors, John Arnould and Charly Bost. You both put a lot of effort towards this/these project(s). Your personal investment and your eternal support made this journey feel like an easy and straight forward diving petrel migration towards the ocean of knowledge. Thank you for sharing your experience and passion for marine wildlife and its conservation. You made an amazing complementary team, always keeping the vessel afloat, and safely navigating through my stubbornness. Charly, your good words brought light in the darkness of chapters, and made the plonplons and jojos the new stars of the southern sky. John, you always lead me to do my best, and pushed me to explore the true meaning of science.

As majestic as you are, there is an incredible forest of mentors behind the respectful trees that supervisors are. Karine Delord, you play a key role in this ecosystem. You have been a continuous technical, scientific and mental support, and I greatly thank you for that. Colin Miskelly, your field experience and adventure stories are legendary, and I really hope that we'll share a dandelion salad again. And before everything began, there were Alice Carravieri, Yves Cherel and Paco Bustamante. You are the core of my love for science, you brought to me the taste of curiosity and the light of rigor.

During this project, there was a lot of fieldwork, and during this lot of fieldwork, there were a lot of people, amazing people, that made this adventure meaningful. First there is

Kerguelen, 15 months between the rest of the mission 65 (e.g. Joris), the mission 66 (e.g. Alexis, Pierre, Arnaud Popchat, Hoel, Aurore, Jessy, Colombe, Meggy and Camille), the mission 67 (e.g. Ernest and Sameul), and 5 months with the mission 68 (e.g. Juju and Uiui). The love of the TAAF family can make everyone fly, even elephant seals. And then, there is one year on Kanowna, the way out of lockdown, where help came from the four corners of the globe. Thank you, Seb, Gaëtan, Marine, Aude, Tim, Louarn, Fanny, Chloé, Théo, Ruth, Popchat, Jono, Brett and Yoni, for energetically but gently fisting all these burrows.

My gratitude also goes to the many people I met before, along, and after!?! this journey at Chizé (Baptiste, Gaëtan, Alice, Olivia, Julien, William, Sophie, Juliette, Alex, Martin, Candice, Oban, Ryan, Carine, and Moul), à la maison (Jean & Alice, Guigui, Cédric & Céleste, Julien & Stéphanie, Lorrain & Céline), and in Australia (Liam, Bell, Colin, Catan, MJ & AG, Paul & Alizee, Tim, Brett & Tesh, Grace & Jono, Surfboard, Susie & the boys, Flip & Floyd, Cátia, Hannah, Mei, Oli, Micheal, Cal & Bec, Miles, Maya & Sam, Jency & Mitch and so many others). I feel extremely lucky to share my life with you, and every day learn from you, except about Vegemite... I am thankful that Australia is only an island, which have kept the rest of the world safe from this curse.

Doing most of my PhD 17 000 km away from my home friends and family could have been a real challenge. But I have been so warmly welcomed in Australia, that it would be lying to say so. In particular, I would like to express my love to the Eizenberg family, who always made me feel welcome in their nest, and most of all, showed me the unexpected quality of the Australian snow. The culture, the kindness, the loved shared, the love of sharing, and the renowned quality of their puns was exemplified by one individual in particular, Yoni. We always say that a PhD is a journey, ending somewhere in Research Harbour, when the boat moors to the postdocs. But science will not be the destination, there is none. For the last three years, you have been more than an unconditional support. This journey could have been a

colourless voyage into the eerie maze of fundamental ecology, and instead became a firework of human adventures where learning was like discovering new colours. Thank you for growing with me.

Et pour finir, je voulais remercier ma famille, qui m'a donné la curiosité d'aller voir au-delà. La famille Fromant est très éclectique, dans ses caractères et ses chemins, et faire une thèse est une belle aventure parmi tant d'autres. Merci de m'avoir fait découvrir la nature, de la biologie des animaux jusqu'à l'âme des arbres. Merci à ma Maman pour toujours avoir été là quand j'en avais besoin, et pour me laisser découvrir le monde sans retenir le lien qui nous unit. Merci à mon Papa pour avoir apporté une touche artistique et de poésie à la connaissance. Tu aurais aimé écouter le bruit du sol quand les oiseaux sont à la maison. Cette thèse est pour toi.

And finally, before jumping into the depths of this thesis, I would like to acknowledge the cost of science to the environment. Collecting data on remote islands implies heavy logistic processes. The important induced carbon footprint highlights the need to achieve the best use of data collected, and reduce the ecological impact of unpublished data.

And like Jean-Michel the philosopher once said: "Everything is possible"

Abstract

Understanding the ecological niche of species is a fundamental pillar in ecology, defined as a hyper-volume within a N-dimensional niche space. Although knowledge of a species' ecological niche is among the most rudimentary information required for conservation assessments and environment monitoring, its constant adjustment along temporal and spatial gradients exacerbates the difficulty in defining this multi-dimensional space. Exploring a species' ecological niche entails investigating at multiple scales, as different environmental threats and niche constraints between intra-species levels may lead to important ecological and conservation consequences.

While Procellariiform seabirds occupy a wide range of ecological niches, due to multiple human-induced threats they face throughout their range, this order is one of the most endangered avian groups. Although the threatened status of the group has boosted the gathering of data to put in place conservation management actions, not all species have received the same attention. Whereas studies on large and easily accessible species have benefited from the development of animal-borne data loggers for more than three decades, small cryptic species (storm petrels, prions and diving petrels) have been excluded from this mine of knowledge. The absence of precise information about their at-sea distribution or foraging ecology has greatly limited ecological niche modelling studies, directly impacting our ability to delineate proper conservation planning.

Recent technological advancements in the miniaturisation of data loggers have now made it possible to collect data on the ecological niche of small procellariiform species. In the present study, a combination of Global Positioning System (GPS), time-depth recorder (TDR), accelerometer, light-level geolocators (GLS) and isotopic analyses were used to investigate the ecological niche of the common (CDP) and the South-Georgian (SGDP) diving petrels. Specifically, the primary objectives of this research project were to: 1) describe the fine scale

foraging ecology of these two diving petrel species during the breeding (incubation and chick-rearing) and non-breeding periods; 2) investigate the inter-annual variations in their ecological niche; 3) determine the ecological differences between populations throughout the Southern Ocean; and 4) study the variations in their foraging ecology throughout the entire annual-cycle in the context of niche segregation between two sibling species.

The results demonstrated that diving petrels exhibit remarkable flying abilities despite their high wing loading, foraging over large areas during the breeding season, and migrating several thousands of kilometres from their colony during the post-breeding period. A multi-population analyses revealed important ecological differences throughout the large distribution of CDP, particularly in terms of phenology and migration area. Although variation in the small species' ecological niche between different environments were expected, the major differences observed in the distribution of CDP support the relevance of multi-population studies. Collecting data over several years substantially strengthens results and provides valuable information to understand the variations and the limits of diving petrel ecological niches. Finally, a stage-dependent and context-dependent niche segregation analysis between CDP and SGDP demonstrated the importance of a multi-tool approach to better describe and understand the co-existence of ecologically similar species.

Focusing on species such as diving petrels, with high foraging constraints and feeding on low trophic-level prey, could help to disentangle the underlying mechanisms of long-term adaptation to climate change. Considering the wide geographic distribution (longitudinal and latitudinal gradients) of the CDP and SGDP throughout different environments of the Southern Hemisphere, these abundant seabirds could act as suitable environmental sentinels to monitor the effects of changing oceanographic conditions.

Résumé

Le concept de niche écologique est un pilier fondamental de l'écologie, définie comme un hyper-volume au sein d'un espace à N-dimensions. Bien qu'étudier la niche écologique d'une espèce soit parmi les informations les plus rudimentaires requises dans le cadre de plans de conservation et de suivi de l'environnement, son ajustement constant le long des gradients temporels et spatiaux exacerbe la difficulté à définir cet espace multidimensionnel. L'exploration de la niche écologique d'une espèce implique une enquête à plusieurs échelles, car différentes contraintes et menaces environnementales aux niveaux inter- et intra-espèce peuvent avoir d'importantes conséquences écologiques et de conservation.

Alors que les procellariiformes occupent un large éventail de niches écologiques, cet ordre est l'un des groupes aviaires les plus menacés, principalement en raison des multiples menaces liées aux activités humaines. Bien que ce statut, de groupe menacé, ait stimulé la collecte de données pour mettre en place des actions de gestion et de conservation, toutes les espèces n'ont pas reçu la même attention. Alors que les études sur les espèces de grande taille et facilement accessibles ont bénéficié du développement technologique de balises pendant plus de trois décennies, les petites espèces cryptiques (océanites, prions et pétrels plongeurs) ont été exclues de cette mine de connaissances. L'absence d'informations précises sur leur distribution en mer ou leur écologie d'alimentation a considérablement limité les études de modélisation de niche écologique, ce qui a un impact direct sur notre capacité à délimiter des programmes de conservation appropriés.

Les récents progrès technologiques dans la miniaturisation des enregistreurs de données ont maintenant permis de collecter des données sur la niche écologique des plus petites espèces de procellariiformes. Dans la présente étude, une combinaison de système de positionnement global (GPS), d'enregistreur de plongée (TDR), d'accéléromètre, de géolocalisateurs (GLS) et d'analyses isotopiques a été utilisée pour étudier la niche écologique du pétrel plongeur

commun (CDP) et de Géorgie du Sud (SGDP). Plus précisément, les principaux objectifs de ce projet de recherche étaient de : 1) décrire l'écologie d'alimentation à petite échelle de ces deux espèces de pétrels plongeurs pendant les périodes de reproduction (incubation et élevage des poussins) et de non-reproduction; 2) étudier les variations inter-annuelles de leur niche écologique ; 3) déterminer les différences écologiques entre les populations de l'océan Austral ; et 4) étudier les variations de leur écologie alimentaire tout au long du cycle annuel dans le contexte de la ségrégation trophique entre deux espèces jumelles.

Les résultats ont démontré que les pétrels plongeurs présentent des capacités de vol remarquables malgré leur charge alaire élevée, se nourrissant de vastes zones pendant la période de reproduction et migrant à plusieurs milliers de kilomètres de leur colonie pendant la période post-reproduction. Une analyse de plusieurs populations a révélé d'importantes variations écologiques au sein des différentes populations de CDP, en particulier en termes de phénologie et de zone de migration. Bien que des variations de la niche écologique des petites espèces entre les différents milieux étaient attendues, les différences majeures observées dans la distribution du CDP soutiennent la pertinence des études inter-populationnelles. La collecte de données sur plusieurs années renforce considérablement les résultats et fournit des informations précieuses pour comprendre les variations et les limites des niches écologiques des pétrels plongeurs. Enfin, une analyse de la ségrégation trophique entre le CDP et le SGDP a démontré l'importance d'une approche intégrant plusieurs techniques et concepts pour mieux décrire et comprendre la coexistence d'espèces écologiquement similaires.

Se concentrer sur des espèces telles que les pétrels plongeurs, avec des contraintes d'alimentation élevées et se nourrissant de proies de faible niveau trophique, pourrait aider à démêler les mécanismes sous-jacents de l'adaptation à long terme au changement climatique. Compte tenu de la large répartition géographique (gradients longitudinaux et latitudinaux) du CDP et du SGDP dans différents environnements de l'hémisphère sud, ces oiseaux marins

pourraient agir comme des sentinelles environnementales appropriées pour évaluer les effets du changement climatique.

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Chapter 1:

General introduction



Photo: diving petrels (*Pelecanoides* sp.) in the Golfe du Morbihan, Kerguelen Archipelago

1.1. Niche concept in ecology

Species ecological niche is a fundamental pillar in ecology. It encompasses and links habitat, movement, behavioural and feeding ecology and is, therefore, defined as a hyper-volume within a N-dimensional niche space (Hutchinson 1957). Although knowledge of a species' ecological niche is among the most important information required for species conservation assessments and environment monitoring, its constant adjustment along temporal and spatial gradients exacerbates the difficulty in defining this multi-dimensional space (Calenge and Basille 2008). This is exemplified by the general contrast between the fundamental niche (the species' theoretical requirements to maintain a positive population growth; Pianka 2000) and the realized niche specific to population/sex/period (the actual niche occupied given biological and environmental constraints, such as morphology, energetic demand, food/habitat availability or competition; Pianka 2000). Exploring a species' ecological niche, therefore, entails investigating at multiple scales (both spatially and temporally), as different environmental threats and niche constraints between intra-species levels may lead to important ecological and conservation consequences.

Specifically, ecological niche is influenced by a combination of intrinsic and extrinsic factors (Begon et al. 1996). Variations in intrinsic factors, such as physiology, morphology or energy requirements can result in niche divergence between and within species (Pianka 2000). Difference in morphology and physiology between ecologically similar species is a key feature leading to divergence in fundamental niches. In allopatry, ecologically similar species may occupy the same niche, while in sympatry, their hyper-volume niches are shaped to avoid competition and enable species co-existence (Leibold and McPeck 2006, Levine and HilleRisLambers 2009, Flores-Escobar et al. 2020). Similar niche partitioning can also occur within a species, between sexes (Shine 1989), ages (Polis 1984) or morphologies (which is often related to sex or age; Smith and Skúlason 1996).

Niche specialisation generally occurs along one or more of the three main axes (Pianka 1974): space (forage in different environments); time (active at different times); and food (select different resources). In addition, the niche hyper-volume is likely to change temporally according to the variation in energy requirements related to different constraints of each discrete stage of the life cycle (Pianka 2000). In particular, central-place foragers often exhibit very different ecological niche between the breeding and the non-breeding periods. As a consequence of being tied to a breeding site, the requirements of reproduction constrain the foraging range while the energetic demand increases (e.g. Krebs and Davies 2009). Similarly, for number of animal groups, such as birds, moult can be a highly energetic process that strongly shapes a species ecological niche (Thiebot et al. 2014).

Extrinsic factors, like temporal or spatial variations in environmental conditions or resource availability, also influence species' ecological niche. Seasonal and inter-annual environmental variations dictate species foraging ecology (distribution and/or diet) (Barta et al. 2008), and strongly influence the timing and output of the breeding season (Haury et al. 1978). Such variations also affect the degree of niche segregation between species. A superabundance of prey may enable overlapping niches (Forero et al. 2004), while niche specialisation may indicate competition for limited food resources (Barger and Kitaysky 2012).

In addition, the different environmental conditions experienced by populations throughout a species distribution is likely to result in a large spectrum of ecological niches. Most notably, because species are distributed along a gradient of more or less favourable conditions, populations breeding at the extent of the species range are more likely to have to adapt their niche to maintain a positive population growth (Pianka 2000). Therefore, considering the large potential for ecological niche to vary at the species level, failing to consider intra-species ecology diversity may lead to a misunderstanding of the potential effects of local threats or environmental changes on population dynamics. Treating species as a stable

and uniform entity is likely to mislead species distribution and population dynamic models, and blur the effectiveness of conservation management (Durell 2000).

1.2. Marine environment and seabirds: constraints and benefits

Marine ecosystems are biologically complex, with each trophic level directly or indirectly affected by others (Doney et al. 2009). The abundance and distribution of marine organisms are determined by physical processes (Pakhomov et al. 1994, Pollard et al. 2002), constantly changing over various spatial and temporal scales (Zimmer and Butman 2000). Mesoscale variability and heterogeneity of such physical processes are particularly important in food web development (Lima et al. 2002).

As top predators, seabirds integrate marine food webs across space and time (Piatt et al. 2004), making them key indicators of marine ecosystem functioning. In the oceans, climate variability is linked to changes in water temperature, salinity, stratification, and current strength, which can result in modifications in primary productivity, food web dynamics, and shifts in prey distribution (Doney et al. 2012, Hoegh-Guldberg and Bruno 2010). Oceanic conditions affect the quality and quantity of prey availability and, in turn, influence the foraging behaviour and diet of seabirds (Durant et al. 2006, Bost et al. 2015).

Seabirds should optimize their feeding strategies in the patchy oceanic environment to maximize their net energy gain per unit of time and allocate sufficient energy to their reproduction and survival, i.e. maximise lifetime fitness (McArthur and Pianka 1966, Charnov 1976). As central-place foragers during the breeding season, the foraging periods of seabirds are defined by an outward movement to a foraging area and a return movement to the colony (Orians and Pearson 1979). Increasing the foraging range, due to prey depletion or shifts in prey location, may increase the energy cost of travel, impacting food deliveries to chicks and,

ultimately, threatening the reproductive success (Burke and Montevecchi 2009, Boersma and Rebstock 2009, Bost et al. 2015).

During the non-breeding period, most pelagic species have a much wider foraging range than during the breeding season, often migrating to completely different environments (Thiebot et al. 2012). This period plays a key role in population dynamics, as seabirds generally face a higher mortality rate during the non-breeding period than during the breeding season (Barbraud and Weimerskirch 2003). Particularly, the majority of seabird species partially or completely renew their plumage during the non-breeding period, which is an energetically demanding process that strongly constrains their niche during this critical period (Dunn et al. 2019, Takahashi et al. 2021). In addition, due to carry-over effects, the conditions encountered during the non-breeding period can also impact reproductive success in the following breeding season (Crossin et al. 2010, Shoji et al. 2015). Consequently, divergent environmental conditions experienced by species and populations throughout their migration and within the moulting areas may differentially influence demographic processes (Reynolds et al. 2011, Frederiksen et al. 2012). Variations of migratory and moult strategies between and within species may lead to long-term effects and carry important ecological and conservation implications (Price et al. 2020).

1.3. Procellariiformes: from large iconic species to small cryptic species

Seabirds forage in a patchy and dynamic environment where prey is unevenly distributed (Hunt 1990, Weimerskirch 2007). They occupy a wide range of ecological niches, feeding on planktonic species, fish or cephalopods, in benthic or pelagic environments, surface feeding or diving (Nelson 1979). Among them, the Procellariiformes constitute a widespread group of more than 130 species of pelagic seabirds (albatrosses, petrels, shearwaters) with about three-quarters occurring in the Southern Hemisphere (Marchant and Higgins 1990).

Procellariiform species are highly adapted to exploit the marine environment, foraging over large areas of the oceans. However, as a result of multiple human-induced threats they face throughout their range (e.g. introduction of invasive species, bycatch, and environmental pollution), the Order of Procellariiformes is one of the most endangered avian groups (Croxall et al. 2012).

Although the threatened status of the group has boosted the gathering of data to put in place conservation management actions (Barbraud et al. 2008), not all species have received the same attention (Rodríguez et al. 2019). Studies on large and easily accessible species (albatrosses, large petrels and shearwaters) have benefited from the development of animal-borne data loggers for more than three decades. However, small cryptic species (storm petrels, prions and diving petrels) have been excluded from this mine of knowledge, mostly due to technological limitation (size and shape of the equipment). The absence of precise information about their at-sea distribution or foraging ecology has greatly limited ecological niche modelling studies, which directly impacts our ability to delineate proper conservation planning (Rodríguez et al. 2019).

The recent miniaturisation of biologgers has, nonetheless, substantially increased the number of small seabird species for which at sea ecology have been successfully investigated (BirdLife International Seabird Tracking Database 2021). Over the last 10 years, light-level geolocators (GLS), Global Positioning System (GPS) and time-depth recorder (TDR) have provided detailed knowledge on the ecological niche of some of the smallest procellariiform species (e.g. Navarro et al. 2013). Yet, the gain of these remarkable technological improvements remains limited for the less accessible species. Indeed, in addition to breeding on remote islands, storm-petrels, prions and diving petrels all nest in small cavities, crevices or fragile burrows (Brooke 2004), which further complicates the monitoring of such species. The high risk of damaging the burrows, when accessing the nest for deployment/retrieval of data

loggers, is a major factor contributing to the limited number of studies of small Procellariiformes (Barbraud et al. 2020). This, combined with their cryptic behaviour (visiting their colonies at night) and high mobility at sea, contributes to the discrepancy of knowledge between the large iconic species and the ubiquitous, yet overlooked, small-sized procellariiform seabirds.

In addition to conservation and management aspects, collecting data about the biology and ecology of small-sized procellariiform species may also be of important ecological interest. As burrowing birds, they are essential ecological engineers of the terrestrial ecosystems (Warham 1996). Mechanical effects on the soil structure and imports of nutrients greatly contribute to island terrestrial ecosystem richness (Polis and Hurd 1996). This pivotal role is strongly supported by the high number of breeding pairs structuring the island systems where their breeding colonies are located (e.g. Barbraud and Delord 2006). Although the size of their burrow and the import of nutrients per individual are limited, small-sized species largely exceed the rest of the procellariiform seabirds by number and biomass. For example, at Kerguelen (Southern Indian Ocean), while only 8 of the 24 Procellariiformes breeding on the archipelago are small species (< 200 g), they represent more than 90% of the breeding pairs (Weimerskirch et al. 1989) and 65% of the biomass of this avian group. This fundamental role of ecological engineers occurs in tandem with their substantial influence on marine ecosystems, consuming nearly 50% of the crustacean biomass eaten by all the seabirds of the archipelago (including the super-abundant subantarctic krill-eating penguins) (Guinet et al. 1996).

As key species, small-procellariiform species may represent valuable models to monitor their environment. In particular, Procellariiformes are long-lived and highly philopatric, central-place foragers during the breeding season, and often migrate to specific areas during the non-breeding periods (Quillfeldt et al. 2015a). They are, therefore, good indicators of the condition of marine ecosystems during the entire year (Barbraud and

Weimerskirch 2003). In contrast to studying large iconic species with high trophic level and large foraging range (Boersma 2008), monitoring species feeding locally and in low trophic levels may help to better understand the link between seabird parameters and the variation in oceanographic conditions (Grémillet and Charmantier 2010). Species feeding on low trophic levels, and with a restricted foraging range, are likely to be more affected by environmental variability, and quicker than upper level species (Furness and Tasker 2000, Hazen et al. 2019). Sensitivity to environmental changes, fast and detectable responses, make such species valuable ecosystem sentinels, clearly linking the indicator parameters with underlying processes.

1.4. Small procellariiforms: diving petrels as model species

Among the small species of Procellariiformes, diving petrels (*Pelecanoides* spp.) have a unique ecological niche. Their distinct morphology (small and compact body shape) (Fig. 1-1) enable strong diving capacities (Zavalaga and Jahncke 1997, Bocher et al. 2000a,b, Navarro et al. 2014, Dunphy et al. 2015) and flying abilities despite a high wing loading (Warham 1977, Rayner et al. 2017). Diving petrels are ubiquitous seabirds in the Southern Hemisphere, and exploit a large range of ecosystems from the Peruvian coast (8°S; Cristofari et al. 2019) to the Antarctic waters (55°S; Marchant and Higgins 1990) (Fig. 1-2). Throughout their large distribution range, diving petrels feed mostly on marine crustaceans (predominantly macrozooplankton: euphausiids and copepods) and fish larvae (Reid et al. 1997, Zavalaga and Jahncke 1997, Bocher et al. 2000a, Schumann et al. 2008, Fromant et al. 2020). Although the diversity in their habitat use and their unique ecological niche make diving petrels relevant species to monitor the marine environment, there are still considerable gaps in the knowledge of their population status (population estimates and trend) and their at-sea distribution and behavioural ecology.



Figure 1-1: Main photo: Adult common diving petrel (*Pelecanoides urinatrix*) captured on Mayes Island (Kerguelen Archipelago) and equipped with a miniaturized GPS (antenna visible on the right end side of the photo). The GPS was attached to two central tail feathers using water proof tape (see Methods in chapters 4 and 5). © A. Fromant.
Top left photo: Flying adult common diving petrel near Mana Island, New Zealand (© C.M. Miskelly).

Of the five recognized species of diving petrels, the Whenua Hou diving petrel (*Pelecanoides whenuahouensis*), which is listed as critically endangered on the IUCN Red List (BirdLife International 2021), is the only species that has received appropriate attention in determining clear population estimates and trends (mainly because there is only one population of about 200 individuals, breeding on a unique site) (Fischer and Tucker 2021). For the four other species, the Peruvian (*P. garnotii*), the Magellanic (*P. magellani*), the common (*P. urinatrix*) and the South Georgian (*P. georgicus*) diving petrels, population estimates are poor (BirdLife International 2021) despite recent isolated initiatives (Barbraud et al. 2020, Cristofari et al. 2019).

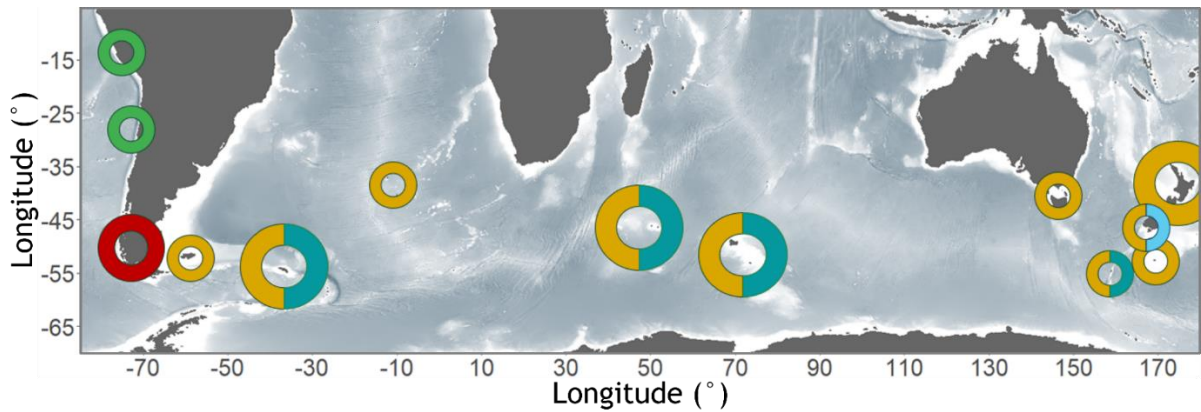


Figure 1-2: Distribution of the five identified species of diving petrels (*Pelecanoides* spp.).

From left to right, Peruvian (green; 20 000 to 25 000 breeding pairs, Red list Category: Near Threatened), Magellanic (red; 3 000 to 150 000 breeding pairs, Red list Category: Least Concern), common (yellow; 6 000 000 to 9 000 000 breeding pairs, Red list Category: Least Concern), South Georgian (dark blue; 5 000 000 to 8 000 000 breeding pairs, Red list Category: Least Concern), and Whenua Hou (light blue; 100 breeding pairs, Red list Category: Critically Endangered) diving petrels (BirdLife International 2021). Larger circles indicate the main populations. Shared circles correspond to species breeding in sympatry (common and South Georgian diving petrels; common and Whenua Hou diving petrels).

While obtaining precise population estimates remains a massive challenge for such cryptic species (Barbraud et al. 2020), robust nest monitoring may represent a first achievable step in order to study their population dynamics. Traditionally, the long-term monitoring of burrow-nesting seabirds implies checking the burrow content, often by hand or using a burrow-scope and playback (Parker and Rexer-Huber 2016). However, these techniques are poorly adapted for small species, breeding in narrow, convoluted and fragile burrows (Barbraud et al. 2020, Parker and Rexer-Huber 2016). Notably, the difficulty to access the nest increases biases such as uncertainty of burrow content or observer bias (Parker and Rexer-Huber 2016) but, overall, long-term regular checking damages the burrow structure and ultimately amplifies the risk of temporary or permanent abandonment (Marks and Leasure 1992). Artificial nest boxes may represent a useful tool to conduct robust long-term studies while limiting these negative impacts. While artificial burrows have been extensively used in conservation management (Ramos et al. 1997, Bolton et al. 2004, Bourgeois et al. 2015), their adaptation for long-term research projects on diving petrels remain to be explored.

In the last decade, deployments of GPS (Global Positioning System; Zavalaga and Alfaro-Shigueto 2018, Zhang et al. 2019, Dunphy et al. 2020), TDR (Time Depth Recorder; Navarro et al. 2014, Dunphy et al. 2015) and GLS (Global Location Sensor; Navarro et al. 2013, 2015, Rayner et al. 2017, Fischer et al. 2021) has started to reveal some aspects of the ecological niche of diving petrels, complementing the information gathered by stable isotope and diet studies (Reid et al. 1997, Bocher et al. 2000a, Cherel et al. 2006, 2014, Fromant et al. 2020a). Nevertheless, although these studies provided important knowledge to delineate the overall shape of the niche hyper-volume of diving petrels, the degree of variation between species, years, seasons, populations or sex remains unknown. Detailed knowledge about these variations will serve both conservation and environmental monitoring purposes.

In particular, the ubiquitous common and South Georgian diving petrels (hereafter CDP and SGDP, respectively), are the two most abundant species of the Genus *Pelacanooides*. The populations of both species exceed several million individuals (Brooke 2004) and are listed as “least concern” on the IUCN Red List (BirdLife International 2021). However, they have experienced multiple local extinctions and substantial habitat loss due to invasive rodents (Brothers 1984, Taylor et al. 2000, Rayner et al. 2017). In addition, while CDP and SGDP are largely distributed throughout the Southern Ocean (and in the sub-tropical waters for the CDP), their at-sea distribution is essentially unknown, especially in the Indian Ocean sector which hosts the largest proportion of the two species (Marchant and Higgins 1990)

For the breeding period, accurate data is limited to few recent studies exploring, during incubation only, the at-sea distribution of CDP (Zhang et al. 2019, Dunphy et al. 2020), or the diving behaviour of CDP and SGDP (Navarro et al. 2014, Dunphy et al. 2015). Additional data using capillary-tube depth gauges has also been collected, but this technique appears to be inaccurate and unreliable to describe the diving behaviour of seabirds (Burger and Wilson 1988, Elliot and Gaston 2009, Navarro et al. 2014). In parallel, two isolated studies have

investigated the distribution of CDP and SGDP during the non-breeding period (Navarro et al. 2015, Rayner et al. 2017). However, considering the large gradient of environments exploited by CDP and SGDP, expanding the knowledge of their ecology seems necessary to better describe their ecological niche at multiple scales (spatially and temporally). In particular, this implies determining their behaviour during the entire annual cycle, and investigating inter-annual and inter-population variations. In addition, CDP and SGDP are the only species of diving petrels breeding in sympatry throughout the Southern Ocean, which provide a unique opportunity to explore the niche segregation of two morphologically and ecologically similar species.

1.5. Objectives and structure of the thesis

The objectives of this PhD were to: 1) provide a tool facilitating long-term research on small-sized burrowing seabirds, the common and South Georgian diving petrels; 2) describe the fine scale foraging ecology of these two diving petrel species during the breeding (incubation and chick-rearing) and non-breeding periods; 3) investigate the inter-annual variations in their ecological niche; 4) determine the ecological differences between populations throughout the Southern Ocean; and 5) understanding the mechanisms in their foraging ecology throughout the entire annual-cycle allowing a trophic niche segregation and ultimately the co-existence of two sibling species, major consumers of the zooplankton stocks.

To achieve these objectives, multi-disciplinary data were obtained from two species of diving petrels: CDP from Kerguelen Islands (southern Indian Ocean; Ile Mayes, 49°28'S 69°57'E), south-eastern Australia (Kanowna Island; 39°10'S 148°16'E) and New Zealand (Mana Island; 41°06'S 174°46'E); and SGDP from Kerguelen Islands (Ile aux Cochons; 49°47'S 70°05'E) (Fig. 1-3). Miniaturized data loggers (GPS, TDR, accelerometer and GLS) were deployed on adult birds to gather information about at-sea movements (during the

breeding and non-breeding periods), diving behaviour and activity budget (during incubation and chick-rearing periods), while isotopic analyses of blood and feathers were used to investigate their trophic niche during the breeding (incubation and chick-rearing periods) and non-breeding periods, respectively. Multi-year data was gathered to improve the quality of the dataset and investigate inter-annual variations in diving petrels foraging niche.

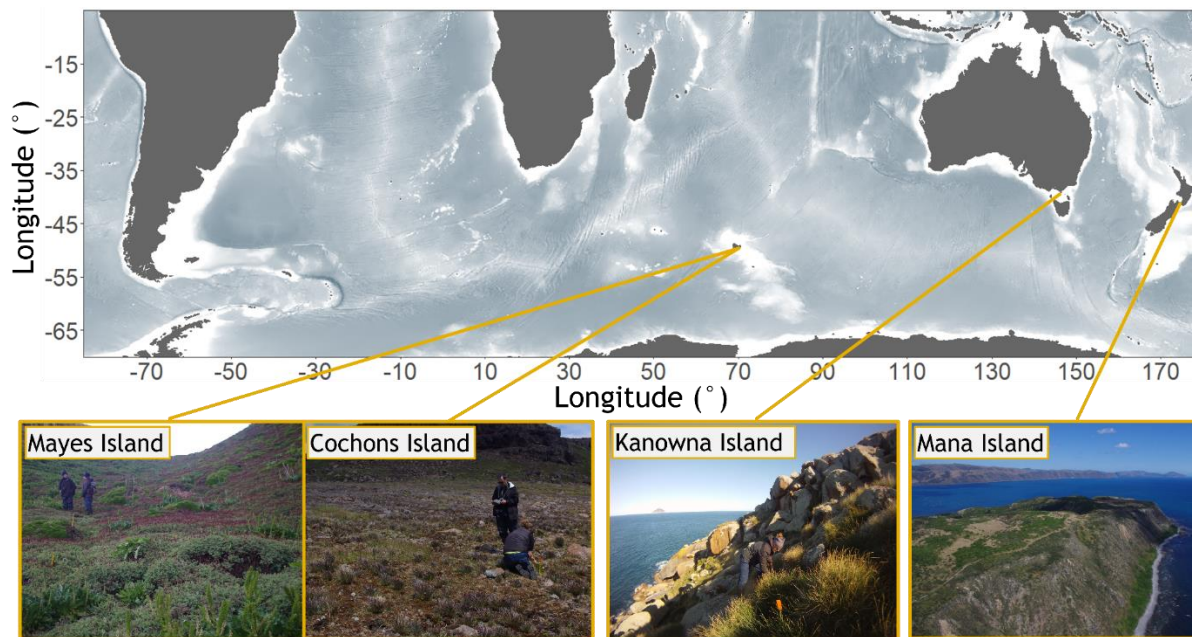


Figure 1-3: Study sites. Common diving petrels were studied from Mayes Island (Kerguelen Archipelago) (Chapters 2, 3, and 5), Kanowna Island (Australia) (Chapters 3 and 4) and Mana Island (New Zealand) (Chapter 3), and South Georgian diving petrels from Cochons Island (Kerguelen Archipelago) (Chapter 5). © C.M. Miskelly and B. Gardner.

This thesis is structured around one technical chapter and three data chapters that have been submitted, or published in peer-reviewed journals.

Chapter 2 evaluates the installation of artificial burrows as a tool to facilitate long-term research on small burrowing seabirds such as diving petrels. This describes a new technique using artificial burrows at existing CDP breeding burrows, and examines the effect of the conversion on chick growth and breeding success, burrow fidelity and occupancy.

Chapter 3 describes the post-breeding movements and timing of moult of CDP from three distantly separated populations in two basins in the Southern Hemisphere. By comparing

these results with three other localities in the Southern Atlantic and Pacific Oceans, this chapter explores the extent to which the timing and location of post-breeding movements contribute to the ecologically and evolutionary divergence of distinct populations of a ubiquitous seabird.

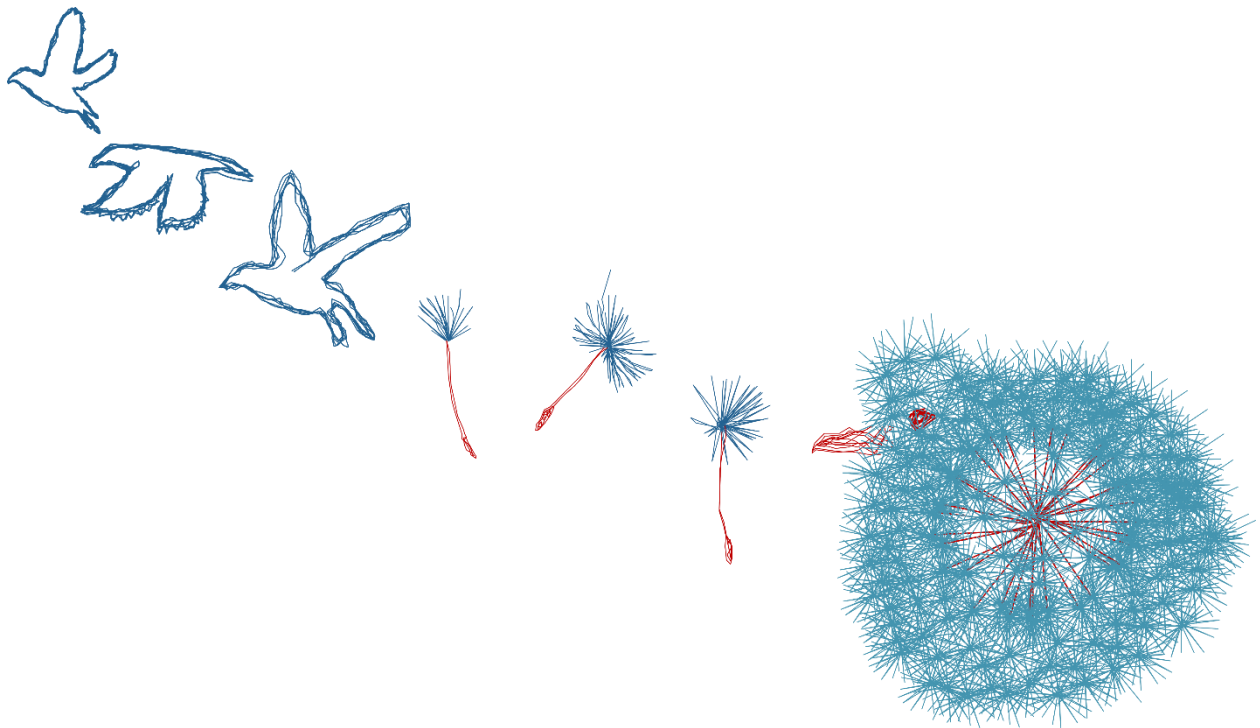
Chapter 4 documents the inter-annual variations over four successive breeding cycles in the breeding success, at-sea movements, foraging behaviour and trophic niche of the CDP in south-eastern Australia. Specifically, this chapter investigates the effect of marine heatwaves on CDP foraging and trophic ecology, and examine the links between such extreme events and the reproductive output of CDP in Bass Strait.

Chapter 5 provides insights into the niche use and partitioning of the morphologically and ecologically similar CDP and SGDP. Specifically, by combining at-sea movement, diving, accelerometer and isotopic datasets throughout their whole annual cycle, this chapter describes the variations in the degree of niche segregation, and investigates whether the processes leading to the niche partitioning are similar during the pre-breeding, incubation, chick-rearing and post-breeding periods.

Finally, chapter 6 (General Discussion) synthesises the insights gained from these preceding chapters, and discusses the spatial and temporal variations in diving petrels ecological niche, and explores the role of diving petrels as environmental indicators of the Southern Ocean.

Chapter 2

Artificial burrows as a tool for long-term studies of diving petrels



A version of this chapter was been published as:

Fromant A, Miskelly CM, Arnould JPY, Bost CA (2020) Artificial burrows as a tool for long-term studies of diving petrels. *Polar Biology* 43(5):435–442.

<https://doi.org/10.1007/s00300-020-02645-y>

2.1. Summary

Long-term studies are essential to determine demographic parameters and population trends in seabirds. However, studies to date have focused mainly on the larger and accessible species. While small seabirds (<200g) play a major role in marine ecosystems, their nesting habitat, which is typically fragile convoluted burrows, largely preclude long-term surveys. Chapter 2 evaluated the installation of artificial burrows as a tool to facilitate ongoing long-term research on small burrowing seabirds. We tested the use and acceptance of artificial burrows during the chick-rearing period of common diving petrels (*Pelecanoides urinatrix*) on Mayes Island, Kerguelen Archipelago, southern Indian Ocean (Fig. 2-1).

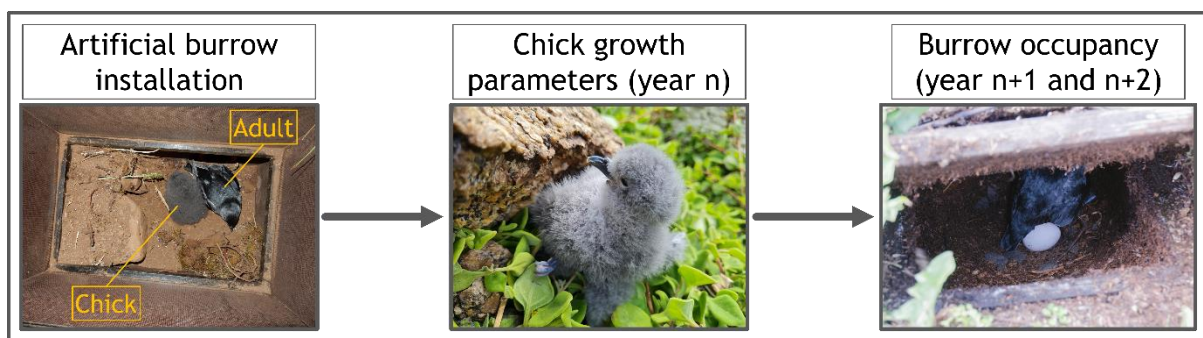


Figure 2-1: Diagram describing the different steps of the study. Artificial burrows were installed during the chick-rearing period.

The growth rate, mass at fledging and fledging rate of chicks were similar between artificial and natural burrows. Similarly, there was no difference in occupancy rate 1 and 2 years after artificial burrows were installed. The present chapter suggests that the installation of artificial burrows during the chick-rearing period of a small burrowing seabird appears to be an effective way to facilitate ongoing monitoring and research. Therefore, we recommend the wider use of artificial burrows to facilitate monitoring and research of other small burrow-nesting Procellariiform species.

2.2. Introduction

The conservation of endangered seabirds is highly dependent on long-term research on demographic parameters and population trends, which requires robust datasets. Although long-term ecological monitoring has improved our understanding of the main threats such as climate change, marine pollution or deterioration of breeding habitat experienced by seabirds (Croxall et al. 2012; Rodríguez et al. 2019; Ropert-Coudert et al. 2019), studies have focused mainly on large surface nesting species (penguins, albatrosses, gannets, gulls) or on large easily accessible burrow nesting species (shearwaters, petrels; Rodríguez et al. 2019). In contrast, for small Procellariiform species, which typically nest in small convoluted burrows, obtaining the required data is particularly challenging, and, therefore, these species remain relatively understudied (Brooke 2004; Rodríguez et al. 2019).

Monitoring burrow-nesting seabirds can imply a wide selection of techniques, more or less invasive, depending on the targeted data collection (Fischer et al. 2018). While any long-term study on breeding biology should aim limited/no impact on the study species, non-invasive technique, such as Radio Frequency Identification (Taylor et al. 2012; Fischer et al. 2017), remote cameras (Taylor et al. 2012; Dilley et al. 2015), or call-playback responses (Berrow 2000; Barbraud et al. 2009; Soanes et al. 2012), are not highly suitable to small seabirds for long-term study (Fischer et al. 2017), and overall do not provide clear information of the nest status. The inspection of the nest chamber usually involves the use (and/or combination) of tools such as burrow-scopes (*e.g.* Lavers 2015; Waugh et al. 2015), or checking by hand the content of the burrow (*e.g.* Schulz et al. 2005). While these techniques are appropriate for some species, though are potential sources of disturbance (Blackmer et al. 2004), they appear less successful for others (Parker and Rexer-Huber 2016). Burrow-scoping and probing by hand are well adapted for large species with straight burrows but are less useful for deeper or more convoluted burrows (Lyver et al. 1998; Parker and Rexer-Huber 2016). In

addition, regular checking of burrow contents may damage the burrow entrance and its internal structure (Marks and Leasure 1992). Indeed, even if an easy access to the burrow entrance is possible by hand (e.g. Barbraud and Delord 2006; Schumann et al. 2013), many burrows require the digging of multiple holes for access to the nest chamber which may result in habitat damage, the collapsing of burrows (Ryan et al. 2006) and increases the risk of disturbance/abandonment (Wilson 1986; Warham 1990; Carey 2009). More critically, regardless of which method is used to access the birds, long-term demographic studies for burrowing seabirds, and particularly small species, are potentially limited by multiple sources of error which need to be taken into account for robust inferences: (1) varying accuracy (uncertainty of burrow content: presence/absence) (Parker and Rexer-Huber 2016); (2) bird accessibility, individual and status identification (burrow occupied by breeding, or failed or non-breeding birds) (Parker and Rexer-Huber 2016); and (3) observer bias (Lyver et al. 1998; MacKenzie et al. 2006).

Despite their major role in the marine ecosystem of the Southern Ocean, small seabirds have received very little attention due to the difficulty in their sampling. While only 8 out of 24 Procellariiform seabirds breeding on Kerguelen Archipelago (Southern Indian Ocean) are small burrowing species (<200g: Antarctic prion (*Pachyptila desolata*), thin-billed prion (*Pachyptila belcheri*), fairy prion (*Pachyptila turtur*), common diving petrel (*Pelecanoides urinatrix*), South Georgian diving petrel (*Pelecanoides georgicus*), Wilson's storm petrel (*Oceanites oceanicus*), black-bellied storm petrel (*Fregetta tropica*), grey-backed storm petrel (*Garrodia nereis*)), they represent 92% and 86% of the breeding pairs and estimated biomass consumption by Procellariiforms in this region, respectively (Weimerskirch et al. 1989; Guinet et al. 1996). This situation highlights the challenge of undertaking long-term demographic studies for small burrow-nesting species, while decreasing as much as possible the sources of bias and consequences of disturbance.

While inspecting small natural burrows is hardly sustainable in multi-decade studies (Wilson 1986), artificial nest boxes have been successfully employed for burrowing petrel species, especially for conservation purposes (Bolton et al. 2004; Gummer et al. 2015). Artificial burrows have been installed in order to decrease inter-specific competition, supplement available breeding habitat, decrease the risk of predation and nest destruction, or establish new breeding sites with chick translocation (e.g., Ramos et al. 1997; Bolton et al. 2004; Miskelly et al. 2009; Bourgeois et al. 2015). For most of these studies, the technique used is to provide additional burrows by establishing artificial nest boxes. However, such a method is hardly compatible with on-going studies, as it takes at least multiple breeding seasons to reach “normal” occupancy rates (e.g. Wilson 1986; Gaston 1996; Bolton et al. 2004; Libois et al. 2012). Overall, in these cases, individuals using artificial burrows seem to be first time breeders (Bourgeois et al. 2015), the lack of experience generally being associated with lower reproductive success (Wooller et al. 1990; Mougin et al. 2002) and could be a source of bias in long-term surveys. This chapter describes the use of artificial burrows installed at existing common diving petrel breeding burrows, and evaluates the effectiveness of this method in order to facilitate long-term studies of small burrowing petrels. By installing artificial burrows at existing breeding burrows we expected an occupancy rate in the following breeding season similar to the one observed in natural burrows.

2.3. Materials and Methods

2.3.1. Study area and study species

The study was carried out on Mayes Island (49°28'S, 69°57'E) in the Morbihan Gulf, Kerguelen Archipelago, during breeding seasons 2015/2016, 2016/2017 and 2017/2018. Due to logistic constraints after the hatching period, it was not possible to collect data on chick growth and fledging success for the season 2016/2017.

Common diving petrels are small seabirds (110-150 g) that feed predominantly on microzooplankton (Bocher et al. 2000a; Fromant et al. 2020a). This species has a circumpolar distribution and breeds on numerous islands of the Southern Ocean, off southern Australia and around New Zealand (Marchant and Higgins 1990). A single egg is laid in a burrow in damp peat beneath tussock grass, shrubs or herbs on very steep coastal slopes (Payne and Prince 1979, Weimerskirch et al. 1989); incubation is shared and takes 54 days (Thoresen 1969); chicks fledge at 44-59 days old (Marchant and Higgins 1990; Miskelly et al. 2001). In the Kerguelen Archipelago, laying occurs in mid-November, hatching in mid-January and fledging in mid-March (Weimerskirch et al. 1989; Bocher et al. 2000a). Chicks are fed nightly until fledging, and typically depart for the sea on the first night that they emerge from the burrow (Richdale 1943, 1965; Miskelly et al. 2009).

2.3.2. *Artificial burrows*

Artificial burrows were installed at randomly selected existing common diving petrel burrows on Mayes Island in early February 2016 (n = 7) and 2018 (n = 5). The boxes were made of ground-treated timber (marine plywood rot-resistant) with a hinged lid as an inspection hatch, and with 8-cm-diameter PVC drainage pipe leading to the entrance (Fig. 2-2). Each nest box measured 340 mm long x 250 mm wide x 150 mm high, and had no base, so that the chick remained sitting on natural substrate. The small pipe diameter precluded the use of the artificial burrows by larger species such as blue petrel (*Halobaena caerulea*) or thin-billed prion (*Pachyptila belcheri*). Artificial burrows were installed around active natural nest chambers during the post-guard stage of chick-rearing, as petrels are considered less prone to desertion at this stage of the breeding cycle (Gummer et al. 2015). Care was taken to leave the burrow entrance looking as natural as possible, and in the same location as the original burrow entrance. The boxes were installed during day time (when adults were foraging at-sea), when

chicks were aged between 12-25 d. Once the chick was removed, the entire pre-existing burrow was replaced with the wooden box and the PVC pipe, making sure that the shape and the ambient conditions (temperature and relative humidity) of the burrow were unchanged (Fischer et al. 2018). Only the first 5 cm of the entrance were preserved untouched. To avoid the birds to dig under the nest chamber, a layer of fine shingle was added under the nest soil (Fig. 2-2). During the burrow installation (that generally took < 1 h), the chick was kept in an insulated box with part of the nest chamber material, the familiar scents limiting the stress of the diving petrel chicks (Cunningham et al. 2012). The original nest soil was returned to the artificial burrow along with the chick.

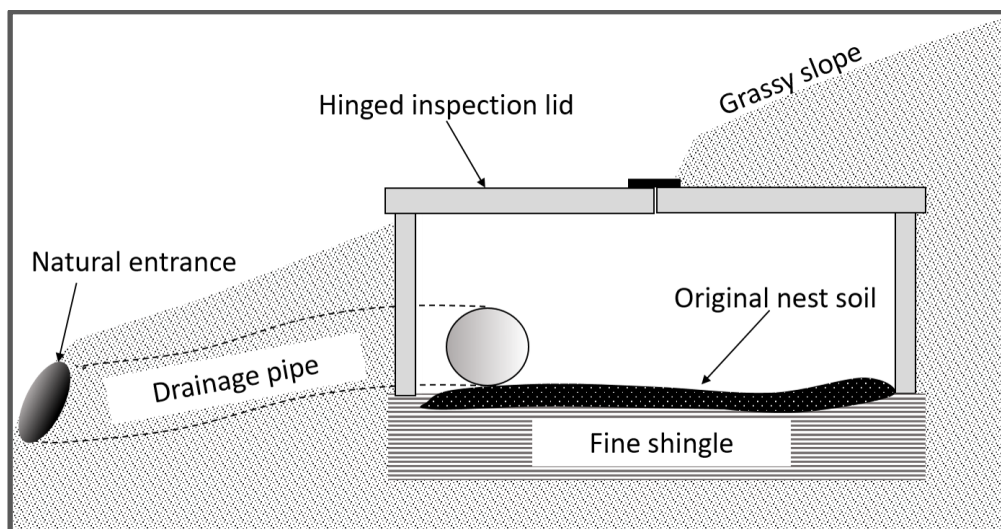


Figure 2-2: Schematic view of artificial nesting chamber for common diving petrel.

Entrance tunnels were on average 60 cm long, and were deliberately curved in order to provide shelter from wind and reduce the amount of light reaching the nest.

2.3.3. Data analysis

Potential effects on breeding behavior of artificial burrow installation were assessed by comparing several parameters of chicks growth and adult burrow occupancy in experimental and control burrows: 1) the variation in body mass of chicks (Pesola spring scale ± 2 g) just before and 2 days after artificial burrow installation (in 2015-2016 and 2017-2018); 2) the

fledging mass and the fledging success of chicks (proportion of chicks fledged in relation to eggs hatched; in 2015-2016 and 2017-2018); 3) the chicks' growth (chicks were weighed on average every 4 days; in 2015-2016 and 2017-2018); and 4) the nest-site fidelity and burrow occupancy in the subsequent years after burrow conversion (in 2016-2017 and 2017-2018).

A Richards logistic growth curve (Richards 1959) was fitted to chick body mass for each group (control and experimental burrows) using the equation

$$Y_t = \frac{A}{1 + e^{-K(t - T)}}$$

where Y_t is the mass at age t (days), A is the asymptotic value (g), K is a constant that determines the curvature of the growth pattern (days⁻¹), and T is the inflection point at which the maximum growth rate is achieved (days) (Richards 1959). We used the 95 % confidence interval of each A , T and K values to determine if the growth curve was different between groups. When the exact hatching date was uncertain, the age of the chick was estimated using data on age-specific wing length (Payne and Prince 1979; Thoresen 1969). The effects of year and burrow type were analyzed with a logistic regression (binomial distribution and logit link) with chick identity included as random effect. For body mass, non-parametric tests were used for statistical analysis due to parameter distributions departing significantly from normality. All statistical analyses were performed using R (R Core Team 2019).

2.4. Results

A total of 522 measurements were taken on body mass from 68 chicks. No inter-annual (2016 and 2018) differences were found in chick growth ($A = 165$ g [95% CI 159-171] and 170 g [95% CI 157-179], $T = 20.0$ d [95% CI 18.6-21.2] and 19.2 d [95% CI 18.1-20.2], and $K = 0.13$ [95% CI 0.10-0.16] and 0.12 [95% CI 0.10-0.13], for 2016 and 2018 chick growths, respectively), fledging date (13-Mar \pm 9 d, $n = 22$; 08-Mar \pm 12 d, $n = 44$, in 2016 and 2018, respectively), mass at fledging (Wilcoxon test, $W = 187$, $p = 0.9452$), fledging success (*GLMM*,

$z = 0.305, p = 0.7600$). Hence, for both control and artificial burrows, data were pooled between years for subsequent statistical analyses.

Table 2-1: Chick mass gain (mean \pm SD), fledging mass (mean \pm SD), average growth parameters (95% confidence interval) and fledging success of common diving petrel from Mayes Island, comparing natural and artificial burrows. For each group, the number of individuals is given in brackets. The differences between groups were not significant. The growth parameters are derived from a logistic growth curve (Richards 1959) fitted to chick body mass for each group (control and experimental burrows), where A is the asymptotic value (g), T is the inflection point at which the maximum growth rate is achieved (days), and K is a constant that determines the curvature of the growth pattern (days⁻¹) (see Materiel and methods for more details).

	Natural burrows (n = 54)	Artificial burrows (n = 12)
Mass gain after 2 days	6.4 \pm 5.8 g	8.0 \pm 7.1 g
Fledging mass	135 \pm 20 g	140 \pm 17 g
Growth parameters	A 165 (159 – 171) g	168 (156 – 171) g
	T 18.6 (17.6 – 19.6) d	19.4 (17.0 – 21.7) d
	K 0.12 (0.10 – 0.14) d ⁻¹	0.11 (0.07 – 0.15) d ⁻¹
Fledging success	74 %	92 %

There was no significant difference in mass gain between experimental chicks and control chicks during the first 2 d after artificial burrow installation (Wilcoxon test, $W = 48, p = 0.6561$) (Table 2-1). Similarly, there was no significant difference in chick body mass at fledging (Wilcoxon test, $W = 244, p = 0.6783$) nor in fledging success (*GLMM*, $z = 1.266, p = 0.2060$) between nests where artificial burrows were installed and control burrows. Chick growth was compared among the 2 groups (artificial and control burrows) using a logistic growth model. There was no significant difference in the maximum mass, neither in the inflection point at which the maximum growth rate is achieved or the curvature of the growth

pattern ($A = 168$ g [95% CI 157-179] and 165 g [95% CI 159-172], $T = 19.4$ d [95% CI 17.0-21.7] and 18.6 d [95% CI 17.6-19.6], and $K = 0.11$ [95% CI 0.07-0.15] and 0.12 [95% CI 0.10-0.14], for artificial and control chick growths, respectively) (Table 2-1, Fig. 2-2).

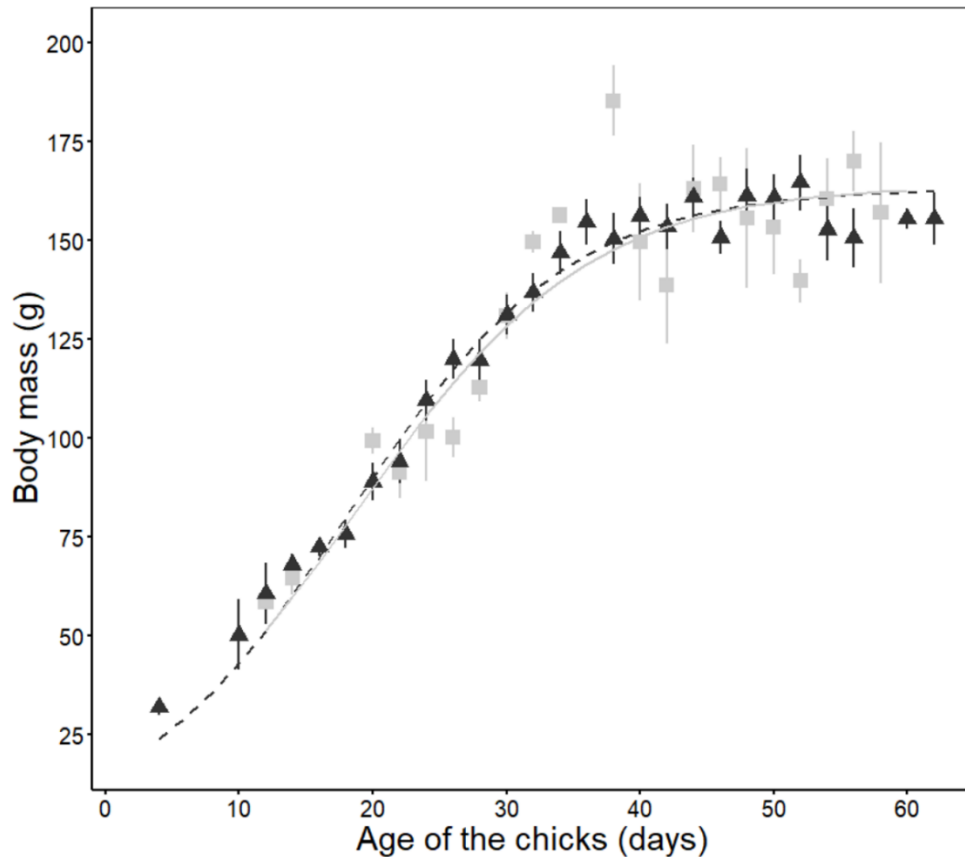


Figure 2-3: Chick growth of common diving petrel from Mayes Island, Kerguelen Archipelago, comparing growth of chicks in artificial burrows (grey squares, $n = 12$) and natural burrows (black triangles, $n = 54$). The curves are the predictions from a logistic growth model fitted to chick body mass over time for artificial (solid grey) and natural burrows (dashed black).

For the 2 subsequent years after deployment, the occupancy of artificial burrows was slightly higher compared to control burrows but not significantly different ($GLMM$, $z = 0.739$, $p = 0.4600$) (Table 2-2). For the 7 artificial burrows installed in 2015-2016, only 2 of the breeding pairs were identified in 2015/2016 (adult previously banded as part of a long-term program). Nevertheless, these 2 burrows were occupied by the same pairs in 2016/2017 and

2017/2018. Similarly, the 5 other burrows installed in 2015/2016 (for which at least 1 of the adult identity was unknown) were re-used in 2017/2018 by at least 1 of the individuals occupying the burrow in 2016/2017.

Table 2-2: Burrow occupancy of common diving petrel in artificial and natural burrows 1 and 2 years after experiment start on Mayes Island, Kerguelen Archipelago. For each group, the number of individuals is given in brackets. The differences between groups were not significant.

	Natural burrows (n = 27)	Artificial burrows (n = 7)
Burrow occupancy Year + 1 (2016/2017)	55.6 %	75.0 %
Burrow occupancy Year + 2 (2017/2018)	56.7 %	83.3 %

2.5. Discussion

The installation of artificial burrows during the chick-rearing period of common diving petrel appears to be an effective way to facilitate ongoing monitoring and research. While the limited sample size could have affected the statistical power to detect small differences, strong similarities in survival or growth rates of common diving petrel chicks and burrow occupancy were found between artificial and natural burrows, and both group of burrows were generally occupied by the same adults.

2.5.1. Burrow acceptance and chick growth

For common diving petrels, Roby (1989) estimated that chicks were fed by both parents on 91% of nights during the chick-rearing period. In such a case, when a chick received 1 meal per parent (for a total of food delivery of between 50 and 70 g), the net mass gain over a 24-hour period was 1-5 g in average. In the present study, it was neither possible to assess the size

of the meals nor to know if the chicks were fed by both parents every night. Nevertheless, the significant gain in mass after 48 hours for all burrows indicates that diving petrels continued to feed their chicks at the same rate in both natural and artificial burrows. A similar pattern was found for Chatham petrels (or ranguru, *Pterodroma axillaris*), where all artificial burrow installations were accepted by the breeding birds, and where the petrels continued to feed their chicks normally after nest boxes installation (Gummer et al. 2015). Similarly, no difference was found in chick growth rates between control and newly installed artificial burrows. The growth rates that we recorded for chicks in both natural and artificial burrows were similar to those for chicks of *P. urinatrix* from South Georgia (Payne and Prince 1979), New Zealand (Richdale 1943; Thoresen 1969) and northern Bass Strait in Australia (Eizenberg 2019). The mass of fledglings and the fledging success of chicks from artificial nest boxes (140 ± 17 g, $n = 12$; 92 %, $n = 12$, respectively) were also similar to data from common diving petrels in natural burrows in previous studies (Miskelly et al. 2009: 135.5 ± 2.0 g, $n = 50$; Thoresen 1969: 87%, $n = 46$ respectively). In the present study, the slightly lower fledging success in control burrows could be linked to predation, as 6 of 14 dead chicks were killed by brown skuas (*Catharacta antarctica lonnbergi*), a species which feeds on numerous petrel species including common diving petrel (Mougeot et al. 1998; Pacoureaux et al. 2019). Use of artificial burrows to provide protection from predators has been shown to increase nest productivity of seabirds (Libois et al. 2012). Furthermore, digging access holes to the nest chambers of natural burrows might increase the risk of subsequent nest depredation (Huntington et al. 1996; Ambagis 2004) and may, therefore, decrease chick survival rate. While the presence of skuas had no significant impact on fledging success rate in our study, predation may impact burrow retention. In order to access diving petrel chicks, skuas excavate the nest chamber, partially or completely destroying the burrow in the process, and rendering it unsuitable for use in subsequent breeding

seasons. For this reason, artificial burrows may further facilitate long-term studies by ensuring that nest chambers remain intact between breeding seasons.

2.5.2. Burrow fidelity and occupancy

The majority of active burrows (both artificial and control) were occupied by the same birds in subsequent breeding seasons (adult birds were banded as part of a long term program; Program IPEV-109). This is in accordance with previous studies of Procellariiformes, a group known to exhibit high year to year nest and mate fidelity (Warham 1990). For common diving petrels from Mana Island in New Zealand, 71 % of pairings (n = 112) were the same and in the same burrow the following year (Miskelly, unpublished data).

In the present study, the slightly higher occupancy rates for artificial burrows could either reflect a preference for artificial nest boxes, or a lower detection rate for birds using natural burrows, or a combination of both factors. A potential preference for artificial burrows should be taken with caution as it could lead to long-term deviations in demographic parameters between populations. Variation in habitat preference could be due to the better stability of artificial burrows and a lower risk of burrow collapsing (Wilson 1986). Indeed, for natural burrows, interference to the entrance and the internal structure caused by enlarging the entrance hole or opening a direct access to the chamber (for extraction of study birds) may decrease the suitability of the burrow in terms of water-proofing, heat retention or access for predators or competing (larger) burrow-nesting species, and therefore, increase the probability of abandonment in the subsequent year (Marks and Leasure 1992; Carey 2009). Additionally, while the probability to detect a bird in an artificial burrow is nearly 100%, it is likely that the detectability in a natural burrow is reduced by its shape, especially for small species such as common diving petrel for which tight or complex burrows are harder to inspect efficiently. For example, Parker and Rexer-Huber (2016) suggested that, for convoluted burrows of 2 different

shearwater species, burrow occupancy rate was underestimated by up to 19% (Cuthbert 2001; Cuthbert and Davis 2002; McKechnie et al. 2007).

2.5.3. Methodological considerations

Like the majority of Procellariiform species, the adult common diving petrels rely essentially on scent cues to relocate their burrow (Bonadonna et al. 2003). Similarly, *P. urinatrix* chicks are highly philopatric (Warham 1990) and are tightly connected to odours from the nest and the colony (Cunningham et al. 2012) and, therefore, the use of wood and/or plastic in artificial burrows could potentially impact the olfactory capabilities of the individuals. However, the results of the present and previous similar studies (e.g. Gummer et al. 2015) have demonstrated the acceptance by adults returning to newly installed artificial burrow. This is likely due to fact that the original nest soil was kept in the artificial burrow, which effectively provided the olfactory signal needed by the birds to relocate the burrow. Similarly, Miskelly et al. (2009) reported the successful return in the breeding colony of translocated chicks raised in wooden nest-boxes, highlighting that the material of the artificial burrow did not affect their olfactory capabilities.

By preventing the risk of predation and nest destruction, and by restricting the access to the artificial burrows for small species only, this technique may cause long-term deviations in demographic parameters compare to natural burrows (Bourgeois et al. 2015). In the same way, artificial burrows could affect the natural conditions of humidity or temperature and provide a habitat that differs from natural conditions. Although in the present study this was not tested, Fischer et al. (2018) reported no difference in the air parameters between natural burrows and similarly designed nest-boxes. Conversely, traditional techniques involving checking of natural burrows are limited by multiple sources of error (accuracy, accessibility, observer bias; Parker and Rexer-Huber 2016), and long-term monitoring of such burrows often

implies digging multiple access holes to the nest chambers, likely increasing the risk of structure deterioration and predation. Therefore, these aspects also suggest potential negative effects on nest productivity or long-term occupancy (Marks and Leasure 1992), leading to long-term deviations in demographic parameters compare to natural burrows. Additionally, because Procellariiformes are long-lived species, parameters influencing population dynamic over several decades are likely to be winter adult survival (Barbraud and Weimerskirch 2003) or juvenile mortality (Barbraud et al. 2011) and, therefore, should not be biased by the type of study burrows. Consequently, the development of artificial burrows, in combination with the monitoring of natural burrows, could become a useful tool in order to determine long-term trends in key demographic parameters. Additionally, expanding the sample sizes and the study duration would provide valuable insights to evaluate the variation in the demographic parameters between natural and artificial burrows in polar or sub/polar environments.

2.5.4. Artificial burrows as long-term studies tools

This study evaluated the installation of artificial burrows as a tool to facilitate ongoing long-term research on small burrowing Procellariiform seabirds such as diving petrels. This technique may lead to a breakthrough in such studies by ensuring burrows with high long-term occupancy rates (Wilson 1986), excluding biases such as uncertainty of burrow content or observer bias, limiting the time needed to inspect the nest and minimizing the disturbance (Gummer et al. 2015), and overall, increasing the longevity of study burrows (Bourgeois et al. 2015) and decreasing the habitat damage and the risk of nest abandonment (Wilson 1986; Marks and Leasure 1992). Additionally, at sites with high between-species competition for nesting burrows (as at Mayes Island, where the present study was conducted), an important function of artificial nest boxes would be to prevent intrusion or excavation of the nest by larger species (Ramos et al. 1997; Bolton et al. 2004). For a small burrowing seabird in a given

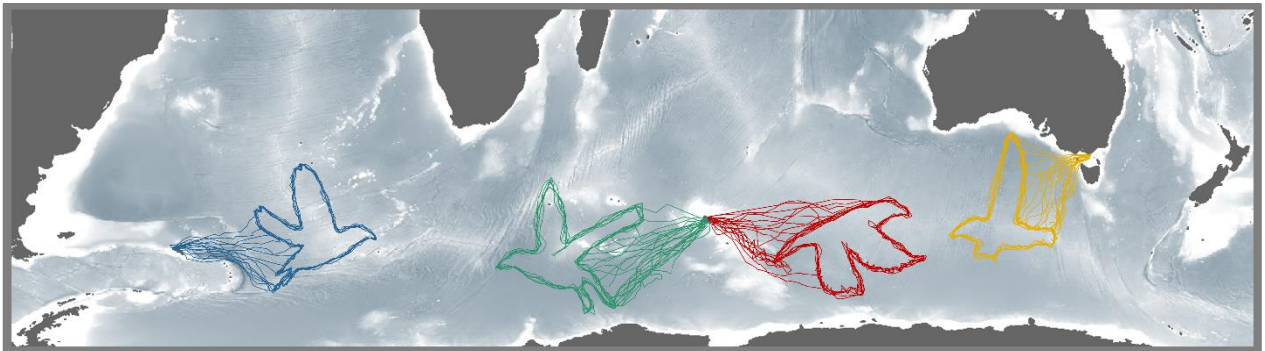
burrow, interspecific competition by bigger species may lead to an enlargement of the nest, pair bond disruption or burrow desertion (Thoresen 1969; Gummer et al. 2015), and therefore interrupt the long-term survey of this burrow. In addition, artificial nest boxes may decrease impacts of habitat change, including potential effects of invasive plants (Frenot et al. 2001). For example, in the study archipelago, the main native plant species, *Pringlea antiscorbutica* (Kerguelen cabbage) and *Azorella selago*, which play key roles in the soil structure, have decreased dramatically during the last 2 decades (Chapuis et al. 2002). As Kerguelen common diving petrels nest in deep soils with ample plant cover, particularly under Kerguelen cabbage (Weimerskirch et al. 1989), a modification in plant community could result in a potential decline in suitable breeding habitat and may have important implication in exacerbating inter-specific competition for nesting sites.

A high proportion of small burrowing petrel species are under-studied, with no (or limited) accurate estimates of population sizes, population trends and demographic parameters (Rodríguez et al. 2019), resulting in a decreased ability to develop appropriate conservation actions. In the Southern Ocean, scientific studies and conservation management focus predominantly on iconic seabirds such as albatrosses or penguins (Heerah et al. 2019). In contrast, the ubiquitous small Procellariiform species that comprise enormous populations, representing a substantial biomass consumption and nutrient fluxes (Guinet et al. 1996), have received comparably little attention. Therefore, a greater research effort should be dedicated to the development of techniques enabling long-term studies of small burrow-nesting birds in order to fill this knowledge gap and improve their conservation actions. Artificial burrows are a relatively cheap and durable method to establish study populations, with little or no negative impact on chick growth rates or mate and burrow retention rates. However, given the small sample size in the present study, other researchers are encouraged to evaluate the potential of

artificial burrows on other small burrow-nesting Procellariiform species to facilitate their long-term studies.

Chapter 3

Temporal and spatial differences in the post-breeding behaviour of the common diving petrel



A version of this chapter has been published as:

Fromant A, Bost CA, Bustamante P, Carravieri A, Cherel Y, Delord K, Eizenberg YH, Miskelly CM, Arnould JPY (2020) Temporal and spatial differences in the post-breeding behaviour of a ubiquitous Southern Hemisphere seabird, the common diving petrel. *Royal Society Open Science* 7(11):200670.

<https://doi.org/10.1098/rsos.200670>

3.1. Summary

The post-breeding period plays a major role in seabird survival and population dynamics. However, our understanding of the migratory behaviour, moulting and feeding strategies of non-breeding seabirds is still very limited, especially for small-sized species. Chapter 3 investigated the post-breeding behaviour of three distant populations (Kerguelen Archipelago, south-eastern Australia, New Zealand) of the common diving petrel (*Pelecanoides urinatrix*), an abundant, widely distributed zooplanktivorous seabird breeding throughout the southern Atlantic, Indian and Pacific oceans (Fig. 3-1).

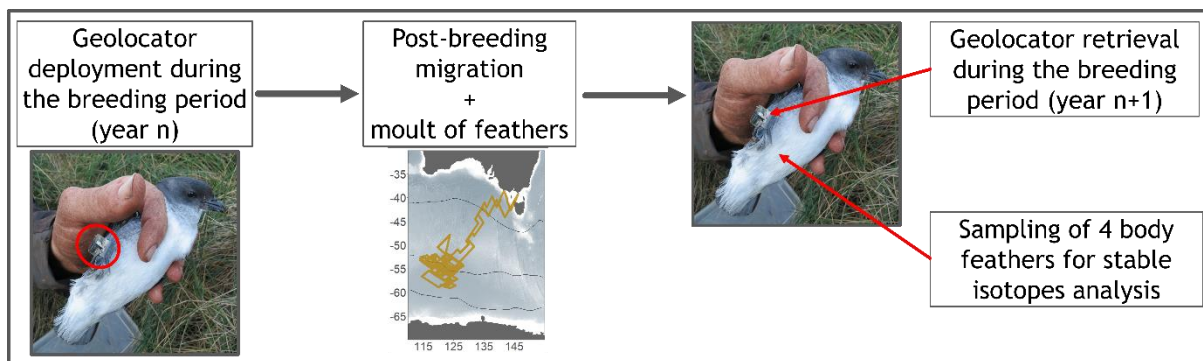


Figure 3-1: Description of sampling period and methods to study the post-breeding migration of diving petrels.

The timing, geographical destination and activity pattern of birds were quantified through geolocator deployments during the post-breeding migration, while moult pattern of body feathers was investigated using stable isotope analysis. Despite the high energetic cost of flapping flight, all the individuals quickly travelled long distances ($> \sim 2500$ km) after the end of the breeding season, targeting oceanic frontal systems. The three populations, however, clearly diverged spatially (migration pathways and destinations), and temporally (timing and duration) in their post-breeding movements, as well as in their period of moult. Philopatry to distantly separated breeding grounds, different breeding phenologies, and distinct post-

breeding destinations suggest that the common diving petrel populations have a high potential for isolation, and hence, speciation. This chapter contributes to improving knowledge of ecological divergence and evolution between populations and inform the challenges of conserving migratory species.

3.2. Introduction

In order to adapt to seasonal environmental changes, many animal species migrate during the non-breeding period (Dingle and Drake 2007). Post-breeding migration is particularly common in seabirds (Newton 2010), some species travelling long distances between breeding and non-breeding habitats (Egevang et al. 2010, Rayner et al. 2011). The post-breeding period is particularly important for plumage replacement for a wide range of seabirds (Marchant and Higgins 1990). This period can, therefore, be energetically challenging (Sillet et al. 2000, Barbraud and Weimerskirch 2003) and the divergent environmental conditions experienced by populations throughout their migration and at the moulting areas may differentially influence demographic processes (Reynolds et al. 2011, Frederiksen et al. 2012, Price et al. 2020). Different migratory and moult strategies within a species may lead to long-term population divergences, and carry important ecological, evolutionary and conservation implications (Friesen 2015).

Distinct populations within a species can have substantial demographic and ecological differences (Fischer et al. 2018, Cristofari et al. 2019, Quillfeldt et al. 2019). As the response of one particular population to environmental changes may not be representative of the entire species, it is important to obtain information from multiple populations (Martin et al. 2007, Thackeray 2016). However, only a few coordinated studies have investigated multiple separate populations of seabirds during the non-breeding period (Frederiksen et al. 2012). This is particularly true in small-sized seabirds, even though they are more likely to be vulnerable to anthropogenic threats than larger species (Rodríguez et al. 2019). In conservation biology, failing to consider population-specific ecology during the non-breeding period may lead to a misunderstanding of the potential effects of local threats or environmental changes on population dynamics of small seabird species (Cristofari et al. 2019). Therefore, knowledge of the distribution and at-sea activity of multiple populations is required in order to determine the

inter-population diversity during this critical period (Martin et al. 2007, Rodríguez et al. 2019, Bolton et al. 2019).

Stable isotope analysis of feathers provides a robust method to study the non-breeding feeding ecology of seabirds (Cherel et al. 2000, Quillfeldt et al. 2005) and investigate inter-population variability (Cherel et al. 2006). Values of $\delta^{13}\text{C}$ in feathers provide information on the feeding habitat occupied during moult (Cherel and Hobson 2007) and $\delta^{15}\text{N}$ values provide highly valuable indications on the trophic niche (Cherel et al. 2007). This approach is nonetheless unable to provide precise temporal and spatial scales of the migratory behavior of seabirds.

Due to the high-energy cost of carrying telemetry devices, there is a tradeoff between the size of animal-borne transmitters and their deployment duration such that their application in seabirds has been constrained to species with larger body size and/or for a relative short period (Soanes et al. 2015). Daylight sensing geolocation provides a lightweight alternative for long-term deployments (geolocation sensing data loggers, GLS) and is increasingly being used to investigate the at-sea distribution and activity of small procellariiform species during the breeding (Navarro et al. 2015, Hedd et al. 2018) and non-breeding periods (Delord et al. 2016, Pollet et al. 2019, Jones et al. 2020).

Non-breeding ecology has been investigated in a wide range of large seabirds in the Southern Ocean (*e.g.* albatrosses, shearwaters and penguins; BirdLife International 2020). While some studies have recently investigated the distribution of multiple populations of small petrels during this period, most have focused on a small proportion of populations and/or limited spatial range of the species (Pollet et al. 2019, Quillfeldt et al. 2015). The common diving petrel (CDP, *Pelecanoides urinatrix*) is a small procellariiform seabird (110-160 g) feeding on macrozooplankton (Reid et al. 1997, Bocher et al. 2000a, Fromant et al. 2020a). This species breeds on numerous islands along a wide latitudinal gradient (35°-55°S)

throughout the Atlantic, Indian and Pacific oceans, with an estimated 8-10 million breeding pairs (Fig. 3-2; Marchant and Higgins 1990), though substantial differences in breeding phenology are evident among populations (Fig. 3-2).

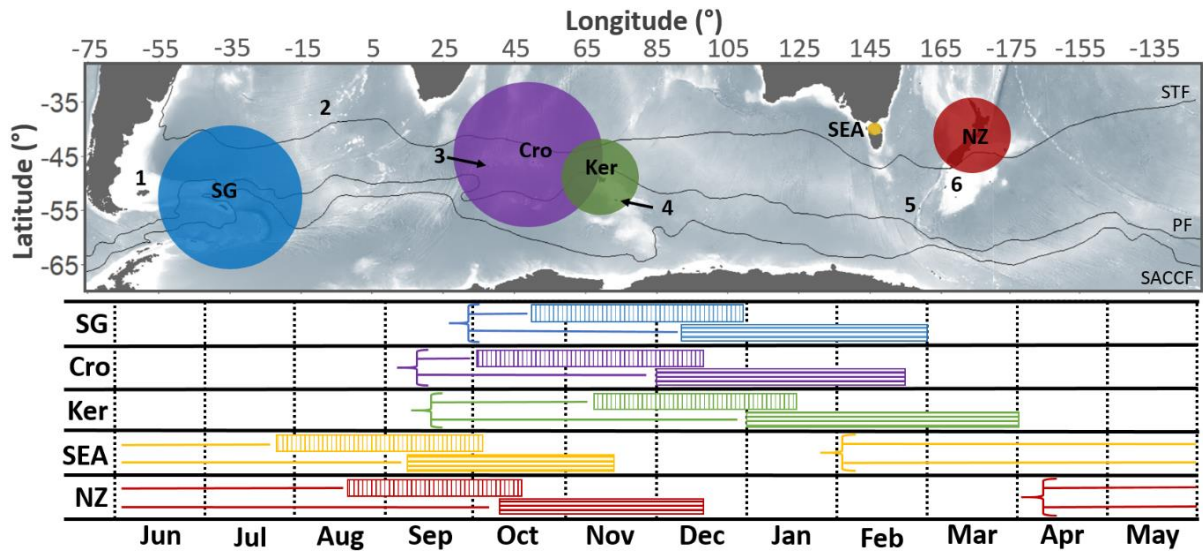


Figure 3-2: Upper panel: Populations estimates of common diving petrels (*P. urinatrix*) throughout its circumpolar distribution. The circles show the proportional sizes of the main populations: South Georgia (SG; blue circle; 3.8 million breeding pairs, Prince and Croxall 1983); Crozet (Cro; purple circle; 3-4 million breeding pairs, Jouventin et al. 1985); Kerguelen (Ker; green circle; 0.5-1 million breeding pairs, Weimerskirch et al. 1989); south-eastern Australia (SEA; orange circle; 0.1-0.2 million breeding pairs, Baker et al. 2002; New Zealand (NZ; red circle; 0.9 million breeding pairs, Richard et al. 2020). The numbers 1 to 6 show small isolated populations (<50 000 breeding pairs): 1) Falklands/Malvinas islands; 2) Gough/ Tristan da Cuna Islands; 3) Prince Edwards Islands; 4) Heard/McDonald Islands; 5) Macquarie Island; 6) New Zealand sub-Antarctic Islands. The black lines represent the approximate location of the Subtropical Front (STF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF).

Lower panel: Phenology of common diving petrels from South-Georgia (SG), Crozet (Cro), Kerguelen (Ker), south-eastern Australia (SEA), and New Zealand (NZ). Blocks with vertical lines correspond to incubation and horizontal lines to chick-rearing period. Arrows followed by horizontal lines show the period when the species is present at a specific breeding site. For Kerguelen, south-eastern Australia and New Zealand, the data correspond to the colonies surveyed in the present study in 2017-18.

Recent tracking studies suggest that CDP head to the subantarctic region during the post-breeding migration (Navarro et al. 2015, Rayner et al. 2017). This observation is well supported by isotopic analysis of feathers of individuals from the Kerguelen Archipelago and

South Georgia (Navarro et al. 2015, Cherel et al. 2006). However, the distribution of CDP during the non-breeding season remains unknown for the majority of breeding sites, particularly in the Indian Ocean sector of the Southern Ocean which hosts large populations (Williams et al. 1979, Jouventin et al. 1985, Weimerskirch et al. 1989, Woehler and Green 1992). Furthermore, it is uncertain if these different populations share the same ecology (spatial, temporal and trophic segregation) and whether they consistently migrate to the same regions. Similarly, there is very limited information about the critical moulting period, and how breeding phenology could influence the subsequent post-breeding activity patterns.

The present chapter investigated the post-breeding behaviour of CDP from three distantly separated breeding sites from two oceanic basins in the Southern Hemisphere, by combining information from GLS and isotopic analyses. The specific aims were to: (1) identify the spatial distribution of post-breeding individuals; (2) describe the timing and duration of their post-breeding movements and moult; and (3) evaluate the potential differences among the focal populations, and discuss their implication for further conservation biology studies. Additionally, by comparing our results with those of CDP populations from three other localities in the southern Atlantic and Pacific oceans (Navarro et al. 2015, Rayner et al. 2017), we explored the extent to which the timing and location of post-breeding movements contribute to the ecological and evolutionary divergence of distinct populations of a ubiquitous seabird species.

3.3. Material and Methods

3.3.1. Study site, study species and animal instrumentation

The study was conducted at three field sites representing separate populations: Ile Mayes (Kerguelen Archipelago, southern Indian Ocean, 49°28'S 69°57'E, hereafter referred as Kerguelen); Kanowna Island (south-eastern Australia, 39°10'S 148°16'E); and Mana Island

(New Zealand, 41°06'S 174°46'E). In order to avoid potential bias due to inter-annual variations, individuals from all three colonies were sampled during the same non-breeding period (November 2017 to September 2018). Additional data was collected for Kerguelen (in 2015-16 and 2016-17) and Kanowna Island (in 2016-17 and 2018-19). Kerguelen is located in subantarctic waters *sensu lato* (between the Polar Front and the Subtropical Front), while both Kanowna and Mana Islands are located farther north, in the temperate subtropical region.

In the present article, migration is defined as the period during which there is an annual to-and-from movement of populations between the breeding site and a migration area (Dingle and Drake 2007). The post-breeding period is defined as the period between the last burrow attendance at the end of the breeding season, and the first return in a burrow the following season. The non-breeding period is the period between two successive breeding cycles. It includes the post-breeding migration away from breeding sites, followed by a more or less prolonged period in the vicinity of breeding sites before initiating the next breeding season.

To study the at-sea distribution of individuals from the three populations during the non-breeding period, adult birds were equipped with leg-mounted GLS (Migrate technology, model C65). The mass of the device attached to a plastic or metal ring with a cable tie was < 1.5 g, corresponding to on average $1.07 \pm 0.1\%$ of body mass (117 g – 175 g). Previous use of such devices on small seabird species have shown limited impact on the feeding ecology or future breeding (Delord et al. 2016, Quillfeldt et al. 2012). Breeding individuals were equipped during the breeding season and were recaptured during the following breeding season for removal of the device. Sex was determined by DNA analysis of a small blood sample (0.1 mL) collected from the brachial vein for the individuals from Kerguelen (Laboratoire Analyses Biologiques, CEBC, France), and of a body feather for those from Kanowna Island (DNA solutions, Australia). The sex of individuals at Mana Island was determined from their sex-specific calls (Marchant and Higgins 1990, Miskelly and Taylor 2007).

Information on moult pattern in Pelecanoididae species is very limited, largely because individuals can be at sea during this stage (Marchant and Higgins 1990). Similarly to alcids, the majority of diving petrel species seem to undergo an annual almost synchronous wing molt of flight feathers during the non-breeding period (Watson 1968, Bridge 2006). For CDP, in south-eastern Australia and New Zealand, adults are thought to start wing moult at sea after chicks have fledged (Marchant and Higgins 1990). In South Georgia, Kerguelen and Heard Island, moult of primaries seems to be initiated just before the end of the chick-rearing period (Marchant and Higgins 1990, Payne and Prince 1979), although sources are discordant (Woehler 1991). However, the accuracy of these records is complicated by the lack of information on the breeding status of the observed individuals. In the present study, the timing of wing moult was inferred from information provided by the GLS on the time spent on the sea surface. Since flight feather renewal directly affects flying ability (Bridge 2006, Gutowsky et al. 2014, Cherel et al. 2016), in particular for species with high wing loading (body mass / wing area) such as diving petrels (Warham 1977), a peak in time spent on the water is likely to reflect the wing moult of flight feathers.

For body feathers, it is likely to be a protracted process initiated during the post-breeding period, similarly to other species of small petrels (Carravieri et al. 2014, Cherel et al. 2014). The continuous moult of body feathers throughout the non-breeding period allows the birds to progressively renew their plumage while maintaining its vital role in thermoregulation (Murphy 1996). Stable isotope ratios in body feathers can be a proxy of the location and trophic level of the individuals when they were synthesised (Cherel et al. 2000, Quillfeldt et al. 2005). Therefore, to investigate the isotopic niche and the moult of body feathers of individuals throughout the non-breeding period, four contour feathers were collected from the middle and lower back of each tracked individual at recapture. Additional samples were collected on adult individuals that were not tracked in order to increase the sample size and to assess temporal

variation (three years of data for both Kerguelen and Kanowna). Handling time at deployment (measurements, banding and GLS attachment) and recapture (device removal, weighing, blood and feather sampling) were minimized and took on average < 5 min.

3.3.2. Data processing and analyses

The GLS measured light intensity every minute and recorded the maximum value for each 5 min interval. The determination of twilights (dawn and dusk), linked to a time base, enabled longitude (timing of local midday and midnight) and latitude (duration of day and night) to be estimated, providing two positions per day with an uncertainty of 200-400 km (Phillips et al. 2004, Halpin et al. 2021). Processing and calculations were conducted using the *GeoLight* package in the R statistical environment (Lisovski et al. 2012, R Development Core Team 2020). As latitude estimations around the equinoxes are unreliable, data for two weeks before and after the equinoxes were excluded before spatial analysis was conducted (Wilson et al. 1992). Additionally, latitude or longitude estimates that were clearly inaccurate (unrealistic speed > 1500 km/day, trajectory or spikes) were removed (Quillfeldt et al. 2015). When outward and inward movements were occurring during the equinox periods (March-April and September-October), the timing of arrival and departure from the breeding colonies was determined from longitudinal directional movements using the raw data (Quillfeldt et al. 2015, Cherel et al. 2016).

Filtered locations were used to generate kernel utilization distribution (UD) estimates with a smoothing parameter (h) of 1.8 (corresponding to a search radius of ~ 200 km) and 1° x 1° grid cell size (based on the mean accuracy of the device). For each population and year, the 50% (core foraging area) and 95% (home range) kernel UD contours were obtained (Worton 1989). The core area was used to estimate the centroid position (mean latitude and longitude)

during the post-breeding period for each individual. Spatial analyses were performed using the *adehabitatHR* R package (Calenge 2006).

The period of maximum proportion of time spent on the water (wet-dry sensor being wet > 90% per day; Rayner et al. 2017) was used to determine the moulting period of flight feathers for each individual (Cherel et al. 2016). This was recorded differently at the three study sites. For Kerguelen and Kanowna Island, wet-dry data were sampled every 30 s with the number of samples wet and maximum conductivity recorded every 4 h. At Mana Island, wet-dry data were sampled every 30 s with number of wet samples and maximum conductivity recorded every 10 min.

The dates of last and first burrow attendance were determined by combining information on activity (wet-dry: 100% dry for a period > 4 h), temperature (for Kerguelen and Kanowna Island only, sampled every 5 min with maximum recorded every 4 h) and movement data (presence of the bird in the vicinity of the breeding region). These data were then used to estimate the duration and the total distance travelled during the post-breeding migration.

For stable isotope analyses, feathers were cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution in an ultrasonic bath, followed by two successive methanol rinses and air dried 24 h at 50°C. Each feather was then cut to produce a fine powder for homogenization before carbon and nitrogen isotope ratio determination using a continuous flow mass spectrometer (Delta V Plus or Delta V Advantage both with a Conflo IV interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash 2000 or Flash EA 1112, Thermo Scientific, Milan, Italy) at the LIENSs laboratory (La Rochelle Université, France). Stable isotope values were expressed in conventional notation ($\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$) where X is ^{13}C or ^{15}N and R represent the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. R_{standard} values were based on Vienna Pee Dee Belemnite for ^{13}C , and atmospheric nitrogen (N_2) for

¹⁵N. Replicates of internal laboratory standards (Caffeine USGS-61 and USGS-62) indicate measurement errors < 0.10 ‰ for $\delta^{13}\text{C}$ and 0.15 ‰ for $\delta^{15}\text{N}$.

As the Southern Ocean is marked by a latitudinal gradient of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Jaeger et al. 2010), low ($\delta^{13}\text{C} < -19.5$ ‰ and $\delta^{15}\text{N} < 9.9$ ‰) and high isotopic values ($\delta^{13}\text{C} > -19.5$ ‰ and $\delta^{15}\text{N} > 9.9$ ‰) in body feathers were interpreted as corresponding to feathers moulted in Antarctic/Subantarctic and Subtropical/neritic waters, respectively (Cherel et al. 2006, Jaeger et al. 2010).

All spatial and statistical analyses were conducted in the R statistical environment 3.6.1 (R Development Core Team 2020). To investigate among-population, inter-annual and sex-related variations on post-breeding migration parameters (departure and return dates, migration duration, total distance travelled and maximum range), general linear models (GLM) were fitted using the *lme4* package (Bates et al. 2014). For all models a Gaussian family was selected (error structure approached the normal distribution), all combinations of variables were then tested and ranked based on their Akaike's Information Criterion (AIC), and the global models were checked to ensure normality and homoscedasticity of the residuals (Zuur et al. 2010) before further statistical tests. Inter-population differences were quantified using analyses of variance (ANOVA or Welch's ANOVA), and *post-hoc* tests were conducted using *t*-tests (parametric), or Kruskal-Wallis and Mann-Whitney *U* tests (non-parametric) depending on the data distributions. Before these analyses, data were checked for normality (Shapiro-Wilk test) and equality of variances (Levene test). Estimates are presented as means \pm standard error (unless specified).

3.4. Results

In total, 21 GLS (9 in 2015-16 and 12 in 2017-18) were deployed on CDPs from Kerguelen, 41 (20 in 2017-18 and 21 in 2017-19) from Kanowna Island, and 10 (in 2017-18)

from Mana Island. Recapture rate was 68% (70% in 2015-16 and 66% in 2017-18) at Kerguelen, 31% (25% in 2017-18 and 38% in 2018-19) at Kanowna Island, and 40% at Mana Island. At Kerguelen, two GLS (one in 2015-16 and one in 2017-18) were found in brown skua (*Catharacta antarctica lonnbergi*) pellets near the colony before the end of the breeding season. Additionally, due to a malfunction, all the GLS deployed at Kerguelen in 2015-16 stopped recording 3-6 months after deployment (just before or soon after departure from the colony) and, therefore, data from these individuals were excluded from further statistical analysis. Because there was no significant difference between the sexes in at-sea distribution, trip parameters, and stable isotope values (Supplementary Table S3-1), data were pooled across sexes in all subsequent statistical analyses.

3.4.1. Post-breeding migration patterns and at-sea activity

All individuals migrated predominantly to the vicinity of the Polar Front, while birds from Kerguelen moved farther south near the SACCF (Southern Antarctic Circumpolar Current Front; Fig. 3-3). In 2017-18 (the only year with data from the three sites), the three populations headed to different post-breeding migration areas within the Southern Ocean. Individuals from Kerguelen and Kanowna Island migrated south-southwest from their respective colonies, while individuals from Mana Island headed east-southeast. Individuals from Kerguelen migrated to more southerly latitudes (55–65°S) than those from both Kanowna Island (51–60°S) and Mana Island (51–59°S). All individuals started their post-breeding migration shortly after their last visit to the burrow (~1-2 days after last burrow attendance). The timing of departure differed significantly among sites according to the differences in breeding phenology (Table 3-1; Kruskal-Wallis test: $\chi^2 = 24.108$, $P < 0.001$). Thus, individuals from Kerguelen departed 107 d and 80 d after birds from Kanowna Island and Mana Island, respectively.

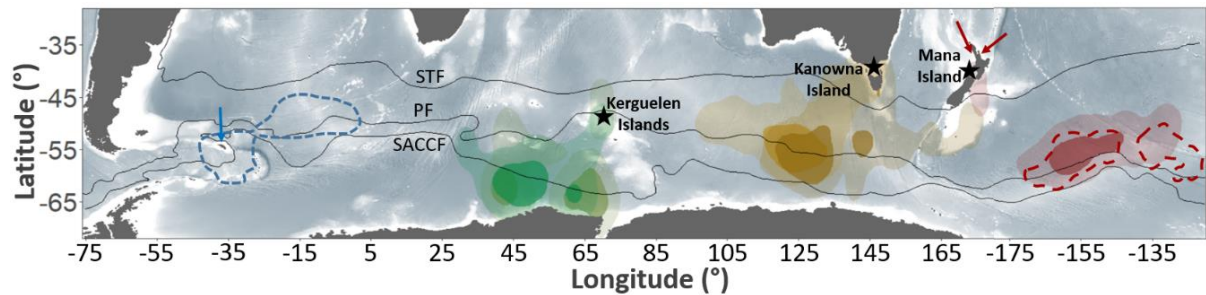


Figure 3-3: Kernel density estimation derived from GLS locations during the post-breeding migration of common diving petrels (*P. urinatrix*) from Kerguelen (light green in 2015-16, $n = 5$; and dark green in 2017-18, $n = 7$), Kanowna (orange in 2017-18, $n = 5$; and brown in 2018-19, $n = 8$), and Mana Islands (red in 2017-18, $n = 4$). Solid colour areas show the 50% (core area) and faint colour the 95% (home range) of the kernel UD. Dotted lines represent the estimated post-breeding distribution of CDPs from South Georgia (blue, adapted from Navarro et al. 2015) and from two colonies in North Island New Zealand (red; adapted from Rayner et al. 2017); the blue and red arrows show the colonies where the species was studied in Navarro et al. (2015) and Rayner et al. (2017), respectively. The black lines represent the approximate location of the Subtropical Front (STF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF). The devices were deployed on breeding birds. For Kerguelen in 2015-16, the GLS stopped recording soon after their deployments (2-4 months), and therefore, the present figure describes a partial view of the CDP distribution for that year.

The duration of the post-breeding migration was on average 120 d and 92 d longer for birds from Kerguelen than from Kanowna and Mana Islands (Table 3-1; Welch's ANOVA: $F_{10.976} = 94.321$, $P < 0.001$). It was also significantly different between the latter two populations (Paired t -test: $t_{6.993} = -5.781$, $P < 0.001$). Most individuals were performing their post-breeding migration between March-September at Kerguelen, between November-February at Kanowna Island, and between December-April at Mana Island (Table 3-1; Fig. 3-4). The total distance travelled during this period was the greatest for individuals from Kerguelen and the shortest for those from Kanowna Island (Table 3-1). In contrast, maximum range from the colony was not related to either the total distance travelled or the duration of the post-breeding migration, with birds from Mana Island going the farthest from their colony and the birds from Kerguelen the nearest (Table 3-1; Mann-Whitney U test: for Mana Island-Kanowna Island $U = 9$, $P = 0.905$; for Kanowna Island-Kerguelen $U = 32$, $P = 0.018$).

Overall, the three populations of CDP displayed a similar activity pattern: they spent a relatively low proportion of time on the water at the start and end of the post-breeding migration (<70 % of each day), and showed a peak of time spent on the water (>90% of each day) 34-41 days after departure (Fig. 3-5; Table 3-1). The timing of this peak differed among populations (ANOVA: $F_{5,426} = 19.855$, $P = 0.002$), but the duration between departure and the maximum time spent on the water did not (ANOVA: $F_{5,007} = 0.435$, $P = 0.782$). In addition, the date of maximum time spent on the water was highly correlated with the date of departure for migration (Supplementary Fig. S3-1; Spearman's correlation test: $S = 189.510$, $P < 0.001$, $\rho = 0.927$).

Table 3-1: Timing and duration of the post-breeding migration, and mean moult date of common diving petrels (*P. urinatrix*) from Kerguelen, Kanowna, and Mana Islands (mean \pm SE). The mean moult date of flight feathers was identified as the peak of time spent on the water (> 90% time per day sitting on water). Birds were equipped with miniaturized saltwater immersion geolocators (see Methods).

	Kerguelen		Kanowna		Mana
	2015-16 (n = 5)	2017-18 (n = 7)	2017-18 (n = 5)	2018-19 (n = 8)	2017-18 (n = 4)
Last burrow occupancy	29-Feb \pm 17 d	26-Feb \pm 5 d	12-Nov \pm 1 d	16-Dec \pm 3 d	08-Dec \pm 2 d
Departure date	02-Mar \pm 16 d	27-Feb \pm 4 d	12-Nov \pm 1 d	17-Dec \pm 3 d	09-Dec \pm 2 d
Outward travel duration (days)	11.0 \pm 2.3 d	15.3 \pm 1.6 d	13.8 \pm 2.1 d	12.4 \pm 1.4 d	7.8 \pm 0.8 d
Post-breeding migration duration (days)	-	211 \pm 6	92 \pm 4	127 \pm 8	119 \pm 3
Inward travel duration (days)	-	7.1 \pm 1.6 d	9.6 \pm 0.9 d	13.1 \pm 3.6 d	9.5 \pm 0.9 d
Return date	-	23-Sep \pm 3 d	08-Feb \pm 5 d	12-Apr \pm 6 d	04-Apr \pm 6 d
First burrow occupancy	-	25-Sep \pm 4 d	11-Feb \pm 5 d	22-Apr \pm 10 d	06-Apr \pm 5 d
Maximum range (km)	-	2,514 \pm 103	3,153 \pm 267	2,769 \pm 119	3,599 \pm 407
Total distance (km)	-	44,232 \pm 2,218	31,603 \pm 2,561	33,309 \pm 3,550	33,514 \pm 1,033
Mean wing moult date	-	10-Apr \pm 5 d	16-Dec \pm 3 d	23-Jan \pm 3 d	14-Jan \pm 2 d
Time between departure and mean wing moult (days)	-	41 \pm 5	34 \pm 3	37 \pm 2	36 \pm 4

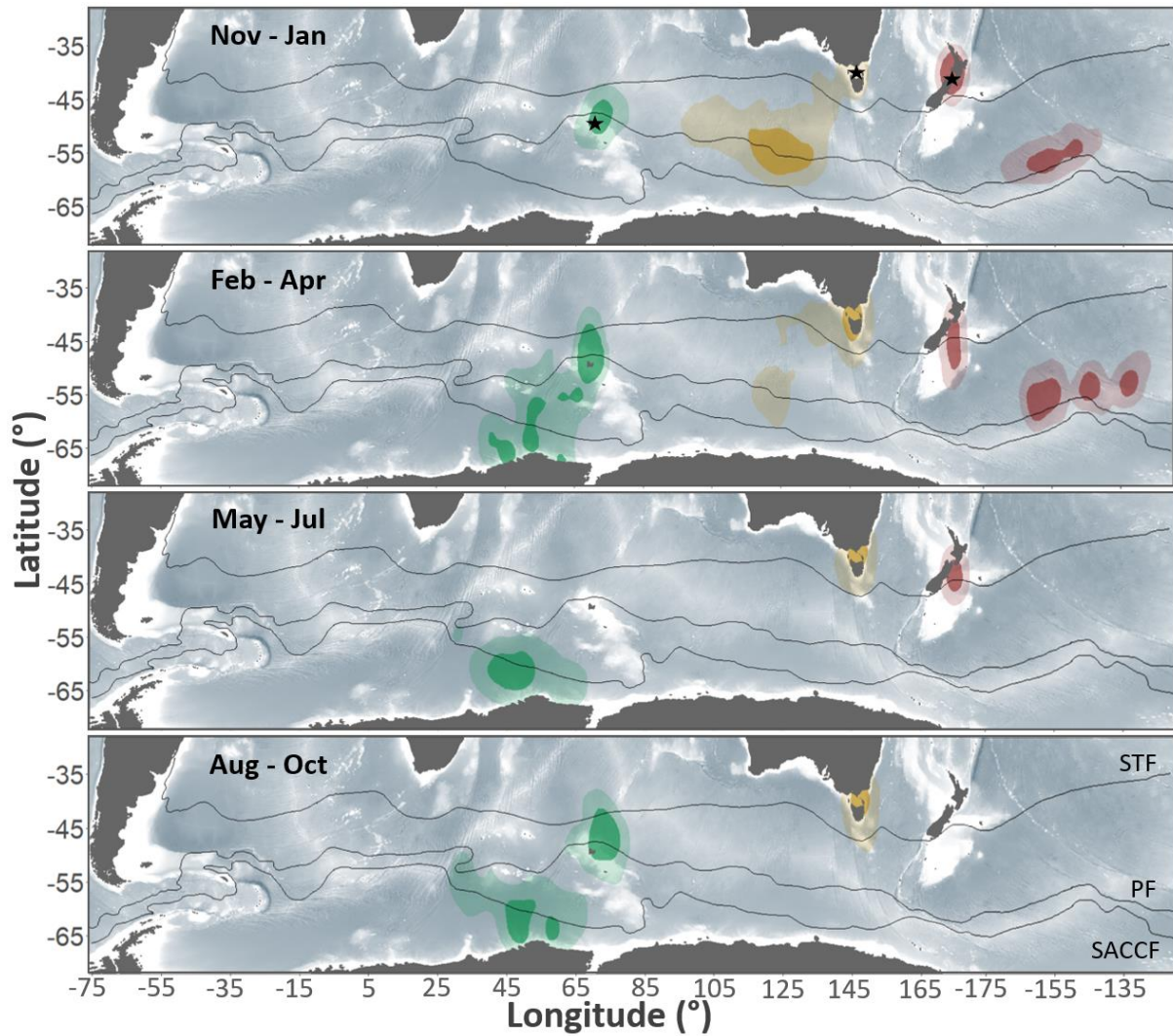


Figure 3-4: Year-round kernel density estimation derived from GLS locations of common diving petrel (*P. urinatrix*) in 2017-18 from Kerguelen (light green, $n = 7$), Kanowna Island (orange, $n = 5$), and Mana Island (red, $n = 4$). Solid colour areas show the 50% (core area) and faint colour the 95% (home range) of the kernel UD. The devices were deployed on breeding birds. Aug-Oct data were not available for Mana Island, as the GLS loggers were recovered in June 2018. See Fig. 3-2 for more details on the species phenology. The black lines represent the approximate location of the Subtropical Front (STF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF).

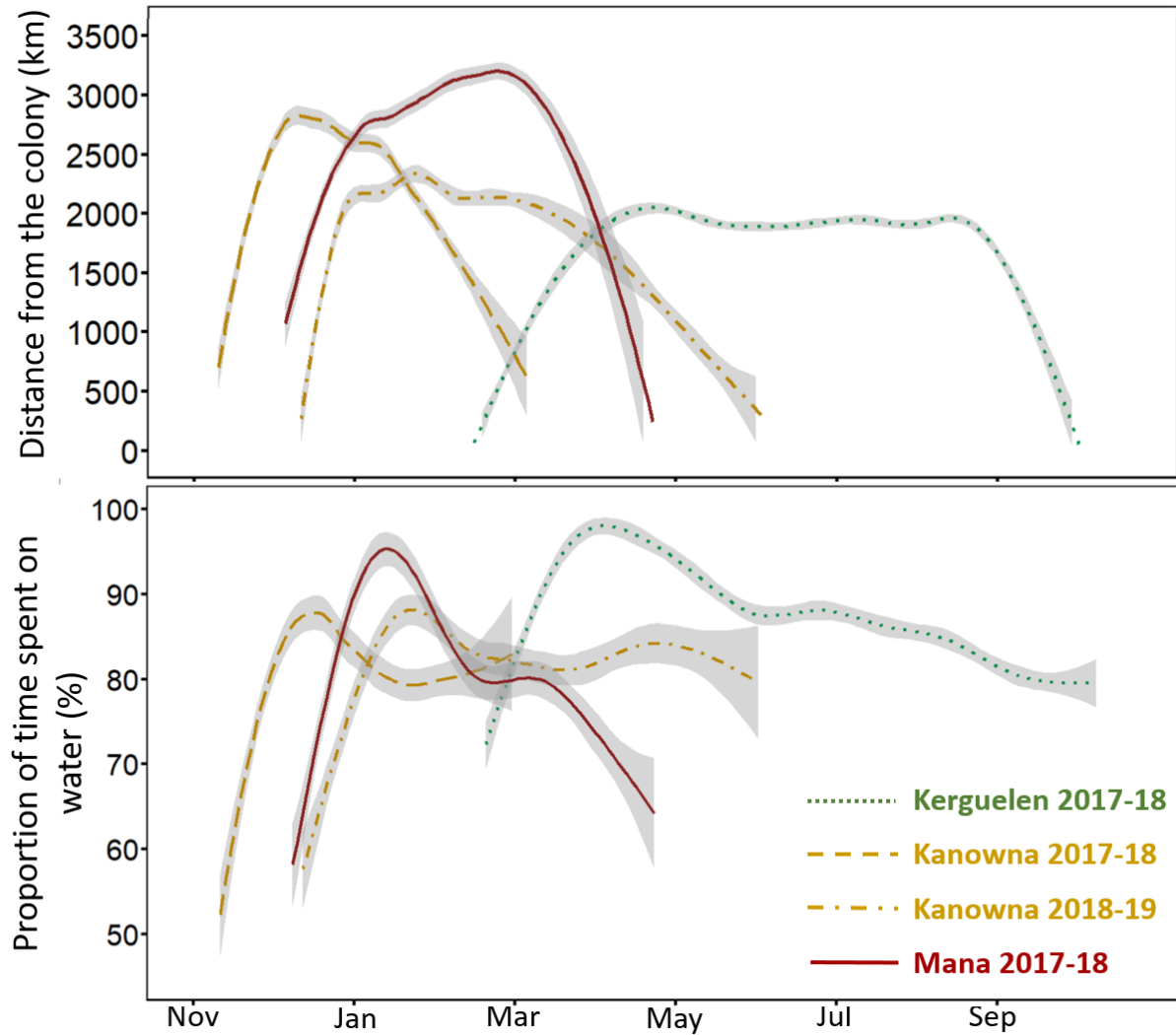


Figure 3-5: Distance from the colony (upper panel) and proportion of time spent on the water per day (lower panel) during the post-breeding migration of common diving petrels (*P. urinatrix*) from Kerguelen (green dotted line, 2017-18, n = 7), Kanowna (orange long-dashed line, 2017-18, n = 5; and orange dot-dashed line, 2018-19, n = 8), and Mana Islands (red solid line, 2017-18, n = 4). Data were fitted with a generalized additive mixed models (GAMMs). The shaded areas along the curves represent the 95% confidence interval.

3.4.2. Stable isotope values

Stable isotope values of body feathers (four per individual) varied substantially, from -26.0 to -15.9 ‰ for $\delta^{13}\text{C}$ and from 3.9 to 15.2 ‰ for $\delta^{15}\text{N}$. Within each population, there were similar patterns, with feathers splitting into two groups (Fig. 3-6). The majority of feathers had low $\delta^{13}\text{C}$ (from -26.1 to -19.5 ‰) and $\delta^{15}\text{N}$ (from 3.8 to 9.9 ‰) values (Group 1), while a smaller group of body feathers exhibited markedly higher isotopic values (from -19.5 to -15.9 ‰ for $\delta^{13}\text{C}$ and from 9.9 to 15.1 ‰ for $\delta^{15}\text{N}$; Group 2).

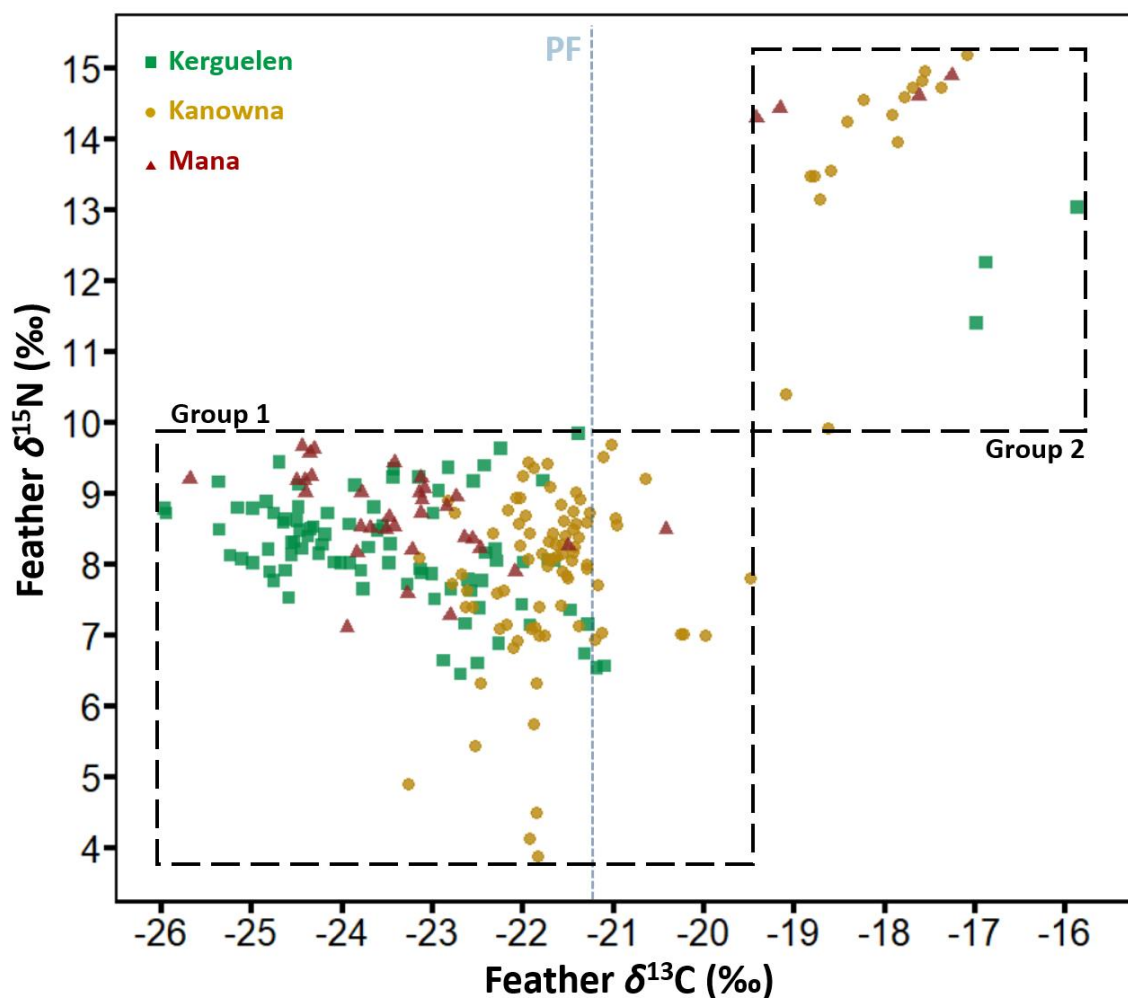


Figure 3-6: Body feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common diving petrels (*P. urinatrix*) from Kerguelen (green squares, $n = 23$), Kanowna (orange dots, $n = 25$), and Mana Islands (red triangles, $n = 10$). Points represent isotopic values of individuals feathers (four body feathers per individual). Isotopic ratios in Group 1 correspond to Antarctic/subantarctic waters and Group 2 to subtropical/neritic waters (Jaeger et al. 2010). The blue dotted line corresponds to the feather $\delta^{13}\text{C}$ estimation of the Polar Front (PF) (Jaeger et al. 2010).

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values differed significantly among populations (Friedman test: $\chi^2 = 101$ for $\delta^{13}\text{C}$ and 52.2 for $\delta^{15}\text{N}$, both $P < 0.001$), with individuals from Kerguelen exhibiting the lowest values of $\delta^{13}\text{C}$ in Group 1 but the highest in Group 2. The $\delta^{15}\text{N}$ values for the individuals from Kanowna Island in Group 1 had a larger range than in the other populations (Fig. 3-6), with extremely low $\delta^{15}\text{N}$ values in six body feathers ($3.9\text{‰} < \delta^{15}\text{N} < 5.7\text{‰}$) from four different individuals (2 females and 2 males). The proportion of body feathers in Group 2 varied among populations (3.4% for Kerguelen, 16.0% for Kanowna Island, and 10.8% for Mana Island) and within populations (Supplementary Fig. S3-2), with either individuals with body feathers only in Group 1 or in both Group 1 and 2 but never with all the four feathers in Group 2. Values of $\delta^{13}\text{C}$ in body feathers of tracked individuals were correlated with latitude of the kernel UD centroid, $\delta^{13}\text{C}$ values decreasing with higher latitudes (Supplementary Fig. S3-3; Spearman's correlation test: $S = 44630$, $P < 0.001$, $\rho = 0.649$).

3.4.3. Inter-annual variations

Multi-year data were collected for GLS tracking (2015-16 and 2017-18 for Kerguelen; 2017-18 and 2018-19 for Kanowna Island; Table 3-1), and stable isotopes (2015-16, 2016-17 and 2017-18 for Kerguelen; 2016-17, 2017-18 and 2018-19 for Kanowna Island; Table 3-2). Trip parameters differed substantially between years at Kanowna Island ($P < 0.01$ in all cases), but not at Kerguelen (Table 3-1). Specifically, individuals from Kanowna Island departed on average 35 days later, stayed away 35 days longer and returned to the breeding region 70 days later in 2018-19 than in 2017-18. However, the maximum range and the total distance travelled were similar between the two years ($P > 0.2$ in both cases), as were post-breeding destinations (Fig. 3-3).

For both regions, feather $\delta^{13}\text{C}$ values were generally consistent among years, except for Kerguelen between 2016-17 and 2017-18 (Table 3-2, Supplementary Fig. S3-4; Mann-Whitney

U test: $U = 754.5$, $P = 0.002$), while $\delta^{15}\text{N}$ values differed greatly among years for Kerguelen (Friedman test: $\chi^2 = 10.806$, $P = 0.004$) and Kanowna (Friedman test: $\chi^2 = 25.220$, $P < 0.001$), with for the latest a mean value of $\delta^{15}\text{N}$ 1.8 ‰ lower in 2018-19 than in 2017-18 (Table 3-2; Mann-Whitney U test: $U = 582$, $P < 0.001$). Additionally, for Kanowna, the proportion of feathers in Group 2 varied from 22.9% in 2016-17 and 20.0% in 2017-18 to 3.1% in 2018-19 (Supplementary Fig. S3-5). Nonetheless, even when considering only the feathers from Group 1, $\delta^{15}\text{N}$ values were 1.4 ‰ lower in 2018-19 than in 2017-18 (Mann-Whitney U test: $U = 457.5$, $P < 0.001$).

Table 3-2: Body feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of common diving petrels (*P. urinatrix*) from Kerguelen, Kanowna, and Mana Islands. Values are means (\pm SD), and n and N refer to the number of feathers and of individuals (four feathers per individual), respectively.

		Kerguelen	Kanowna	Mana
Feather $\delta^{13}\text{C}$ (‰)	2015-2016	-23.3 \pm 1.6 (n = 24; N = 6)	-	-
	2016-2017	-22.8 \pm 1.9 (n = 40; N = 10)	-20.9 \pm 1.8 (n = 48; N = 12)	-
	2017-2018	-24.1 \pm 1.2 (n = 28; N = 7)	-21.1 \pm 1.3 (n = 20; N = 5)	-22.8 \pm 1.8 (n = 40; N = 10)
	2018-2019	-	-21.5 \pm 0.8 (n = 32; N = 8)	-
Feather $\delta^{15}\text{N}$ (‰)	2015-2016	8.7 \pm 0.9 (n = 24; N = 6)	-	-
	2016-2017	8.4 \pm 1.2 (n = 40; N = 10)	9.3 \pm 3.1 (n = 48; N = 12)	-
	2017-2018	7.9 \pm 0.7 (n = 28; N = 7)	9.4 \pm 1.5 (n = 20; N = 5)	9.3 \pm 1.9 (n = 40; N = 10)
	2018-2019	-	7.6 \pm 1.4 (n = 32; N = 8)	-

3.5. Discussion

By combining GLS tracking with stable isotope analysis of body feathers, the present study described the post-breeding movements and timing of moult of CDP from three populations breeding across two oceanic basins in the Southern Hemisphere. Despite the high

wing loading of CDPs (Warham 1977) and their high daily energy expenditure (Roby and Ricklefs 1986, Green and Brothers 1989), all the individuals in the present study travelled long distances (20,000 – 55,000 km) during the post-breeding migration. Our results show also strong inter-population differences in the phenology, distribution and activity of CDP during the non-breeding period. This highlights the importance of using a multi-population approach in ecology in order to fully understand the mechanisms of species adaptation to local environmental variations.

3.5.1. Spatial distribution

Common diving petrels from the three study regions all migrated to oceanic frontal systems of the Southern Ocean. However, their post-breeding destinations were markedly different among the three focal populations, and differed also from those of birds from South Georgia, which remained in the southern Atlantic Ocean (Fig. 3-3; Navarro et al. 2015). Birds from Mana Island in New Zealand migrated south-east in accordance with previous findings from two colonies on the east and west coasts of North Island (Fig. 3-3; Rayner et al. 2017). This suggests behavioural homogeneity within the New Zealand population.

Given their high wing loading and very limited soaring capabilities (Pennycuick 1996), the flight energy expenditure of CDP is relatively high (Roby and Ricklefs 1986). Therefore, the different migratory destinations and path headings among the populations could reflect individuals exploiting the nearest productive habitats during the non-breeding period (Navarro et al. 2015, Rayner et al. 2017). Indeed, CDP from South Georgia, south-eastern Australia and New Zealand all travel to the highly productive Polar Front region (Navarro et al. 2015, Rayner et al. 2017, Moore and Abbott 2002). The observation that individuals from New Zealand did not travel directly towards the Polar Front could reflect longitudinal differences in the productivity of this oceanographic feature (Moore and Abbott 2002). Such regional variations

have also been shown to play an important role in the distribution of grey petrels (*Procellaria cinerea*) and sooty shearwaters (*Ardenna grisea*) breeding in New Zealand (Shaffer et al. 2009, Torres et al. 2015).

Alternatively, the inter-population differences in post-breeding migratory destinations of CDP could reflect competition avoidance. Spatial segregation is often considered to be a mechanism to reduce competition between species and/or populations (Bolton et al. 2019). The Polar Front is known to be exploited by a wide range of other seabirds in the region (Bost et al. 2009, Delord et al. 2013, Hindell et al. 2020), including the closely related South Georgian diving petrel (*P. georgicus*; Fromant et al. 2022). Consequently, the observation that post-breeding CDP from Kerguelen do not target the closest Polar Front area, but head farther south, could be due to intra- and inter-specific competition occurring in the densely populated southern Indian Ocean (Marchant and Higgins 1990).

3.5.2. *Timing of migration and moult*

Breeding phenology in seabirds has been shown to follow a gradient, with nesting periods being delayed with increasing latitude (Burr et al. 2016). In the present study, there was a 3-4 months difference between the timing departure in migration of individuals from Kanowna Island and Kerguelen. However, only a 20-day shift in breeding phenology should be expected due to the 10° latitudinal difference between the two sites (*i.e.*, a 2-day delay per degree of latitude; Burr et al. 2016, Baker 1939). Interestingly, within the Kerguelen Archipelago, CDP nesting and feeding in the Golfe du Morbihan (a closed coastal habitat) have been shown to breed one month later than the individuals nesting on offshore sites (Weimerskirch et al. 1989). Additionally, in the present study, the breeding phenology of CDP from Kanowna Island varied substantially among years. These suggest that local oceanographic

conditions of foraging areas during the breeding season play a key role in determining the phenology of CDP.

In the present study, a substantial increase in the proportion of time spent on water 30-40 d after migration departure was found in all sites and years. Such a pronounced pattern of activity has been associated with the renewal of flight feathers in several small procellariiform species (Jones et al. 2020, Cherel et al. 2016). Migratory diving birds, such as some species of alcids and diving petrels, are known to undergo a rapid wing moult in early post-breeding period, temporary affecting their flight ability (Bridge 2006). The physiological cost of a quasi-flightless period seems to be mediated by their diving and feeding capacities that remain efficient during wing moult (Bridge 2004). Although, this result could simply indicate a period of intensive feeding, the strong correlation between the peak timing and the migration departure suggests that this event is strongly influenced by the breeding phenology. The onset of flight feather renewal in other Procellariiformes has similarly been related to the end of the breeding season (Arroyo et al. 2004).

The important intra-individual variance in isotopic values of body feathers indicates they grew in different locations and, therefore, at different periods from the end of the breeding season to throughout the non-breeding period (Cherel et al. 2016, Carravieri et al. 2014, Bugoni et al. 2015). The results indicate most body feathers moulted in Antarctic/subantarctic waters but a small proportion moulted in sub-tropical or coastal areas (Cherel et al. 2006). However, the proportion of body feathers with Antarctic $\delta^{13}\text{C}$ value differed among the three study populations which could be related to the timing and duration of migration. Indeed, at Kanowna Island, inter-annual differences in isotopic values were associated with unprecedented changes in breeding phenology between consecutive seasons for this species (Supplementary Fig. S3-5; Eizenberg et al. 2021). These unexpected results indicate that the moult of body feathers was delayed according to the change in breeding phenology. This reinforces the findings showing

that, the timing of breeding is an important factor in determining the moult schedule of body feathers (Pastor-Prieto et al. 2019). Additionally, a longer post-breeding migration duration lowered the number of isotopic values corresponding to sub-tropical/neritic waters. This suggests that most of the body feathers were moulted within the first four months after the end of the breeding season.

3.5.3. Duration of the post-breeding migration

In addition to inter-population differences in the timing and destinations of post-breeding migration, the present study revealed important differences in its duration, with individuals at Kerguelen remaining away from the colony for four and three months longer than those at Kanowna Island and Mana Island. These results are consistent with previous studies indicating that adults are absent from the colony for six to eight months at South Georgia (Croxall and Prince 1980), Crozet (Jouventin et al. 1985) and Kerguelen Islands (Bocher et al. 2000b), while on New Zealand's North Island birds are away for half this duration (Rayner et al. 2017). The CDP from south-eastern Australia and New Zealand, then, come back and stay in the vicinity of their respective breeding colony 5-6 months before initiating the next breeding cycle.

For both south-eastern Australia and New Zealand populations, a decrease in marine productivity in the area where they migrate in post-breeding (Moore and Abbott 2002) and/or an increase of food availability near their breeding grounds at the end of summer (February-March; Young et al. 1993) could induce an early return from their migration area. Such a pattern has been observed in thin-billed prions (*Pachyptila belcheri*) from the Falkland/Malvinas Islands (Quillfeldt et al. 2019) that, in contrast to conspecifics from Kerguelen, return earlier to the breeding grounds from substantially shorter migration periods to distant open waters in order to exploit an extensive local shelf area.

Conversely, this difference could be linked to the predictability of food resources in the vicinity of the breeding areas (Frederiksen et al. 2004). In south-eastern Australia and New Zealand, the locally abundant coastal krill *Nyctiphanes australis* (Young et al. 1993) is a key food source for CDP (Fromant et al. 2020a, Miskelly *pers. Obs.*). However, this euphausiid undergoes extreme inter-annual variations in biomass and distribution, considerably affecting the reproductive success of various fish (Young et al. 1993) and seabird species (Mills et al. 2008, Manno et al. 2014). Populations spending a long period near the colony before the reproductive season are more likely to follow local environmental cues to adapt their phenology (Frederiksen et al. 2004), which may explain the significant delay in the breeding period observed between the years in the present study at Kanowna Island (Eizenberg et al. 2021). In contrast, CDP at Kerguelen and South Georgia, where marine productivity is relatively more predictable (Reid et al. 1997, Bocher et al. 2001), may be able to return from migration closer to the mating period.

3.5.4. Implications for conservation

Six factors have been considered as potential barriers to gene flow between seabird populations: physical isolation; contrasted breeding phenology; strong philopatry; differences in ocean regime; and divergence in breeding and non-breeding distributions (Friesen 2015). In addition to the obvious physical isolation between the main CDP populations and their small range in their foraging areas during the breeding period (Navarro et al. 2013, Zhang et al. 2019), the present study has provided evidence of segregation in the post-breeding migratory destinations of eastern CDP populations. Similarly, there are inter-population differences in diving behaviour (Bocher et al. 2000a,b, Navarro et al. 2014, Dunphy et al. 2015), diet (Ridoux 1994, Reid et al. 1997, Bocher et al. 2000a, Fromant et al. 2020a) and phenology (Thoresen 1969, Payne and Prince 1979, Eizenberg et al. 2021, **Chapter 2**), though these differences may

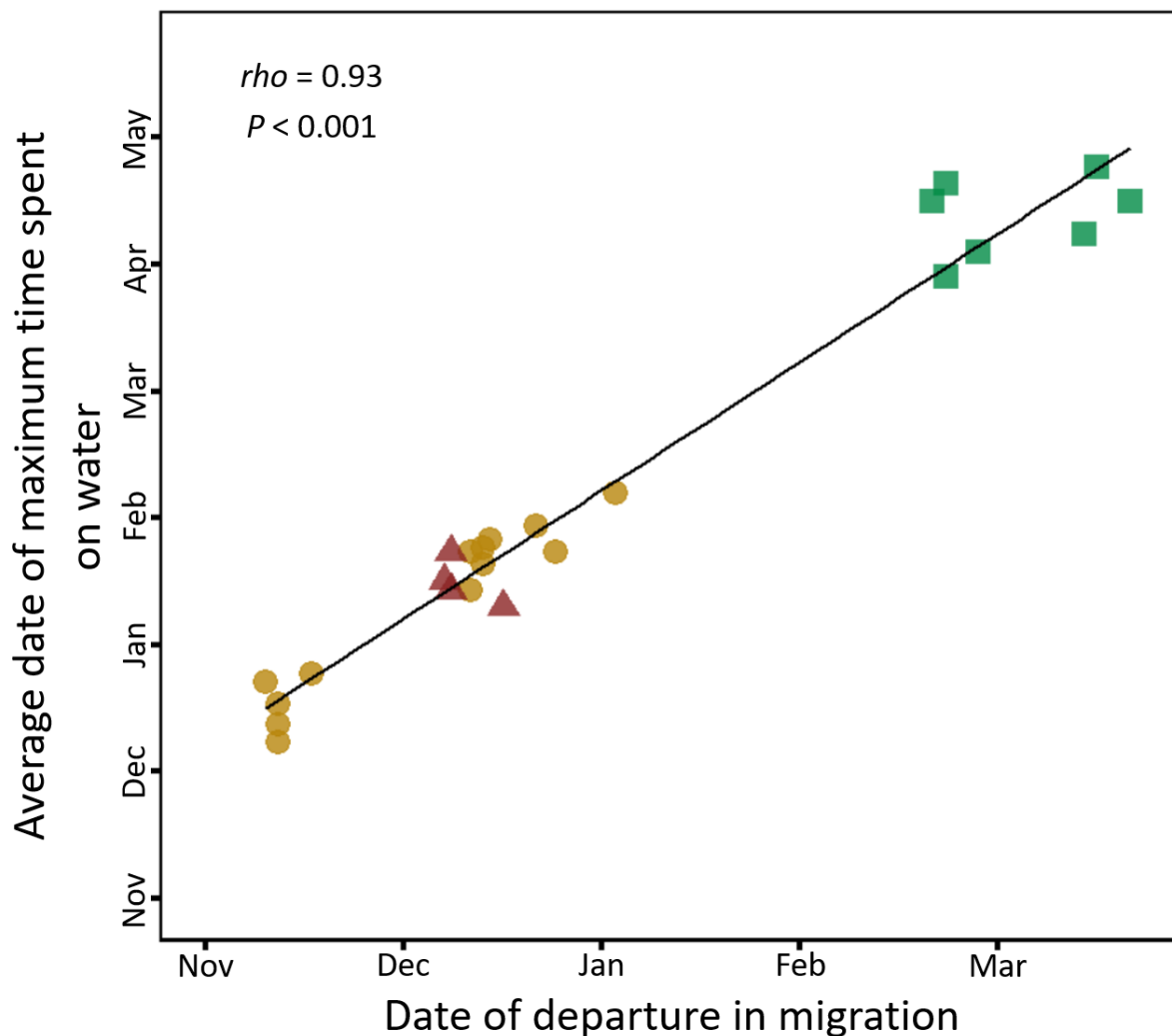
be mainly related to the local oceanographic environment during the breeding season. Finally, because CDP are highly philopatric (Warham 1990, Bonadonna et al. 2003, Cunningham et al. 2012), the results of the present study provide further evidence that the species has a high potential for population differentiation (Rayner et al. 2011). Indeed, Cristofari et al. (2019) recently revealed significant isolation and low inter-population flux in Peruvian diving petrel (*Pelecanoides garnotii*) colonies at very short distances (350 km).

Conservation biology often considers species as single taxonomical, biological and ecological entities, and not considering the presence of sub-species may mislead in determining the species' status and, thus, appropriate conservation strategies (Martin et al. 2007). It is, therefore, of importance to revisit the genetic and taxonomic relationships among the different populations of CDP, as recently done for the South Georgian diving petrel (Paterson et al. 2000, Fischer et al. 2018) and the Peruvian diving petrel (Cristofari et al. 2019). Meanwhile, caveats remain for the spatial distribution of juveniles and failed-breeders. Natal dispersal is a major factor influencing population structure and metapopulation dynamics (Greenwood 1980), and despite the CDP being highly philopatric (Warham 1990, Bonadonna et al. 2003, Cunningham et al. 2012), knowledge of first year individuals could have important implications for conservation.

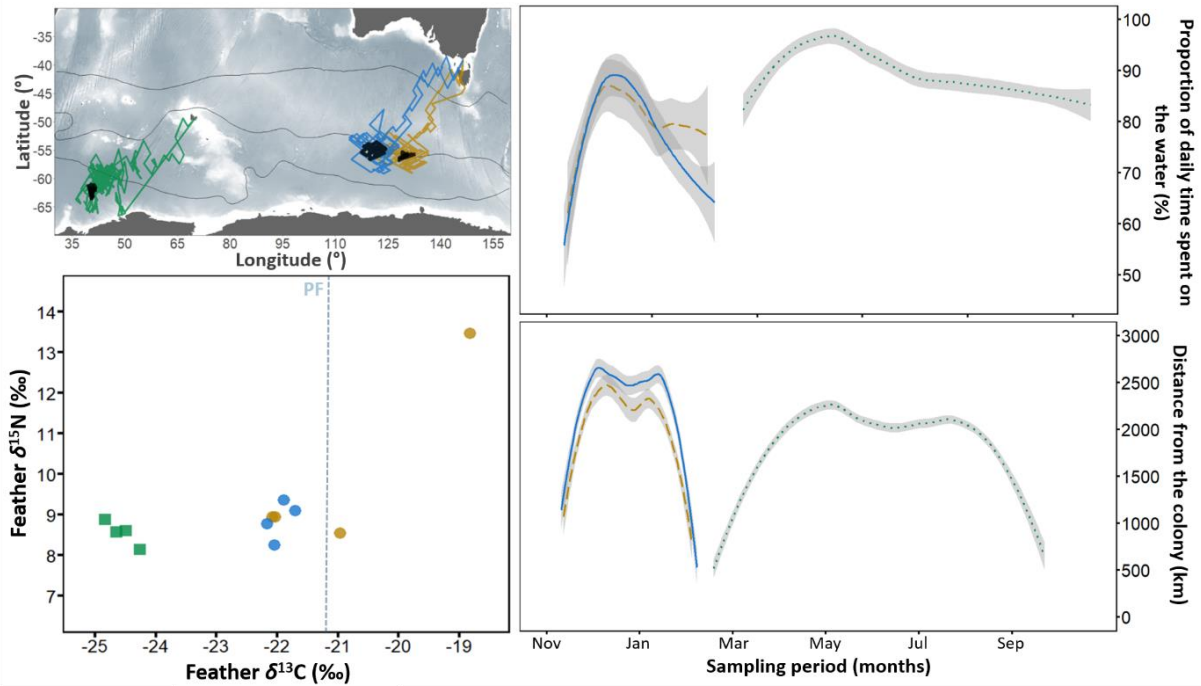
In summary, the present study has provided clear evidence that CDP travel to Antarctic or subantarctic productive waters during the post-breeding migration. However, major temporal, spatial and trophic differences throughout the species' distribution highlight the relevance of multi-population studies (Frederiksen et al. 2012). Further information is required in order to better understand the genetic and taxonomic structure (Rodríguez et al. 2019), and the degree of isolation, of sub-populations/sub-species (Murphy and Harper 1921). It is notably vital for small remote populations such as those from Gough Island, Marion Island, Macquarie Island and Campbell Island that are or have been exposed to the threat of invasive rodents

(Brothers 1984, Barker et al. 2005, Dilley et. 2015). The approach used in the present study, investigating the phenology and distribution outside the breeding season to evaluate the population diversity, could be expanded to a wide range of seabird species, especially the under-studied small-sized Procellariiformes (Rodríguez et al. 2019). This could improve the knowledge of evolutionary divergence among populations (Lombal et al. 2020) and assist in the challenging conservation of migratory species (Dunn et al. 2019).

3.6. Supplementary material

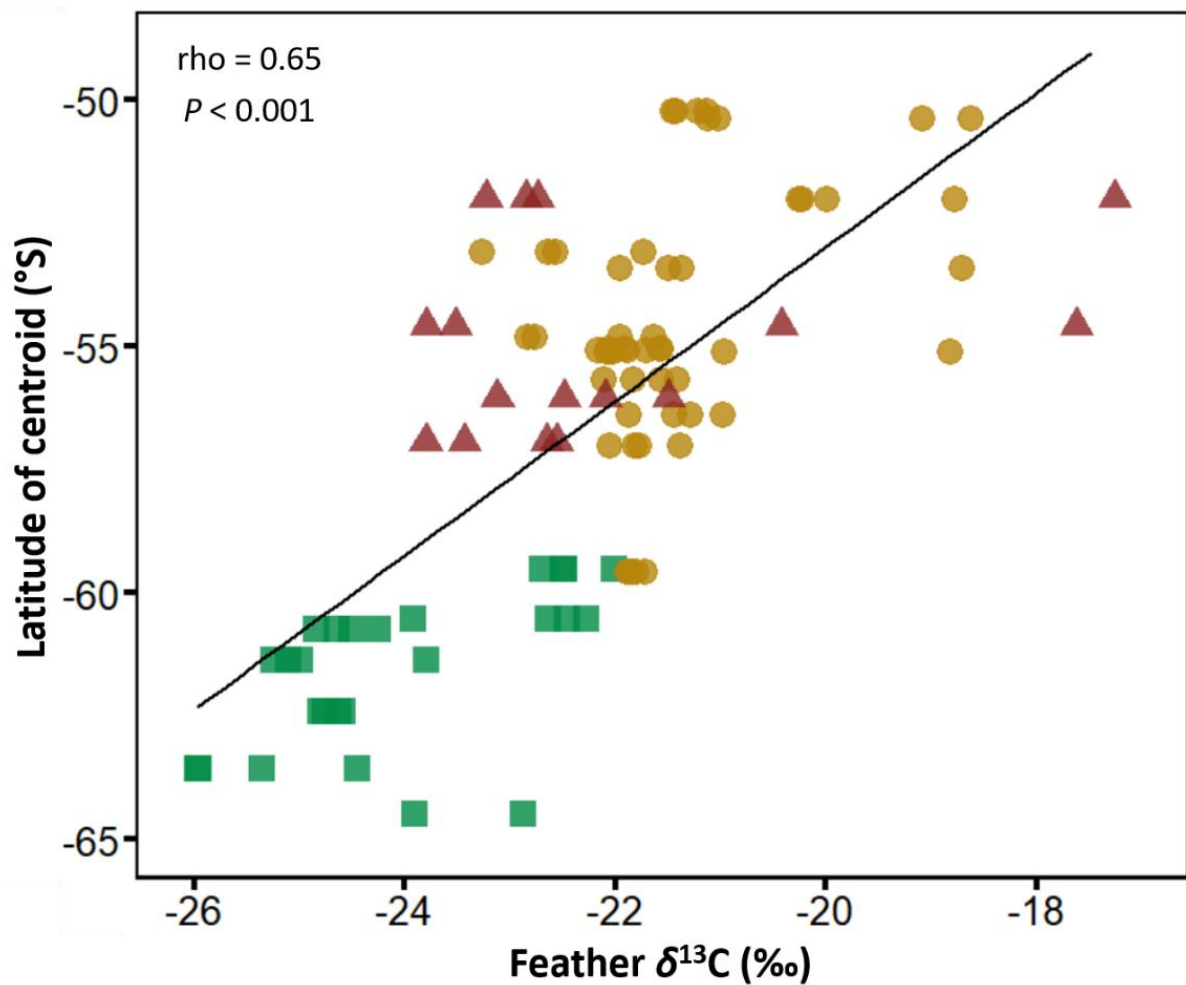


Supplementary Figure S3-1: Correlation between departure date and the average date of maximum time spent on the water (mean moult period) for common diving petrels from Kerguelen (green squares, 2017-18, N = 7), Kanowna Island (orange dots, 2017-18 and 2018-19, N = 13), and Mana Island (red triangles, 2017-18, N = 4). The Mean moult date was identified as the peak of time spend on the water (> 90% time per day sitting on water). Birds were equipped with miniaturized saltwater immersion geolocators.

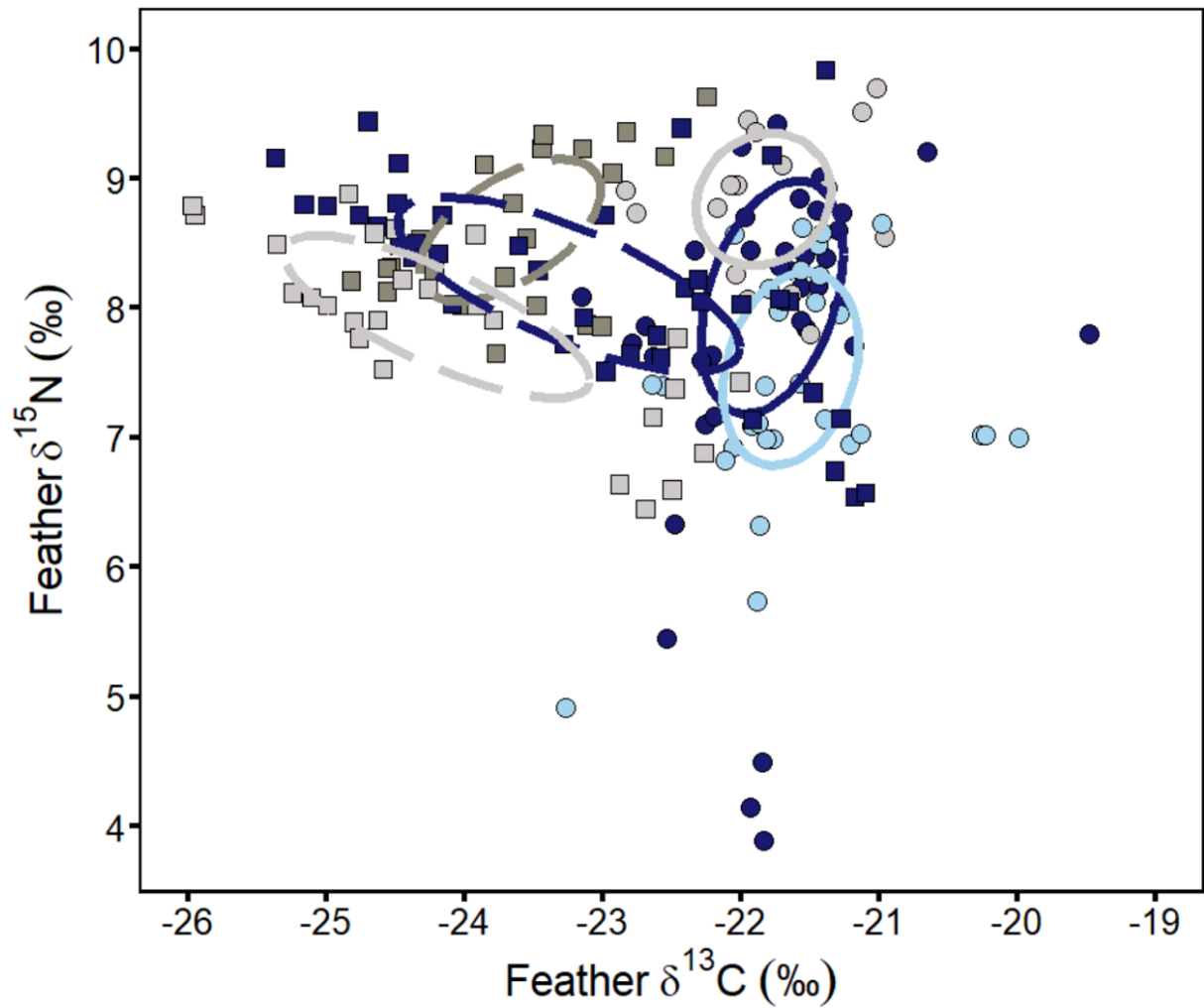


Supplementary Figure S3-2: Example of inter-population and intra-population variation of migratory behaviour during the post-breeding migration of common diving petrels from Kerguelen (1 individual in green) and Kanowna (2 individuals in blue and yellow).

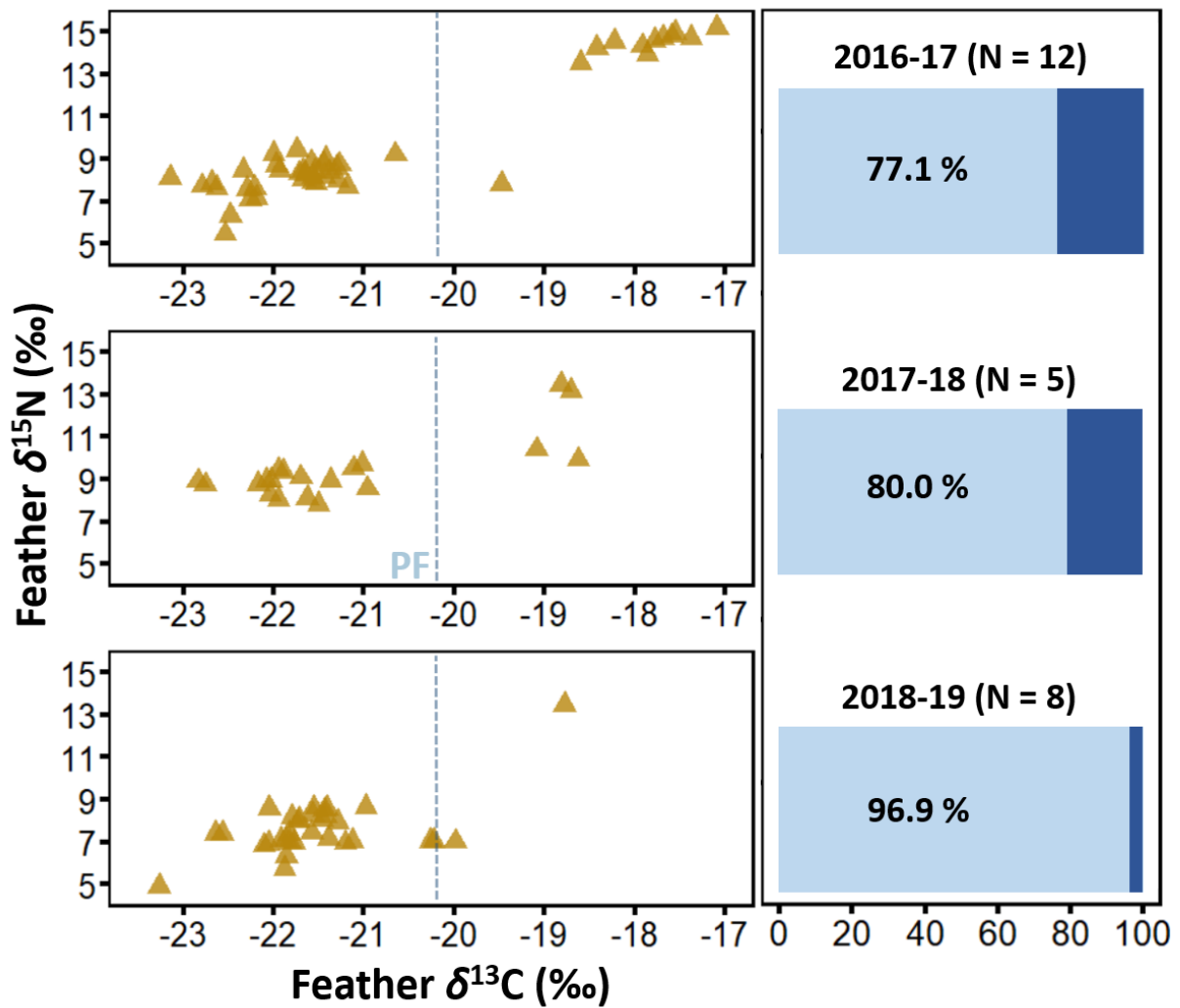
Lower left: stable carbon and nitrogen isotope values of body feathers (four per individual). The dotted line corresponds to the feather $\delta^{13}\text{C}$ estimation of the Polar Front (PF) (Jaeger et al. 2010); Upper left: individual track derived from geolocator data. For each track, the estimated moult period of flight feathers is highlighted in black; Upper right: daily time spent on the water for each individual; Lower Right: distance from the colony for each individual. Data for upper and lower right panels were fitted with a generalized additive mixed models (GAMMs). The shaded areas along the curves represent the 95% confidence interval.



Supplementary Figure S3-3: Correlation between stable carbon isotopic values ($\delta^{13}\text{C}$) of body feathers (four per individuals) and the latitude of centroid of the 50% kernel utilization distribution (core area) for common diving petrels from Kerguelen (green squares; 2017-18, N = 7), Kanowna Island (orange dots; 2017-18 and 2018-19, N = 13), and Mana Island (red triangles; 2017-18, N = 4).



Supplementary Figure S3-4: Niche overlap of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in body feathers (Group 1) of common diving petrel from Kerguelen (squares and dashed line) and Kanowna (dots and solid line). Dark grey = 2015-16 (Kerguelen only, N = 6), blue navy = 2016-17 (Kerguelen N = 10, Kanowna N = 12), grey = 2017-18 (Kerguelen N = 7, Kanowna N = 5), light blue = 2018-19 (Kanowna only, N = 8). Solid lines represent the standard ellipses corrected for sample size (SEAc; 40% probability of containing a subsequently sampled datum regardless of sample size; Jackson et al. 2011).



Supplementary Figure S3-5: Inter-annual variation of isotopic values in body feathers of common diving petrel from Kanowna (four feathers per individual). The right panel presents the proportion of feathers moulted in Antarctic/subantarctic waters (percentage; light blue) or in subtropical/neritic waters (dark blue). The dotted line corresponds to the feather $\delta^{13}\text{C}$ estimation of the Polar Front (PF) (Jaeger et al. 2010). Departure in post-breeding migration was unknown in 2017, but was, early November and early December in 2018 and 2019, respectively (Eizenberg et al. 2021).

Supplementary Table S3-1: Results of the GLM models explaining trip parameters (duration of post-breeding period, departure date, return date, maximum range, and total distance travelled) for common diving petrels Kerguelen (2015-16, n = 5; 2017-18 = 7), Kanowna (2017-18, n = 5; 2018-19, n =8) and Mana Islands (2017-18, n = 4).

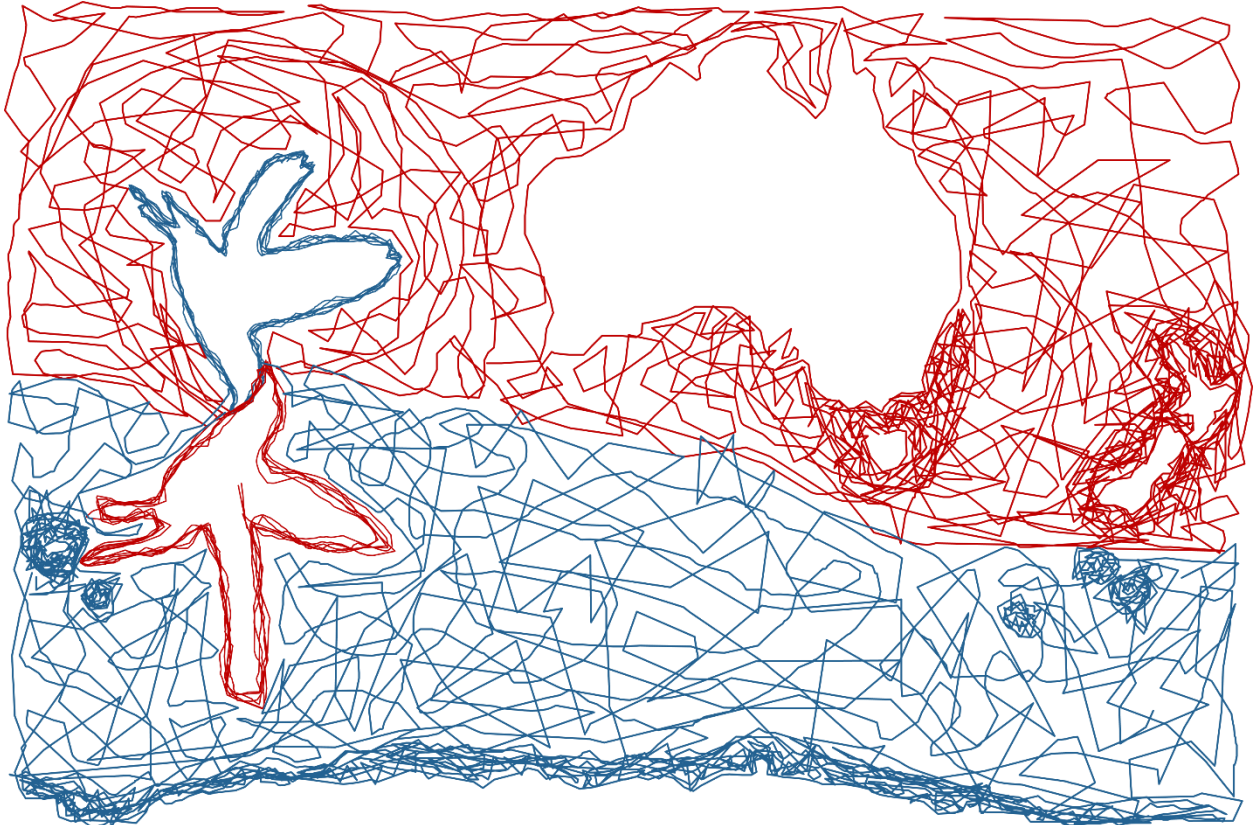
Explanatory variables, deviance explained, Akaike Information Criterion (AIC) and Delta AIC (difference in AIC with the best model) are given for each model. Models are ranked according to their respective AIC value and significant variables in each model are highlighted in bold.

	Model	Deviance	AIC	Delta AIC
Total duration of post-breeding period	DURATION ~ POPULATION + YEAR	91.1 %	216.6	0.0
	DURATION ~ POPULATION + YEAR + SEX	91.3 %	219.9	3.4
	DURATION ~ POPULATION	84.6 %	226.2	9.6
	DURATION ~ 1	0.0 %	268.9	52.4
	DURATION ~ YEAR	11.3 %	269.9	53.4
	DURATION ~ SEX	1.1 %	272.6	56.1
Departure date	DEPARTURE ~ POPULATION + YEAR	92.1 %	234.0	0.0
	DEPARTURE ~ POPULATION + YEAR + SEX	92.3 %	237.1	3.1
	DEPARTURE ~ POPULATION	85.5 %	246.9	12.9
	DEPARTURE ~ YEAR	27 %	292.1	58.1
	DEPARTURE ~ 1	0.0 %	296.9	62.9
	DEPARTURE ~ SEX	3.7 %	299.8	65.8
Return date	RETURN ~ POPULATION + YEAR	98.3 %	206.5	0.0
	RETURN ~ POPULATION + YEAR + SEX	98.5 %	207.2	0.7
	RETURN ~ POPULATION	92.3 %	239.7	33.1
	RETURN ~ YEAR	15.4 %	299.7	93.1
	RETURN ~ 1	0.0 %	299.8	93.2
	RETURN ~ SEX	3.1 %	303.1	96.5
Maximum range	RANGE ~ POPULATION	38.4 %	442.0	0.0
	RANGE ~ POPULATION + YEAR	44.8 %	442.8	0.8
	RANGE ~ POPULATION + YEAR + SEX	45.3 %	446.6	4.5
	RANGE ~ YEAR	16.8 %	450.7	8.7
	RANGE ~ 1	0.0 %	452.1	10.0
	RANGE ~ SEX	2.3 %	455.4	13.3
T ot	DISTANCE ~ POPULATION + SEX	52.6 %	516.7	0.0

DISTANCE ~ POPULATION	40.8 %	518.2	1.6
DISTANCE ~ POPULATION + YEAR + SEX	53.1 %	520.4	3.7
DISTANCE ~ 1	0.0 %	527.4	10.7
DISTANCE ~ YEAR	10.9 %	528.5	11.8
DISTANCE ~ SEX	4.0 %	530.3	13.6

Chapter 4

Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of the common diving petrel.



A version of this chapter has been published as:

Fromant A, Delord K, Bost C-A, Eizenberg YH, Botha JA, Cherel Y, Bustamante P, Gardner BR, Brault-Favrou M, Lec’hvien A, Arnould JPY (2021) Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird. *Progress in Oceanography* 198:102676.

<https://doi.org/10.1016/j.pocean.2021.102676>

4.1. Summary

The reproductive success of birds is strongly driven by environmental conditions at different time scales. Thus, during periods of low food availability, breeding success is constrained by the ability of adults to adapt their foraging effort and feeding behaviour to maintain regular incubation shifts and chick provisioning. However, while large seabirds can buffer disruptions in prey availability, the ecophysiological constraints of smaller species may limit their behavioural flexibility. By combining information on at-sea movements, foraging habitat, trophic niche, and breeding success, Chapter 4 evaluated the effects of intense variability in oceanographic conditions on common diving petrels (*Pelecanoides urinatrix*) at the northern extent of their range in south-eastern Australia during four consecutive breeding seasons. Unusually low breeding success (6 and 0%) was observed during two years with intense heatwave events, which were associated with higher foraging effort (foraging trips twice longer) and a substantial shift in trophic niche (lower blood $\delta^{15}\text{N}$ values). These findings suggest that common diving petrels in Bass Strait may have reached a critical threshold above which buffering the effects of environmental variability on their reproductive output is not possible. The clear cascading impacts that marine heatwaves have on zooplankton feeders illustrate the profound bottom-up effect induced by such extreme environmental variations (Fig. 4-1), and suggest strong impact on higher-trophic levels. The wide, circumpolar breeding distribution of the common diving petrel, and its high sensitivity to variations in oceanographic conditions, suggest that this species may be a suitable model to study short-term and long-term behavioural responses to the effects of climate change throughout the Southern Ocean.

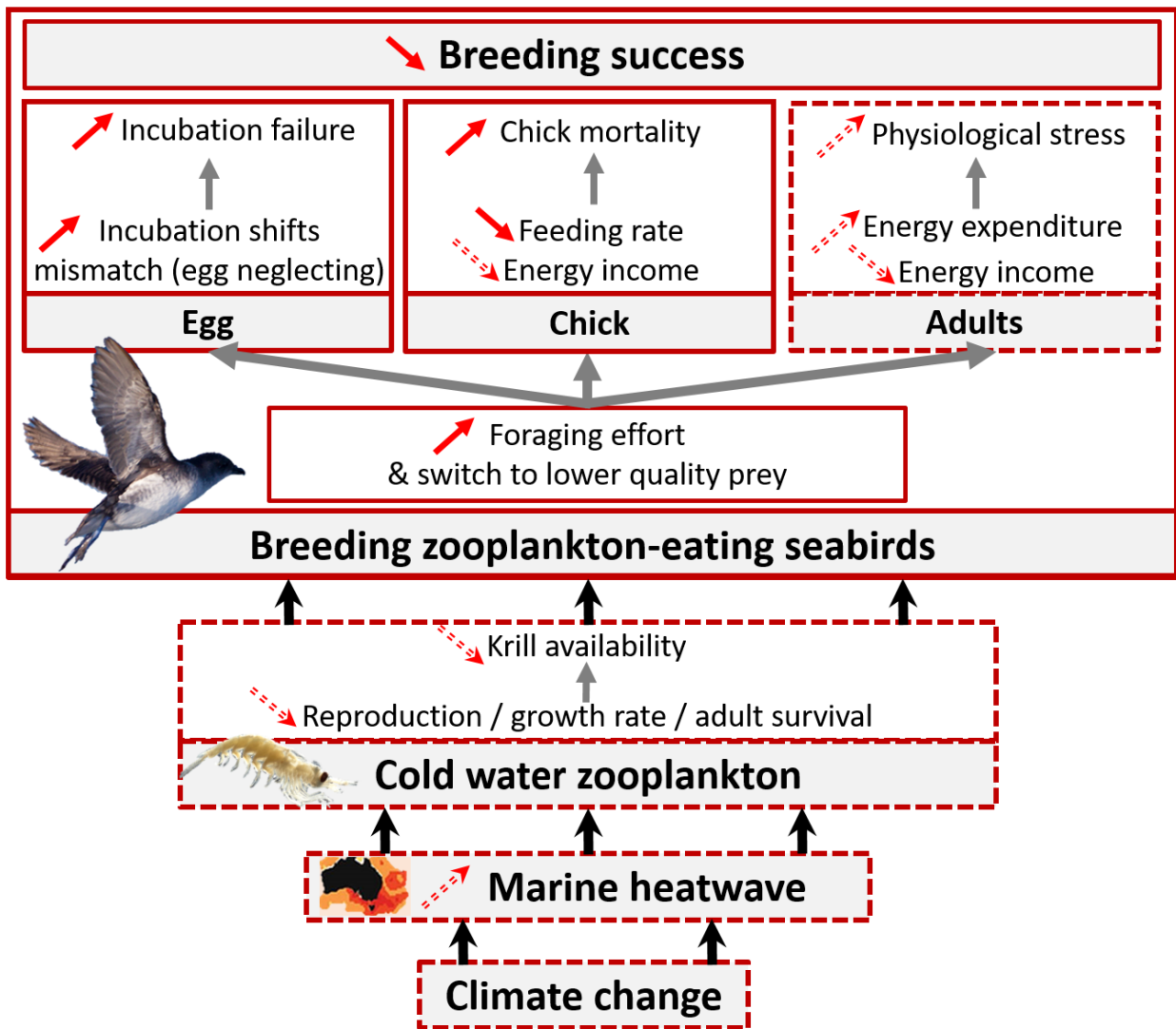


Figure 4-1: Cause-effect diagram illustrating the bottom-up effect of marine heatwaves on the breeding output of zooplankton-eating seabirds presented in Chapter 4. For species breeding on the edge of their distribution range, the predicted intensification of marine heatwaves is likely to strengthen the detrimental effects on their breeding output. Full red blocks and arrows are results observed in the present study; Dotted red blocks and arrows are adapted from the literature (Young et al. 1993, Harding et al. 2007, Cohen et al. 2014, Oliver et al. 2017, Evans et al. 2020) (photo ©: A. Slotwinski and G. Jones).

4.2. Introduction

Seabirds forage in a patchy and dynamic environment where prey is unevenly distributed (Hunt 1990, Weimerskirch 2007). The variation in physical characteristics of the ocean such as temperature, salinity or currents, strongly influence the distribution and availability of prey which, in turn, determine the foraging behaviour of consumers (Franks 1992). Individuals must be flexible in their foraging behaviour and diet, according to spatio-temporal variations in the abundance and distribution of prey species. Thus, seabirds should adapt their strategy at different time scales (i.e. daily, seasonally or annually) to ensure survival and maximise reproductive output (Haury et al. 1978, Weimerskirch et al. 1993). However, climate change is likely to challenge species, as the anticipated increased alterations in the distribution, abundance and diversity of prey should affect their capacity to cope with environmental variability (Chambers et al. 2011).

Seabirds have been extensively used as ecological indicators of the impacts of environmental variations (Cairn 1992, Piatt et al. 2007, Bost et al. 2008). During periods of low prey abundance, breeding seabirds can adjust their behaviour by increasing their foraging effort and/or adapting their diet (Harding et al. 2007, Cohen et al. 2014). However, behavioural plasticity varies greatly between species and/or populations (Gilmour et al. 2018), and seabirds with less flexible foraging strategies or capabilities may not cope with drastic environmental variability (Quillfeldt & Masello 2013, Jakubas et al. 2020). Due to their relatively easier access for data collection, the majority of studies have focused on large iconic species, resulting in knowledge being mostly restricted to species of higher trophic level, broad diet and/or large foraging range (Chiaradia et al. 2010, Price et al. 2020). Consequently, our understanding of the links between seabird parameters and variation in oceanographic conditions is limited (Grémillet & Charmantier 2010), with little information available for species feeding locally on low trophic level prey.

This is exemplified by small pursuit-diving seabirds with high flight costs that might be less able to buffer the consequences of reduced prey availability and longer foraging trips (Elliott et al. 2013). While significant advances have been made in recent years for small Northern Hemisphere alcids (*e.g.* Grémillet et al. 2012, Amélineau et al. 2019, Jakubas et al. 2020), information on the at-sea movements and foraging behaviour of Southern Hemisphere diving petrels (Procellariidae), and their capacity to adapt, is deficient (Chastel et al. 1995, Cherel et al. 2014). This is of concern considering the wide distribution and large biomass the species comprises (Marchant & Higgins 1990). For example, the common diving petrel (*Pelecanoides urniatrix*, study species) is a ubiquitous species of the Southern Ocean estimated to 20-30 million individuals (conservative estimation based on the estimated breeding pairs; Marchant & Higgins 1990, Brooke 2004) and contributing to 600-900,000 tonnes of crustacean biomass consumption annually (estimation based on the average consumption per individual; Guinet et al. 1996).

During the breeding season, common diving petrels exhibit a unimodal foraging trip duration strategy. This contrasts with most of the other small Procellariiformes that display a dual foraging strategy by alternating short and long foraging trips (Weimerskirch et al. 1994, Chastel et al. 1995). Across its wide distribution encompassing different environmental conditions, the common diving petrel consistently does short daily trips, during both the incubation (Navarro et al. 2013, Zhang et al. 2018, Dunphy et al. 2020) and chick-rearing periods (Roby 1989, Weimerskirch et al. 1994, Fromant et al. 2020a). This consistent behavioural pattern between populations and across breeding stages could highlight a very high efficiency in foraging and illustrate the species adaptation capacity to different local environments. Conversely, this could indicate a low behavioural plasticity resulting in common diving petrels breeding only where this unimodal foraging behaviour can persist.

Throughout the species range, common diving petrels show differences in breeding phenology (Chapter 3), diet (Reid et al. 1997, Bocher et al. 2000a, Fromant et al. 2020a) and diving behaviour (Bocher et al. 2000a,b, Navarro et al. 2014, Dunphy et al. 2015), showing how populations adapt to specific conditions. However, it is uncertain if these variations demonstrate behavioural flexibility at the species and/or population level. In particular, the absence of combined multi-year datasets on the trophic and foraging behaviour at a given locality impedes our understanding of how small, abundant seabirds such as diving petrels adapt to inter-annual environmental changes.

Despite its relatively low primary productivity, Bass Strait, the shallow (50-100 m) continental shelf area between mainland Australia and Tasmania, hosts 60% of Australian seabirds (Ross et al. 2001). Currents within Bass Strait are complex and dynamic, fluctuating spatially, seasonally and annually, and being influenced by tides, winds and density-driven flows (Sandery & Kämpf 2007). This region is also one of the most rapidly changing areas of the global ocean, characterised by warming waters and changing currents (Cai et al. 2005, Poloczanska et al. 2007). These ongoing changes are likely to deeply influence the abundance and distribution of cold water zooplanktonic communities (Evans et al. 2020), and could potentially affect zooplanktivorous species such as common diving petrels (Chambers et al. 2011, Evans et al. 2021). In particular, coastal krill (*Nyctiphanes australis*), the main prey of common diving petrel in Bass Strait (Schumann et al. 2008, Fromant et al. 2020a), exhibits high sensitivity to increased ocean temperatures (Young et al. 1993, Mills et al. 2008). Furthermore, Bass Strait represents the northern extent of the common diving petrel range, and the predicted modification of oceanographic parameters in the region are likely to have a profound effect on this small and geographically isolated population (Schumann et al. 2014). Exploring the foraging and trophic ecology of common diving petrels in such a challenging environment will provide valuable information on the extent of its behavioural flexibility and

contribute to our understanding of the capacity of small planktonic feeders to buffer contrasted environmental fluctuations.

The present study was conducted over four consecutive years on common diving petrels breeding in Bass Strait. Its aims were to determine: (1) their at-sea movements and habitat use; (2) trophic niche; and 3) inter-annual variation in relation to environmental parameters and reproductive output. Specifically, south-eastern Australia experienced over the last decade successive intense summer marine heatwaves (prolonged periods where ocean temperatures are above the climatological average; Oliver et al. 2017, Perkins-Kirkpatrick et al. 2019). If these extreme rises in sea surface temperature induce major shifts in zooplankton population structure (Evans et al. 2020), the cascading effect that marine heatwaves have on upper trophic levels remains unknown. We predicted that (1) diving petrel trip duration and foraging area would increase in response to the negative effect of marine heatwaves on cold-water zooplanktonic prey; (2) the shifts in prey availability would induce a modification in the birds' trophic niche; and (3) the resultant increased in foraging effort would negatively impacts their breeding success.

4.3. Materials and Methods

4.3.1. Study site and animal instrumentation

The study was conducted during the incubation and chick-rearing periods over four consecutive years (2017-2020) on Kanowna Island (39°15'S 146°30'E) in northern Bass Strait, south-eastern Australia. This island is a breeding site for seven seabird species (Fromant et al. 2020d), including 250-500 pairs of common diving petrels (2-4% of the northern Bass Strait population; Schumann et al. 2014). Some study nests (20-30 per year) were randomly located at the start of each breeding season to record the birds' phenology. Control nests (2017: 16; 2018: 66; 2019: 63; 2020: 46) were monitored in early incubation, post-hatching and before

fledging to calculate the average reproductive success for the colony (hatching, fledging and breeding success). In addition, during chick-rearing in 2017, burrows ($n = 40$) were monitored weekly in order to estimate the potential effects of short-term deployments of miniaturized devices on adult body mass, chick growth and breeding success (see Supplementary text; Table S5-1).

To evaluate the at-sea distribution of common diving petrels during the breeding period, adult breeding birds were equipped with miniature GPS data loggers (nanoFix-GEO, Pathtrack Ltd, Otley, United-Kingdom), attached to two tail feathers using waterproof tape (Tesa 4651; Beiersdorf AG). The total mass of the devices corresponded to $2.25 \pm 0.18\%$ of body mass (134 ± 11 g) and, thus, was unlikely to have impacted the feeding ecology or breeding performance of individuals (see Supplementary text). During incubation, both partners alternate between 1 d foraging at sea and 1 d incubating (Weimerskirch et al. 1994, Zhang et al. 2018), while during chick-rearing (post-brooding stage), both individuals forage at sea during the day and come back to the nest every night to feed the chick (Marchant & Higgins 1990). Accordingly, during incubation, the study birds were captured in their burrow in the afternoon (corresponding to the end of their shifts) while during the chick-rearing period they were captured at night after feeding the chick.

When individuals were recaptured, a blood sample (0.2 mL) was collected from the brachial vein for stable isotope analyses and sexing. For all birds, sex was determined by DNA analysis (DNA solutions, Wantirna South, Australia) from either blood or a single body feather. Individuals were weighed (± 2 g; Pesola), and culmen, tarsus (± 0.1 mm; Vernier calipers) and wing length (± 1 mm; ruler) were measured. Handling time at deployment (banding, weighing and device attachment) and recapture (device removal, measurements, blood and feather sampling) was usually less than 5 min.

4.3.2. Environmental data and habitat selection modelling

Environmental data were used to run two distinct sets of analysis: (1) using sea surface temperature (SST) to explore the variation in foraging ecology and breeding outputs of common diving petrels following summer marine heatwave events. Hereafter, a marine heatwave event is defined as daily SST above the seasonally varying 90th percentile (climatological mean for the period 1981-2010) for more than 5 consecutive days (Oliver et al. 2017, 2021); (2) using dynamic environmental covariates (see details in section 2.2.2.) to describe the habitat selection and determining the physical features explaining the foraging distribution of breeding common diving petrels in Bass Strait.

Inter-annual variations of oceanographic conditions

Sea surface temperature has been shown to be the main feature influencing the occurrence and abundance of zooplankton species in south-eastern Australia (Evans et al. 2020, 2021). In particular, the distribution and availability of coastal krill, the main common diving petrel prey in Bass Strait (Schumann et al. 2008, Fromant et al. 2020a), vary substantially between years in relation to SST (Young et al. 1993, Mills et al. 2008). Specifically, summer marine heatwaves with prolonged period of SST above the optimal temperature range of coastal krill (12-18 °C; Sheard 1953) alter the reproduction, survival, and potentially disrupt the availability of this key planktonic species for several months (Ritz & Hosie 1982, O'Brien 1988). Therefore, for each summer, the duration and intensity of periods strictly above the optimal temperature range of coastal krill (>19 °C; Sheard 1953) were determined. Monthly averages of SST for the summer period (December-February) were extracted for each gridded cell (0.25° resolution; dataset MULTIOBS-GLO-PHY-TSUV-3D-MYNRT-015-012 downloaded from Copernicus [<http://marine.copernicus.eu/>]) within the boundary of the observed home range of common diving petrels in Bass Strait (38.5-41.0 °S, 144.0-148.0 °E).

Habitat selection modelling

To investigate the influence of environmental variables on the at-sea movements and foraging behavior of breeding common diving petrels, habitat selection in relation to habitat availability was determined using a presence-pseudoabsence approach in R software (Hindell et al. 2020, R Core Team 2020). Specifically, for each real track ($n = 187$), 20 pseudo-tracks were simulated by means of a first-order vector autoregressive model fitted using the package *availability* (Raymond et al. 2016). Simulations were created with constraints on sampling frequency, distances, turning angles and departure/arrival locations to maintain the characteristics of the real tracks. Furthermore, pseudo-tracks were bound by a land mask to ensure that all simulated locations were at sea.

Ten dynamic environmental covariates that have been shown to potentially influence marine predators and their habitat use (Reisinger et al. 2018, Hindell et al. 2020) were incorporated in the habitat selection modelling: SST, sea floor temperature, salinity, mixed layer thickness, sea surface height anomaly, northward velocity, eastward velocity, wave height, wave direction, wave period. Daily environmental data were downloaded from Copernicus. Northward and eastward velocities were used to calculate current speed as:

$$\text{current speed} = \sqrt{\text{northward velocity}^2 + \text{eastward velocity}^2}$$

In addition, bathymetric data were downloaded from the GEBCO 15-arc second grid [<http://www.gebco.net>] and used to calculate sea floor slope by means of the *terrain* function from the *raster* package. Given that environmental covariates differed substantially in resolution (0.004 to 0.083°), all layers were standardized to the coarsest resolution (0.083°) and spatiotemporally matched to each real and pseudo-location using the *raster* package (Hijmans 2018). Dynamic covariates were averaged for the duration of each track before being matched to each location.

4.3.3. Tracking and stable isotope processing and analysis

Tracking and spatial analysis

The GPS data loggers were programmed with a sampling interval of 10 and 5 min during the incubation and chick-rearing periods, respectively. Prior to analysis, land-based points were removed and a speed filter with a threshold at $20 \text{ m}\cdot\text{s}^{-1}$ was applied to remove erroneous locations (Spear & Ainley 1997). Because of poor satellite reception during intense diving activity, linear interpolation was necessary to correct for unequal sampling frequencies between foraging and commuting periods. For each complete trip (1-7 per individual bird) the following basic parameters were calculated: 1) time of departure and return; 2) trip duration; 3) total horizontal distance travelled; 4) maximum distance from the colony; and 5) bearing at departure and distal location.

For heavily wing-loaded species such as diving petrels, alcid or cormorants, typical foraging trips consist of departing from the colony rapidly with a constant bearing to a particular area for foraging, and returning in a direct flight path to the colony (Weimerskirch 2007, Amélineau et al. 2016). Diving petrels forage by diving from the sea surface, which impedes the distinction between foraging and resting behaviors when using GPS only. Foraging/resting (hereafter foraging) areas were defined as areas where instantaneous speed was $\leq 10 \text{ km}\cdot\text{h}^{-1}$, following the method previously used on ecologically similar species (e.g. Amélineau et al. 2016, Jakubas et al. 2020). The remaining positions (speeds $> 10 \text{ km}\cdot\text{h}^{-1}$) were assumed to represent flying between the colony and the foraging areas or between two feeding areas. In the analysis of the relationship between the proportion of time spent foraging and the total distance travelled, 1 d trips and 2 d trips were analyzed separately in order to discount the effect of staying at-sea overnight (3 d trips were not included because of the low sample size). Indeed, in the case of an at-sea overnight stay (common diving petrels do not forage at night;

Navarro et al. 2013), the absence of commuting to the colony at the end of the first day, and from the colony at the start of the second day, up weights the proportion of time spent foraging compared to commuting.

Locations identified as foraging were used to generate kernel utilization distribution (UD) estimates using the package *adehabitatLT* (Calenge 2006). For each year and breeding stage, the 50% (core foraging area) and 95% (home range) kernel UD contours were obtained (Worton 1989, Montevecchi et al. 2012). To investigate spatial variation in foraging area, the percentage overlap in foraging distribution between years and breeding stages were estimated using Bhattacharyya's affinity (BA), where 0 indicates no overlap and 1 a complete overlap.

Isotopic niche analysis

Stable isotope analyses of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in whole blood were used to investigate temporal change in the common diving petrel trophic niche, reflecting dietary integration of approximately two to four weeks (Bearhop et al. 2002). Prior to analyses, samples were freeze-dried, ground to powder and homogenized. The relative abundance of carbon and nitrogen isotopes was determined with a continuous-flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Isotopic results are presented in the δ notation relative to Vienna PeeBee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.10 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The C:N mass ratios of samples were calculated as the ratio between the mass percentages in carbon and nitrogen. The consistently low C:N values of blood (<4.0) verified that low lipid content did not necessitate lipid extraction (Cherel et al. 2005a). The isotopic niche position and width was compared between years and breeding stages using the ellipse area-based metrics of the *SIBER* package (Jackson et al. 2011). The isotopic niche was

estimated by the 40% standard ellipse area corrected for small sample size (SEAC), the Bayesian standard ellipses areas (SEAB) on 10^5 replicates was used to measure the overlap of the isotopic niches between each breeding stage, and the total area of the convex hull (TA) to provide an indication of the niche width (Jackson et al. 2011).

4.3.4. Statistical analyses

To examine seasonal and inter-annual differences in SST, a one-way ANOVA and Tukey's *post-hoc* analysis were used. Habitat selection was assessed using boosted regression trees (BRT) (Friedman 2001) to determine the importance of each environmental covariate on the probability of habitat used in relation to availability. To ensure that individuals contributed equally to the analysis, modelling was restricted to the first foraging trip of each individual. Prior to analysis, collinearity between predictor effects was assessed and, if correlations were > 0.6 , the environmental covariate with the highest average correlations was excluded from the model (sea floor temperature, wave height). The BRT were fitted using the *dismo* package (Hijmans et al. 2016) and locations were modelled as a binomial response, where all real locations were represented by 1 and all pseudo-locations were represented by 0. The BRT were fitted with a tree complexity of 5 and total of 6450 trees were fitted at a learning rate of 0.05 (Elith et al. 2008). Model performance was evaluated using 10-fold cross validation and represented by the area under the receiver operating characteristic curve (AUC).

Effects on foraging parameters (i.e. time of departure and return, trip duration, total horizontal distance travelled, maximum distance from the colony, and bearing at departure and distal location) were investigated generating multiple Generalized Linear Mixed Models (GLMM) using the package *glmmADMB* (Bolker et al. 2012). Year, breeding stage and sex were considered as fixed effects, and individual was added as a random effect, with a Gaussian family. Models were ranked based on their Akaike's Information Criterion (AIC) and were

checked to ensure normality and homoscedasticity of residuals (Zuur et al. 2010) before further statistical analysis. Data normality and homogeneity of the variance were assessed with Shapiro-Wilk and Bartlett tests, respectively. *Post-hoc* analyses were conducted using pairwise comparisons of least-squares means between years, breeding stages and sex (package *emmeans*; Lenth 2020) with the Tukey method for p-value adjustment. The variation between years and stages in the trip orientation (bearing at departure and at distal location) was investigated by calculating the angular difference (Rao's spacing test, $\alpha = 0.05$; package *circular*; Lund et al. 2017). Differences between years and breeding stages $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were tested by using 2-way semi-parametric permutation multivariate analyses of variance test (PERMANOVA) on the Euclidean distance matrix (Anderson 2001). Spearman's rank correlation was used to test whether there was a correlation between the proportion of time spent foraging and trip duration. Hatching success (eggs hatched as a proportion of eggs laid), fledging success (chicks fledged as a proportion of eggs hatched) and breeding success (chicks fledged as a proportion of eggs laid) were compared between years using a Pearson's chi-squared test. All statistical analyses were conducted in the R statistical environment 4.0.0 (R Core Team 2020).

4.4. Results

4.4.1. Environmental variables and habitat selection

Inter-annual variations of oceanographic conditions

During the whole study period, SST varied strongly, ranging from 10.9 to 21.5 °C, exhibiting an annual cycle with significant differences between the seasons (ANOVA, $F_{641.1} = 69.925$, $P < 0.001$), and significant inter-annual variations (ANOVA, $F_{197.63} = 58.194$, $P < 0.001$). Importantly, the average temperature in summer preceding the common diving petrel breeding season in 2018 (18.5 ± 0.9 °C) and 2019 (18.2 ± 1.1 °C) were significantly warmer

than in 2017 (17.1 ± 1.0 °C) and 2020 (16.5 ± 1.3 °C), and it was above the average summer temperature for the period 1981-2010 (17.2 ± 1.1 °C). During the summer period, SST in Bass Strait was above the optimal temperature range of coastal krill (the main common diving petrel prey; >19 °C) for 84 days in 2018 (32 d > 20 °C), and 94 days in 2019 (28 d > 20 °C), while it was only 37 days above 19 °C in 2017 (0 d > 20 °C) and 6 days in 2020 (0 d > 20 °C) (Fig. 4-2).

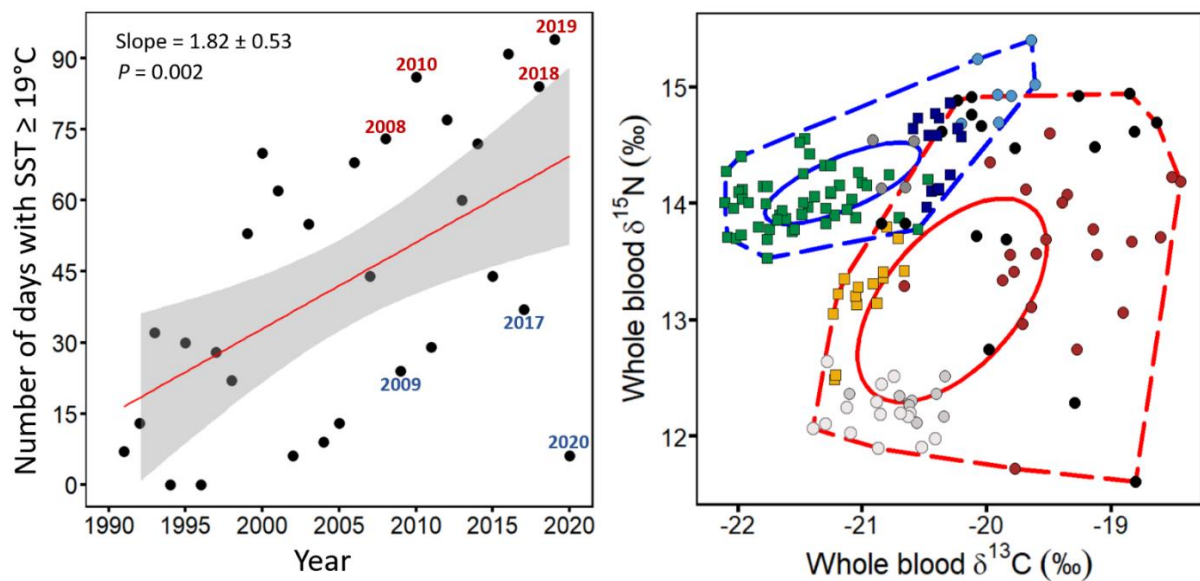


Figure 4-2: Left panel: Number of days per year with mean sea surface temperature above 19°C in Bass Strait, south-eastern Australia. Each dot corresponds to one year, and dots with a specified year correspond to the periods when blood samples were collected from common diving petrels on Kanowna Island (2008-2010 in Fromant et al. 2020a; 2017-2020 in the present study). The 19 °C threshold was selected based on the optimal temperature range of coastal krill (12-18 °C; Sheard 1953). A linear model was fitted to the data (red line; the analyses of residual and autocorrelation function plots showed no temporal autocorrelation pattern).

Right panel: Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common diving petrels from Kanowna Island during cold (blue 40% ellipse and 100% total convex hull; 2009, 2017 and 2020) and warm years (red 40% ellipse and 100% total convex hull; 2008, 2010, 2018 and 2019).

Incubation, dot symbols: red = 2018; black = 2019; light blue = 2020. Chick-rearing, square symbols: green = 2017; yellow = 2018; dark blue = 2020. Grey dots were adapted from Fromant et al. (2020a) (light grey, incubation 2008; dark grey, incubation 2009; open grey, incubation 2010).

Table 4-1: Model performance (AUC) and relative importance of environmental variables for the habitat selection models for common diving petrels (*P. urinatrix*) from Kanowna (Bass Strait, south-eastern Australia).

Model	AUC	Salinity	Sea surface temperate	Sea surface height	Wave period	Wave direction	Current speed	Sea floor slope	Bathymetry	Mixed layer thickness	
Combined years and breeding stages	0.96	18.4%	11.4%	11.2%	10.8%	12.3%	11.2%	10.3%	8.0%	6.5%	
2017 Chick-rearing	0.96	41.5%	9.4%	8.2%	8.5%	8.4%	5.6%	7.2%	8.8%	2.5%	
2018	Incubation	0.96	28.5%	5.6%	8.5%	12.8%	13.7%	5.1%	7.0%	5.1%	
	Chick-rearing	0.96	7.1%	9.3%	12.1%	12.2%	17.8%	10.9%	14.2%	1.2%	
2019 Incubation	0.97	14.1%	20.3%	16.5%	12.6%	10.4%	6.4%	5.4%	5.1%	9.1%	
2020	Incubation	0.97	11.6%	9.7%	7.6%	11.5%	19.4%	5.4%	12.6%	7.5%	14.6%
	Chick-rearing	0.94	23.8%	15.6%	8.0%	5.7%	13.6%	15%	9.4%	8.6%	0.4%

Habitat selection modelling

The final BRT model returned an AUC score of 0.96 ± 0.01 and identified salinity, wave direction and SST as the most important factors for predicting habitat selection (Table 4-1; Fig. S4-1). Salinity had a variable relative influence of 18.4%, with fitted functions indicating that the probability of habitat selection decreased with increasing salinity. Both wave direction and SST had a lower variable relative influence (12.3% and 11.4%, respectively). For wave direction, fitted functions indicated that the probability of selection was relatively constant, although there were two slight peaks with wave direction from ESE (110°) and WNW ($280\text{-}300^\circ$). For SST, fitted functions indicated that the probability of selection peaked at 12.5°C , after which it remained relatively constant (Fig. S4-1).

The main variables influencing the habitat selection models varied between years and breeding stages (Table 4-1; Fig. S4-2). Similarly, the relative influence of each variable differed among the models. Salinity had a high relative influence for all the models except for chick-rearing 2018 (7.1%), while sea surface height and SST were significant only in the model for incubation 2019 (Fig. S4-2).

4.4.2. Breeding success

Breeding success varied substantially between the four years of the study (Pearson's Chi-squared test, $\chi^2 = 127.73$, $P < 0.001$), from 69% in 2017 ($n = 16$) and 84% in 2020 ($n = 50$), to 6% in 2018 ($n = 66$) and 0% in 2019 ($n = 63$) (Table 4-2). The very low breeding success in 2018 and 2019 was related to a delayed breeding season (a 30-50 days delay compared to the breeding seasons of 2017 and 2020; Kruskal-Wallis test: $\chi^2 = 112.75$, $P < 0.001$), and related to low egg and chick survival (Table 4-2; Pearson's Chi-squared test, $\chi^2 = 46.291$, $P < 0.001$ and $\chi^2 = 90.391$, $P < 0.001$, respectively). The low hatching and breeding success in warmer years were associated with longer trips in 2018 (no data in 2019), larger foraging areas

(in both 2018 and 2019) and lower whole blood $\delta^{15}\text{N}$ values (in both 2018 and 2019) (see Sections 3.3. and 3.4.).

Table 4-2: Hatching, fledging and breeding success of common diving petrel (*P. urinatrix*) from Kanowna Island (Bass Strait, south-eastern Australia). For each parameter, values not sharing the same superscript letter (a, b or c) are significantly different ($P < 0.05$; Pearson’s chi-squared test).

Year	Hatching success	Fledging success	Breeding success
2017	81% (n = 16) ^a	90% (n = 32) ^a	69% (n = 16) ^a
2018	36% (n = 66) ^b	17% (n = 24) ^b	6% (n = 66) ^b
2019	41% (n = 63) ^b	0% (n = 26) ^c	0% (n = 63) ^c
2020	92% (n = 50) ^a	91% (n = 46) ^a	84% (n = 50) ^a

4.4.3. Foraging parameters and at-sea distribution

At-sea movement data were obtained from a total of 67 trips in incubation (36 individuals) and 122 trips during chick-rearing (65 individuals). Data for both the incubation and chick-rearing periods within the same season were collected in 2018 and 2020. Due to logistical constraints, no data were obtained during incubation in 2017. In 2019, all the study nests failed (young chicks found dead in the burrow) before any birds could be equipped during the chick-rearing period.

There were no significant differences between the sexes (48 females and 53 males) in trip parameters ($P > 0.05$ in all cases) and, therefore, data from both sexes were pooled in all subsequent statistical analyses.

Foraging parameters and at-sea distribution according to the breeding stage: incubation vs chick rearing

Within the same breeding season (in 2018 and 2020), habitat distribution differed between the incubation and chick-rearing periods (Fig. 4-3; home ranges during incubation was 42% larger than during chick-rearing in 2018, and 10% in 2020; $BA_{\text{incubation/chick-rearing}} = 0.26$ in

2018 and 0.48 in 2020). In 2018, the total distance travelled was significantly different between the incubation and chick-rearing stages (Table S4-1; Mann-Whitney U test: $U = 483$, $P = 0.020$). However, no significant differences in the trip parameters were found between the two breeding stages in 2020.

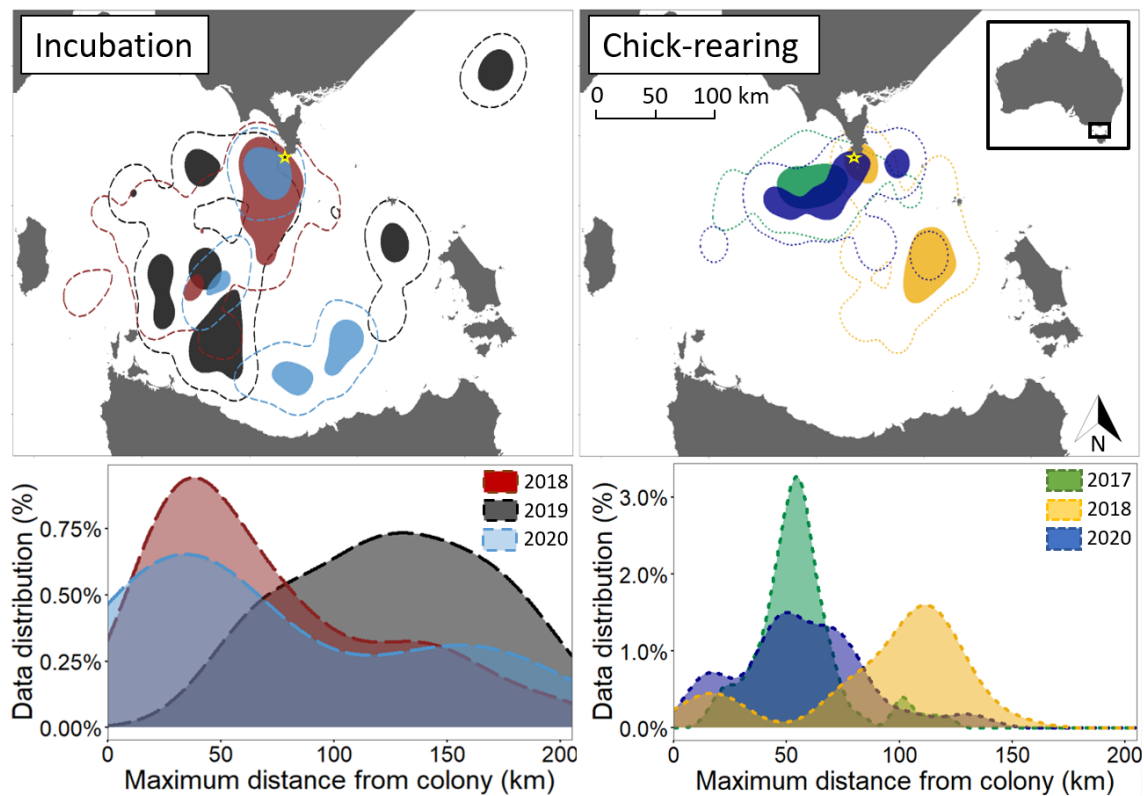


Figure 4-3: Upper panels: Foraging kernel density distribution estimated from GPS locations of common diving petrels in incubation (upper left) and chick-rearing (upper right) from Kanowna Island, south-eastern Australia. Solid and open kernel areas show the 50 and 95% of the kernel utilization distribution, respectively (core area and home range, respectively). **Lower panels: Distribution density for maximum distance from colony to foraging locations per foraging trip of common diving petrel in incubation (lower left) and chick-rearing (lower right) periods.**

Individuals consistently departed from the colony earlier during incubation than during the chick-rearing period (Table S4-1; Mann-Whitney U test: $U = 6064$, $P < 0.001$), but no clear pattern was observed for the timing of return (Mann-Whitney U test: $U = 4758$, $P = 0.062$).

However, the time between departure and sunrise, and the time between sunset and return, were positively correlated to the total distance travelled. The sampling period did not influence the distance travelled per trip nor the proportion of time foraging, with no relation found between the daylight duration (a proxy of available foraging time) and both the total distance travelled (Spearman's correlation test: $S = 1024604$, $P = 0.221$, $\rho = 0.089$) and the proportion of time spent foraging (Spearman's correlation test: $S = 1202794$, $P = 0.239$, $\rho = -0.086$).

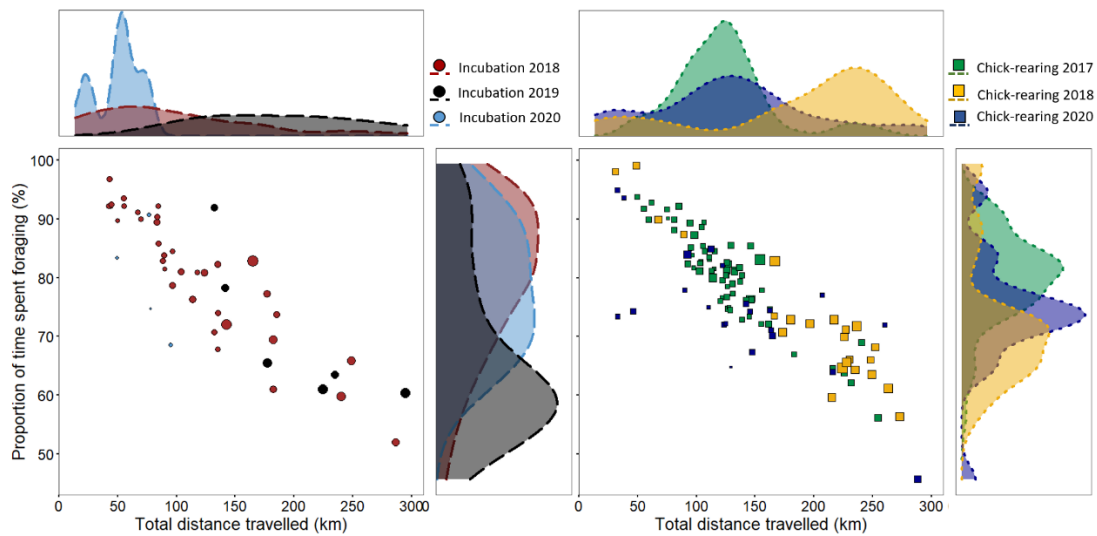


Figure 4-4: Correlation between the proportion of time spent foraging and total distance travelled per 1-day trip of common diving petrels (*P. urinatrix*) in incubation (left panels) and during the chick-rearing periods (right panels). The vertical and upper panels give the distribution density of the proportion of time spent foraging per trip and the total distance travelled per trip, respectively. The size of each point is proportional to the trip duration (< 24h). Trips longer than 24h with overnight period at sea were not included in this figure.

Foraging parameters and at-sea distribution according to the years

Home range differed inter-annually in size and location during both the incubation and chick-rearing periods (Fig. 4-3). The home range was the smallest in 2020 during the incubation and chick-rearing periods, and it was the largest in incubation 2019 and chick-rearing 2018. All parameters of foraging trips varied inter-annually, i.e. in terms of duration, total distance travelled, and maximum distance from the colony (Fig. 4-3; Table S4-2; Kruskal-Wallis test, $P < 0.001$ for all parameters).

In incubation, the proportion of foraging trips that were of 1 d duration varied from 74.5% in 2018, 46.2% in 2019 and 66.7% in 2020. During the chick-rearing period, the proportion ranged between 100.0% in 2017 and 2020, and 80.0% in 2018. The longest trips (3 days) were observed during the incubation periods 2018 and 2019. Similarly, the proportion of time at sea spent in foraging/resting state varied inter-annually and between incubation and the chick-rearing periods (Kruskal-Wallis test: $\chi^2 = 69.74$, $df = 3$, $P < 0.001$); it was negatively correlated with the total distance travelled, for both 1 d trips (Fig. 4-4; Spearman's correlation test: $S = 1254374$, $P < 0.001$, $\rho = -0.840$) and 2 d trips (Spearman's correlation test: $S = 2890$, $P = 0.002$, $\rho = -0.632$).

4.4.4. Isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied substantially between years and breeding stages (Table 4-3; Fig. 4-5; PERMANOVA, $F_5 = 50.81$, $R^2 = 0.677$, $P = 0.001$; ANOVA, $P < 0.001$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Table 4-3: Summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in whole blood of common diving petrels (*P. urinatrix*) from Kanowna Island (Bass Strait, south-eastern Australia) during the incubation and chick-rearing periods. Values are means \pm SD, with the number of individuals given in brackets. Values not sharing the same superscript letter (a, b, c, d or e) are significantly different ($P < 0.05$; multiple comparisons with Tukey method for p-value adjustment).

Year	2017		2018		2019		2020	
	Breeding stage	Chick-rearing	Incubation	Chick-rearing	Incubation	Incubation	Chick-rearing	
Blood $\delta^{13}\text{C}$ (‰)		-21.5 ± 0.4^a (n = 51)	-19.4 ± 0.5^b (n = 23)	-21.0 ± 0.2^c (n = 16)	-19.7 ± 0.7^b (n = 20)	-19.9 ± 0.2^b (n = 9)	-20.4 ± 0.1^d (n = 15)	
Blood $\delta^{15}\text{N}$ (‰)		14.0 ± 0.2^a (n = 51)	13.6 ± 0.6^b (n = 23)	13.2 ± 0.4^c (n = 16)	14.0 ± 1.0^{abe} (n = 20)	15.0 ± 0.2^d (n = 9)	14.5 ± 0.3^e (n = 15)	

This variation was characterized by limited isotopic niche overlap between stage/year (Table S4-3). During the same breeding season, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly

higher in incubation than during the chick-rearing period. Values of $\delta^{13}\text{C}$ were minimum in chick-rearing 2017 and maximum in incubation 2018 (ranging from -22.2 to -18.4 ‰), while $\delta^{15}\text{N}$ values were minimum in incubation 2019 and maximum in incubation 2020 (from 11.6 to 15.4 ‰). The isotopic niche width was larger in incubation 2018 and 2019 (Fig. 4-5; Table S4-3; TA in incubation 2018 = 3.47 and in incubation 2019 = 4.61) than during the 2020 incubation period (TA = 0.21). No such variations were observed during the chick-rearing period.

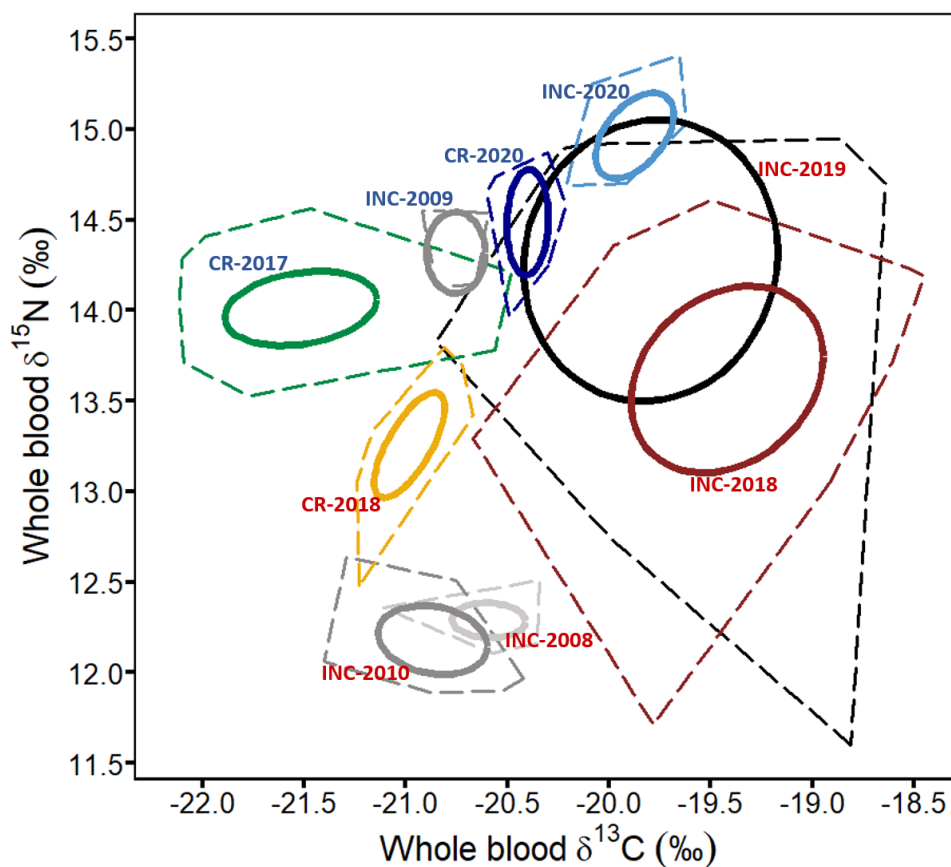


Figure 4-5: Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common diving petrels (*P. urinatrix*) from Kanowna Island in incubation (INC: red, 2018, n =23; black, 2019, n = 20; light blue, 2020, n = 9) and chick-rearing (CR: green, 2017, n = 51; yellow, 2018, n = 16; dark blue, 2020, n = 15). Incubation 2008-2010 (grey) are whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common diving petrels in incubation from Kanowna Island obtained from Fromant et al., 2020a (2008, n = 10; 2009, n = 4; 2010, n = 15). Full lines correspond to the 40% ellipse and dashed lines 100% total convex hull. The blue and red writing represent cold and warm years, respectively (see Fig. 4-2).

4.5. Discussion

Using a combination of GPS tracking and stable isotope analyses, the present study documented for the first time substantial variations over four successive breeding cycles in the at-sea movements, foraging behaviour and trophic niche of a small planktonic forager, the common diving petrel. The salient features of the results can be summarized as following: i) these inter-annual variations coincided with drastic fluctuations in reproductive success and were associated with intense summer marine heatwave events; ii) during years of low breeding success, common diving petrels strongly increased their foraging effort and shifted their trophic niche, likely in response to important variations in prey availability; iii) the clear cascading effects that marine heatwaves have on the breeding and foraging ecology of this zooplankton feeder illustrate the rapid bottom-up effect induced by extreme environmental variations.

4.5.1. Foraging behaviour, at-sea distribution and habitat use

In all studied years, the foraging activity of the common diving petrels breeding on Kanowna Island was consistently restricted to the shallow continental shelf of Bass Strait. Although, diving petrel species seem to appear morphologically better suited for short foraging trips during breeding (Navarro et al. 2013), common diving petrels in Bass Strait exhibited relatively long foraging trips (average maximum distance from the colony = 71 ± 3 km) both during the incubation and chick-rearing periods. In all breeding stages and years, the diving petrels from Kanowna Island foraged farther away from the colony and conducted foraging trips 2-6 times longer than conspecifics in New Zealand (Zhang et al. 2018, Dunphy et al. 2020) and Peruvian diving petrels (*Pelecanoides garnotii*) in Peru (Zavalaga & Alfaro-Shigueto 2018).

The overall foraging distribution of common diving petrels in the present study was in accordance with at-sea observation of the species in south-eastern Australian waters (Reid et

al. 2002), and matches the habitat distribution of their main prey, i.e. coastal krill (O'Brien 1988, Schumann et al. 2008). Blood isotope values in 2017-2020 were within the same range as those previously measured in common diving petrels from the Bass Strait (Fromant et al. 2020a) and New Zealand (Dunphy et al. 2020). The average blood $\delta^{15}\text{N}$ value (14.0 ‰) corresponds to one trophic level above the values of coastal krill ($\delta^{15}\text{N} = 11.7$ ‰; Cherel et al. 2005b), thus confirming the importance of this prey item in the diet of Australian common diving petrels (Schumann et al. 2008, Fromant et al. 2020a). However, the wide isotopic niche and the large differences in at-sea distribution suggested seasonal and inter-annual prey variation in the diet of diving petrels in Bass Strait.

Seabirds increase their foraging efficiency by identifying persistent oceanographic features where prey encountering is predictable (Weimerskirch 2007, Bost et al. 2009). In central Bass Strait, however, the oceanographic processes influencing the productivity are highly spatially and temporally variable (Sandery & Kämpf 2007, Huang & Wang 2019). The higher foraging effort and wide isotopic niche of common diving petrels in Bass Strait could, therefore, be due to the sparse distribution of their prey (O'Brien 1988), leading them to search farther and more widely than other diving petrel populations or similar species (Ryan & Nel 1999, Zavalaga & Alfaro-Shigueto 2018, Dunphy et al. 2020).

Salinity, wave direction and sea surface temperature appeared to be the most meaningful variables to describe the foraging distribution of the common diving petrel in Bass Strait. Higher preference to low salinity and low sea surface temperature is likely to reflect the optimal environmental conditions influencing their prey distribution (Sheard 1953, Evans et al. 2020). Such preferences are consistent with distribution models based on at-sea observation of common diving petrels in south-eastern Tasmania, with bird sightings being negatively correlated to SST and salinity (Evans et al. 2021).

However, the important inconsistencies in the habitat selection models between breeding stages and years may suggest a more complex association between potential prey and oceanographic features, and illustrate the oceanographic complexity of the region (Sandery & Kämpf 2007). Additionally, the mismatch in resolution between tracking and environmental variables data may have failed to capture the scale at which the phenomenon occurs, impeding our interpretations. A finer resolution should enable in the future to fully understand what parameters influence the at-sea movements of common diving petrels.

4.5.2. Inter-annual variation in breeding success, foraging behaviour and trophic niche

The present study was characterised by two consecutive years of remarkably low breeding success (6% in 2018 and 0% in 2019; Marchant & Higgins 1990, Chastel et al. 1995). At Kerguelen, the overall high breeding success of common diving petrels (46-86% over seven years; Chastel et al. 1995) suggests that, during years of lower food availability, this species seems to be able to maintain its breeding output by increasing its foraging effort (Chastel et al. 1995). However, the same authors concluded that substantial shortage in food availability during the whole breeding season would likely induce an important decrease in breeding success.

In the present study, during years of very low breeding success, common diving petrels exhibited i) a higher distance travelled and lower nest attendance (longer trip duration), and ii) proportionately less time spent foraging per trip (longer foraging commutes). This higher foraging effort was associated with substantial variation in their isotopic niche (e.g. lower blood $\delta^{15}\text{N}$ values), suggesting a potential dietary shift from rich temperate zooplanktonic species to lower quality subtropical prey (Cohen et al. 2014, Evans et al. 2020). Such adjustments in relation to prey depletion is well documented among seabirds (Harding et al. 2007, Bost et al. 2015, Barbraud et al. 2018). However, the large decrease in breeding success of common

diving petrel in Bass Strait, despite important modification in their foraging effort and trophic niche, underline the magnitude of the apparent disruption in prey availability.

As a key zooplankton species (Ritz & Hosie 1982), variability in abundance of coastal krill has been observed to influence the foraging behaviour and demographic parameters of various marine predators (Mills et al. 2008, Manno et al. 2014). For example, in New Zealand, delayed breeding period, longer foraging trips and low breeding success of the zooplanktivorous red-billed gull (*Chroicocephalus novaehollandiae scopulinus*) were linked to the absence of coastal krill in years of positive sea temperature anomaly (Mills et al. 2008). Similarly, in south-eastern Australia, a close relationship has been documented between coastal krill and the capture biomass of barracoota (*Thyrsites atun*) and jack mackerel (*Trachurus declivis*) by commercial fisheries, mitigated by the absence of coastal krill during years of high sea temperature anomaly (Young et al. 1993).

In the present study, summers preceding the very low breeding success of common diving petrel (2018 and 2019) were characterized by exceptionally long periods of SST above the optimal temperature range of coastal krill. The abnormal temperature conditions observed during these two successive summers is likely to have altered the availability of this key zooplanktonic species (Young et al. 1993, Mills et al. 2008). Previous marine heatwaves events in the region resulted in a shift of dominant species from large-bodied cold-water euphausiids to smaller size subtropical copepods (Evans et al. 2020). The depletion in the common diving petrel main prey in Bass Strait may have forced individuals to adapt their foraging ecology to prey of lower energetic value. In contrast, the mild SST in summer 2017 (fitting the 1981-2010 average) and the even colder summer 2020 were related to a much higher breeding success (69 and 84%, respectively), indicating prey abundance. The large spectrum of SST observed in this study, within and outside the optimal temperature of coastal krill, therefore, illustrates a strong link between the oceanographic conditions, prey availability and predator breeding success.

The important inter-annual variations in blood isotopic values of common diving petrel (Fromant et al. 2020a, this study) are consistent with a substantial shift in their trophic niche during warmer years (Fig. 4-2). Alternatively, these variations could result from the spatiotemporal modification in the isotopic baselines in Bass Strait, leading ultimately to fluctuation in the isotopic values of common diving petrel prey (Jaeger & Cherel 2011; Polito et al. 2019). However, the large isotopic niche width occupied by common diving petrels in 2018 and 2019 suggests a diversification in their diet, which may indicate a shortage in availability of their main prey following these marine heatwave events (Layman et al. 2007).

In South-Georgia, the reproductive performance of “krill-dependent” macaroni penguins (*Eudyptes chrysolophus*) decreased during years of poor Antarctic krill (*Euphausia superba*) availability (Waluda et al. 2012). These years were characterised by a broader diet, which was associated with increased energy and/or time costs. This is consistent with the greater foraging effort and wider isotopic niches observed for the common diving petrel in the present study during years of marine heatwaves. Likewise, in New Zealand, Hutton’s shearwaters (*Puffinus huttoni*) adapted their behaviour by diving significantly deeper during the same marine heatwave events (Oliver et al. 2017, Perkins-Kirkpatrick et al. 2019, Bennet et al. 2020).

While the inter-annual variations in foraging ecology of the common diving petrel observed in the present study were concomitant with marine heatwaves in Bass Strait, their underlying mechanisms are poorly understood (Perkins-Kirkpatrick et al. 2019). Indeed, the thermal regime of Bass Strait is affected by several climatic and oceanographic features (Sandery & Kämpf 2007), and further investigations are required to understand the link between environmental conditions, prey availability and the birds feeding and foraging behaviour.

4.5.3. *A potentially difficult future for small diving seabirds*

Reduction in prey availability during the breeding season in seabirds has been shown to result in increased foraging effort (e.g. Harding et al. 2007, Bost et al. 2015), lowered adult fitness and survival rate (Cohen et al. 2014, Piatt et al. 2020), and altered chick growth and breeding success (Quillfeldt et al. 2007, Waluda et al. 2012). Some seabird species can buffer disruptions in prey availability (Sommerfeld et al. 2015, Jakubas et al. 2020). However, as central place foragers, the high energetic demands during the breeding season sets a physiological limit that determines the effects of environmental variation on reproductive success and adult survival. The threshold that delineates seabird behavioural flexibility varies greatly among species and ecosystems, and is influenced by factors such as intra- and inter-specific competition or geographic constraints.

Modification of zooplankton communities and abundance in marine systems in response to unprecedented periods of warming waters (McKinstry & Campbell 2018, Evans et al. 2020) is likely to exacerbate the long-term bottom-up effect on higher-trophic levels (Möllmann et al. 2008, Sandford et al. 2019, Osborne et al. 2020). This may particularly intensify over the coming decades as such events are predicted to increase in magnitude and frequency (Oliver et al. 2019). In addition, considering the various anthropogenic perturbations in marine ecosystems (e.g. overfishing and pollution) and the rapidly changing oceanographic conditions, seabird flexibility may be increasingly challenged by the predicted intensification of extreme events such as marine heatwaves (Grémillet & Boulinier 2009, Oliver et al. 2019).

Due to their high wing-loading (Warham 1977), the limited capacity of small diving seabird species to extend their foraging range during years of poor prey availability may impede their ability to adapt to more extreme environmental variations (Elliott et al. 2013). Additionally, unlike all other procellariiform species, the absence of stomach oil for diving petrels compels adults to deliver meals to their chick at high frequency (Roby 1989, Eizenberg

et al. 2021). With more intense marine heatwaves predicted (Oliver et al. 2019), these constraints may affect diving petrel capacity to adapt to more frequent extreme events, and ultimately impact colony recruitment and drive local population/species declines (Bost et al. 2015, Péron et al. 2012). Indeed, the small population size of Peruvian (Cristofari et al. 2019) and Whenua Hou (*Pelecanoides whenuahouensis*; Fischer et al. 2018) diving petrels, or the geographic isolation of common diving petrels in Bass Strait (Chapter 3) may exacerbate the long-term effects of climate change.

In conclusion, the present study highlighted the sensitivity of a small macrozooplanktonic avian feeder, the common diving petrel, to environmental variability. While the time-series of the present study was relatively short, marine heatwave events were found to have a major impact at a regional scale on the food webs on which rely diving petrels. This suggests that common diving petrels in Bass Strait may have reached a critical threshold above which buffering the effects of such intense events on their reproductive output is not possible. In addition, the long-term effects of marine heatwaves on marine predators remain undescribed, and understanding their impact on adult survival is a key point for long-lived species. Focusing on species such as diving petrels, with high foraging constraints and feeding on low trophic-level prey, could help to disentangle the underlying mechanisms of long-term adaptation to climate change. Considering the wide geographic distribution (longitudinal and latitudinal gradients) of the common diving petrel throughout different environments of the Southern Hemisphere, this abundant seabird could act as a suitable environmental sentinel to monitor the effects of changing oceanographic conditions.

4.6. Supplementary materials

Supplementary text: Estimating the potential effects of short-term deployments of miniaturised devices on adult common diving petrels.

In October/November 2017, adult birds were equipped during the chick-rearing period with lightweight GPS ($n = 38$; nanoFix-GEO, Pathtrack Ltd, Otley, United-Kingdom) attached to two tail feathers using waterproof tape. The total mass of the equipment (GPS) corresponded to $2.3 \pm 0.2\%$ of the birds' body mass ($1.8 - 2.7\%$, $n = 38$). The devices were deployed for 1 to 4 consecutive days (2.2 ± 0.8 days), and all the GPS were recovered. Individuals were weighed (± 2 g; Pesola) before and after the deployment and retrieval of the device, respectively.

All the individuals remained in their burrow after handling until departure time the next morning. Birds equipped with a GPS departed on average 1.47 ± 0.05 hours before sunrise and return 1.67 ± 0.02 hours after sunset. This is in accordance with field observation and passive acoustic studies showing that common diving petrels leave the colony on average 1-2 hours before sunrise and return to the colony 1-2 hours after sunset (Thoresen 1969; Ranjard et al. 2017; Fromant et al. unpublished data).

All untracked birds and individuals equipped with a GPS did daily trips. There was no significant variation in body mass of instrumented individuals between the deployment and the retrieval (130 ± 2 g and 134 ± 2 g, respectively; $n = 38$; Mann-Whitney U test: $U = 1085$, $P = 0.151$). Similarly, there was no difference between the body mass of birds when retrieved and control individuals (134 ± 2 g and 133 ± 1 g, respectively; $n = 38$ and 89 , respectively; Mann-Whitney U test: $U = 2191.5$, $P = 0.737$). These results are consistent with Navarro et al. (2014) that found no effect of TDRs deployment on trip duration and body mass of common and South Georgian diving petrels in South Georgia.

Growth curve analysis method (Mirman 2014) was used to investigate the potential effect of GPS deployment of parent birds on chick growth. Chicks were monitored approximately every 3-5 d, depending on weather conditions. Individuals were weighed in a cloth bag with a Pesola spring scale (± 2 g), bill and tarsus measurements were taken with Vernier callipers (± 0.1 mm) and wing length was measured with a shoulder stopped ruler (± 1.0 mm). The growths of body mass, wing length, tarsus length and bill length were modelled with a third-order orthogonal polynomial and fixed effects on all age terms of conditions (Control = no deployment *versus* Instrumented = adults equipped with a GPS). The model also included chick-ID random effects and chick-ID by condition random effects. For all studied parameters (body mass, wing length, tarsus length and bill length), there was no significant effect of device deployment on the intercept term nor the curvature (Table S4-4), which indicates similar growth rates between the two groups.

Similarly, fledging success and fledging body mass of chicks did not differ between control and experimental groups (91% and 95% fledging success; 128 ± 3 g and 126 ± 2 g for control and experimental groups, respectively; paired *t*-test: $t_{11.755} = 0.622$, $P = 0.546$).

Table S4-1: Summary of foraging trip metrics (mean \pm SE) for GPS-equipped common diving petrels (*P. urinatrix*) on Kanowna Island, Bass Strait, south-eastern Australia. In 2017, no bird was tracked during incubation due to logistical constraints. In 2019, no bird was tracked during the chick-rearing period because of the early breeding failure of all the study individuals. For each parameter, values not sharing the same superscript letter (a, b or c) are significantly different ($P < 0.05$; Mann-Whitney U test for distance and time related parameters, and Rao's spacing test for bearings).

	2017	2018	2019	2020		
	Chick-rearing	Incubation	Chick-rearing	Incubation	Incubation Chick-rearing	
Number of trips (n)	n = 70	n = 47	n = 30	n = 13	n = 7	n = 22
Number of individuals (N)	N = 38	N = 18	N = 12	N = 12	N = 6	N = 15
Females (F) ; Males (M)	F = 16; M = 22	F = 9; M = 9	F = 6; M = 6	F = 6; M = 6	F = 3; M = 3	F = 8; M = 7
Maximum distance from colony (km)	55.4 \pm 2.3 ^a	73.1 \pm 7.5 ^{ab}	92.0 \pm 7.0 ^b	127 \pm 12.1 ^b	75.5 \pm 27.0 ^{ab}	56.7 \pm 6.1 ^a
Total distance travelled (km)	126 \pm 40.1 ^a	171 \pm 18.2 ^a	224 \pm 19.5 ^b	305 \pm 33.8 ^b	182 \pm 68.3 ^{ab}	134 \pm 14.5 ^a
Trip duration (h)	16.6 \pm 0.1 ^a (1 d trip)	23.9 \pm 2.1 ^{ab} (1-3 d trip)	24.0 \pm 1.8 ^{bc} (1-2 d trip)	35.2 \pm 5.0 ^c (1-3 d trip)	23.1 \pm 5.8 ^{ab} (1-2 d trip)	16.2 \pm 0.2 ^a (1 d trip)
Time between departure and sunrise (min)	87.9 \pm 5.8 ^{ab}	102 \pm 7.4 ^c	92.2 \pm 7.0 ^{bc}	137 \pm 14.6 ^d	123 \pm 17.0 ^{cd}	77.5 \pm 6.6 ^a
Time between sunset and return (min)	101 \pm 3.9 ^a	120 \pm 8.3 ^a	173 \pm 14.0 ^{bc}	215 \pm 19.9 ^c	119 \pm 33.8 ^{ab}	91.8 \pm 9.4 ^a
Bearing at departure (°)	227 \pm 4.2 ^a	215 \pm 4.8 ^a	138 \pm 5.4 ^a	205 \pm 15.7 ^a	210 \pm 18.5 ^a	193 \pm 10.7 ^a
Bearing of distal point (°)	233 \pm 3.8 ^a	218 \pm 4.9 ^a	135 \pm 4.3 ^a	216 \pm 15.2 ^a	209 \pm 14.0 ^a	194 \pm 12.3 ^a

Table S4-2: Results of the GLMM models explaining trip parameters for common diving petrels from Kanowna Island in incubation (2018, N = 18; 2019, N = 12; 2020, N = 6) and during the chick-rearing period (2017, N = 38; 2018, N = 12; 2020, N = 15).

Explanatory variables, Akaike Information Criterion (AIC), Delta AIC (difference in AIC with the best model) and Log-likelihood are given for each model. Models are ranked according to their respective AIC value.

Model	AIC	Delta AIC	Log-likelihood
Total trip duration ~ YEAR * BREEDING STAGE	1261.7	0	-622.9
Total trip duration ~ YEAR	1264.0	5.2	-626.0
Total trip duration ~ BREEDING STAGE	1295.0	36.1	-643.5
Total trip duration ~ SEX	1310.2	51.4	-651.1
Total trip duration ~ 1	1312.0	53.1	-652.9
Total distance per trip ~ YEAR * BREEDING STAGE	1991.0	0	-987.5
Total distance per trip ~ YEAR	2010.4	22.2	-999.2
Total distance per trip ~ BREEDING STAGE	2057.7	69.5	-1024.8
Total distance per trip ~ SEX	2063.7	75.3	-1027.8
Total distance per trip ~ 1	2069.6	81.3	-1031.8
Maximum distance per trip ~ YEAR * BREEDING STAGE	1677.7	0	-830.8
Maximum distance per trip ~ YEAR	1691.3	16.3	-839.7
Maximum distance per trip ~ BREEDING STAGE	1732.9	57.9	-862.5
Maximum distance per trip ~ SEX	1739.7	64.7	-865.9
Maximum distance per trip ~ 1	1744.1	68.9	-869.0
Start direction ~ YEAR * BREEDING STAGE	1682.7	0	-833.3
Start direction ~ YEAR	1738.6	60.2	-863.3
Start direction ~ BREEDING STAGE	1768.6	90.1	-880.3
Start direction ~ SEX	1769.9	91.5	-880.9
Start direction ~ 1	1774.2	95.8	-884.1
Maximum range direction ~ YEAR * BREEDING STAGE	1665.3	0	-824.7
Maximum range direction ~ YEAR	1722.4	66.6	-855.2
Maximum range direction ~ BREEDING STAGE	1756.4	100.9	-874.2
Maximum range direction ~ SEX	1758.4	102.5	-875.2
Maximum range direction ~ 1	1762.7	106.8	-878.3

Table S4-3: Total area of the convex hull (TA), Bayesian standard ellipses areas (SEAB) and SEAB overlap of isotopic values in whole blood of common diving petrels (*P. urinatrix*) from Kanowna Island, south-eastern Australia. INC = incubation; CR = Chick-rearing.

		CR 2017	INC 2018	CR 2018	INC 2019	INC 2020	CR 2020
TA		1.23	3.47	0.34	4.61	0.28	0.21
SEAB		0.30	1.08	0.16	2.22	0.19	0.11
Overlap	- CR	-	0.00	0.06	0.05	0.00	0.03
2017							
Overlap	- INC	-	-	0.02	0.48	0.05	0.03
2018							
Overlap	- CR	-	-	-	0.05	0.00	0.02
2018							
Overlap	- INC	-	-	-	-	0.09	0.05
2019							
Overlap	- INC	-	-	-	-	-	0.15
2020							
Overlap	- CR	-	-	-	-	-	-
2020							

Table S4-4: Parameter estimates for the analysis of the effect of equipment on chick growth curves.

		Estimate	Std.Error	t	p
Body mass	Intercept	-1.40	2.89	-0.46	0.628
	Linear	2.17	6.26	-0.34	0.729
	Quadratic	-0.08	3.92	-0.02	0.983
Wing length	Intercept	-0.49	1.10	-0.44	0.660
	Linear	-1.39	2.00	-0.69	0.490
	Quadratic	-0.23	1.45	-.15	0.870
Tarsus length	Intercept	0.07	0.30	0.24	0.804
	Linear	0.28	0.43	0.66	0.506
	Quadratic	-0.27	0.30	-0.90	0.366
Bill length	Intercept	0.50	0.30	1.65	0.097
	Linear	-1.11	1.19	-0.93	0.350
	Quadratic	0.82	0.83	0.99	0.321

Figure S4-1: Fitted functions for each environmental covariate used to assess the probability of habitat selection of common diving petrels (*P. urinatrix*) from Kanowna Island, south-eastern Australia. Environmental covariates include (in increasing order of importance): salinity (SAL), wave direction (WVD), sea surface temperate (SST), sea surface height (SSH), current speed (CUR), wave period (WVP), sea floor slope (SLO), bathymetry (DEP) and mixed layer thickness (MLT).

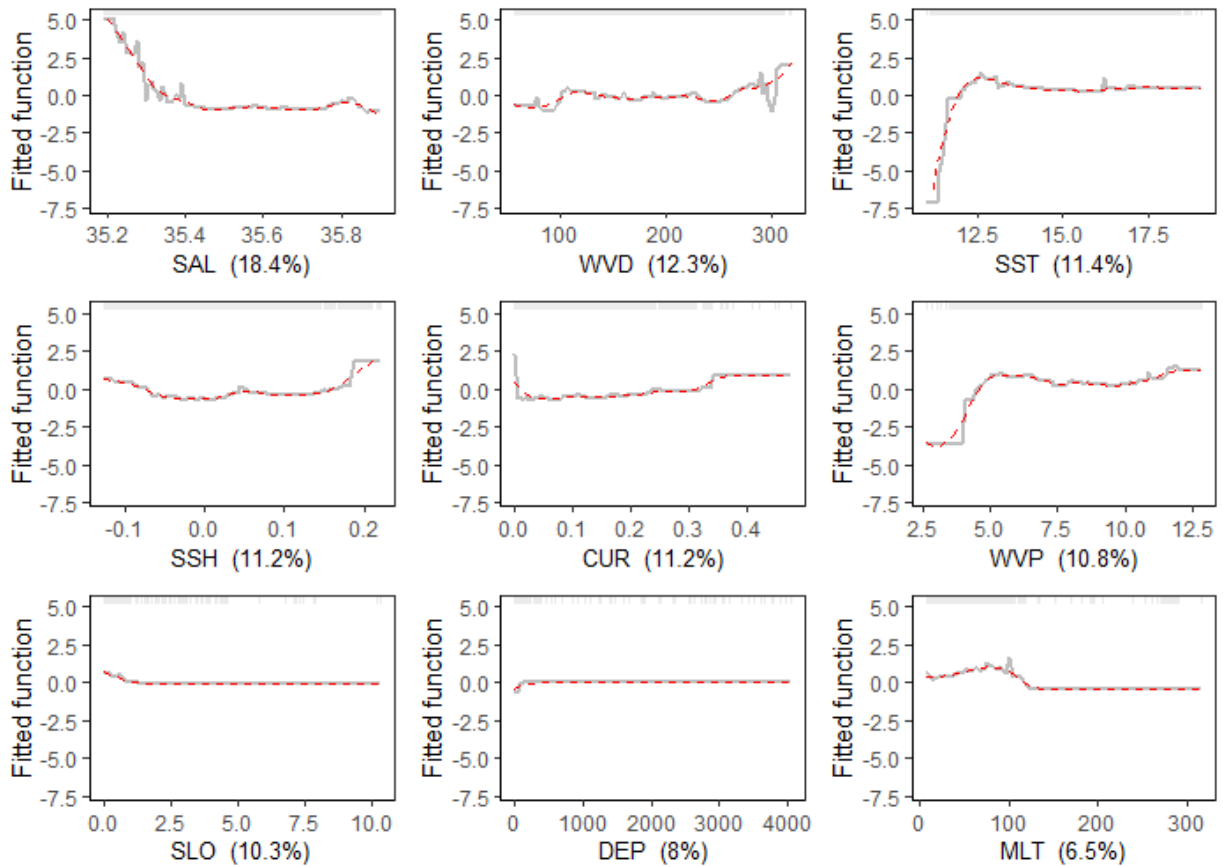


Figure S4-2: Fitted functions for each year and breeding stage of habitat selection of common diving petrels (*P. urinatrix*) from Kanowna Island, south-eastern Australia.

Environmental covariates: salinity (SAL), sea surface height (SSH), sea surface temperature (SST), wave period (WVP), current speed (CUR), wave direction (WVD), sea floor slope (SLO), bathymetry (DEP) and mixed layer thickness (MLT).

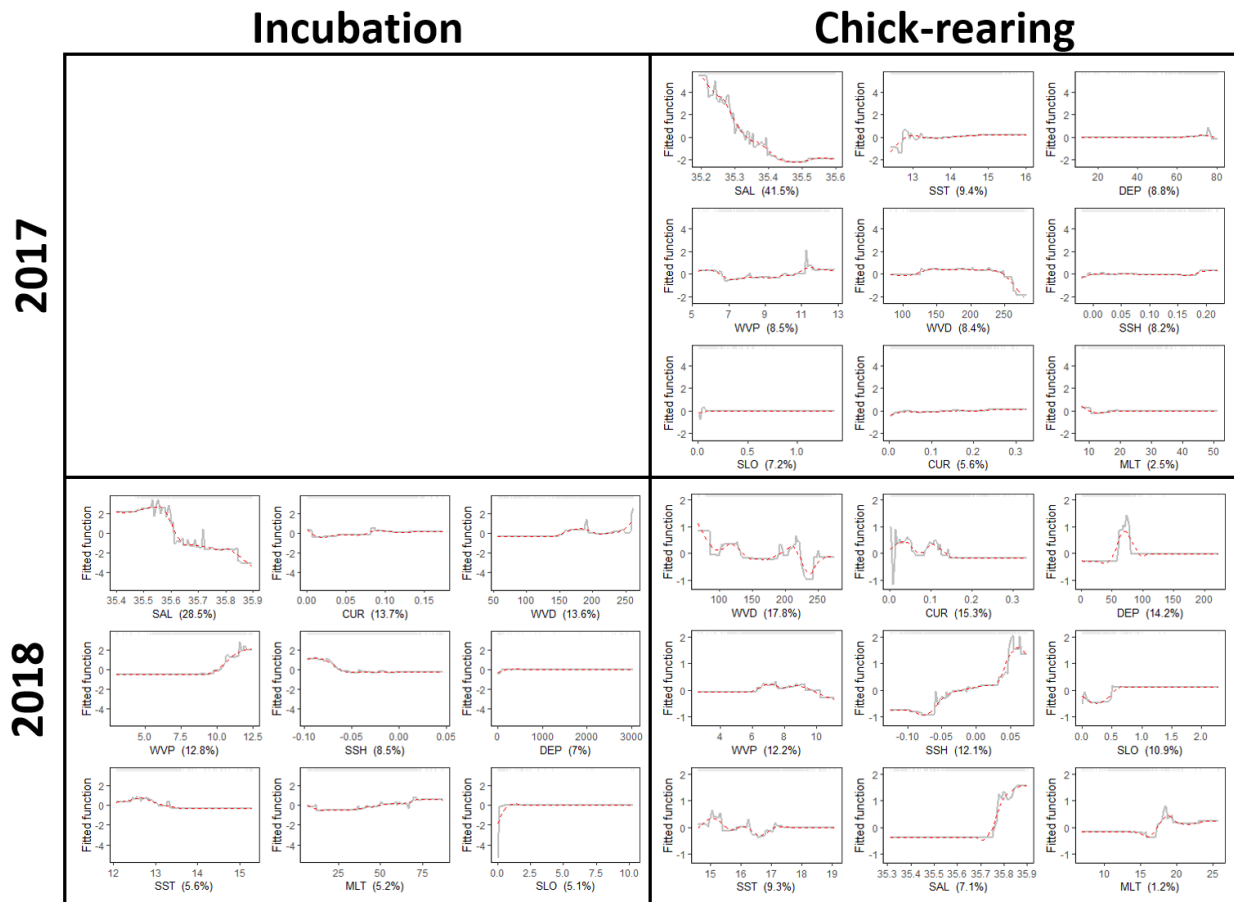
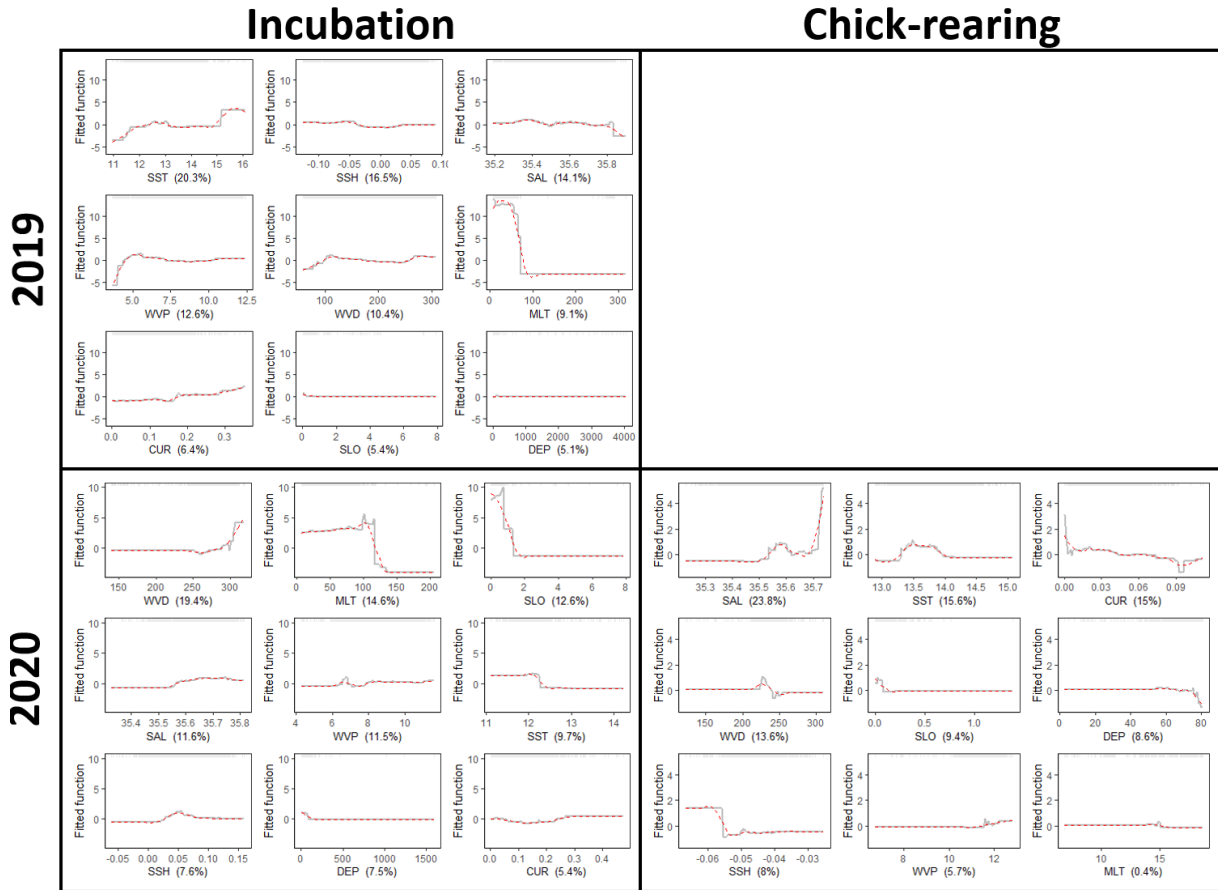
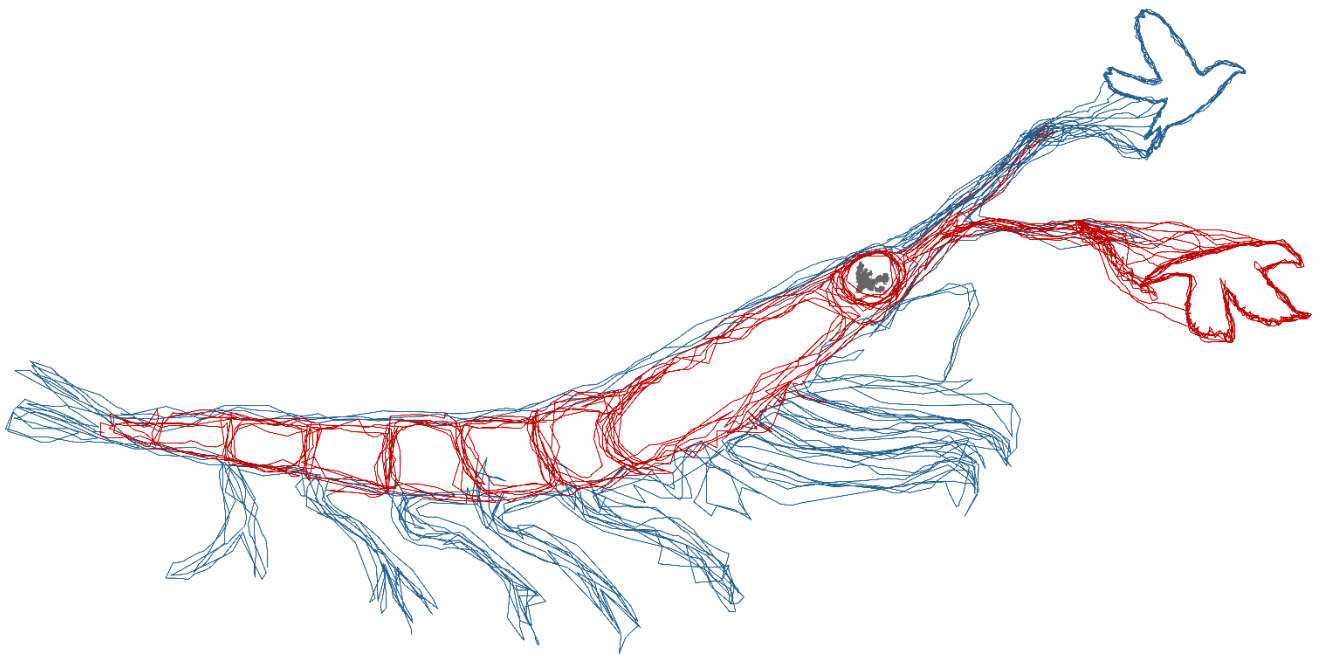


Figure S4-2:



Chapter 5

Year-round niche segregation in two sympatric sibling seabirds: the common and South Georgian diving petrels



A version of this chapter has been submitted as:

Fromant A, Arnould JPY, Delord K, Sutton GJ, Carravieri A, Bustamante P, Miskelly CM, Kato A, Brault-Favrou M, Cherel Y, Bost CA (2022) Stage-dependent niche segregation: insights from a multi-dimensional approach of two sympatric sibling seabirds. *Oecologia* 199: 537-548.

<https://doi.org/10.1007/s00442-022-05181-0>

5.1. Summary

Niche theory predicts that to reduce competition for the same resource, sympatric ecologically similar species should exploit divergent niches and segregate in one or more dimensions. Seasonal variations in environmental conditions (extrinsic factors) and energy requirements (intrinsic factors) can influence the mechanisms and the degree of niche segregation. However, studies have overlooked the multi-dimensional aspect of niche segregation over the whole annual cycle, and key facets of species co-existence still remain ambiguous. Chapter 5 provides insights into the niche use and partitioning of two morphologically and ecologically similar seabirds of the Southern Ocean, the common diving petrel (CDP, *Pelecanoides urinatrix*) and the South Georgian diving petrel (SGDP, *P. georgicus*). Using phenology, at-sea distribution, diving behavior and isotopic data gathered across five annual cycles (during the incubation, chick-rearing and non-breeding periods), we show that the degree of partitioning was highly stage-dependent (Table 5-1). During the breeding season, the greater niche segregation during chick-rearing than incubation supported the hypothesis that resource partitioning increases during energetically demanding periods. During the post breeding period, while the observed species-specific latitudinal differences were expected, CDP and SGDP also migrated in very divergent directions (south west for CDP and east for SGDP). This may indicate the implication of processes other than inter-species niche competition. In addition, a review of CDP and SGDP segregation throughout their distribution range highlighted differences in partitioning between breeding sites (Kerguelen vs South Georgia). Such variations suggest that niche segregation mechanisms should be carefully interpreted in different environments. This Chapter demonstrates the importance of integrative approaches combining concepts and techniques from different fields to better understand the co-existence of ecologically similar species. The stage-dependent and context-dependent niche segregation shown here highlights the need for whole-year and multiple-site studies of niche

partitioning of sympatric species. This is particularly relevant in order to fully understand the short and long-term effects of ongoing environmental changes on species distributions and communities.

Table 5-1: Summary of spatial (at-sea distribution and dive depth) and trophic segregation between common (CDP) and South-Georgian (SGDP) diving petrels from Kerguelen Islands during the whole annual cycle. The degree of segregation is symbolized as a gradient from no segregation (–) to strong segregation (+++).

Period	Dimension	Degree of segregation	Comment
Pre-breeding	Distribution	-	Overlapping (both species off-shore)
	Dive depth		No data
	$\delta^{13}\text{C}$ (‰)		No data
	$\delta^{15}\text{N}$ (‰)		No data
Incubation	Distribution	±	Overlapping (both species mostly foraging off-shore)
	Dive depth	-	CDP = SGDP
	$\delta^{13}\text{C}$ (‰)	+	Large distribution of values for CDP
	$\delta^{15}\text{N}$ (‰)	+	For similar $\delta^{13}\text{C}$, CDP < SGDP
Chick-rearing	Distribution	+++	Full spatial segregation (CDP foraging inshore)
	Dive depth	+++	CDP >> SGDP
	$\delta^{13}\text{C}$ (‰)	+++	CDP >> SGDP
	$\delta^{15}\text{N}$ (‰)	+++	CDP >> SGDP
Post-breeding	Distribution	+++	Full segregation (latitudinal and longitudinal)
	Dive depth		No data
	$\delta^{13}\text{C}$ (‰)	++	CDP < SGDP
	$\delta^{15}\text{N}$ (‰)	++	CDP > SGDP

5.2. Introduction

The concept of niche is central in ecology, defined as a hyper-volume within an N-dimensional niche space (Hutchinson 1957), and has found important applications in fundamental ecology, evolution, species management and conservation (Putman and Flueck 2011, Green 2020). Niche theory predicts that in order to limit the competition for the same resource, sympatric ecologically similar species should exploit divergent niches and segregate in one or more dimensions (MacArthur 1958, Holt 2009). Niche segregation has been observed in a diverse range of taxa including plants (Monson et al. 1983), invertebrates (Finke and Snyder 2008) and vertebrates (Latham 1999), in both terrestrials and marine environments (Ainley et al. 2009). Investigating niche segregation is essential to gather knowledge about how and why species co-exist, especially for sibling species. In addition, it is also of particular relevance to evaluate the species' ability to adjust the characteristics of its niche hyper-volumes over time and space. This step is an essential prerequisite for assessing a species' capacity to buffer current and future environmental changes.

Seabirds are a particularly good model taxon to study niche segregation as they aggregate in large mixed-species populations in spatially restrained breeding and foraging habitats (Ainley et al. 2009). Although there is an ongoing interest in niche segregation in seabirds (Barger et al. 2016, Petalas et al. 2021), the strong three-dimensional aspect of the marine environment challenges our understanding of the underlying mechanisms driving niche partitioning. In particular, segregation in seabirds can occur temporally (daily and seasonally, i.e. both during the breeding and non-breeding period; Jouventin et al. 1988, Granroth-Wilding and Phillips 2019), spatially (in both horizontal and vertical dimensions; Masello et al. 2010, Navarro et al. 2013, Kokubun et al. 2016), and trophically (Bocher et al. 2000a, Cherel et al. 2002, Whitehead et al. 2017). However, very few studies have investigated the niche partitioning in more than two dimensions (Thiebot et al. 2012, Navarro et al. 2015, Harris et

al. 2020), thereby complicating the possibility to distinguish the causes and mechanisms leading to segregation.

High latitude seabirds typically experience varying influences of extrinsic and intrinsic factors throughout their annual cycle. Seasonal variations in oceanographic conditions and prey availability (extrinsic factors) can influence the patterns of niche partitioning, as trophic segregation might highlight competition for limited food resources (Barger and Kitaysky 2012), while a superabundance of prey enables overlapping niches (Forero et al. 2004). In addition, the degree of niche segregation might change according to the variation in energy requirements (intrinsic factors) related to the different constraints of each breeding stage and moult (Calado et al. 2018). During the breeding season, niche partitioning of ecologically similar species is likely to be at its maximum during the chick-rearing period, when offspring provisioning adds on to adults self-supplying (Cherel et al. 2014, Barger et al. 2016). Similarly, outside the breeding season, the high energetic demand of the moult may increase inter-species competition during this critical period (Dunn et al. 2019, Takahashi et al. 2021). However, most niche segregation studies have focused on one stage of the annual cycle at a time, mainly during the breeding season when seabirds are easily accessible. Therefore, key facets of species co-existence still remain ambiguous. Clearly, more attention is needed concerning the description of niche segregation throughout the entire annual cycle.

In the Southern Ocean, albatrosses, petrels and penguins represent a wide range of sympatric seabirds with various physiological and ecological adaptations to the marine environment (Croxall 1984; Warham 1990). However, conventional foraging studies (tracking of at-sea movements and diving behaviour) have focused mainly on larger species mostly because of technological and practical reasons. In addition, the primary investigation of niche segregation in such studies revolves around the flying characteristics of albatrosses (Phillips et al. 2004a), or the diving capacities of penguins (Wilson 2010).

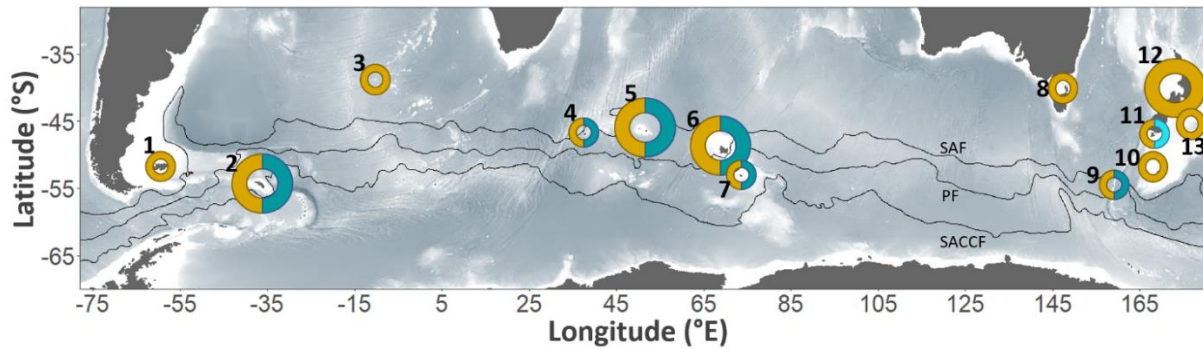


Figure 5-1: Distribution of common (CDP; yellow) and South Georgian (SGDP; blue) diving petrels. 1: Falklands/Malvinas Islands; 2: South Georgia; 3: Gough/Tristan da Cunha Islands; 4: Prince Edward Islands; 5: Crozet Islands; 6: Kerguelen Islands; 7: Heard/McDonald Islands; 8: south-eastern Australia; 9: Macquarie Island; 10: Auckland/Campbell Islands; 11: Stewart Island islets; 12: New Zealand; 13: Chatham Islands. Larger circles show populations with more than 500 000 individuals of each species (Marchant & Higgins 1990). Shared circles show sympatric populations of CDP and SGDP. Light blue for Stewart Island islets (11) corresponds to Whenua Hou diving petrel (*P. whenuahouensis*), a species recently described and closely related to SGDP (Fischer et al. 2018). The black lines represent the approximate location of the Subantarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF).

Among seabirds of the Southern Ocean (Croxall 1984), diving petrels (*Pelecanoides* spp.) are unique in their morphology (small and compact), notable for their diving (Navarro et al. 2014) and flying abilities (Rayner et al. 2017; Bost et al. 2022; Chapter 4). Among the five recognized species of diving petrels (Fischer et al. 2018; Marchant and Higgins 1990), the common diving petrel (CDP, *P. urinatrix*) and the South Georgian diving petrel (SGDP, *P. georgicus*) have a circumpolar distribution and breed sympatrically in several archipelagos of the Southern Ocean (Fig. 5-1; Marchant and Higgins 1990). Throughout their large distribution, both CDP and SGDP exhibit overlapping breeding and post-breeding periods (Fig. 5-2; Payne and Prince 1979; Jouventin et al. 1985; Weimerskirch et al. 1989). These two sibling species have been shown to locally segregate by foraging at different depths (Navarro et al. 2013; Bocher et al. 2000a) and habitats (Cherel et al. 2006; Navarro et al. 2015), or feeding on different prey (Ridoux 1994; Reid et al. 1997; Bocher et al. 2000a). However, site-specific and stage-specific inconsistencies preclude a global picture of their segregation. In particular, the

lack of investigations over the whole annual cycle, combined to the limited number of dimensions explored, complicate our ability to fully describe and understand the niche segregation of these two sympatric species.

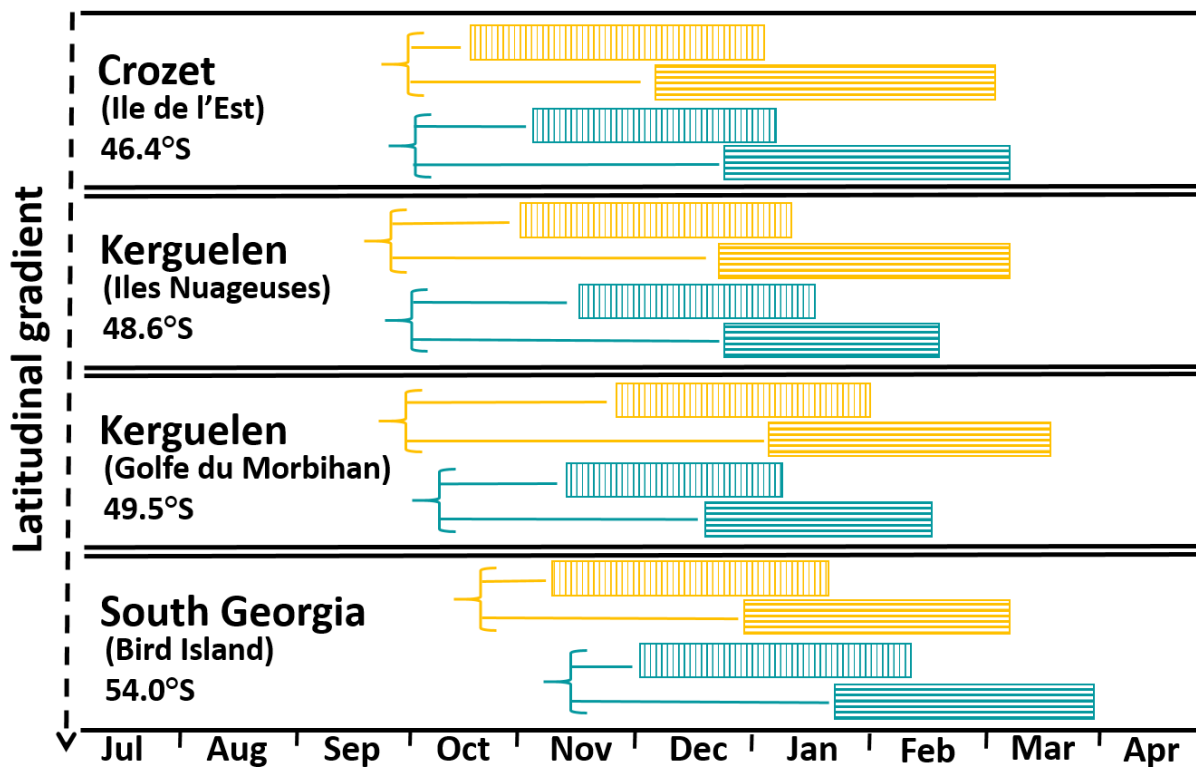


Figure 5-2: Phenology of common (yellow) and South Georgian (blue) diving petrels breeding in sympatry. Blocks with vertical lines correspond to incubation, and horizontal lines show the chick-rearing period. Horizontal lines indicate the pre-breeding period (from when birds return to the colony to the start of the breeding period). Phenology data were adapted from Jouventin et al. (1985) (Crozet), Weimerskirch et al. (1989) (Kerguelen), and Payne & Prince (1979) and Reid et al. (1997) (South Georgia). For Kerguelen, Ile Nuageuses are a group of offshore islands while Golfe du Morbihan is a semi-closed embayment, north-west and south-east of the archipelago, respectively.

In the present chapter, we investigated the niche segregation between CDP and SGDP at Kerguelen Islands, southern Indian Ocean, by quantifying the hyper-volume differences of these two morphologically and ecologically similar congeners throughout their whole annual cycle. Using an integrative approach combining phenology, at-sea movement, diving, accelerometer, and isotopic data, we addressed three main questions: (1) do CDP and SGDP

differ in their timing of breeding, distribution, diving behaviour and isotopic niche? (2) does the degree of niche segregation vary throughout their annual cycle?; and (3) are the processes leading to niche partitioning similar during the pre-breeding, incubation, chick-rearing and post-breeding periods?

Based on previous trophic and isotopic analysis (Bocher et al. 2000a; no accurate distribution and diving behaviour data available at Kerguelen) we predicted that niche segregation between the two species is mostly driven by 1) differences in diving behaviour and spatial partitioning during the breeding period, and 2) spatial partitioning during the post-breeding period (similarly to what was observed among other small-sized procellariiform species; Quillfeldt et al. 2015, Jones et al. 2020). Since niche segregation can be more pronounced during energetically challenging periods (Barger et al. 2016), we also predicted stronger behavioural and/or trophic differences during the chick-rearing period, and during the first months of the post-breeding period, when adults renew their plumage (Chapter 3).

5.3. Materials and Methods

5.3.1. Study site and animal instrumentation

Fieldwork was conducted at Kerguelen Islands, Southern Indian Ocean across five consecutive annual cycles (2015/2016 to 2019/2020) (details of year- and stage-specific sample sizes are given in Table S5-1). The annual cycle was divided into four distinct periods: the incubation and chick-rearing periods during the breeding season, and the post-breeding migration (from departure to return to the colony) and pre-breeding period (from return to the colony to the start of the breeding season) during the non-breeding season. Although both species breed in sympatry on some islands of the archipelago (Weimerskirch et al. 1989), for logistical and practical reasons, the study colonies we used were located on two islands 6 km apart within the Gulfe du Morbihan, where large populations of diving petrels breed: CDP at

Ile Mayes (49°28'S, 69°57'E) and SGDP at Ile aux Cochons (49°47'S, 70°05'E). Both species breed in burrows and the nest chamber was accessed by an artificial entrance covered with a removable stone lid. This access system reduced the disturbance of the natural tunnel and facilitated rapid access to the birds which were captured in the nest burrow for all procedures (Chapter 2).

To evaluate the at-sea distribution and diving behaviour of the two study species during both the incubation and chick-rearing periods, miniature GPS (2.0 g; nanoFix-GEO, Pathtrack Ltd, Otley, United Kingdom), time-depth recorder (TDR; 2.7 g; Cefas G5, Cefas Technology Ltd, Lowestoft, United Kingdom) and depth-accelerometer (4.0 g; AxiDepth, TechnoSmArt Ltd, Italy) data loggers were deployed using adhesive water proof tape (Tesa 4651, Beiersdorf AG, Germany) on two central tail feathers (for GPS and TDR) or on back feathers (for accelerometers). The GPS loggers were programmed to record locations at 10 min and 5 min interval during the incubation and chick-rearing periods, respectively. Both TDRs and depth-accelerometer data loggers were programmed to record pressure and hence dive depth (± 5 cm), and temperature ($\pm 0.1^\circ\text{C}$) every 1 s. In addition, accelerometers measured tri-axial body acceleration at 25 Hz. Because of the small size of the species (<180 g), only one type of device was deployed on each individual at a time. The total mass of logger attachments was between 1.5-2.5% and 2.0-2.9% of CDP (120-180 g) and SGDP (110-150 g) body weight, respectively. Equipped individuals were recaptured after 1 to 3 foraging trips dependent on recapture opportunities.

To determine the at-sea distribution of CDP and SGDP during the non-breeding period (post-breeding migration and pre-breeding period), adult birds were equipped with leg-mounted GLS (Migrate Technology, model C65, United Kingdom). The mass of the device attached to a metal ring with a cable tie was less than 1.5 g, corresponding to $1.1 \pm 0.1\%$ (mean

\pm SD) of body mass. Breeding individuals were equipped at the end of the breeding season and were recaptured during the following breeding season for removal of the device.

Blood (0.2 mL) was collected from the brachial vein for stable isotope measurements and sexing when each individual was recaptured. For all birds, sex was determined by DNA analysis (Laboratoire Analyses Biologiques, CEBC, France). Individuals were weighed (\pm 2 g; Pesola), and culmen, tarsus (\pm 0.1 mm; Vernier calipers) and wing length (\pm 1 mm; ruler) were measured. Handling time at deployment and recapture was $<$ 10 min.

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in whole blood and body feathers can be used as proxies of the foraging habitat and diet/trophic level, respectively. Specifically, isotopic values of whole blood (hereafter blood) reflect dietary integration of approximately two to four weeks (Bearhop et al. 2002), while body feathers reflect dietary intake when they were synthesized (Cherel et al. 2000). Like for most small-sized procellariiforms, the moult of body feathers for diving petrels is a protracted process happening mostly after the end of the breeding season (Carravieri et al. 2014, Chapter 3). The Southern Ocean is marked by a strong latitudinal isotopic gradient, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ decreasing with increasing latitudes (Jaeger et al. 2010). In addition, at the local scale, coastal waters are generally characterized by high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines that propagate throughout the food web up to top predators (Cherel et al. 2014), thus allowing discrimination of coastal and pelagic foraging grounds of seabirds. Isotopic analyses were carried out on blood and body feathers to investigate the isotopic niche of CDP and SGDP during the breeding (incubation and chick-rearing) and post-breeding periods, respectively. For the post-breeding period, four body feathers were collected from the middle and lower back of each individual tracked with a GLS. Additional samples were collected on other breeding individuals in order to increase the sample size.

5.3.2. *Data processing and analyses*

Access constraints to the breeding colonies of CDP and SGDP, and the breeding period distributed over several months (large intra-species heterogeneity of laying dates; Marchant and Higgins 1990), precluded the collection of accurate data of laying, hatching, and fledging dates. Therefore, to obtain an overview of the breeding phenology of both species, chicks were monitored and measured during the breeding season 2015-2016 (CDP = 25, SGDP = 27), and hatching dates were determined using the method described by Eizenberg et al. (2021). The wing length–age relationship (Thoreson 1969, Payne and Prince 1979) was used as a proxy to determine the hatching date. Approximations of laying and fledging dates were then estimated using the duration of the incubation (CDP = 55 d; SGDP = 47 d) and chick-rearing (CDP = 54 d; SGDP = 48 d) periods (Payne and Prince 1979, Jouventin et al. 1985). For each chick, the hatching date was averaged using 2-4 different measurements over a three-week period.

All GPS data were processed within the R statistical environment (R Core Team 2020). Prior to behavioral modeling, land-based points were removed and a speed filter with a threshold at $20 \text{ m}\cdot\text{s}^{-1}$ was applied to remove erroneous locations (Spear and Ainley 1997). Because of poor satellite reception during intense diving activity, linear interpolation was necessary to correct for unequal sampling frequencies between foraging and commuting. Foraging trips were defined as the time spent at sea between the departure from and the return to the burrow. For each complete trip, the following basic trip parameters were calculated: trip duration, total horizontal distance travelled, and maximum distance from the colony. Incomplete trips were only used to estimate maximum distance from the colony. Because diving petrels forage by diving from the sea surface, two behavioral states were identified: flying, and foraging/resting (foraging hereafter). To enable the comparison between CDP and SGDP, the discrimination between both states was determined using the conservative instantaneous speed threshold method (Petalas et al. 2021):

Speed threshold = $2 * (\text{Drift Speed} * \text{Average Flight Speed}) / (\text{Drift Speed} + \text{Average Flight Speed})$.

The average speed threshold of $9.1 \text{ km}\cdot\text{h}^{-1}$ was obtained assuming a drift speed of $5 \text{ km}\cdot\text{h}^{-1}$ (Petalas et al. 2021), and an average flight speed of $50 \text{ km}\cdot\text{h}^{-1}$ for both species. Average flight speed was estimated from the analysis of flying bouts using the raw data. Regular distance between location points over large distances (35 to 225 km) were used to select continuous flying bouts, and speed was averaged for each species ($\text{CDP} = 49 \pm 13 \text{ km}\cdot\text{h}^{-1}$; $\text{SGDP} = 50 \pm 11 \text{ km}\cdot\text{h}^{-1}$). Values equal or lower to the speed threshold were assigned as foraging, and the remaining positions (instantaneous speed $> 9.1 \text{ km}\cdot\text{h}^{-1}$) were defined as flying (see Bost et al. 2022 for more details).

Processing and calculations of GLS data were conducted using the *GeoLight* package in the R statistical environment (Lisovski et al. 2012; R Core Team 2020). The device records the maximum light intensity for each 5 min interval, and the determination of morning and evening twilights enables longitude (timing of local midday and midnight) and latitude (duration of day and night) to be estimated, providing two positions per day with an average accuracy of 200-400 km (Wilson et al. 1992; Phillips et al. 2004b; Halpin et al. 2021). Filtered locations were used to generate kernel utilization distribution (UD) estimates using the same method as Chapter 3. The 50% (core foraging area) and 95% (home range) kernel UD contours were obtained (Worton 1989). Spatial analyses were performed using the *adehabitatHR* R package (Calenge 2006).

Dive data obtained from depth recorders and accelerometers were corrected for depth drift and processed using *diveMove* package (Luque and Fried, 2011). For each dive, the following dive parameters were calculated: time at the beginning and end of a dive, dive duration, dive depth, duration of descent, bottom time, ascent duration, and post-dive interval.

The species relative dive efficiency was estimated by dividing the bottom duration during dives by the total time spent during one dive cycle for that particular cycle (Wilson 2010).

Accelerometer data were filtered to separate dynamic acceleration attributed to animal movement from static acceleration using a 1 s running mean. The Vectorial Dynamic Body Acceleration (VeDBA) was calculated using the following equation:

$$VeDBA = \sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}$$

where X, Y and Z are the dynamic acceleration (dyn) of horizontal (surge), vertical (heave) and lateral (sway) movements, respectively. Mean and Total VeDBA per dive were used as proxies for diving effort (Qasem et al. 2012). Behavioral modes were identified from the combined accelerometer and depth data through *k*-means clustering analysis in the Ethographer package in IgorPro (Wavemetrics Inc., Portland OR, USA, version 6.3.7.2) (Sakamoto et al. 2009). Briefly, this method is a type of unsupervised clustering analysis that groups similar kinds of signals into clusters and was performed on the x-axis due to its greater variation. Three categories (surface resting, flying, and diving) were identified from the accelerometers, and were further classified using depth data to discriminate between the high amplitude observed in both flying and diving behavioural modes. The duration of each of the behaviour categories were determined for each individual and summed to obtain daily activity budgets.

Blood was freeze-dried, ground to powder and homogenized, and sub-samples were weighed (0.4 mg) with a microbalance. To remove surface dirt, feathers were washed in a chloroform-methanol solution and oven dried for 24h as described by Carravieri et al. (2013). For each individual, feathers were homogenized by cutting them with scissors into small fragments (Fromant et al. 2016). The relative abundance of carbon and nitrogen isotopes was determined with a continuous-flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Isotopic results are

presented in the δ notation relative to Vienna PeeDee Belemnite and atmospheric nitrogen (N_2) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.10 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. The C:N mass ratios of the samples were calculated as the ratio between the mass percentages of carbon and nitrogen. The consistently low C:N values (<4.0 , Post et al. 2007) verified that the low lipid content of blood did not necessitate lipid extraction (Cherel et al. 2005).

All statistical analyses were conducted within the R statistical environment (R Core Team 2020). Since some deployments resulted in multiple successive trips from a single individual, effects (species, stage, and year) on foraging and diving parameters were investigated by generating multiple Generalized Linear Mixed Models (GLMMs) using the package *glmmADMB* (Bolker et al. 2012). Species, year, and breeding stage were considered as fixed effects, and individual was added as a random effect. In addition, to investigate factors influencing diving behavior (dive depth, dive duration and mean VeDBA per dive), Generalized Additive Mixed Models (GAMMs) were fitted using the *mgcv* package (Wood 2018). Models were ranked based on their Akaike's Information Criterion (AIC) and were checked to ensure normality and homoscedasticity of residuals (Zuur et al. 2010) before further statistical analyses. Data normality and homogeneity of the variance were assessed with Shapiro-Wilk and Bartlett tests, respectively. *Post-hoc* tests were conducted using non-parametric statistics (Kruskal-Wallis and Mann-Whitney *U* tests) when parametric test assumptions of normality were unmet. To investigate at-sea spatial segregation, the percentage overlap in foraging distribution between species and for each stage were estimated using Bhattacharyya's Affinity (BA) index (Fieberg and Kochanny 2005) using the *adehabitatHR* R package (Calenge 2006). BA index (0 signifying no overlap in UD, and 1 = complete overlap) is a statistical measure for the degree of similarity amongst UD, and the amount of space-use shared among species. The isotopic niche position and width were compared between species

and breeding stages using the ellipse area-based metrics of the SIBER package (Jackson et al. 2011). The isotopic niche was estimated by the 40% standard ellipse area corrected for small sample size (SEAC), and the Bayesian standard ellipses areas (SEAB) on 10^5 replicates was used to measure the overlap of the isotopic niches between species for each stage of the annual cycle.

5.4. Results

All the morphological measurements, trip parameters and stable isotopes results were compared between sex for both species. Of the 40 inter-sex comparisons, only 3 were statistically significant (Table S5-2): wing length for SGDP (female > male; t -test: $t_{34.979} = 2.304$, $P = 0.027$), total distance travelled per trip in chick-rearing for SGDP (female > male; Mann-Whitney U test: $U = 85$, $P = 0.036$), and blood $\delta^{15}\text{N}$ in incubation for CDP (female < male; t -test: $t_{41.378} = -3155$, $P = 0.003$). Because of the limited inter-sex differences for both CDP and SGDP, data were pooled in all subsequent statistical analyses. Similarly, because of the small inter-annual variations in foraging behavior (trip parameters and diving behavior) and stable isotope values, data were pooled by species and stage.

5.4.1. Morphological differences

Morphological differences between CDP and SGDP were investigated using measurements of body mass, wing length, tarsus length, and bill length of adult breeding individuals. Although all the measurements overlapped between the two species (Fig. 5-3), CDP had significantly larger body mass, and longer wing, tarsus and bill lengths (Table 5-2). The difference between the two species was emphasized by CDP being disproportionately heavier than SGDP (Fig. 5-3), resulting in a higher wing load (ratio body mass / wing length, CDP = 1.16 ± 0.08 ; SGDP = 1.08 ± 0.08 ; t -tests: $t_{60.001} = 4.146$, $P < 0.001$).

Table 5-2: Morphological measurements (mean \pm SD) of adult common and South-Georgian diving petrels from Kerguelen Islands. Individuals from both species were measured between 2016 and 2020.

	Common diving petrels (n = 39)	South Georgian diving petrels (n = 43)	Test
Body mass (g)	147 \pm 12 (122 – 186)	128 \pm 10 (110 – 150)	<i>t</i> -test: $t_{65.916} = 7.348, P < 0.001$
Wing length (mm)	126 \pm 4 (115 – 132)	119 \pm 3 (113 – 126)	<i>t</i> -test: $t_{65.334} = 8.383, P < 0.001$
Tarsus length (mm)	26.4 \pm 1.5 (22.5 – 29.1)	24.6 \pm 0.9 (23.0 – 27.1)	<i>t</i> -test: $t_{59.883} = 7.119, P < 0.001$
Bill length (mm)	16.2 \pm 0.5 (15.1 – 17.2)	15.5 \pm 0.8 (13.8 – 16.9)	<i>t</i> -test: $t_{74.910} = 5.096, P < 0.001$

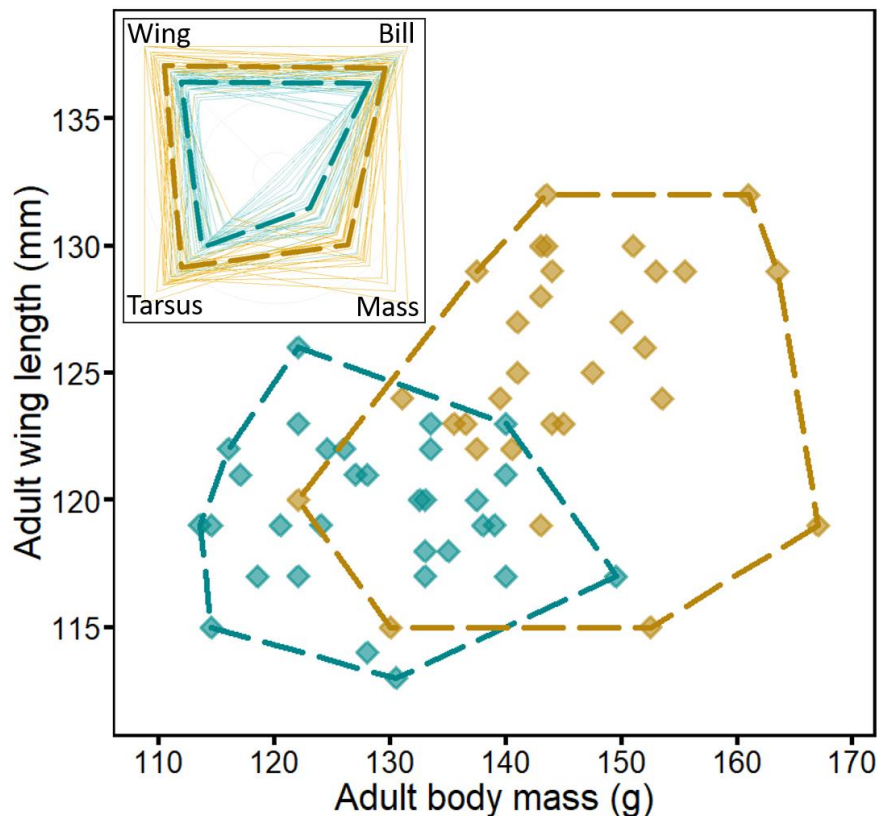


Figure 5-3: Main panel: morphological differences between adult common (yellow) and South Georgian (blue) diving petrels breeding at Kerguelen Islands. The dashed lines indicate the morphological range of each species.

Top left panel: radial chart indicating the intra- and inter-species morphological variations. These are relative values estimated as the proportion of the maximum individual values for both species combined (Value / Maximum Value (CDP : SGDP)). Each faint line corresponds to one individual, and the bold dashed lines correspond to the mean value for each species.

5.4.2. Phenology

The average laying date of CDP (28-Nov \pm 10; ranging from 15-Nov to 18-Dec) was estimated to be 18 days later than SGDP (10-Nov \pm 10; ranging from 27-Oct to 12-Dec; *t*-tests: $t_{47.238} = -6.291$, $P < 0.001$). Similarly, owing to the longer incubation and chick-rearing duration period for CDP, the mean hatching date of CDP (22-Jan \pm 10) was estimated to occur on average 26 days later than SGDP (27-Dec \pm 10; *t*-tests: $t_{47.238} = -9.082$, $P < 0.001$), and the fledging date was 32 days later for CDP (16-Mar \pm 10) than SGDP (13-Feb \pm 10; *t*-tests: $t_{47.238} = -11.176$, $P < 0.001$). The incubation period of CDP overlapped during 29 d of the SGDP incubation period (62% overlap), and also 26 d with the SGDP chick-rearing period (55% overlap) (Fig. 5-2).

5.4.3. Spatial segregation: at-sea distribution and diving behaviour

Over the 5 years of the study, at-sea movement data were obtained from a total of 104 GPS trips (incubation = 19; chick-rearing = 85) and 21 GLS trips; diving data were obtained from a total of 45 trips (incubation = 11; chick-rearing = 34), and accelerometry data from 38 trips (incubation = 11; chick-rearing = 27) (details in Table S5-1). Due to logistical constraints, no tracking data were obtained during the incubation and chick-rearing periods during the 2016-2017 breeding season.

During the incubation period, both CDP and SGDP travelled 200-400 km south of Kerguelen, along the shelf-slope of the Kerguelen Plateau (Fig. 5-4A), with considerable overlap in their foraging distribution (BA indices for 50% UDs = 0.62). Although, one CDP individual undertook a short foraging trip within the Golfe du Morbihan (Fig. 5-4A; Table 5-3), there was no significant difference for offshore trips between both species, neither in duration (CDP = 45 ± 1 h; SGDP = 45 ± 24 h; Mann-Whitney *U* test: $U = 3$, $P = 0.700$), nor in distance travelled (CDP = 777 ± 154 km; SGDP = 653 ± 98 km; Mann-Whitney *U* test: $U = 7$,

$P = 0.400$) or maximum distance from the colony ($CDP = 331 \pm 71$ km; $SGDP = 322 \pm 108$ km; Mann-Whitney U test: $U = 14$, $P = 0.762$).

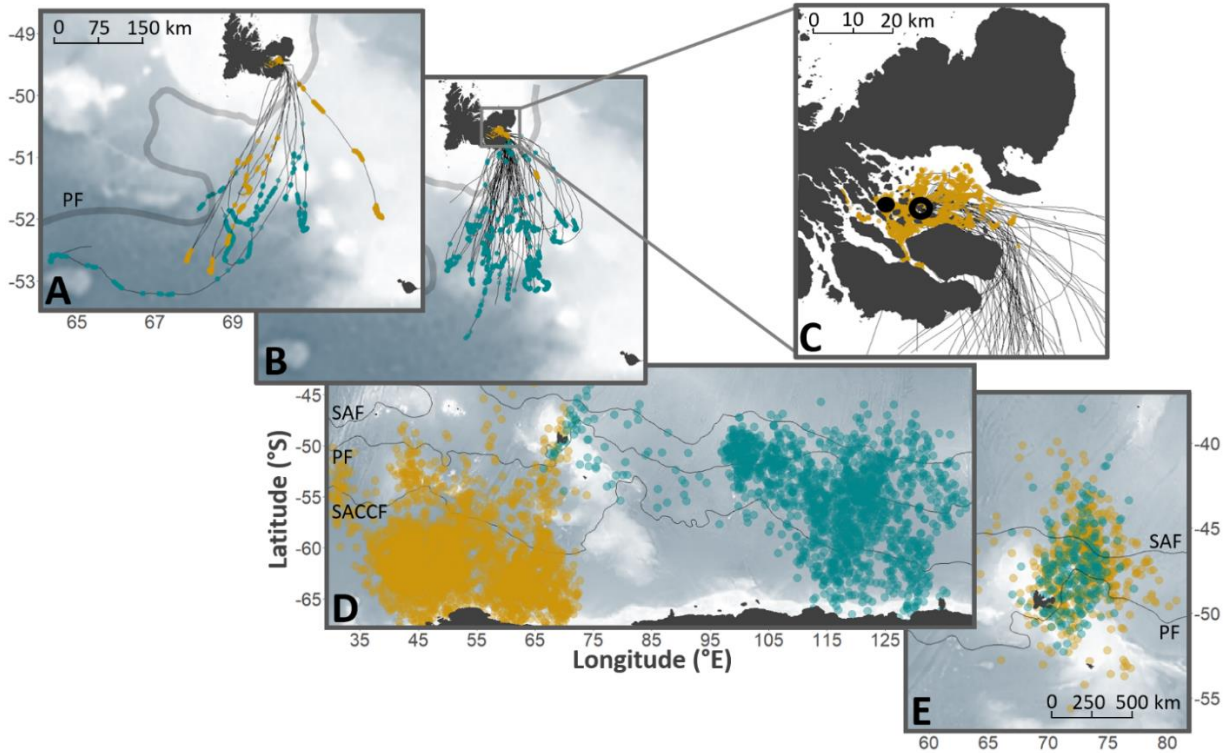


Figure 5-4: At-sea distribution of common (yellow) and South Georgian (blue) diving petrels from Kerguelen Islands. Tracks in incubation (A) and chick-rearing (B and C) were collected using GPS, where dots indicate positions with speed < 9.1 km·h⁻¹ (proxy of foraging locations; see Methods for more details). Data in post-breeding (D) and pre-breeding (E) were collected using GLS (2 locations per day). In panel C, the full black circle indicates the location of Ile Mayes where CDP were studied, and the open black circle the location of Ile aux Cochons where SGDP were studied. The two islands are situated in the central part of the Golfe du Morbihan, and are 6 km apart. SAF = Subantarctic Front; PF = Polar Front; SACCF = Southern Antarctic Circumpolar Current Front.

Similarly, CDP and SGDP exhibited comparable dive characteristics during the incubation period (Table 5-3; Fig. 5-5). Both species were diving to similar depths (Mann-Whitney U test: $U = 14$, $P = 0.808$), and for similar durations (Mann-Whitney U test: $U = 24$, $P = 0.214$). Nonetheless, CDP and SGDP differed in their mean VeDBA values. During the incubation period, while diving at a similar depth, SGDP exhibited higher mean VeDBA values

than CDP (Fig. S5-1), for both dive duration ($F_{6,020} = 178.60$, $P < 0.01$) and depth ($F_{6,215} = 165.03$, $P < 0.01$), indicating they were more active underwater than CDP.

Table 5-3: Overall tracking data (mean \pm SD) of common and South-Georgian diving petrels during the incubation and chick-rearing periods at Kerguelen Islands. For each parameter, values not sharing the same superscript letter (a, b or c) are significantly different (Mann-Whitney U test: $P < 0.05$).

	Common diving petrels		South-Georgian diving petrels	
	Incubation	Chick-rearing	Incubation	Chick-rearing
GPS data (N individuals; n trips)	N = 6; n = 6	N = 31; n = 39	N = 6; n = 6	N = 37; n = 46
Trip duration (h)	40 \pm 10 ^a	19 \pm 1 ^b	45 \pm 24 ^{ac}	28 \pm 10 ^c
Total distance travelled (km)	506 \pm 388 ^a	84 \pm 23 ^b	653 \pm 98 ^a	535 \pm 115 ^a
Maximum distance from colony (km)	227 \pm 171 ^{ab}	19 \pm 10 ^c	322 \pm 108 ^a	208 \pm 68 ^b
Dive data (N individuals; n trips)	N = 7; n = 7	N = 12; n = 21	N = 4; n = 4	N = 11; n = 13
Dive depth (m)	6.5 \pm 0.5 ^a	15.2 \pm 3.2 ^b	6.6 \pm 0.8 ^a	6.1 \pm 2.6 ^a
Dive duration (s)	28 \pm 3 ^a	44 \pm 6 ^b	25 \pm 3 ^{ac}	23 \pm 5 ^c
Time activity budget (N individuals; n trips)	N = 7; n = 7	N = 10; n = 19	N = 4; n = 4	N = 6; n = 8
Flying (%)	53.4 \pm 14.0 ^{ab}	50.9 \pm 12.9 ^b	33.0 \pm 4.8 ^a	49.2 \pm 19.0 ^{ab}
Resting (%)	27.5 \pm 13.5 ^{ab}	25.6 \pm 12.9 ^b	49.9 \pm 4.2 ^a	33.4 \pm 18.7 ^{ab}
Diving (%)	19.1 \pm 5.1 ^{ab}	23.5 \pm 4.7 ^b	17.1 \pm 3.2 ^a	17.4 \pm 3.3 ^a

During the chick-rearing period, CDP and SGDP strongly segregated in their at-sea distribution, dive depth, and dive duration (Table 5-3; Fig. 5-4B and C). While SGDP continued to forage at a distance, along the shelf-slope of the Kerguelen Plateau, CDP foraged almost exclusively inshore, within the Golfe du Morbihan (Fig. 5-4B and C). This switch in foraging habitat by CDP resulted in a decrease in the prospecting distance (distance travelled per trip one sixth, and trip duration one half of that displayed by SGDP). This was associated with an increased diving effort for CDP, with birds diving significantly deeper (Mann-Whitney

U test: $U = 2$, $P < 0.001$) and longer (Mann-Whitney U test: $U = 1$, $P < 0.001$) than SGDP at that time (Table 5-3; Fig. S5-2). The relationship between dive bottom duration, post-dive duration and dive depth indicated divergent relative dive efficiencies (Fig. 5-6), with CDP appearing to be more efficient divers than SGDP with increasing depths. This difference in diving behavior between the two species was similar to the magnitude of change in diving behavior by CDP between incubation and chick-rearing.

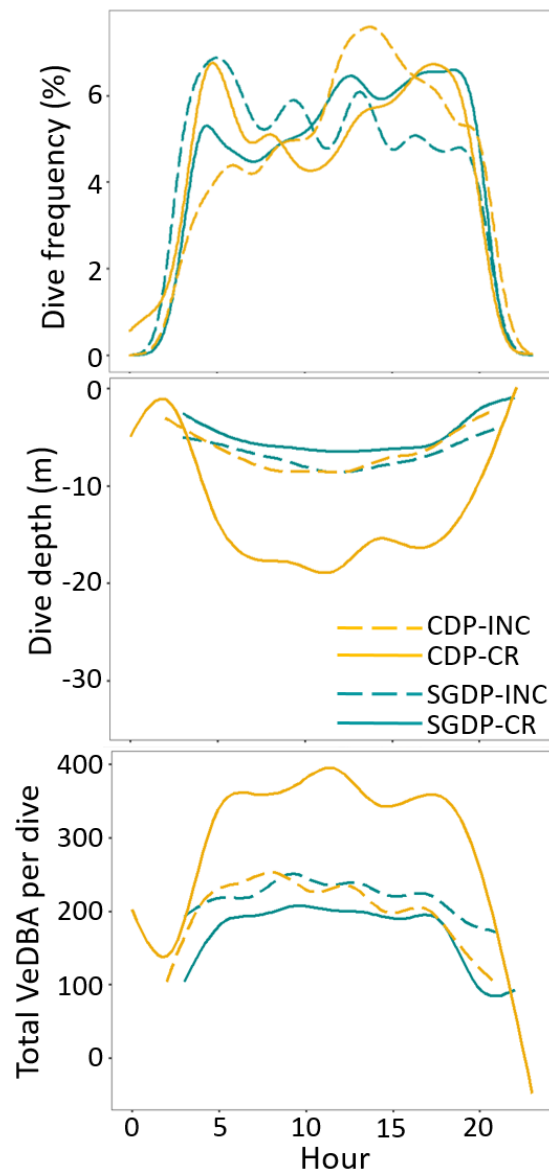


Figure 5-5: Temporal variation for dive frequency, dive depth and total VeDBA (Vectorial Dynamic Body Acceleration) per hour of the day (24h period) predicted by generalized additive mixed models. CDP = common diving petrels; SGDP = South Georgian diving petrels; INC =incubation period; CR = chick-rearing period.

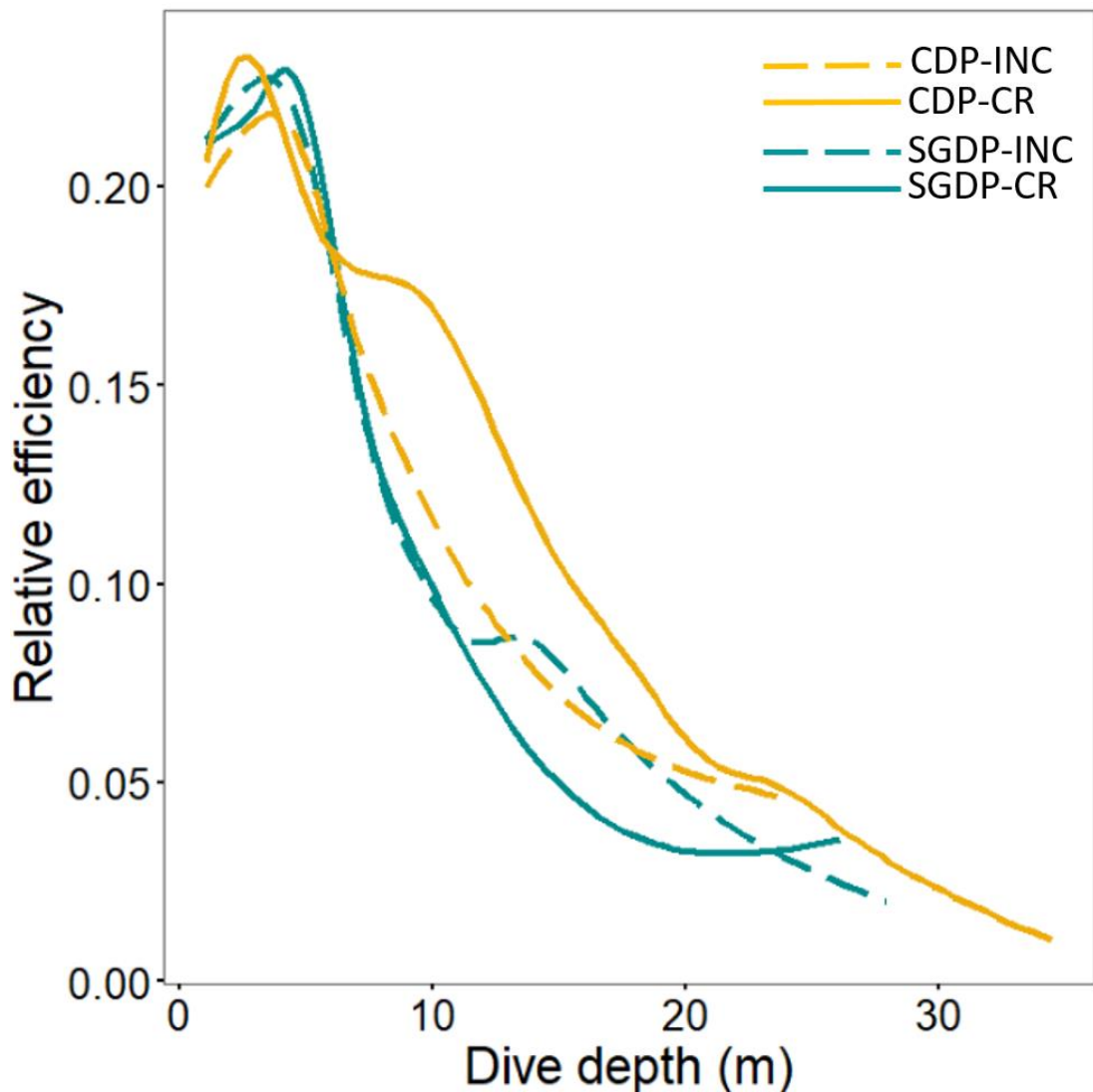


Figure 5-6: Relative diving efficiency (Wilson 2010) of common and South Georgian diving petrels during both incubation and chick-rearing periods predicted by generalized additive mixed models. The efficiency is calculated by dividing the duration of the bottom phase by the total time spent during one dive cycle (dive duration + post-dive duration) for that particular depth. CDP = common diving petrels; SGDP = South Georgian diving petrels; INC =incubation period; CR = chick-rearing period.

During incubation, the overall proportion of time spent flying/resting/diving was not significantly different between the two study species (Table 5-3). Both species were diving during less than 20% of their foraging trips, and were diving almost exclusively during daylight hours. However, CDP spent significantly more time diving compared to SGDP during chick-rearing (Mann-Whitney U test: $U = 20$, $P = 0.003$). The proportion of time spent flying or

resting varied greatly between individuals within each species-stage group. The inter-individual variation in daily and hourly activity was mainly related to the relative proportion of these two states (flying vs resting), while the inter-individual variation of time spent diving was much lower (Table 5-3). Similarly, the within-individual daily proportion of flying/resting activity varied between trips, but the proportion of time spent diving was stable (Fig. S5-3).

Table 5-4: Trip parameters (mean \pm SD) of the post-breeding migration of common and South-Georgian diving petrels from Kerguelen Islands.

	Common diving petrels		South-Georgian diving petrels		Wilcoxon (U) Test (CDP 2017-18 vs SGDP 2017-18)
	2015-16 (n = 5)	2017-18 (n = 7)	2015-16 (n = 3)	2017-18 (n = 4)	
Last burrow attendance	29-Feb \pm 34 d	26-Feb \pm 8 d	24-Jan \pm 8 d	02-Feb \pm 1 d	$U = 28, P = 0.011$
Departure date	02-Mar \pm 33 d	27-Feb \pm 11 d	28-Jan \pm 8 d	03-Feb \pm 1 d	$U = 28, P = 0.010$
Outward travel duration (days)	11 \pm 5	15 \pm 4	9 \pm 2	6 \pm 1	$U = 28, P = 0.009$
Post-breeding migration duration (days)	-	207 \pm 15	-	242 \pm 5	$U = 8, P = 0.022$
Inward travel duration (days)	-	7 \pm 4	-	24 \pm 3	$U = 8, P = 0.022$
Return date	-	23-Sep \pm 8 d	-	03-Oct \pm 6 d	$U = 2, P = 0.051$
First burrow attendance	-	25-Sep \pm 9 d	-	05-Oct \pm 5 d	$U = 3, P = 0.104$
Maximum range (km)	-	2 514 \pm 273	-	3 953 \pm 507	$U = 8, P = 0.017$
Total distance travelled (km)	-	44 232 \pm 5 869	-	88 220 \pm 9 165	$U = 8, P = 0.006$

During the post-breeding period, CDP and SGDP differed markedly in their at-sea distributions. Directly after the breeding season (1-5 days after the last burrow attendance), both species migrated in divergent directions (2 000-5 000 km apart; Fig. 5-4D). While CDP migrated south-west to an area along the Southern Antarctic Circumpolar Current Front (SACCF), SGDP headed south-east between the Polar Front (PF) and the SACCF. The maximum migration range was significantly larger for SGDP (Mann-Whitney U test: $U = 8, P$

= 0.016; Table 5-4), as well as the total distance travelled (Mann-Whitney U test: $U = 8$, $P = 0.006$) and the total duration of migration (Mann-Whitney U test: $U = 8$, $P = 0.002$). For CDP, outward movements (movements to the migration area; facing dominant south-west winds) took longer than inward travels (return travels; heading north-east). This pattern was opposite for SGDP (south-east outward movements shorter than north-west inward movements; Table 5-4). After returning from migration (late September for CDP; early October for SGDP), both species spent most of the pre-breeding period north-east of the Kerguelen Plateau within 1000 km of their colony locations (Fig. 5-4E). During this period, the at-sea distribution of CDP and SGDP completely overlapped (BA indices for 50% UD_s = 0.94).

5.4.4. Isotopic niche

Both species were characterized by large variations in the stable isotope values of blood and feathers. For CDP, blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied from -23.7 to -16.5 and from -26.0 to -15.3 ‰, and from 7.6 to 12.5 and from 6.4 to 14.1 ‰, respectively (Table S5-3). For SGDP, the intra-species variation was smaller, with blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranging from -23.9 to -20.5 and from -24.4 to -18.9 ‰, and from 7.8 to 9.8 and from 3.9 to 11.6 ‰, respectively (Table S5-3).

During incubation, despite total convex hull areas partially overlapping (Fig. 5-7), stable isotope values in blood were significantly different between species for $\delta^{13}\text{C}$ (t -tests: $t_{50.095} = 6.391$, $P < 0.001$), but not for $\delta^{15}\text{N}$ (t -tests: $t_{54.974} = 1.371$, $P = 0.175$). While inter-individual variation for SGDP was low (Table S5-3; Fig. 5-7), isotopic values of incubating CDP stretched out into two groups: a low value group ($\delta^{13}\text{C} < -21.5$ ‰, and $\delta^{15}\text{N} < 9.5$ ‰), and a high value group ($-21.5 < \delta^{13}\text{C} < -17$ ‰, and $9.5 < \delta^{15}\text{N} < 12.5$ ‰). The first group, comprising the majority of CDP samples, showed similar $\delta^{13}\text{C}$ values between the two species, but lower $\delta^{15}\text{N}$ values than SGDP (Fig. 5-7).

Unlike during incubation, total convex hull areas did not overlap during chick-rearing, both species fully segregating in their isotopic signatures during this breeding stage (Fig. 5-7; for $\delta^{13}\text{C}$, $t_{58.359} = 22.803$, $P < 0.001$; $\delta^{15}\text{N}$, $t_{60.663} = 17.648$, $P < 0.001$). All SGDP individuals exhibited low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values close to those during incubation (Table S5-3; all $\delta^{13}\text{C} < -21.4$ ‰ and $\delta^{15}\text{N} < 9.3$ ‰), while CDP showed almost exclusively higher values with $\delta^{13}\text{C} > -20.0$ ‰ and $\delta^{15}\text{N} > 10$ ‰.

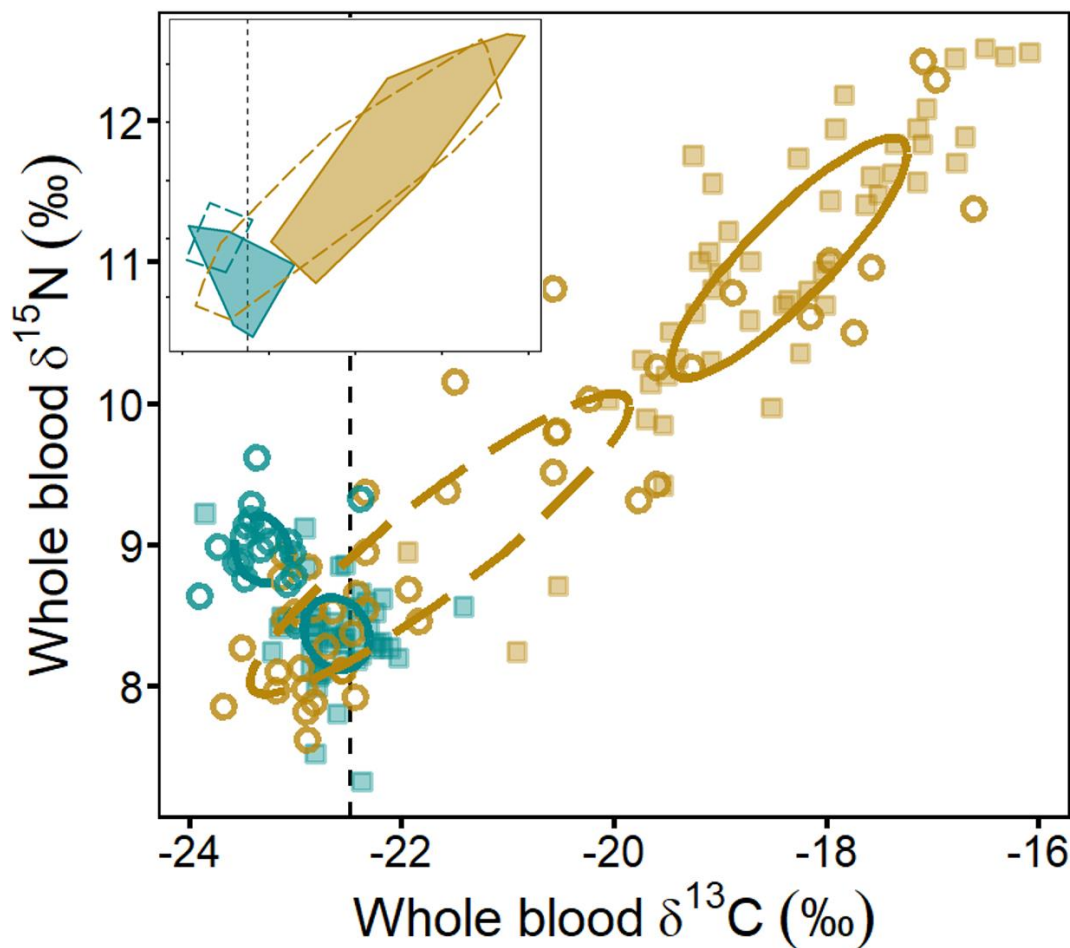


Figure 5-7: Main panel: whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common (yellow) and South-Georgian (blue) diving petrels from Kerguelen Islands. Open circles = incubation; Full squares = chick-rearing. The blue and yellow lines represent the standard ellipses corrected for sample size (SEAc) based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values during the incubation (dashed line) and chick-rearing periods (solid line). The black vertical line corresponds to the value for the Polar Front (PF; $\delta^{13}\text{C} = -22.5$ ‰) (Jaeger et al. 2010).

Top left panel: total convex hull area (total amount of niche space occupied; Layman et al. 2007).

During the non-breeding period (moulting period; Fig. 5-8), although total convex hull areas of the two diving petrels partially overlapped, CDP exhibited significantly lower feather $\delta^{13}\text{C}$ values (t -tests: $t_{234.57} = -9.943$, $P < 0.001$) and higher $\delta^{15}\text{N}$ values than SGDP (t -tests: $t_{166.07} = 10.206$, $P < 0.001$). SGDP had a larger range of $\delta^{15}\text{N}$ values than CDP, including a group of low values (< 5.0 ‰). Conversely, both species exhibited few outliers that were characterized by both high $\delta^{13}\text{C}$ (> -20 ‰) and $\delta^{15}\text{N}$ (> 11 ‰) values (Fig. 5-8).

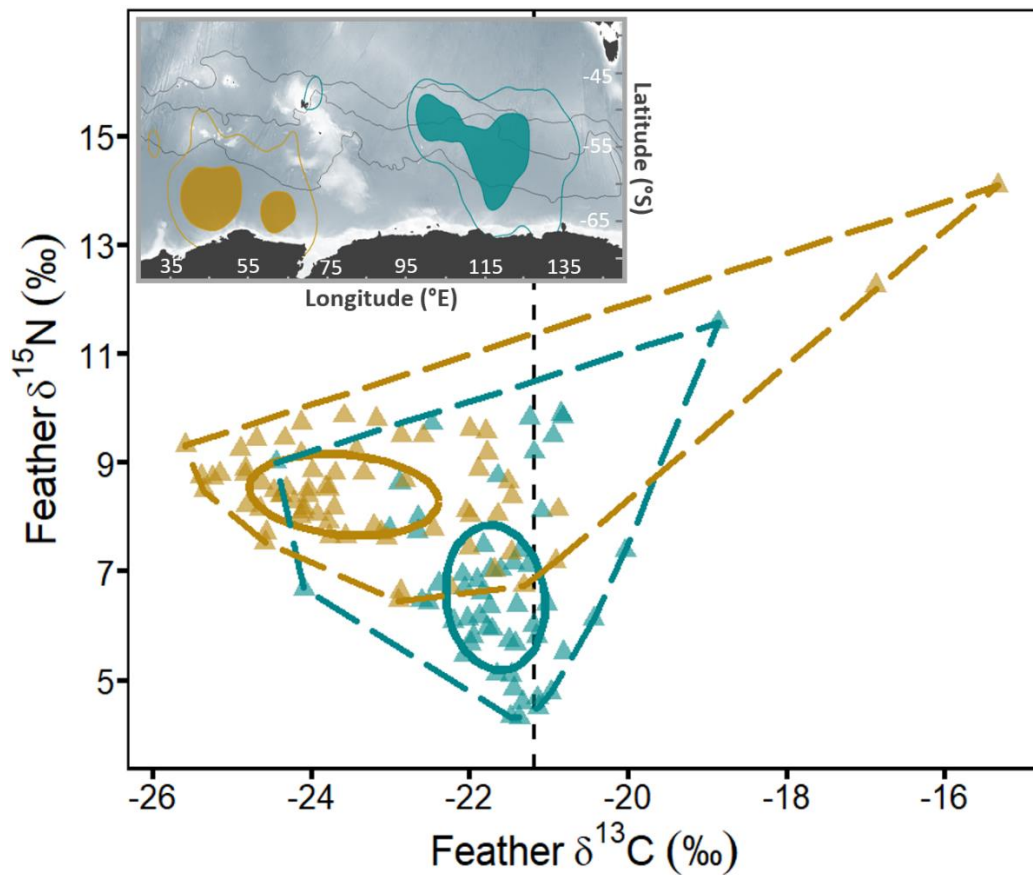


Figure 5-8: Main panel: body feathers $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common (yellow) and South Georgian (blue) diving petrels from Kerguelen. Solid lines represent the standard ellipses corrected for sample size (SEAc) based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and dashed lines correspond to the total convex hull area (total amount of niche space occupied; Layman et al. 2007). The black vertical line corresponds to the value for the Polar Front (PF; $\delta^{13}\text{C} = -21.2$ ‰) (Jaeger et al. 2010). **Top left panel: kernel density estimation (50 and 95 %) of common (yellow) and South Georgian (blue) diving petrels during the post breeding period (see Figure 5-4).**

5.5. Discussion

This study provides unique insights into the niche segregation of two congeneric species throughout their whole annual cycle, by combining at-sea movement, diving, accelerometer, and isotopic datasets. The degree of partitioning was highly stage-dependent, emphasized by the complete niche segregation between CDP and SGDP during the chick-rearing period (Table 5-5). Such seasonal variation supports the hypothesis that resource partitioning between sympatric similar species increases during energetically demanding periods (Barger et al. 2016). The variation between breeding stages was likely related to differences in the processes involved in niche segregation, such as competitive exclusion or niche specialization. Such niche specialization is a key factor allowing the coexistence of very large populations of these two sibling species of diving petrels at Kerguelen. In post-breeding, although species-specific latitudinal differences were expected, the complete separated migration paths and overwintering grounds of CDP and SGDP appear to involve processes other than inter-species niche segregation, such as past evolutionary divergence.

5.5.1. Phenology: influence of oceanographic conditions

The analysis of the phenology of both diving petrel species from Kerguelen Islands showed that SGDP started breeding 2-3 weeks earlier than CDP, which was in accordance with historical data from the Golfe du Morbihan study site (Weimerskirch et al. 1989). However, this marginal allochrony is inconsistent with the general pattern observed elsewhere in the Southern Ocean (e.g. South-Georgia, Crozet and Kerguelen offshore islands), where CDP typically begin breeding slightly earlier than SGDP (Payne and Prince 1979, Jouventin et al. 1985, Weimerskirch et al. 1989). Timing of breeding is a species/population specific life history trait (Lack 1954, Perrins 1970), expected to be synchronized with optimal environmental conditions according to the species ecology. The similar phenology of SGDP

populations throughout the species distribution highlights a preference for foraging in offshore waters, where the timing of maximum productivity is constant at a large spatial scale (Labat et al. 2005). Conversely, the substantial variation in the phenology of CDP at both large and local scales (Weimerskirch et al. 1989; Chapter 3), may be driven by a stronger influence of local inshore conditions (Weimerskirch et al. 1989, Lescroël and Bost 2005).

Interspecific differences in timing of breeding can also be interpreted as a mechanism to reduce competition between ecological similar species (Granroth-Wilding and Phillips 2019). Nevertheless, the relatively long incubation duration of CDP tends to extend the period during which both species share the same foraging area (i.e. during both the incubation and the early chick-rearing periods of SGDP). This, in addition to the important inconsistencies between breeding sites, downplays the importance of such slight allochryony as a competition avoidance induced mechanism.

5.5.2 Incomplete segregation in the early breeding period: competitive exclusion theory

Both CDP and SGDP shared similar pelagic foraging areas during the pre-breeding and incubation periods. For both species, the similarity was emphasized by a clear shift in foraging area from the north-east part of the Kerguelen Plateau in pre-breeding, to the south during the incubation period. Such habitat switching between pre-breeding and incubation is common within seabirds (Cherel et al. 2014; Quillfeldt et al. 2020) and is likely to be related to the limited range that a diving petrel can reach between two incubation shifts (1-3 d; Navarro et al. 2014, Dunphy et al. 2020, Chapter 4). As central place foragers, breeding seabirds must find a trade-off between performing short enough foraging trips and accessing productive areas. While the north-eastern sector of the Kerguelen Plateau is known to be highly productive (Blain et al. 2007), its distant location (500-800 km from the study colonies) may force CDP and

SGDP to exploit a closer foraging area, matching the requirements of undertaking short incubation shifts.

Interestingly, the constraint of exploiting a closer foraging area at the start of the breeding season did not trigger spatial segregation in either the horizontal or the vertical dimension. The exploitation of waters along the south-western shelf-slope of the plateau by both species during incubation was characterized by similar trip parameters (trip duration, distance travelled and dive depths). However, and despite large overlap in their isotopic niche, stable isotope analyses revealed subtle trophic differences. For similar values of $\delta^{13}\text{C}$ (proxy indicating similar water mass), SGDP exhibited slightly higher $\delta^{15}\text{N}$ values than CDP (0.5 to 1 ‰ higher), suggesting that both species may partially differ in their targeted prey. Although both diving petrel species are known to feed on pelagic euphausiid and copepods species (Bocher et al. 2000a,b), the knowledge of their diet during the incubation period is still limited (Bocher et al. 2000b).

During the incubation period, in addition to the difference in blood $\delta^{15}\text{N}$ values, SGDP exhibited higher diving effort (higher mean VeDBA) than CDP, despite similar dive characteristics (dive depth and duration). The exploitative competition theory (Wootton 1994) predicts that the larger species (CDP) forages more efficiently, thus outcompeting and excluding the smaller one (SGDP; Clutton-Brock et al. 1987). The larger species occupies the niche where intake rates are highest while minimizing diving effort, whereas the smaller species is constrained to increase its diving effort to catch any other available high-quality food. In the scenario where both species target and forage on similar prey patches, the higher effort observed in SGDP imply that they must swim harder to access remaining prey. To supplement their intake under competition, SGDP may need to forage on larger prey that are potentially harder to catch, resulting in the observed higher blood $\delta^{15}\text{N}$ values and diving effort when compared to CDP. In addition, when the two species fully segregate during the chick-rearing

period (see next section), SGDP occupy the niche left vacant by CDP. In particular, this is illustrated by the shift of SGDP isotopic niche towards the niche previously occupied by CDP, supporting the exploitative competition hypothesis.

In South Georgia, the co-existence of CDP and SGDP appears to induce similar exploitative competition during the incubation period, with an isotopic niche segregation arising from SGDP constrained to diving deeper than CDP (Navarro et al. 2013, 2014). Similar to Kerguelen, this potential inter-specific competition may result in SGDP pushing the trade-off between prey size and catch towards larger prey (Reid et al. 1997), which would be facilitated by their wider bill compared to CDP (Trallero et al. 2019). However, while body size difference appears to be the main factor driving competitive exclusion, and has been largely documented in various cases in both terrestrial and marine environments (Wignall et al. 2020; Wearmouth and Sims 2008), our understanding of such predator-prey interactions will remain unclear without direct observation of foraging behaviour in the field.

5.5.3. Complete niche segregation in chick-rearing: niche specialization theory

During the chick-rearing period, CDP and SGDP fully differed in their at-sea distribution, diving behavior and isotopic niche. This substantial change in the degree of segregation between the two species was driven by a drastic shift in CDP foraging ecology. While SGDP foraged in similar offshore areas and depths during both the incubation and chick-rearing periods, CDP foraging habitat during chick-rearing was restricted to the coastal area (Golfe du Morbihan), switching from open ocean to a semi-closed embayment. This resulted in a substantial decrease in trip duration and distance travelled than during incubation, and when compared to both the incubation and chick-rearing periods of SGDP. This profound shift in at-sea distribution of CDP during the chick-rearing period coincided with substantial modifications in their diving behaviour (increased depth, duration and mean VeDBA per dive).

Noticeably, by diving 2-3 times deeper in chick-rearing compared to incubation, CDP occupied a very different foraging niche during this period, likely in response to a shift in the prey targeted (Bocher et al. 2000b).

The change in foraging niche occupied by CDP during the incubation and chick-rearing periods is further supported by the substantial shift in isotopic niche. This complete spatial and isotopic niche segregation has been previously illustrated by stomach content analyses, showing that CDP rely mostly on the swarming amphipod *Themisto gaudichaudii* during this period (Bocher et al. 2000a). In the Golfe du Morbihan, this crustacean displays a strong seasonal variation with a peak of abundance in summer (from late January to March; Labat et al. 2005), precisely matching the chick-rearing period of CDP. As income breeders (Chastel et al. 1995), diving petrels are expected to match the energy-demanding chick-rearing period with a peak of resource availability (Lack 1954, Perrins 1970). Thus, it is likely that the observed switch in CDP foraging habitat between incubation and chick-rearing is triggered by the summer high density of *T. gaudichaudii* in the Golfe du Morbihan (Bocher et al. 2001).

In addition, the overall pattern of isotopic values shifting from offshore to inshore environments between incubation and chick-rearing masks the fact that some CDP individuals already started feeding in the Golfe du Morbihan while still incubating. This suggests that CDP switched foraging behaviour as soon as *T. gaudichaudii* became available within the gulf. Such results may provide key information to understand the central role of *T. gaudichaudii* in the breeding cycle of CDP at Kerguelen, as well as in the process of niche segregation between CDP and SGDP. Indeed, surprisingly, SGDP did not appear to take advantage of this reliable and locally superabundant prey during neither the incubation period nor the energetically demanding chick-rearing period.

Spatial and trophic segregations are considered to result from competitive exclusion (the bigger species accessing the best resource), or niche specialization (induced by

morphological and/or physiological differences) (Phillips et al. 2004a). Although, both processes may be applicable in the present case, the total absence of SGDP from the *T. gaudichaudii* niche strongly suggests partitioning arising from physical capabilities and diving performance. Indeed, for a breath-hold diving species, maximum dive depth and duration generally increase with body mass (Schreer and Kovacs 1997; Watanabe et al. 2011), while prey capture is proportional to the time that an individual allocates to the bottom phase of a dive (Wilson 2010). Following the model of depth/time relative efficiency developed by Wilson (2010), CDP appears to be the most efficient of the two species at depths in excess of 10 m.

The relative absence of surface feeders in the Golfe du Morbihan (Bocher et al. 2001; Chérel et al. 2014; present study), in addition to the depths (>10 m) exploited by CDP and coastal penguin species feeding on *T. gaudichaudii* (Bocher et al. 2000a, 2001; present study), confirm that this abundant prey is mainly restricted to depths deeper than 10 m. Therefore, the relatively lower efficiency of SGDP at deeper depths, associated with their smaller body size, may restrict their access to *T. gaudichaudii* in the Golfe du Morbihan. Although SGDP are able to dive as deep as 20 m (Navarro et al. 2014; present study), when compared to CDP for similar dive depth and duration, the higher mean VeDBA observed for SGDP suggests these individuals have a lower diving capacity.

In addition, the lower wing loading of SGDP may also reflect their adaptation to flying over longer distances than CDP (Navarro et al. 2013; Thaxter et al. 2010). Notable differences in diving performances and energetic expenditure of the SGDP appear to be key factors explaining the exploitation of more distant areas to target more accessible macrozooplankton species at shallower depth on the Kerguelen shelf. For SGDP, the energetic cost of repeated deep and long dives may exceed the cost of undertaking longer trips but foraging on more accessible prey in conditions of limited exploitative competition. Therefore, the complete niche

segregation observed between CDP and SGDP during the chick-rearing period may result from niche specialization and not direct competition.

At South Georgia, Reid et al. (1997) reached the same conclusions based on stomach content analyses of both species during the chick-rearing period, interpreting the difference in targeted prey as differential diving capabilities. In the extensive literature exploring niche partitioning between similar species or sex, niche specialization commonly originates from body size differences and divergent relative efficiencies to exploit the environment (Wearmouth and Sims 2008; Barbraud et al. 2019). For example, the between-sex difference in wing loading for albatrosses may advantage females in lower wind conditions (Phillips et al. 2011), which ultimately appears to induce latitudinal habitat specialization (Weimerskirch et al. 1997; Shaffer et al. 2001; Phillips et al. 2004a). Similarly, niche segregation in alcids during the chick-rearing period appears to be caused by differential flying and/or diving capabilities (Thaxter et al. 2010).

5.5.4. Post-breeding migration: historical distribution and congeneric segregation

During the inter-breeding period, CDP and SGDP headed in divergent directions and spent winter 4 000 km apart, in the vicinity of the Southern Antarctic Circumpolar Current Front for CDP, and farther north, near the Polar Front for SGDP. The stable isotopic signatures in body feathers supported the idea of latitudinal segregation, with lower $\delta^{13}\text{C}$ values for CDP indicating a moulting area farther south than for SGDP (Jaeger et al. 2010). Adult diving petrels migrate to wintering areas directly after the end of the breeding season (Rayner et al. 2017, Chapter 3, Fischer et al. 2021), and renew their plumage during the first months of this period (Marchant and Higgins 1990, Chapter 3). Because moult is an energetically/nutritional demanding process, seabirds are likely to renew their plumage where the surrounding waters are productive (Cherel et al. 2016), which may incite ecologically similar species to limit

competition and migrate to different areas. Previous studies on winter distribution of small-sized petrels and prions from Kerguelen showed clear inter-species latitudinal segregation, which was explained by differences in preferred water masses (Quillfeldt et al. 2015, 2017). In the present study, however, migrating in opposite directions does not fully support the hypothesis of environmental condition preferences only. In particular, SGDP migrated to an area overlapping with the migration/moulting area of CDP from Australia (Chapter 3) and Whenua Hou diving petrels (*P. whenuahouensis*) from New Zealand (Fischer et al. 2021).

Interestingly, the recent studies investigating the post-breeding distribution of three different diving petrel species (Navarro et al. 2015; Rayner et al. 2017; Chapter 3; Fischer et al. 2021; present study) all revealed that diving petrels migrate to well defined population/species-specific areas (see Thiebot et al. 2012). This contrasts with the highly dispersive behavior generally observed with other small-sized procellariiform species (Quillfeldt et al. 2015, 2017; Navarro et al. 2015; Pollet et al. 2019; Jones et al. 2020). In particular, the ecological theory of segregation predicts that individuals should disperse when they are no longer tied to their breeding grounds. Therefore, the observed segregation in migration area may not be a response to the selective pressure arising from present competition avoidance between sympatric species, but instead, could reflect past evolutionary divergence (Peck-Richardson et al. 2018). Divergent but consistent species-based and population-based cultural patterns may suggest that each species/population is responding to different life history traits (Thiebot et al. 2012). The evolution of wintering ecological optimum for each species/population may, therefore, involve historical distribution shift of water masses but also the sequence of colonization(s) and speciation within diving petrels in the Southern Ocean.

In addition, by heading south-east, Kerguelen SGDP may as well segregate from large populations of conspecifics breeding farther west on Crozet Islands. Two species can indeed segregate in other dimensions than space when their distribution overlaps (Thiebot et al. 2013),

while two synchronous populations of the same species must segregate spatially in order to avoid competition for the same resource. Thus, perceived inter-breeding segregation between sympatric sibling species could rather result from intra-species (populations) competition avoidance.

5.5.5. Variations in niche segregation: effects of local short-term and large-scale historical factors

The present investigation over the entire annual cycle demonstrated important stage-specific variations in the degree and mechanisms of niche segregation. Such results point to multiple, non-exclusive causal factors of niche segregation. The evolution of species optimum through competition may have lead SGDP to exploit a niche where CDP are absent or rarely present (as seen during the incubation period). Alternatively, and/or both species have evolved separately, and developed different capacities/preferences related to their optimal environment (such as the segregation observed during the chick-rearing and post-breeding period) (Wereszczuk and Zalewski 2015).

Any study *of* niche segregation is only a snapshot of a continuous process and, thus, the evolutionary mechanisms leading to morphological differences and niche specialization remain relatively obscure. However, the unique characteristics of the niche occupied by CDP during the chick-rearing period at Kerguelen may provide valuable clues helping to disentangle the concept of evolutionary niche segregation. In fact, juvenile CDP appear to stay in the Golfe du Morbihan after the breeding season, foraging at similar depths and feeding on same prey as adults during the chick-rearing period (Bocher et al. 2000b). The ability to dive deep enough to access resources during early life may work as a major selective pressure for CDP at Kerguelen, resulting in morphological differences that lead to niche specialization. Although

the origins and effects of niche segregation processes are probably interconnected, this adds a local geographic dimension in the hyper-volume ecological niche.

In South Georgia, for instance, while CDP and SGDP appear to segregate throughout the entire annual cycle (Reid et al. 1997; Anderson et al. 2009; Navarro et al. 2013, 2015), the degree and factors leading to niche partitioning differ from those at Kerguelen (Fig. 5-9). The lower degree of segregation in South Georgia could originate from the super abundance of Antarctic krill (*Euphausia superba*), easing the coexistence of these two species. These differences between breeding sites highlight that generalizations on the causes and characteristics of niche partitioning should be drawn with caution when studying different environments. Investigating the niche segregation between CDP and SGDP throughout their entire distribution would, therefore, be a unique opportunity to further understand the mechanisms involved in the co-existence of sympatric species. In particular, the key question left open is, what is the role of niche segregation in the process of speciation and colonization of such ubiquitous species?

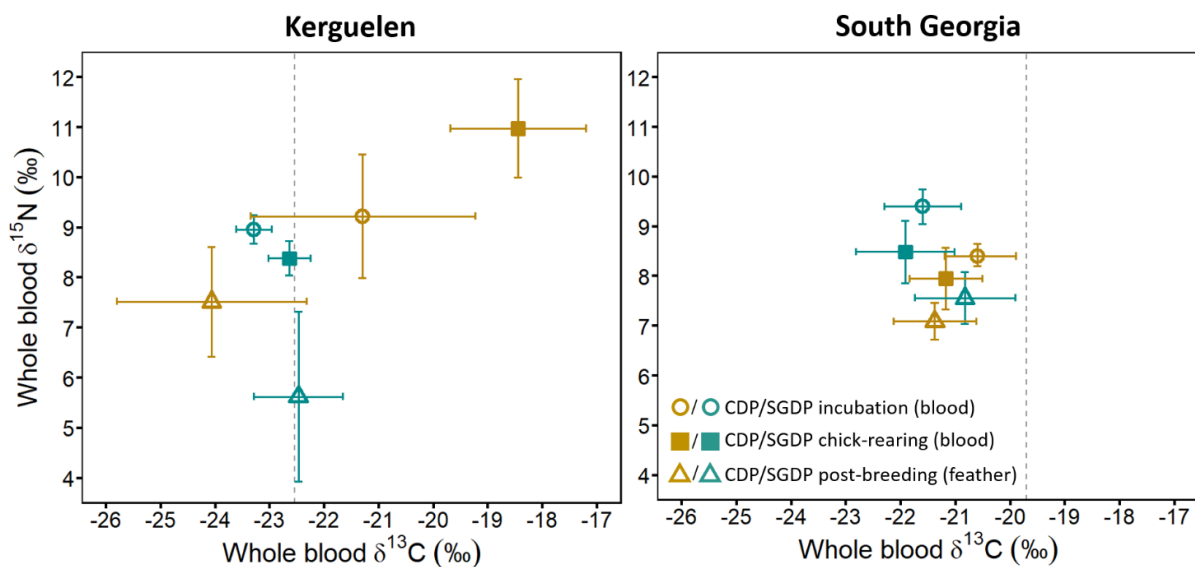


Figure 5-9: Isotopic comparison between Kerguelen and South Georgia islands of whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common (yellow) and South Georgian (blue) diving petrels in incubation (circles), chick-rearing (squares) and post-breeding (triangles). Isotopic values of feathers were corrected to allow an accurate comparison with blood values using mean corrections factors from

Cherel et al. (2014). Isotopic values for South Georgia were adapted from Anderson et al. (2009) (chick-rearing and post-breeding) and Navarro et al. (2013) (incubation). The dotted vertical lines correspond to the value for the Polar Front (for Kerguelen: $\delta^{13}\text{C} = -22.5\text{‰}$, Jaeger et al. 2010; for South Georgia: $\delta^{13}\text{C} = -19.7\text{‰}$, Phillips et al. 2009).

5.5.6. Conclusion

Overall, the present study demonstrates the importance of integrating approaches from different fields (foraging and trophic ecology, ecophysiology, phenology and morphometry) to describe the co-existence of ecologically similar species. The degree of partitioning and the mechanisms involved were highly stage-dependent, allowing a better understanding in the coexistence of very large populations of two sibling species of diving petrels. The investigation over the entire annual cycle indicates that CDP and SGDP segregate in at least three dimensions (horizontal, vertical and trophic). During the breeding season, the differences in body size and diving/flying capacity seem to be key factors explaining the niche segregation of such similar species. Highly productive environments in polar and sub-polar regions support a great variety of zooplankton species, allowing the coexistence of large seabird populations. However, the strong link between the cycle of zooplanktonic species and their consumers, as shown here at Kerguelen and previously at South Georgia, highlights the dependence of coexisting sibling species to the stability and productivity of their environment. In the context of climate change, the fragile equilibrium between species living in sympatry is likely to be modified, and, with the evolution of their ecosystems, their niche is going to change accordingly. Investigating the ecology and niche segregation of ubiquitous species experiencing rapid environmental modifications throughout their whole distribution is, therefore, fundamental to fully understand the short and long-term effects of climate change.

5.6. Supplementary materials

Table S5-1: Summary of deployed tracking loggers and collected isotopic samples (whole blood and body feathers) from adult common and South Georgian diving petrels from Kerguelen Islands. Abbreviation: SIA = stable isotope analysis.

Species	Status	Year	GPS/GLS		Dive		Accelerometry		SIA
			<i>Deployed (retrieved)</i>	<i>Complete trips</i>	<i>Deployed (retrieved)</i>	<i>Complete trips</i>	<i>Deployed (retrieved)</i>	<i>Complete trips</i>	
Common diving petrels	Incubation	2015-2016	6 (4)	0					10
		2016-2017							12
		2017-2018							
		2018-2019	8 (6)	4	5 (5)	5	5 (5)	5	17
		2019-2020	2 (2)	2	5 (2)	2	5 (2)	2	7
		Total	16 (12)	6	10 (7)	7	10 (7)	7	46
	Chick-rearing	2015-2016	10 (10)	6					10
		2016-2017							
		2017-2018	15 (15)	13	1 (1)	2			15
		2018-2019	8 (6)	9	7 (7)	13	7 (7)	13	13
		2019-2020	8 (8)	11	4 (4)	6	4 (4)	6	12
		Total	41 (39)	39	12 (12)	21	11 (11)	19	50
	Inter-breeding	2015-2016	9 (6)	0					20
		2016-2017							12
		2017-2018	12 (8)	7					15
		2018-2019							20
		2019-2020							
		Total	21 (14)	7					67
South Georgian diving petrels	Incubation	2015-2016							7
		2016-2017							
		2017-2018							
		2018-2019	10 (6)	5	2 (0)	0	2 (0)	0	9
		2019-2020	2 (1)	1	4 (4)	4	4 (4)	4	6
		Total	12 (7)	6	6 (4)	4	6 (4)	4	22
	Chick-rearing	2015-2016	9 (9)	9					7
		2016-2017							
		2017-2018	19 (19)	21	6 (5)	5			23
		2018-2019	9 (8)	10	7 (6)	8	7 (6)	8	15
		2019-2020	6 (6)	6					6
		Total	43 (42)	46	13 (11)	13	7 (6)	8	51
	Inter-breeding	2015-2016	10 (3)	0					20
		2016-2017							12
		2017-2018	8 (4)	4					15
		2018-2019							20
		2019-2020							
		Total	18 (7)	4					67

Table S5-2: Inter-sex comparison of morphological measurements, trip parameters and whole blood and body feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of common (CDP) and South Georgian (SGDP) diving petrels from Kerguelen Islands. Values are means \pm SD, and statistically significant results are highlighted in bold.

	CDP Female	CDP Male	Test CDP (Female vs Male)	SGDP Female	SGDP Male	Test SGDP (Female vs Male)	
Measurements	Body mass (g)	145 \pm 8 (n = 16)	146 \pm 14 (n = 23)	<i>t</i> -test: $t_{36.434} = -0.367$, <i>P</i> = 0.716	131 \pm 10 (n = 22)	128 \pm 11 (n = 23)	<i>t</i> -test: $t_{42.939} = 0.860$, <i>P</i> = 0.394
	Wing length (mm)	127 \pm 3 (n = 13)	125 \pm 5 (n = 18)	<i>t</i> -test: $t_{28.757} = 1.557$, <i>P</i> = 0.130	120 \pm 3 (n = 20)	118 \pm 3 (n = 17)	<i>t</i> -test: $t_{34.979} = 2.304$, <i>P</i> = 0.027
	Tarsus length (mm)	26.3 \pm 1.7 (n = 13)	26.7 \pm 1.3 (n = 18)	<i>t</i> -test: $t_{22.537} = -0.618$, <i>P</i> = 0.542	24.7 \pm 0.9 (n = 20)	24.8 \pm 0.9 (n = 18)	<i>t</i> -test: $t_{35.947} = -0.143$, <i>P</i> = 0.887
	Bill length (mm)	16.2 \pm 0.4 (n = 13)	16.2 \pm 0.6 (n = 18)	<i>t</i> -test: $t_{28.890} = -0.408$, <i>P</i> = 0.687	15.4 \pm 0.6 (n = 20)	15.7 \pm 0.7 (n = 18)	<i>t</i> -test: $t_{34.071} = -1.595$, <i>P</i> = 0.120
Incubation period	Trip duration (h)	37 \pm 13 (n = 3)	45 \pm 2 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 2, <i>P</i> = 0.800	60 \pm 11 (n = 3)	32 \pm 21 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 8, <i>P</i> = 0.200
	Total distance travelled (km)	506 \pm 400 (n = 3)	506 \pm 532 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 2, <i>P</i> = 0.800	768 \pm 101 (n = 3)	452 \pm 102 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 9, <i>P</i> = 0.100
	Maximum distance from colony (km)	217 \pm 182 (n = 3)	237 \pm 198 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 4, <i>P</i> = 1.000	379 \pm 136 (n = 3)	265 \pm 32 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 8, <i>P</i> = 0.200
	Dive depth (m)	6.7 \pm 0.5 (n = 5)	6.2 \pm 0.3 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 12, <i>P</i> = 0.250	7.3 \pm 0.4 (n = 2)	6.0 \pm 0.4 (n = 2)	na
	Dive duration (s)	29 \pm 4 (n = 5)	27 \pm 1 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 9, <i>P</i> = 0.786	27 \pm 1 (n = 2)	22 \pm 4 (n = 2)	na
	Blood $\delta^{13}\text{C}$ (‰)	-22.0 \pm 1.6 (n = 18)	-20.9 \pm 2.2 (n = 26)	<i>t</i> -test: $t_{41.847} = -1.874$, <i>P</i> = 0.068	-23.5 \pm 0.2 (n = 10)	-23.2 \pm 0.4 (n = 12)	<i>t</i> -test: $t_{14.519} = -1.625$, <i>P</i> = 0.126
	Blood $\delta^{15}\text{N}$ (‰)	8.6 \pm 1.6 (n = 18)	9.6 \pm 1.3 (n = 26)	<i>t</i> -test: $t_{41.378} = -3.155$, <i>P</i> = 0.003	9.0 \pm 0.2 (n = 10)	9.0 \pm 0.3 (n = 12)	<i>t</i> -test: $t_{14.929} = 0.277$, <i>P</i> = 0.786
Chick-rearing period	Trip duration (h)	19 \pm 1 (n = 13)	18 \pm 2 (n = 25)	Mann-Whitney <i>U</i> test: <i>U</i> = 195, <i>P</i> = 0.332	31 \pm 12 (n = 17)	24 \pm 7 (n = 12)	Mann-Whitney <i>U</i> test: <i>U</i> = 132, <i>P</i> = 0.199
	Total distance travelled (km)	84 \pm 30 (n = 7)	85 \pm 23 (n = 14)	Mann-Whitney <i>U</i> test: <i>U</i> = 47, <i>P</i> = 0.913	579 \pm 114 (n = 11)	485 \pm 99 (n = 10)	Mann-Whitney <i>U</i> test: <i>U</i> = 85, <i>P</i> = 0.036
	Maximum distance from colony (km)	18 \pm 5 (n = 11)	19 \pm 6 (n = 19)	Mann-Whitney <i>U</i> test: <i>U</i> = 89, <i>P</i> = 0.524	210 \pm 72 (n = 16)	216 \pm 69 (n = 19)	Mann-Whitney <i>U</i> test: <i>U</i> = 162, <i>P</i> = 0.756

	Dive depth (m)	15.3 ± 2.8 (n = 6)	15.5 ± 3.4 (n = 14)	Mann-Whitney <i>U</i> test: <i>U</i> = 40, <i>P</i> = 0.904	5.3 ± 1.0 (n = 6)	7.2 ± 3.6 (n = 5)	Mann-Whitney <i>U</i> test: <i>U</i> = 10, <i>P</i> = 0.429
	Dive duration (s)	44 ± 4 (n = 6)	44 ± 6 (n = 14)	Mann-Whitney <i>U</i> test: <i>U</i> = 38, <i>P</i> = 0.779	22 ± 2 (n = 6)	24 ± 8 (n = 5)	Mann-Whitney <i>U</i> test: <i>U</i> = 15, <i>P</i> = 1.000
	Blood δ¹³C (‰)	-18.8 ± 1.3 (n = 20)	-18.1 ± 1.1 (n = 25)	<i>t</i> -test: <i>t</i> _{37.315} = -1.912, <i>P</i> = 0.064	-22.6 ± 0.4 (n = 23)	-22.7 ± 0.4 (n = 24)	<i>t</i> -test: <i>t</i> _{44.998} = 0.751, <i>P</i> = 0.457
	Blood δ¹⁵N (‰)	10.9 ± 1.0 (n = 20)	11.3 ± 0.7 (n = 25)	<i>t</i> -test: <i>t</i> _{34.128} = -1.544, <i>P</i> = 0.131	8.4 ± 0.3 (n = 23)	8.4 ± 0.3 (n = 24)	<i>t</i> -test: <i>t</i> _{44.960} = -0.021, <i>P</i> = 0.983
Inter-breeding period	Post-breeding migration duration (days)	206 ± 19 (n = 4)	210 ± 10 (n = 3)	Mann-Whitney <i>U</i> test: <i>U</i> = 7, <i>P</i> = 0.857	239 (n = 1)	244 ± 6 (n = 3)	na
	Migration maximum range (km)	2 528 ± 256 (n = 6)	2 341 ± 236 (n = 6)	Mann-Whitney <i>U</i> test: <i>U</i> = 27, <i>P</i> = 0.180	3 517 (n = 1)	4 165 ± 326 (n = 4)	na
	Migration total distance travelled (km)	42 941 ± 6 248 (n = 4)	45 954 ± 6 081 (n = 6)	Mann-Whitney <i>U</i> test: <i>U</i> = 4, <i>P</i> = 0.629	81 462 (n = 1)	91 598 ± 9 975 (n = 3)	na
	Feathers δ¹³C (‰)	-23.4 ± 1.9 (n = 28)	-23.2 ± 1.7 (n = 31)	<i>t</i> -test: <i>t</i> _{53.720} = -0.387, <i>P</i> = 0.700	-21.6 ± 1.0 (n = 20)	-21.9 ± 0.6 (n = 25)	<i>t</i> -test: <i>t</i> _{29.477} = 1.138, <i>P</i> = 0.264
	Feathers δ¹⁵N (‰)	8.5 ± 1.4 (n = 28)	8.5 ± 1.0 (n = 31)	<i>t</i> -test: <i>t</i> _{48.846} = -0.113, <i>P</i> = 0.911	6.9 ± 1.8 (n = 20)	6.6 ± 1.6 (n = 25)	<i>t</i> -test: <i>t</i> _{37.882} = 0.562, <i>P</i> = 0.578

Table S5-3: Whole blood and body feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm SD) of common and South-Georgian diving petrels from Kerguelen Islands. Significantly different values (Mann-Whitney U test: $P < 0.05$) are indicated by different superscript letters/symbols, for each year (row; difference between species-stage group; a, b, c or d), and for each species-stage group (columns; inter-annual variation; *, # or &). In order to allow statistical comparisons between blood and feathers, isotopic values of feathers were corrected using mean corrections factors from Cherel et al. (2014) (underlined values = corrected values).

	Common diving petrels			South Georgian diving petrels			
	Inter-breeding (feathers)	Incubation (blood)	Chick-rearing (blood)	Inter-breeding (feathers)	Incubation (blood)	Chick-rearing (blood)	
$\delta^{13}\text{C}$ (‰)	2015-2016	-23.1 \pm 1.3* (n = 20)	-22.2 \pm 1.0 ^{a*} (n = 10)	-19.0 \pm 1.2 ^{b*} (n = 10)	-21.3 \pm 1.3* (n = 12)	-23.2 \pm 0.4 ^{a*} (n = 7)	-23.0 \pm 0.5 ^{a*} (n = 7)
	2016-2017	-23.5 \pm 2.1* (n = 12)	-20.6 \pm 2.4 ^{*#} (n = 12)	-	-	-	-
	2017-2018	-23.2 \pm 1.4* (n = 15)	-	-18.8 \pm 1.0 ^{a*} (n = 15)	-21.8 \pm 0.6* (n = 23)	-	-22.4 \pm 0.3 ^{a#} (n = 23)
	2018-2019	-23.3 \pm 2.2* (n = 20)	-22.1 \pm 1.7 ^{a*} (n = 17)	-17.8 \pm 1.0 ^{c*} (n = 13)	-21.8 \pm 0.8* (n = 20)	-23.4 \pm 0.3 ^{b*} (n = 9)	-22.9 \pm 0.1 ^{bd*} (n = 15)
	2019-2020	-	-19.2 \pm 1.8 ^{a#} (n = 7)	-18.2 \pm 1.5 ^{a*} (n = 12)	-	-23.1 \pm 0.2 ^{b*} (n = 6)	-22.7 \pm 0.2 ^{b*#} (n = 6)
	Means	-23.3 \pm 1.7 <u>-24.1 \pm 1.7^a</u>	-21.3 \pm 2.1^b	-18.4 \pm 1.2^c	-21.7 \pm 0.8 <u>-22.5 \pm 0.8^d</u>	-23.3 \pm 0.3^e	-22.7 \pm 0.4^d
$\delta^{15}\text{N}$ (‰)	2015-2016	8.8 \pm 0.9* (n = 20)	9.3 \pm 0.8 ^{a*#} (n = 10)	11.2 \pm 0.9 ^{b*} (n = 10)	7.9 \pm 2.0* (n = 12)	9.2 \pm 0.2 ^{a*} (n = 7)	8.8 \pm 0.4 ^{a*} (n = 7)
	2016-2017	8.9 \pm 1.2* (n = 12)	9.4 \pm 1.5 ^{*#} (n = 12)	-	-	-	-
	2017-2018	8.3 \pm 0.7* (n = 15)	-	10.8 \pm 0.7 ^{a*} (n = 15)	6.8 \pm 1.5 [#] (n = 23)	-	8.4 \pm 0.2 ^{b#} (n = 23)
	2018-2019	8.3 \pm 1.5* (n = 20)	8.7 \pm 1.2 ^{ab*} (n = 17)	11.4 \pm 0.8 ^{c*} (n = 13)	6.2 \pm 1.3 [#] (n = 20)	8.9 \pm 0.2 ^{b#} (n = 9)	8.4 \pm 0.2 ^{a#&} (n = 15)
	2019-2020	-	10.1 \pm 0.9 ^{a#} (n = 7)	10.6 \pm 1.4 ^{a*} (n = 12)	-	8.7 \pm 0.2 ^{b#} (n = 6)	7.9 \pm 0.4 ^{c&} (n = 6)
	Means	8.4 \pm 1.1 <u>7.5 \pm 1.1^a</u>	9.2 \pm 1.2^b	11.0 \pm 1.0^c	6.5 \pm 1.7 <u>5.6 \pm 1.7^d</u>	9.0 \pm 0.3^b	8.4 \pm 0.4^e

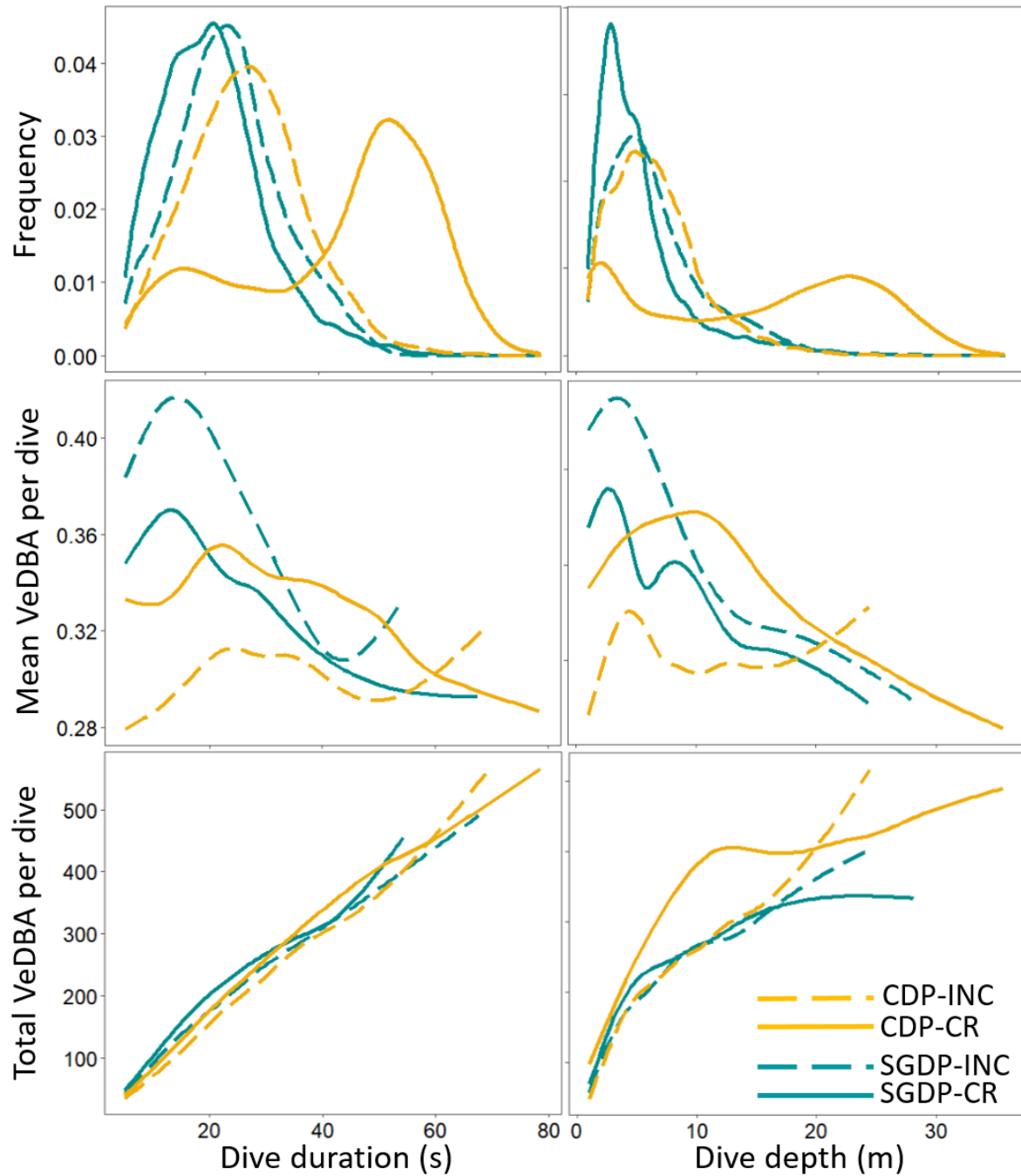


Figure S5-1: Effect of dive duration and dive depth on mean and total VeDBA per dive predicted by generalized additive mixed models. CDP-INC = common diving petrels during the incubation period; CDP-CR = common diving petrels during the chick-rearing period; SGDP-INC = South Georgian diving petrels during the incubation period; SGDP-CR = South-Georgian diving petrels during the chick-rearing period.

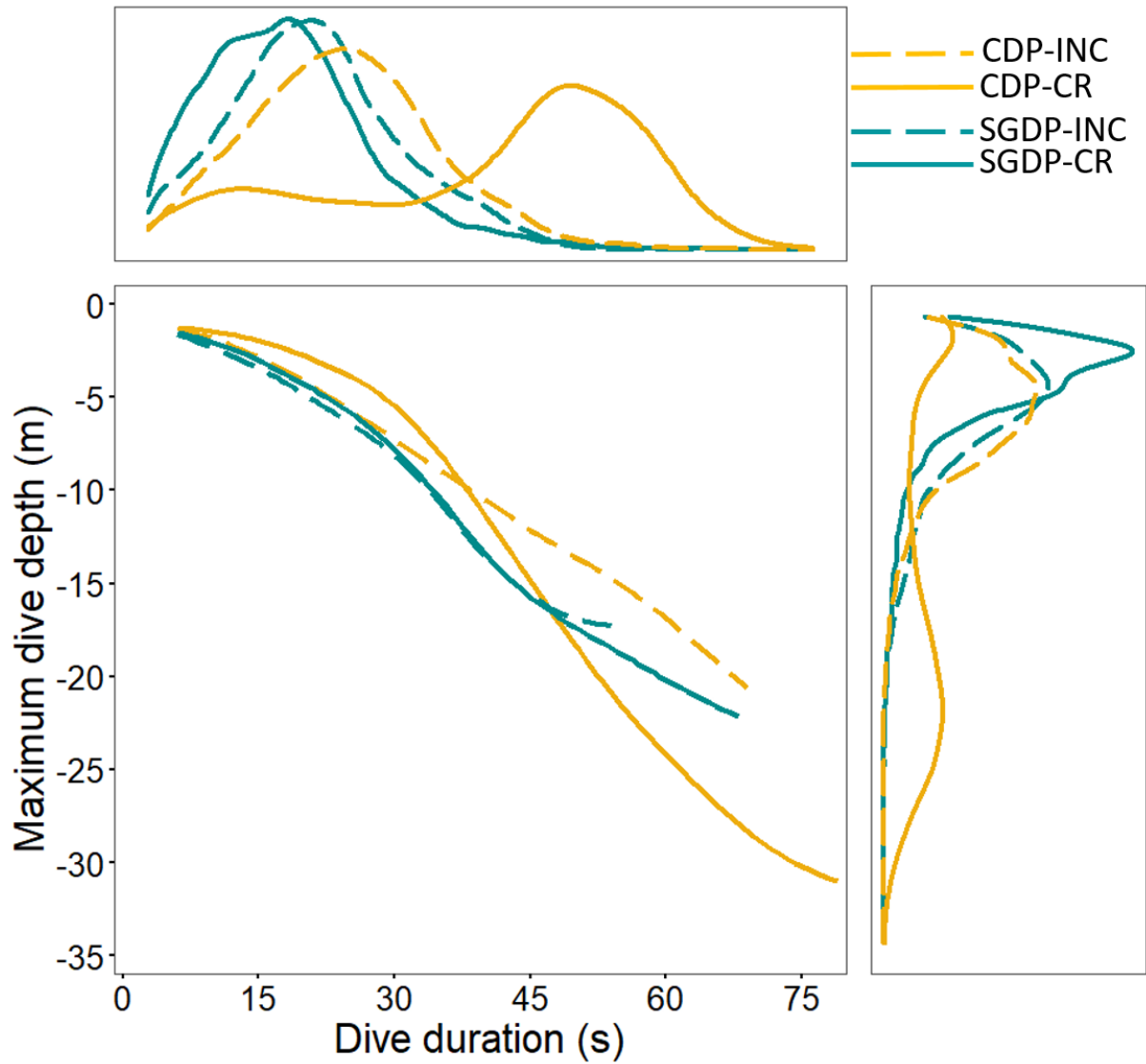


Figure S5-2: Correlation between dive depth and dive duration predicted by generalized additive mixed models. Upper and right panels provide the data distribution of dive duration and dive depth, respectively. CDP-INC = common diving petrels during the incubation period; CDP-CR = common diving petrels during the chick-rearing period; SGDP-INC = South-Georgian diving petrels during the incubation period; SGDP-CR = South Georgian diving petrels during the chick-rearing period.

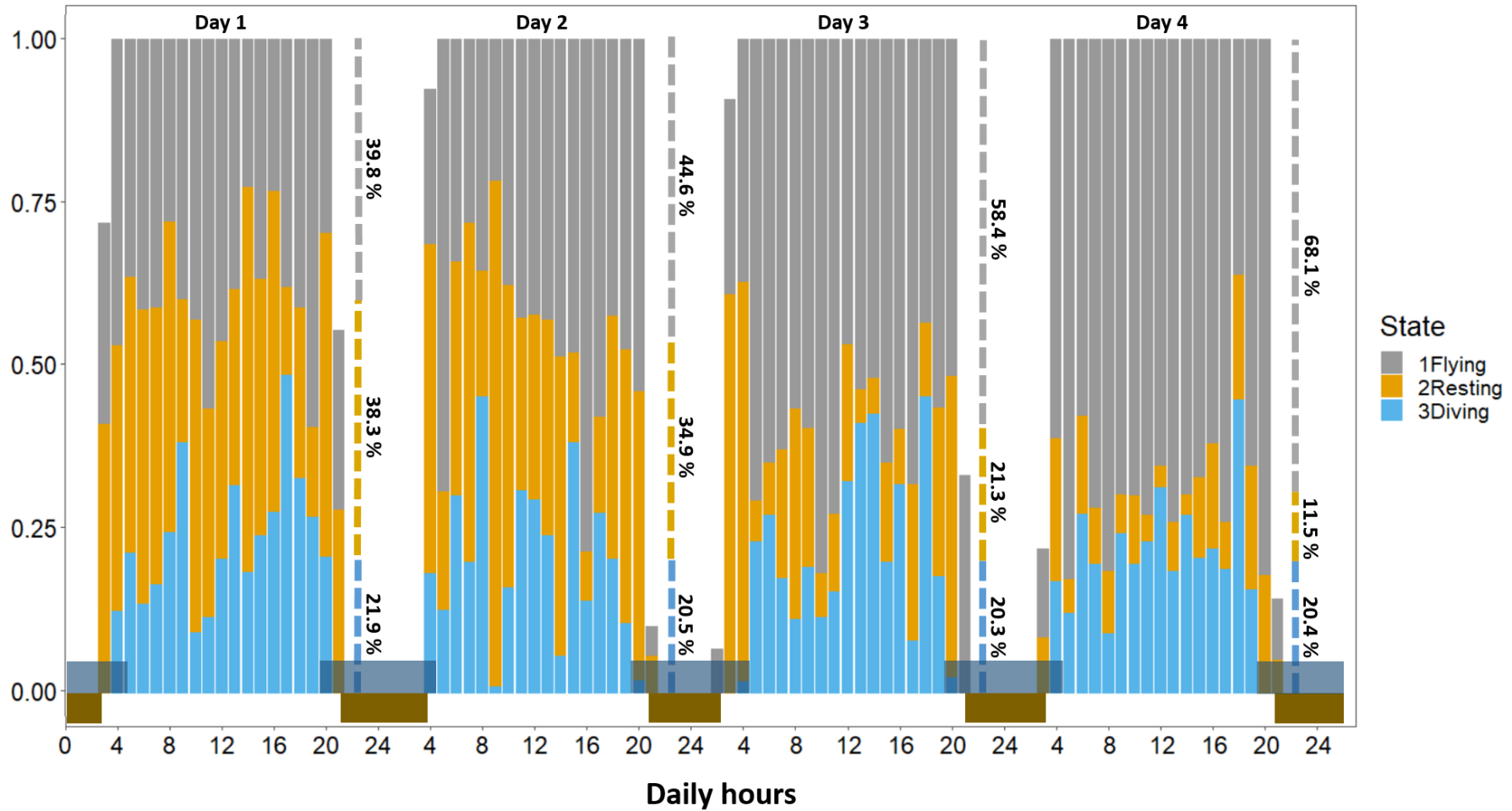


Figure S5-3: Example of intra-individual variation of daily activity budget. These data were obtained from one adult common diving petrel equipped with an accelerometer during the chick-rearing period. The vertical dashed lines indicate the proportion of the overall activity budget for each day. Shaded dark blue indicates the night period (bottom part of the chart), and brown corresponds to the period when the bird was inside the burrow (derived from temperature data).

Chapter 6

General discussion



Photo: Diving petrels (*Pelecanoides* sp.) in the Golfe du Morbihan, Kerguelen Archipelago (© A. Fromant)

6.1. Introduction

The Procellariiformes are one of the most endangered avian groups (Croxall et al. 2012) owing to the numerous natural and anthropogenic threats throughout their distribution (Sydeman et al. 2012). Identifying and assessing the impacts of such environmental modifications requires precise knowledge of species' ecological niches during the whole annual cycle and throughout their distribution (Chambers et al. 2011). Information on the at-sea ecology of species, during both the breeding and the non-breeding seasons, is essential for conservation assessments and environmental monitoring purposes (Rodriguez et al. 2019). While animal-borne data loggers have been developed, improved and miniaturized over the last four decades, knowledge of the ecology of smaller species has remained limited until very recently and, consequently, so has our ability to assess the threats that these species are facing (Rodriguez et al. 2019).

Benefiting from the recent technological advances and further data logger miniaturizations, the overall objectives of the present study were to investigate the ecological niches of the two most abundant diving petrel species, the common (CDP) and the South-Georgian (SGDP) diving petrels, and explore the potential variations between years, seasons, populations and sex. In addition, as large populations of CDP and SGDP breed in sympatry at Kerguelen Islands, a second objective was to study the degree of niche partitioning and the mechanisms involved in the co-existence of these two morphologically and ecologically similar species. In the first instance, the study evaluated the efficacy of artificial burrows as a tool to facilitate ongoing research projects on diving petrels (Chapter 2). The conversion of natural burrows during the chick-rearing period appeared to be an effective method and may benefit the collection of essential data for conservation biology of such cryptic species. The results of the three subsequent chapters have demonstrated that diving petrels exhibit remarkable flying abilities despite their high wing loading, foraging over large areas during the breeding season

(Chapters 4 and 5) and migrating several thousands of kilometres from their colony during the post-breeding period (Chapters 3 and 5).

Studying the species' ecology during the entire annual cycle highlighted substantial seasonal variations in their ecological niche, mainly induced by differences in at-sea distribution, diving behaviour and isotopic niche (Chapters 3, 4, and 5). The multi-population analyses revealed important ecological differences throughout the wide distribution of CDP (Chapters 3, 4 and 5), particularly in terms of phenology and migration area (Chapter 3). Although variations in ecological niche in these small species were expected between different environments, the major differences observed during the post-breeding period throughout the distribution of CDP support the relevance of multi-population studies. Collecting data over several years (Chapters 3, 4 and 5) substantially strengthens these results, and also provides valuable information for understanding the variations and limits in the ecological niches of diving petrels. Finally, the stage-dependent and context-dependent niche segregation between CDP and SGDP demonstrate the importance of integrative approaches to better describe and understand the co-existence of ecologically similar species.

The present discussion expands on the major findings of these combined studies. The gathered information about the ecology of diving petrels is discussed with reference to the broader context of seabird ecology, the impacts of climate change, and the potential role of diving petrels as environmental indicators.

6.2. At-sea distribution and trip parameters during the breeding season

For central-place foragers, such as seabirds, duration and distance of foraging trips are energetically constrained by the need to return to the nest for incubation shifts or to feed their offspring. Consequently, breeding seabirds have to maximize their foraging efficiency by identifying optimum foraging areas within limited distance from the colony (Stephens and

Krebs 1986, Hunt 1990), in particular for species with limited moving abilities (penguins) or high wing loading (e.g. alcids and diving petrels) (Roby and Ricklefs 1986).

6.2.1. Foraging range of diving petrels: to infinity and beyond

In the present study, at-sea movement data of breeding individuals were collected for CDP (at Kerguelen Islands and in south-eastern Australia) and SGDP (Kerguelen Islands) during both the incubation and chick-rearing periods. Overall, this study has shown unexpected trip characteristics, both CDP and SGDP exhibiting remarkable distances travelled per trip. Among the Procellariiformes, diving petrels differ drastically from other species due to their high wing loading (Warham 1977). During the breeding season, because of the high energetic flight costs (Roby and Ricklefs 1986) and the pressure to minimize commutes, diving petrel species have usually been considered as coastal (Warham 1977, Ryan and Nel 1999) or foraging in a restricted range from the colony (Jouventin et al. 1988). Similarly, the short trip duration (Jouventin et al. 1988, Chastel et al. 1995, Reid et al. 1997) combined with the important energetic cost of flapping flight (Roby and Ricklefs 1986, Green and Brothers 1989) suggested a short foraging range. Recently, the results of GPS tracking of breeding CDP (Zhang et al. 2019, Dunphy et al. 2020) and Peruvian diving petrels (Zavalaga and Alfaro-Shigueto 2018) appear to support the notion of restricted foraging ranges in breeding diving petrels. Both species displayed maximum distances from the colony <50 km and total distances travelled in daily trips <100 km.

However, in the present study, breeding CDP and SGDP had maximum foraging ranges four to six times larger than previously recorded (Chapters 4 and 5; Bost et al. 2022). Both at Kerguelen Islands and in south-eastern Australia, the maximum distance travelled per trip for CDP approached 300 km for 1-day trips and 900 km for 2-day trips. The smaller SGDP regularly exceed 400 km for 1-day trips (maximum of 630 km) and 800 km for 2-day trips.

Such results highlight that information about the maximum foraging range are crucial in delineating species' ecological niche, and carry important conservation implications. Indeed, recent tracking studies demonstrated that prior estimations of distribution range of small procellariiform species during the breeding season were generally underestimated by a factor of three to five (Pollet et al. 2014).

6.2.2. Spatial and temporal variations in foraging range

Although such magnitude in the maximum range of diving petrels was not expected, important variations were observed between stages (Chapters 4 and 5), years (Chapter 4) and breeding sites (Chapters 4 and 5, Zhang et al. 2019, Dunphy et al. 2020). For example, CDP from Kerguelen Islands exhibited substantial differences in their at-sea distribution between incubation and chick-rearing, switching from long offshore trips during incubation (> 200 km from the colony) to short coastal trips in chick-rearing (< 20 km from the colony) (Chapter 5). Similarly, CDP from south-eastern Australia displayed important variations in at-sea distribution and foraging range between breeding stages (though in a lower magnitude), but above all, showed important inter-annual variations related to modifications in environmental conditions (Chapter 4). Finally, CDP also exhibited spatial differences at a large scale throughout the species distribution (both during incubation and chick-rearing periods; Chapters 4 and 5, Navarro et al. 2013, Zhang et al. 2019, Dunphy et al. 2020), and at a local scale (Dunphy et al. 2020). In addition to these differences in at-sea distribution and foraging range, CDP also appear to exhibit important variations in their diving behaviour according to the breeding stage in terms of diving depth and diving effort (discussed in section 6.2.2.).

These results provide evidence that such dissimilarities are tightly linked to the local environment, with major differences in oceanographic conditions likely reflecting variations in prey type and abundance (Reid et al. 1997, Ridoux 1994, Bocher et al. 2000a, Fromant et al.

2020a). While CDP feed predominantly on macro-zooplankton species in all breeding locations, the differences in dominant prey species and their specific ecology seem to dictate the specificities of CDP foraging behaviour for each population, and/or each breeding stage. This is particularly well illustrated at Kerguelen Islands, where the drastic shift in foraging area is likely triggered by the sharp seasonal cycle of the hyperiid *Themisto gaudichaudii* in the Golfe du Morbihan (Chapter 5, Labat et al. 2005). Such temporal and spatial variations in foraging behaviour demonstrate an unexpected level of ecological and behavioural plasticity (Jouventin and Mougin 1981, Bost and Jouventin 1990). Comparable patterns have been observed in the ecologically and morphologically similar alcid species of the Northern Hemisphere. In particular, the small planktivorous little auks (*Alle alle*) exhibit clear behavioural plasticity (in their distribution, diving, and trophic ecology) between breeding sites (Grémillet et al. 2012), years (Amélineau et al. 2016) and seasons (Jakubas et al. 2016). Specifically, when the environmental conditions are unfavourable, this high wing loading species (similar flight patterns than CDP; Roby and Ricklefs 1986) has successfully been able to adapt its foraging range to access productive feeding grounds (Jakubas et al. 2020). However, the response to environmental variations appeared to be non-linear, with birds switching from always more distant foraging locations to closer but potentially less predictable areas (Grémillet et al. 2015).

6.2.3. Towards the limits of maximum trip duration

In the present study, determining the full flying capacities of diving petrels revealed an unexpected ability to exploit distant oceanic features (Chapters 4 and 5), and described the extent of their foraging range. However, the flying capacities of diving petrels may not be the only key criteria explaining their at-sea distribution during the breeding season. In addition to the high flight loading, diving petrels appeared to be strongly constrained in their trip duration

by the maximum duration of incubation shifts, and the high frequency of chick feeding. Indeed, unlike the rest of the Procellariiformes, diving petrels do not produce stomach oil, a high energetic mixture of neutral dietary lipids enhancing longer intervals between feeding events (Roby et al. 1997). The absence of stomach oil limits the fasting ability of diving petrels (both adults and chicks) to just a few days.

In the present study, this was illustrated by the absence of foraging trips exceeding three days for either CDP (86% of 1-day trips, 11% of 2-day trips, and 3% of 3-day trips) or SGDP (85% of 1-day trips, 11% of 2-day trips, and 4% of 3-day trips). During the incubation period for CDP from Kanowna Island, all the incubation shifts were of one or two days (1.2 ± 0.6 d on average; estimated from birds tracked for two or more consecutive trips). Any 3-day trip at-sea resulted in the egg left unincubated for at least one day as the partner never extending their incubation shift longer than two days. Similarly, during the chick-rearing period, chick growth and survival were severely affected during years when both parents were not able to feed their offspring every night (Chapter 4, Eizenberg et al. 2021).

Similar to the little auk, the behavioural plasticity of diving petrels may be determinant in their capacity to successfully extend their foraging range. For such high wing loading species, while exploiting remote feeding grounds is expected to be of important energetic costs, the potential predictability and productivity of a distant oceanographic feature can maintain a positive cost/benefit balance (Chapter 5). However, when functioning at their maximum foraging capabilities, such species may not cope with any additional degradation in food availability (Chapter 4). In this context, fully understanding the species ecological and ecophysiological constraints at different spatial and temporal scales is essential to identifying and predicting the impact of environmental changes.

Table 6-1: Variations of maximum dive depth of common and South Georgian diving petrel. MDG = Maximum depth gauge; TDR = Time-depth recorder.

Species	Breeding stage	Population	Device	Maximum dive depth	Reference
Common diving petrel	Incubation	South Georgia	TDR	10.4 ± 4.6 (n = 20)	Navarro et al. 2014
		Kerguelen	MDG	27.7 ± 4.5 (n =30)	Bocher et al. 2000b
			TDR	20.5 ± 2.5 (n = 7)	Present Study
	Chick-rearing	New Zealand	TDR	10.7 ± 0.7 (n = 15)	Dunphy et al. 2015
		Kerguelen	MDG	32.7 ± 4.8 (n =122)	Bocher et al. 2000a
			TDR	31.9 ± 2.5 (n =12)	Present Study
		South-eastern Australia	TDR	10.2 ± 3.6 (n =27)	Fromant et al. unpublished data
		New Zealand	MDG	10.9 ± 6.1 (n = 6)	Taylor 2008
South Georgian diving petrel	Incubation	South Georgia	TDR	18.1 ± 3.6 (n = 6)	Navarro et al. 2014
		Kerguelen	TDR	20.1 ± 3.6 (n = 4)	Present Study
	Chick-rearing	South Georgia	MDG	25.7 ± 11.4 (n = 6)	Prince and Jones 1992
		Kerguelen	MDG	25.7 ± 5.1 (n = 87)	Bocher et al. 2000a
			TDR	21.4 ± 4.9 (n = 11)	Present Study

6.3. Diving behaviour of diving petrels

6.3.1. Revisiting the maximum dive depth of common and South Georgian diving petrels

For most of air-breathing vertebrates, diving capacities generally increase with body mass (Schreer and Kovacs 1997), with the greater physiological characteristics of larger species (e.g. oxygen storage capacity) predicting deeper and longer dives (Halsey et al. 2006). Whether or not diving petrels fit in with these predictions has been questioned for several decades due to important discrepancies between studies describing their maximum dive depth. The concerns mainly arise from the use of capillary tube maximum-depth gauges (MDG) in most of the studies investigating diving petrel diving capacities. Indeed, this pioneering device, that records a single value of maximum dive depth for the entire deployment, can be imprecise when deployed for a long duration, especially on species with high diving rates (Burger and Wilson 1988, Elliott and Gaston 2009). In particular, two recent studies using more accurate electronic time-depth recorder (TDR) dive behaviour data loggers (Navarro et al. 2014, Dunphy et al. 2015) found a maximum dive depth for CDP and SGDP 2-4 times shallower than previously estimated by MDG studies (Prince and Jones 1992, Chastel 1994, Bocher et al. 2000a,b).

However, because diving behaviour can vary substantially in relation to prey availability and distribution (Bocher et al. 2000b), the variations observed between these studies could simply be related to the different environmental conditions experienced by the study populations (Table 6-1). Indeed, using a previously derived allometric relationship for maximum dive depth [depth (m) = $158.49 * (\text{body mass})^{1.04}$] in alcids (Schreer and Kovacs 1997), which are morphologically and ecologically very similar to diving petrels (Roby and Ricklefs 1986), maximum dive depth of CDP and SGDP at Kerguelen Islands is estimated to be 28 and 24 m, respectively (using a body mass of 147 g for CDP and 128 g for SGDP; Chapter 5). Interestingly, these estimations differed substantially from the values recorded using TDR in South Georgia (for both CDP and SGDP; Navarro et al. 2014) and New Zealand (for CDP;

Dunphy et al. 2015) but fit relatively well to the values collected with MDG at Kerguelen Islands (for both CDP and SGDP; Bocher et al. 2000a) (Table 6-1).

In the present study, maximum dive depths recorded with TDR for both CDP and SGDP at Kerguelen Islands were in the same range as the values recorded with MDG (Table 6-1) and matching the estimations from the allometric model for alcids. These findings suggest the following: (1) the results previously collected using MDG appear to provide accurate estimations of maximum dive depth in diving petrels and confirm their diving abilities; (2) the diving capacities of diving petrels at Kerguelen Islands are very similar to alcids of similar weight; and (3) the combined results from the studies using TDR or MDG highlight the important spatial and temporal variations in diving petrel diving behaviour.

6.3.2. Spatial and temporal variability in diving behaviour of diving petrels: the case of the common diving petrel

Throughout its large distribution, the CDP exhibits important variations in its at-sea foraging distribution (section 6.1.2), and diving behaviour. In addition to diving three times deeper at Kerguelen Islands than elsewhere (Table 6-1), CDP from this subantarctic archipelago had dive durations 2-4 times longer than previously reported (Chapter 5, Navarro et al. 2014, Dunphy et al. 2015). Such variations in dive behaviour between populations are likely to reflect differences in foraging habitat and prey species. In south-eastern Australia and New Zealand, CDP feed predominantly on coastal krill (Schumann et al. 2008, Fromant et al. 2020a), a species also heavily predated by surface feeders such as fairy prions (*Pachyptila turtur*; Manno et al. 2014, Fromant et al. 2020a) or red-billed gulls (*Chroicocephalus novaehollandiae scopulinus*; Mills et al. 2008). As coastal krill forms large swarms close to the surface in coastal waters (O'Brien 1988), the short and shallow dives of CDP in the region, as well as their foraging trip characteristics, seem to mirror the availability of their main prey.

Similarly, at Kerguelen Islands, the diving behaviour of CDP during the chick-rearing period appears to be strictly linked to the local vertical distribution of the hyperiid *Themisto gaudichaudii* (Bocher et al. 2000a,b, Chapter 5), a keystone species in the Golfe du Morbihan ecosystem (Bost et al. 1994, Bocher et al. 2000a). However, unlike CDP in Australia or New Zealand feeding near the surface, CDP at Kerguelen Islands are forced to dive much deeper to access their main prey. While *Themisto gaudichaudii* can occur near the surface elsewhere (Kane 1966, Pakhomov and McQuaid 1996), the absence of surface-feeding species in the Golfe du Morbihan (Bocher et al. 2001) strongly suggest that this prey is found at deeper depths at Kerguelen Islands making it only accessible to diving species.

Although these large variations in CDP diving characteristics could be due to behavioural plasticity to adapt to different environments, the differences between populations could also be the consequence of micro-evolution (Grémillet et al. 2012). Indeed, the species comprises multiple populations with subtle morphological variations (Murphy and Harper 1921, Woehler 1991). Each of these populations breed several thousands of kilometres apart and, while there is no information about their genetic structure, it is likely that there is a restricted gene flow among populations (Chapter 3). Therefore, it cannot be excluded that the foraging behaviour diversity observed in the CDP is a result of population-specific niche-specialisation.

Furthermore, investigation of the foraging behaviour of CDP during the whole breeding season in the present study highlighted substantial intra-population variations in at-sea distribution and diving behaviour between breeding stages (Chapter 5). These large differences in CDP ecological niche within the same population are of a similar range as inter-population variations, and support the idea that CDP exhibit clear behavioural plasticity. In addition, there are still important knowledge gaps about the foraging behaviour of CDP throughout its distribution. In particular, there are no GPS or TDR data during the chick-rearing period in

South Georgia or New Zealand. As observed in Chapters 4 and 5, it appears to be essential to study the whole breeding season in order to fully describe the species' ecological niche.

6.4. At-sea distribution of diving petrels during the non-breeding period

Until very recently, the little information available about diving petrels during the non-breeding period suggested that they were not migratory birds (Warham 1977) or were potentially dispersing over vast areas (Cherel et al. 2006). In the present study, the tracking of diving petrels during the non-breeding period highlighted clear migratory patterns and specific migration areas (post-breeding migration) of three populations of CDP (Kerguelen Islands, south-eastern Australia, New Zealand) and SGDP from Kerguelen Islands (Chapter 3 and 5). In all cases, this period was characterized by a rapid outward movement (away from the breeding colony) towards relatively well-defined areas, located several thousand kilometres away from the breeding sites. This clearly corresponds to *true* migratory behaviour (Berthold 2001). Beyond simply describing the distribution of diving petrels during the non-breeding period, these results also provided valuable information about the similarities and differences in migration behaviour between species and populations of diving petrels.

6.4.1. Migration vs dispersion: a common pattern of diving petrels

During the breeding season, as central-place foragers, seabirds are restrained to a limited space, and have to target productive areas within their foraging range (Orians and Pearson 1979, Weimerskirch 2007). During the non-breeding season, however, seabirds can forage over much larger spatial scales. In the Southern Ocean, tracking studies have revealed that small procellariiform species such as prions often exhibit a dispersal behaviour, spreading to species-specific preferred environments in variable directions (Quillfeldt et al. 2015a,b, 2017, Jones et al. 2020). This environmental specialisation in the Southern Ocean appears to

take place along a latitudinal gradient related to the circumpolar structure of water masses (Quillfeldt et al. 2015a). Similarly, stable isotope analyses also suggest species-specific ecological preferences during the non-breeding period for several species, including CDP and SGDP (Cherel et al. 2006, Navarro et al. 2015). Based on this information, it was expected that diving petrels would also disperse widely to water masses reflecting their species-specific preferences.

In the present study, however, CDP and SGDP appeared to migrate to specific areas and did not exhibit the dispersal behaviour commonly observed in other small Procellariiformes (Chapters 3 and 5). Similar behaviour has been recorded with the WHDP from New Zealand (Fischer et al. 2021), as well as SGDP from South-Georgia (Navarro et al. 2015), and CDP from South-Georgia (Navarro et al. 2015) and New Zealand (Rayner et al. 2017). Compared to diving petrels, other small Procellariiformes have efficient aerial search strategies (Navarro et al. 2013), which enable them to cover large foraging areas where prey is scarce and unpredictably distributed. Their ability to fly long distances with minimal energetic costs facilitates a continuous search effort throughout entire ocean basins. In contrast, for high wing loading species there is an advantage to migrating towards more spatially and temporally predictable areas, minimising the cost of flight and increasing their net energy gain.

Detailed tracking data of diving petrels during the non-breeding period (Chapters 3 and 5, Rayner et al. 2017, Fischer et al. 2021) support this hypothesis. In all cases a rapid and direct transit between the colony and a distinct migration area was observed. Interestingly, for all three species studied, the Antarctic Polar Front appears to be a key oceanic feature in the distribution of diving petrels in the Southern Ocean. This front corresponds to the northern limit of the Antarctic waters (Park et al. 1993) and is the location of significant phytoplankton growth and subsequent high biomass of zooplankton such as copepods (Urban-Rich et al. 2001), which are a major resource in diving petrel diets (Reid et al. 1997, Ridoux 1994).

Interestingly, CDP from Kerguelen Islands did not follow this apparent preference for the Polar Front, with all individuals from this population migrating to Antarctic waters further south than the Polar Front. This may suggest that, unlike other small procellariiform species (Quillfeldt et al. 2015a), sea surface temperature is not the only variable explaining the latitudinal distribution of diving petrels. Additional information is needed to fully understand the environmental factors driving the distribution of diving petrels during the non-breeding period. In particular, investigating diving petrels from Crozet Archipelago which host large populations of CDP and SGDP, may help to disentangle the role of inter- and intra-species segregation in at-sea distribution during the post-breeding migration (Chapter 5).

6.4.2. Population-specific migration pattern: phenology, bearing and distribution

Both CDP and SGDP are circumpolar species, breeding on remote islands in three different ocean basins (Marchant and Higgins 1990). Therefore, because of their limited flying capacities, it was expected that populations breeding several thousands of kilometres apart would not migrate to the same area during the non-breeding period. Indeed, the present results, combined with the information from three other tracking studies (Navarro et al. 2015, Rayner et al. 2017, Fischer et al. 2021), demonstrated clear inter- and intra-species variations in migration area. However, these differences were also characterised by population-specific timing of movement and directions taken by the migrating birds (Fig. 6-1). Individuals from the same population were synchronised in their departure to, and return from, migration areas and followed the same paths. These results may suggest variations in life history traits at the population level, leading to population-based cultural patterns (Thiebot et al. 2012). The behaviour of each individual would, therefore, be more representative of its population of origin rather than to the entire species.

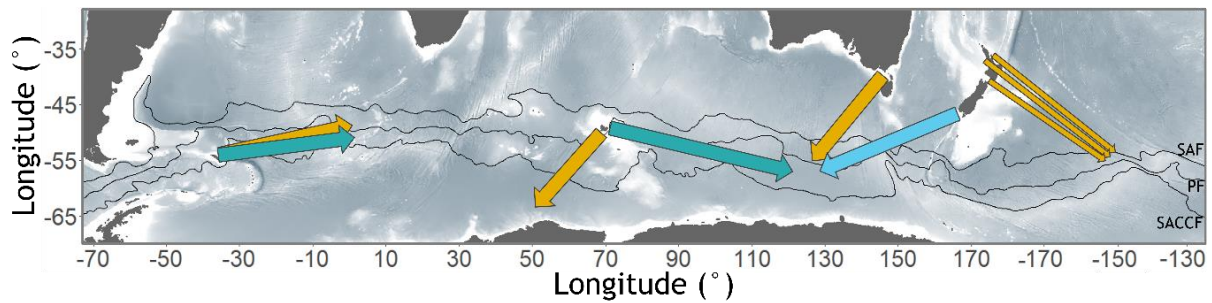


Figure 6-1: Inter- and intra-species variations in post-breeding migration patterns of common (yellow), South Georgian (dark blue) and Whenua Hou (light blue) diving petrels. Data adapted from Navarro et al. (2015) (CDP and SGDP from South Georgia), Rayner et al. (2017) (CDP from New Zealand North Island), Fischer et al. (2021) (WHDP from New Zealand South Island), and Chapters 3 and 5 (CDP and SGDP from Kerguelen Islands, CDP from south-eastern Australia, and CDP from New Zealand North Island).

In the Southern Indian Ocean, a similar pattern was observed in three species of *Eudyptes* penguins (Thiebot et al. 2013). For these species with high movement constraints (Thiebot et al. 2013), the post-breeding migration pattern appeared to be primarily population-specific rather than species-specific. In the present study, this notion of population-based cultural migration appears to be well exemplified by the clear inter- and intra-species variations with four supporting aspects (Fig. 6-1): (1) CDP individuals from three different colonies from the same population all migrated in the same area (CDP from New Zealand North Island; Chapter 3, Rayner et al. 2017); (2) distant populations from the same species migrating to different areas and/or heading in different directions (Chapter 4); (3) two sympatric species migrating in the same direction to the same area (CDP and SGDP from South Georgia; Navarro et al. 2015); and (4) two sympatric species migrating in opposite directions, an ocean basin apart (CDP and SGDP from Kerguelen Islands; Chapter 5). The divergent patterns these examples provide illustrate the complexity in understanding the individual decision processes at the colony, population and species level. Therefore, it is still very unclear what cues trigger specific migration patterns. Possibly, future research on early life and the learning process of young individuals may provide valuable information.

6.5. Niche segregation: what does it inform about species ecology?

The SGDP breeds exclusively on subantarctic islands, often in large populations exceeding several millions individuals (Marchant and Higgins 1990). However, despite a large distribution, SGDP systematically breed in sympatry with the closely related CDP. Because CDP and SGDP cannot be easily differentiated at sea, information about their ecology and niche segregation was mostly limited to diet and isotopic analyses, and/or to a specific period of the breeding cycle. The present study investigated the ecological niche (at-sea distribution, diving behaviour and isotopic niche) of both species at Kerguelen Islands during the whole annual cycle and explored the temporal variation in the degree of niche segregation (Chapter 5). Overall, these results indicated that the niche partitioning of CDP and SGDP at Kerguelen Islands was highly stage-dependent, emphasized by a shift from limited segregation during the incubation period to complete niche segregation during the chick-rearing and non-breeding periods.

During the breeding season, the shift in the degree of segregation resulted from the clear switch of CDP ecological niche (at-sea distribution and diving behaviour) between the incubation and the chick-rearing periods, while SGDP maintained a very consistent behaviour during the whole breeding season. This could suggest a difference in behavioural plasticity between the two species, with CDP adapting their foraging behaviour to spatial and temporal environmental variations, while SGDP having to rely on stable oceanic features such as the Polar Front (Chapter 5). This behavioural “stability” of SGDP between breeding stages appears to also be reflected in the consistent phenology between breeding sites, which strongly contrasts with the variability observed for the CDP (Chapters 3, 4 and 5). Variability among breeding sites is a common feature for coastal foragers, resulting from the temporal variations in resource availability (Bost and Jouventin 1990).

For many seabird species, phenology is determined at a crossroad between species ecology and the peak of prey availability (Lack 1954, Perrins 1970), which ultimately delimits the species' breeding range to where these requirements are met. Therefore, the specificity of ecological requirements and the species behavioural plasticity are likely to reflect the distribution of the species. In the present study, the constant foraging behaviour of SGDP at the local scale appears to reflect its narrow distribution at the species scale. Conversely, the behavioural plasticity of CDP at the local scale matches the diversity of environments exploited throughout its circumpolar distribution (Fig. 6-2). Exploring the degree of species' ecological niche flexibility may be a key aspect in understanding the mechanism of niche segregation. In the context of climate change, the difference between species in their ability to adapt to new environmental conditions may result in very divergent population dynamics (Forcada and Trathan 2009, Jenouvrier 2013). In particular, species relying on specific oceanic features such as oceanic fronts may not cope with large scale environmental changes (Bost et al. 2015).

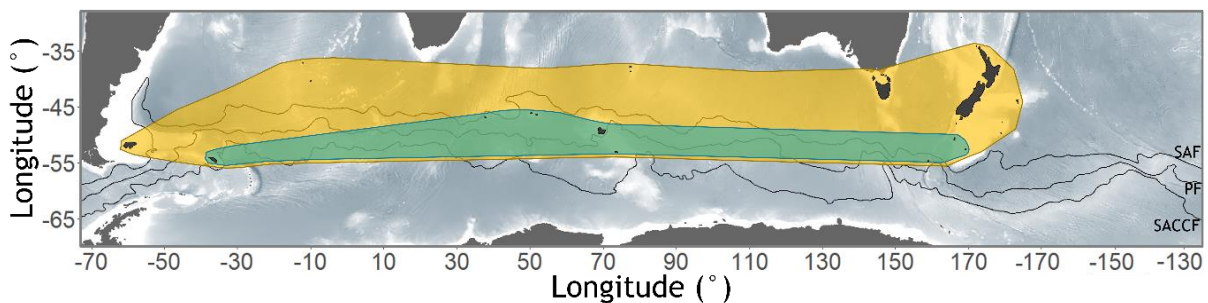


Figure 6-2: Breeding distribution of common (yellow) and South Georgian (blue) diving petrel. This is a historic distribution that includes breeding sites of species that were extirpated as a result of human related activities (Marchant and Higgins 1990).

6.6. Threats and perspectives for diving petrels

6.6.1. Challenges faced by diving petrels and small seabird species

In the present body of work, the investigation of the ecological niche of diving petrels revealed inter- and intra-species variability, highlighting to some extent behavioural flexibility.

However, although these small procellariiform species exhibited unexpected flying and diving abilities, they also revealed clear eco-physiological limits that may constrain their capacity to buffer environmental changes.

During the breeding season, one of the key limitations of diving petrels appears to arise from the convergence between their high metabolic rate and the absence of stomach oil, constraining the maximum trip duration to one or two days (Chapter 4, Eizenberg et al. 2021, Fromant et al. 2022b). Seabird species with strong physiological constraints often rely on the influence of stable ocean features such as up-wellings, oceanic fronts or sea ice (Abrams and Griffiths 1981, Lønne and Gabrielsen 1992, Ainley et al. 1998). Any change in prey distribution and/or prey quality is likely to affect their foraging success, and ultimately the population dynamics. In the Southern Ocean, long term trends indicate a southward shift in cold water zooplankton species due to the modification of optimal habitats towards higher latitudes (Veytia et al. 2020). In particular, for species and populations breeding north of the Polar Front, this may result in increasing the distance to reach optimal foraging zones. For example, for king penguins (*Aptenodytes patagonicus*) at Crozet Islands, breeding success is negatively impacted during years of increased distance to their main foraging zone, the Antarctic Polar Front (Péron et al. 2012, Bost et al. 2015).

At the northern extent of their breeding range, CDP are already facing important environmental changes (Chapter 4). In south-eastern Australia, CDP breeding success have been jeopardised by warming sea surface water (Cai et al. 2005) and the intensification of marine heatwave events (Oliver et al. 2019, Eizenberg et al. 2021). These events induce a drastic shift in zooplankton abundance and community composition (Evans et al. 2020). With warming waters, nutritionally rich cold water crustaceans are replaced by gelatinous zooplankton and small crustaceans that are of poorer nutritional quality (Atkinson et al. 2004, Richardson 2008). In response to warmer sea surface water, cool-water associated zooplankton

species can also temporally move deeper into the water-column (Richardson 2008). Therefore, instead of extending their foraging range or feeding on lower quality prey (Chapter 4), diving petrels may dive deeper to potentially access nutritionally richer prey. In the present study, diving petrels exhibited substantial variations in their diving metrics between species, populations and breeding stages (Chapter 5, Section 6.2.2). However, and it is highly uncertain if these species can buffer environmental changes through deeper dives because diving petrels are ultimately limited in their diving depth capacity (due to their body size). Allometric models for alcid estimate that both CDP and SGDP are diving near their theoretical maximum dive depth at Kerguelen Island (Section 6.2.1), which may suggest that any increase in depth of available prey could have important consequences for their foraging and breeding success. Although, the maximum dive capacity may be underestimated here, the niche segregation between CDP and SGDP at Kerguelen Islands exemplifies the limited diving capacities of SGDP, when during the chick-rearing period this species appears to fly farther rather than diving deeper.

Alternatively, to compensate with the poleward shift of their favourable foraging area, subantarctic populations could colonise new breeding sites owing to the retreat of permanent ice cover from the southernmost islands (Siegert et al. 2019). However, the potential candidate islands that could provide suitable breeding habitat are limited to a small number of sites in the south-west of the Atlantic sector of the Southern Ocean. Indeed, for both the Indian and Pacific sectors, there are no islands between the already occupied breeding sites and Antarctica, 2000 km farther south. This will likely impede the possibility for diving petrels to colonise alternative breeding sites that could otherwise have provided suitable foraging areas (Constable et al. 2014).

Although knowledge about foraging behaviour and foraging plasticity are essential to predict the effects of climate change on small burrowing seabirds, predicting their future

population trajectories must also involve a better understanding of the threats in their terrestrial breeding habitat. In addition to playing an important role in marine ecosystems, burrowing seabirds are key ecosystem engineers of the terrestrial environment in which they breed (Warham 1996). However, this habitat is exposed to several environmental threats that greatly influence short- and long-term population dynamics. In particular, the impacts of invasive rodents on breeding seabirds have been identified for several decades (Rodríguez et al. 2019). Although some species and populations are still at great risk, the development of ambitious rodent eradication management plans may reduce this threat in the future. Furthermore, most breeding habitats are facing the understudied (or overlooked) threat of slowly spreading, but not less harmful, invasive plant species and their induced changes in soil structure. For example, at Kerguelen Islands the native plant species *Pringlea antiscorbutica* and *Azorella selago*, fundamental to CDP nesting habitat (Weimerskirch et al. 1989), have been slowly replaced by introduced grass species such as *Poa annua* (Frenot et al. 2001). In addition to modify the soil structure, this directly impacts small burrowing petrels which struggle to penetrate dense grass cover area (Beach et al. 1997).

In addition to these modifications of the terrestrial ecosystem, seabirds are increasingly impacted by intense environmental events, such as storm surges, heavy rain, heatwaves and bushfires. Recent examples of unusual rain events have highlighted the threats to Antarctic species (Ropert-Coudert et al. 2014), yet little is known of the potential effect on burrowing petrels in the subantarctic and temperate regions. For example, during the present study, the 2017/2018 breeding season of SGDP at Kerguelen Islands was impacted by intense rain due to an unusual intrusion of a tropical storm. During this single-day event, 38% of the chicks died due to burrow flooding (Fromant et al. unpublished data). Interestingly, this death toll was not observed for the CDP, which breed in steeper and less exposed habitat on these subantarctic islands (Weimerskirch et al. 1989; see Fig. 1-3). This illustrates a need to also focus research

towards the breeding habitat in relation to extreme environmental events, and how it may affect species differently.

The combined knowledge of breeding habitat ecology and foraging ecology may be the last major component of the species hyper-volume ecological niche. Seabirds, and in particular burrowing species, represent an essential link between marine and terrestrial ecosystems. Predicting their capacity to buffer environmental changes, therefore, requires a better understanding of the relationships between these two environments.

6.6.2. Perspectives and future research: diving petrels and environmental indicators

Through cascading processes, the effects of climate change on low trophic levels are transferred to upper species in the food web (Constable et al. 2014). In this context, marine predators can inform about ecosystem functions and provide insights into ocean processes through their large distribution (Bestley et al. 2020). The inherent difficulties in collecting data from the marine environment make it essential to use environmental indicators, particularly given the urgency to understand and predict the impact of climate change on remote ecosystems. In the Southern Ocean, several species, such as seals, penguins and albatrosses have been studied for this purpose. Although these species provide valuable information on their environments, three main limitations make it necessary to investigate additional environmental indicators: (1) due to their relatively easier access and their size (allowing tracking device deployment), data collection is largely biased toward the largest species, excluding a major part of the predator biomass (Guinet et al. 1996); (2) since it is difficult to segregate causative mechanisms (Constable et al. 2014), for populations affected by fishery mortality or current/past exploitation, the confounding effects of these factors with climate-related variations impede clear interpretations of the impacts of environmental changes; and (3) for top predator species, their high trophic level often results in an important lag between

the environmental perturbation and the species response, thus complicating even more their role as environmental indicators.

Diving petrels exhibit key characteristics that make them valuable marine environment indicators (Hazen et al. 2019): they are conspicuous (easily accessible during the breeding season; Chapter 2), sensitive to ecosystem processes (phenology, breeding parameters and foraging behaviour; Chapters 3, 4 and 5), and quick in their responses to seasonal and annual variations in food availability (Chapters 4 and 5). In addition, diving petrels offer a large set of measurable attributes that can provide information about different processes over multiple spatial and temporal scales (Chapters 3, 4 and 5). In particular, in addition to the detailed information provided by demographic measurements (chick-growth rates and reproductive success; Eizenberg et al. 2021), biologging can improve our ability to link foraging ecology and environmental changes. Since diving petrels have a unimodal foraging strategy (Chapters 4 and 5), foraging range, diving depth and trip duration may be particularly good parameters to detect variations in prey availability.

Long-term monitoring also necessitates the development of non-invasive, or minimum impact, methods. In addition to stable isotope analyses, faecal DNA metabarcoding may become a systematic tool to investigate seasonal and inter-annual variations of the species trophic niche (Cavallo et al. 2018). In particular, the short foraging trip characteristics of diving petrel could provide a fertile ground to explore daily variations in prey availability. Such information could ultimately be related to the at-sea distribution, and the foraging and diving behaviour of adults. In addition, artificial burrows may facilitate the collection of such samples while limiting the risk of long-term disturbance (Chapter 2).

Finally, one of the key missing aspects regarding diving petrels, and generally small burrowing seabirds, is the absence of accurate population estimates and trends. Few recent studies have provided precious information but only at a very local scale (Schumann et al.

2014, Barbraud et al. 2020, Fischer et al. 2020). The overall conservation status of CDP and SGDP is based on approximate population estimates made 40 to 50 years ago (see Marchant and Higgins 1990), which may considerably mislead any future management plans. In parallel, the taxonomy of the various populations of diving petrels should be explored, notably using DNA sequencing (Rodríguez et al. 2019). In particular, the important inter-population variations in phenology, foraging behaviour and migration pattern of CDP and SGDP suggest population divergence (Chapters 3, 4 and 5). The limited genetic information (Grosser et al. 2021) may have clear conservation implications, as the status of isolated population is overlooked by the assumption that ubiquitous species are made of a single taxonomical, biological and ecological entity.

6.7. Conclusion

A species' ecological niche is shaped by an intricate interplay between interacting environmental, behavioural and physiological factors. Understanding their specific contribution requires collecting information of the species' ecology at different spatial and temporal scales. The present study described important aspects of the foraging ecology of common and South Georgian diving petrels throughout their whole annual cycle. The integrating approaches from different fields, as well as the investigation of spatial and temporal variations revealed the extent and the limits of their ecological niche. Focusing on species such as diving petrels, with high foraging constraints and feeding on low trophic-level prey, could help to disentangle the underlying mechanisms of long-term adaptation to climate change. Considering the wide geographic distribution (longitudinal and latitudinal gradients) of the CDP and SGDP throughout different environments of the Southern Hemisphere, these abundant seabirds could act as suitable environmental sentinels to monitor the effects of changing oceanographic conditions. Nevertheless, ecological research is at the centre of a

perpetually readjusting crossroads between the lack of fundamental knowledge, the development of new technologies, the need for better conservation, and the increasing awareness of animal welfare. Navigating this complex interplay requires working collaboratively in order to increase the value of each data set collected and the conservation benefits, while minimizing the disturbance to the species

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Authorship statement (Chapter 2)


1. Details of publication and executive author

Title of Publication		Publication details
Artificial burrows as a tool for long-term studies of diving petrels		Polar Biology 1-8 https://doi.org/10.1007/s00300-020-02645-y
Name of executive author	School/Institute/Division if based at Deakin; Organisation and address if non-Deakin	Email or phone
Aymeric Fromant	School of Life and Environmental Sciences	afromant@deakin.edu.au

2. Inclusion of publication in a thesis

Is it intended to include this publication in a higher degree by research (HDR) thesis?	Yes	If Yes, please complete Section 3 If No, go straight to Section 4.
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3. HDR thesis author's declaration

Name of HDR thesis author if different from above. (If the same, write "as above")	School/Institute/Division if based at Deakin	Thesis title
As above		
If there are multiple authors, give a full description of HDR thesis author's contribution to the publication (for example, how much did you contribute to the conception of the project, the design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)		
Conception of the project, data collection, data analysis, drafting and writing the manuscript		
<i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i>	Signature and date	 05/10/2021

4. Description of all author contributions

Name and affiliation of author	Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)
Charles-André Bost CEBC, CNRS - Université de La Rochelle	Conception of the project, data collection, edited and revised the manuscript
Colin M Miskelly Museum of New Zealand Te Papa Tongarewa	Conception of the project, data collection, edited and revised the manuscript
John PY Arnould School of Life and Environmental Sciences, Deakin University	Conception of the project, edited and revised the manuscript




5. Author Declarations

I agree to be named as one of the authors of this work, and confirm:

- i. that I have met the authorship criteria set out in the Deakin University Research Conduct Policy,
- ii. that there are no other authors according to these criteria,
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Name of author	Signature*	Date
John PY Arnould		05/10/2021
Colin M Miskelly		06/10/2021
Charles-André Bost		05/10/2021

6. Other contributor declarations

I agree to be named as a non-author contributor to this work.

Name and affiliation of contributor	Contribution	Signature* and date

* If an author or contributor is unavailable or otherwise unable to sign the statement of authorship, the Head of Academic Unit may sign on their behalf, noting the reason for their unavailability, provided there is no evidence to suggest that the person would object to being named as author

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Data format	Storage Location	Date lodged	Name of custodian if other than the executive author
Electronic	CEBC	March-2020	Charly Bost
Electronic	Deakin share drive Arnould's Lab	Sep-2021	John Arnould

This form must be retained by the executive author, within the school or institute in which they are based.

If the publication is to be included as part of an HDR thesis, a copy of this form must be included in the thesis with the publication.

Authorship statement (Chapter 3)

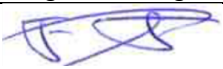
1. Details of publication and executive author

Title of Publication		Publication details
Temporal and spatial differences in the post-breeding behaviour of a ubiquitous Southern Hemisphere seabird, the common diving petrel		Royal Society Open Science 7(11):200670 https://doi.org/10.1098/rsos.200670
Name of executive author	School/Institute/Division if based at Deakin; Organisation and address if non-Deakin	Email or phone
Aymeric Fromant	School of Life and Environmental Sciences	afromant@deakin.edu.au

2. Inclusion of publication in a thesis

Is it intended to include this publication in a higher degree by research (HDR) thesis?	Yes	If Yes, please complete Section 3 If No, go straight to Section 4.
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3. HDR thesis author's declaration

Name of HDR thesis author if different from above. (If the same, write "as above")	School/Institute/Division if based at Deakin	Thesis title
As above		
If there are multiple authors, give a full description of HDR thesis author's contribution to the publication (for example, how much did you contribute to the conception of the project, the design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)		
Conception of the project, data collection, sample analysis, data analysis, drafting and writing the manuscript		
<i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i>	Signature and date	 05/10/2021

4. Description of all author contributions

Name and affiliation of author	Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)
Charles-André Bost CEBC, CNRS - Université de La Rochelle, France	Conception of the project, data collection, edited and revised the manuscript
Paco Bustamante LIENSs, CNRS - Université de La Rochelle, France	Sample analysis, edited and revised the manuscript
Alice Carravieri LIENSs, CNRS - Université de La Rochelle, France	Data collection, sample analysis, edited and revised the manuscript
Yves Cherel CEBC, CNRS - Université de La Rochelle, France	Conception of the project, sample analysis, edited and revised the manuscript
Karine Delord	Data collection, data analysis, edited and revised the manuscript

CEBC, CNRS - Université de La Rochelle, France	
Yonina H Eizenberg School of Life and Environmental Sciences, Deakin University, Australia	Data collection, edited and revised the manuscript
Colin M Miskelly Museum of New Zealand Te Papa Tongarewa, New Zealand	Conception of the project, data collection, edited and revised the manuscript
John PY Arnould School of Life and Environmental Sciences, Deakin University, Australia	Conception of the project, edited and revised the manuscript



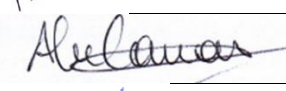





5. Author Declarations

I agree to be named as one of the authors of this work, and confirm:

- vi. that I have met the authorship criteria set out in the Deakin University Research Conduct Policy,*
- vii. that there are no other authors according to these criteria,*
- viii. that the description in Section 4 of my contribution(s) to this publication is accurate,*
- ix. that the data on which these findings are based are stored as set out in Section 7 below.*

If this work is to form part of an HDR thesis as described in Sections 2 and 3, I further

- x. consent to the incorporation of the publication into the candidate's HDR thesis submitted to Deakin University and, if the higher degree is awarded, the subsequent publication of the thesis by the university (subject to relevant Copyright provisions).*

Name of author	Signature*	Date
Charles-André Bost		05/10/2021
Paco Bustamante		05/10/2021
Alice Carravieri		07/10/2021
Yves Cherel		05/10/2021
Karine Delord		05/10/2021
Yonina H Eizenberg		05/10/2021
Colin M Miskelly		06/10/2021
John PY Arnould		05/10/2021

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I agree to be named as a non-author contributor to this work.

Name and affiliation of contributor	Contribution	Signature* and date

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Data format	Storage Location	Date lodged	Name of custodian if other than the executive author
Electronic	CEBC	November-2020	Charly Bost
Electronic	Deakin share drive Arnould's Lab	Sep-2021	John Arnould

This form must be retained by the executive author, within the school or institute in which they are based.

If the publication is to be included as part of an HDR thesis, a copy of this form must be included in the thesis with the publication.

Authorship statement (Chapter 4)


1. Details of publication and executive author

Title of Publication		Publication details
Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird		Progress in Oceanography 198:102676 https://doi.org/10.1016/j.pocean.2021.102676
Name of executive author	School/Institute/Division if based at Deakin; Organisation and address if non-Deakin	Email or phone
Aymeric Fromant	School of Life and Environmental Sciences	afromant@deakin.edu.au

2. Inclusion of publication in a thesis

Is it intended to include this publication in a higher degree by research (HDR) thesis?	Yes	If Yes, please complete Section 3 If No, go straight to Section 4.
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3. HDR thesis author's declaration

Name of HDR thesis author if different from above. (If the same, write "as above")	School/Institute/Division if based at Deakin	Thesis title
As above		
If there are multiple authors, give a full description of HDR thesis author's contribution to the publication (for example, how much did you contribute to the conception of the project, the design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)		
Conception of the project, data collection, data analysis, drafting and writing the manuscript		
<i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i>		Signature and date  05/10/2021

4. Description of all author contributions

Name and affiliation of author	Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)
Karine Delord CEBC, CNRS - Université de La Rochelle, France	Data analysis, edited and revised the manuscript
Charles-André Bost CEBC, CNRS - Université de La Rochelle, France	Conception of the project, edited and revised the manuscript
Yonina H Eizenberg School of Life and Environmental Sciences, Deakin University, Australia	Data collection, edited and revised the manuscript
Jonathan A Botha MAPRU, Nelson Mandela University, South Africa	Data collection, data analysis, edited and revised the manuscript
Yves Cherel CEBC, CNRS - Université de La Rochelle, France	Sample analysis, edited and revised the manuscript

Paco Bustamante LIENSs, CNRS - Université de La Rochelle, France	Sample analysis, edited and revised the manuscript
Brett R Gardner Werrabee Open Range Zoo, Zoos Victoria, Australia	Data collection, edited and revised the manuscript
Maud Brault-Favrou LIENSs, CNRS - Université de La Rochelle, France	Sample analysis, edited and revised the manuscript
Arnaud Lec’hvien School of Life and Environmental Sciences, Deakin University, Australia	Data collection, edited and revised the manuscript
John PY Arnould School of Life and Environmental Sciences, Deakin University, Australia	Conception of the project, edited and revised the manuscript






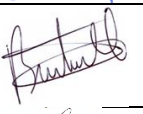

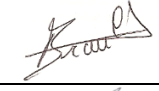

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- xiii. that the description in Section 4 of my contribution(s) to this publication is accurate,*
- xiv. that the data on which these findings are based are stored as set out in Section 7 below.*

If this work is to form part of an HDR thesis as described in Sections 2 and 3, I further

- xv. consent to the incorporation of the publication into the candidate’s HDR thesis submitted to Deakin University and, if the higher degree is awarded, the subsequent publication of the thesis by the university (subject to relevant Copyright provisions).*

Name of author	Signature*	Date
Karine Delord		05/10/2021
Charles-André Bost		05/10/2021
Yonina H Eizenberg		05/10/2021
Jonathan A Botha		07/10/2021
Yves Cherel		05/10/2021
Paco Bustamante		05/10/2021
Brett R Gardner		05/10/2021
Maud Brault-Favrou		05/10/2021
Arnaud Lec’hvien		05/10/2021

John PY Arnould		05/10/2021
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Electronic	Deakin share drive Arnould's Lab	Sep-2021	John Arnould

This form must be retained by the executive author, within the school or institute in which they are based.

If the publication is to be included as part of an HDR thesis, a copy of this form must be included in the thesis with the publication.

Authorship statement (Chapter 5)


1. Details of publication and executive author

Title of Publication		Publication details
Year-round niche segregation in two sympatric sibling seabirds: the common and South Georgian diving petrels		Submitted to Ecology
Name of executive author	School/Institute/Division if based at Deakin; Organisation and address if non-Deakin	Email or phone
Aymeric Fromant	School of Life and Environmental Sciences	afromant@deakin.edu.au

2. Inclusion of publication in a thesis

Is it intended to include this publication in a higher degree by research (HDR) thesis?	Yes	If Yes, please complete Section 3 If No, go straight to Section 4.
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3. HDR thesis author's declaration

Name of HDR thesis author if different from above. (If the same, write "as above")	School/Institute/Division if based at Deakin	Thesis title
As above		
If there are multiple authors, give a full description of HDR thesis author's contribution to the publication (for example, how much did you contribute to the conception of the project, the design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)		
Conception of the project, data collection, data analysis, drafting and writing the manuscript		
<i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i>	Signature and date	 05/10/2021

4. Description of all author contributions

Name and affiliation of author	Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)
John PY Arnould School of Life and Environmental Sciences, Deakin University	Conception of the project, edited and revised the manuscript
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Grace J Sutton School of Life and Environmental Sciences, Deakin University	Data analysis, edited and revised the manuscript
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Museum of New Zealand Te Papa Tongarewa	
Akiko Kato CEBC, CNRS - Université de La Rochelle, France	Data analysis, edited and revised the manuscript
Maud Brault-Favrou LIENSs, CNRS - Université de La Rochelle, France	Sample analysis, edited and revised the manuscript
Yves ChereI CEBC, CNRS - Université de La Rochelle, France	Conception of the project, data collection, sample analysis, edited and revised the manuscript
Charles-André Bost CEBC, CNRS - Université de La Rochelle	Conception of the project, data collection, edited and revised the manuscript




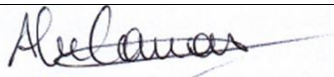



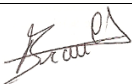


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