Does complexity in behavioral organization allow seabirds to adapt to changes in their environment?

Xavier Meyer

UNIVERSITÉ DE STRASBOURG

ÉCOLE DOCTORALE Vie et Santé (ED414)

IPHC, Département Ecologie, Physiologie & Ethologie (UMR7178)

THÈSE présentée par :

Xavier MEYER

soutenue le : **09 septembre 2016**

pour obtenir le grade de : **Docteur de l'université de Strasbourg**

Discipline/ Spécialité : Sciences du Vivant/Ecologie & Ethologie

Does complexity in behavioral organization allow seabirds to adapt to changes in their environment?

Un comportement complexe est-il adapté pour faire face à une perturbation de l'écosystème chez les oiseaux marins?

THÈSE dirigée par :

Dr. SUEUR Cédric	Maître de conférences, Université de Strasbourg
Dr. ROPERT-COUDERT Yan	Directeur de recherche, CEBC, Villiers-en-Bois

RAPPORTEURS :

Pr. ALADOS Concepción L.	Professeur, Institut Pirenaico de Ecología
Pr. DENEUBOURG Jean-Louis	Professeur, Université libre de Bruxelles

---

AUTRES MEMBRES DU JURY :

Dr. MASSEMIN Sylvie	Maître de conférences, Université de Strasbourg
Dr. MACINTOSH Andrew J.J.	Associate Professor, Kyoto University

Does complexity in behavioral organization allow seabirds to adapt to changes in their environment?

Un comportement complexe est-il adapté pour faire face à une perturbation de l'écosystème chez les oiseaux marins?

Thèse présentée pour obtenir
le grade de docteur de l'Université de Strasbourg
Discipline: Science du Vivant
Spécialité: Ecologie et Ethologie

Xavier Meyer

Soutenue publiquement le 9 septembre 2016

Devant le jury composé de :

Pr. Concepción L. Alados	Maître de conférences. IPE, Saragosse	Rapporteur externe
Pr. Jean-Louis Deneubourg	Maître de conférences. UBL, Bruxelles	Rapporteur externe
Dr. Sylvie Massemin	Maître de conférences. UNISTRA, Strasbourg	Rapporteur interne
Dr. Cédric Sueur	Maître de conférences. UNISTRA, Strasbourg	Directeur de thèse
Dr. Yan Ropert-Coudert	Directeur de recherche. CNRS, Villiers-en-Bois	Co-directeur de thèse
Dr. Andrew J.J. MacIntosh	Professeur associé. WRC-CICASP, Kyoto	Co-directeur de thèse

A mes grands-pères, Gérard et René

Remerciements

Adélie penguins,
Adélie Land, Antarctica

Remerciements/ Acknowledgments:

Et voilà, c'est la fin. Difficile de réaliser que cette thèse se fini et ferme ainsi un chapitre de trois ans de ma vie. Une thèse est loin de se dérouler de façon linéaire et peut aisément se comparer à une étape de haute-montagne sur le tour de France : passage de col dans la difficulté, parfois en s'effondrant, puis descente vers la vallée, et ainsi de suite jusqu'à l'effort final, la rédaction et la soutenance de thèse. Et bien que ça semble dans les deux cas un exercice solitaire, c'est tout le contraire en réalité : une thèse n'est pas possible sans le soutien d'un grand nombre de personnes et j'espère que je n'oublierai personne. Si c'est le cas, je m'en excuse d'avance.

Tout d'abord, je souhaite exprimer toute ma gratitude à Sylvie Massemin, Concepción L. Alados et Jean-Louis Deneubourg d'avoir accepté d'évaluer ce travail de thèse.

Je remercie Odile Petit et François Criscuolo de m'avoir accueilli au DEPE, et Charly Bost et Henri Weimerskirch de m'avoir accueilli au CEBC lors de mes séjours là-bas.

En continuant dans l'analogie avec le cyclisme (oui oui, écrire ses remerciements devant l'étape Vielha Val d'Aran/Andorre Arcalis, ça inspire et laisse des traces), un coureur (un thésard) n'est rien sans son (ses) directeur(s) de thèse. Tout simplement, merci Yan, thanks Andrew et merci Cédric. Yan, merci pour tout, pour m'avoir fait confiance, m'avoir offert l'opportunité de faire cette thèse et pour le soutien que tu m'as apporté tout au long de ma thèse tant professionnellement que personnellement. Merci de m'avoir permis d'aller voir mes modèles d'étude en chair et en plumes, sur le terrain à Phillip Island comme à DDU. Tu m'as tellement appris durant cette thèse, scientifiquement, professionnellement et humainement, que les mots me manquent pour exprimer ma reconnaissance à ton égard.

J’espère continuer à travailler avec toi dans l’avenir. Et promis, les « thus » et « aforementioned », je travaille à les limiter.

Andrew, thank you for everything, to have shared with me your enthusiasm and your knowledge about fractals (but also your talent for pool and darts), to have teach me how to be rigorous in science and finally thanks for all the comments you did on my papers and my thesis. It really helped me to push my thinking further, not only about my thesis topic but also about science in general. I did not succeed to visit you in Japan but I really hope it will be possible in a close future.

Cédric, on se connait depuis mon M1 maintenant (5 ans, ça passe vite dis donc). Merci pour m’avoir pris en stage à l’époque et de m’avoir ensuite poussé à aller voir Yan pour discuter thèse avec lui. Merci pour ta confiance, tes conseils et tes encouragements, pour avoir essayé de « stresser » un peu ma nature (dans le bon sens) qui fait que j’ai souvent l’air ailleurs ou sous l’influence de substances psychotropes (ce qui n’est pas le cas ;-)).

This thesis would not have been possible without the participation of Akiko Kato and Andre Chiaradia. Akiko, arigatou gozaimasu for processing and managing diving dataset, for your patience when you explained me how to do diving analysis on Igor and for all the comments you did on my papers. Andre, muito obrigado por tudo! I enjoyed working with you! Thank you for having welcomed me in Phillip Island and having shared of your knowledge with me. I had a great time in Phillip Island and I would like to thank Matt to have been such a nice company in the volly house and during the fieldwork. Finally, I would also like to thank Thomas Mattern for his help and contribution on New Zealand’s little penguin foraging behavior.

Un grand merci à toutes les personnes que j'ai côtoyé et qui ont rendu mon séjour dans les contrées glacées de la Terre Adélie si merveilleux. J'aimerais remercier tous les membres de la TA64, mais plus particulièrement Elsa, Christophe, Pierre, Alban, Didier, Victor et Nono pour les bons petits plats et desserts, Aymeric, Sep' et Fabien. Merci Marie de m'avoir briefé sur les Adélie et merci Andrew (aka the rapper) et Thierry (aka penguin sheriff) pour la très bonne ambiance au sein de la team 1091 tout au long de la campagne d'été.

Cette thèse aurait été bien triste sans le groupe de thésards du DEPE (mais aussi du CEBC), qui avec les détours par le Wawa et le Public House, les randonnées (« Ne vous inquiétez pas, on est presque au bout »), les soirées destruction de mobilier (« promis je n'ai pas deux mains gauches Mathilde » ;-)), lecture au congélateur et douche Kubor ont enchanté cette thèse. Pour tout cela, mais également les fous-rire de tous les jours, les pronostics foireux de l'Euro et leur soutien, merci Quentin, Agnès, Fanny, Palmyre, Philippine, Nancy, Hannah, Manon, Anthony, Emilio, Mathieu, Mathilde, Amandine, Flo et Valéria à Strasbourg et Pierre, Sophie, Flo, Rémy, Yves, Loriane, Carine, Julien, Joffrey, Camille (on va le sortir ce papier Adélie ;-)) et Sam à Chizé. Plus particulièrement, j'aimerai remercier : Emilio, le barbu dothrak chilien, pour toutes nos discussions géopolitiques et filmographiques passionnantes, les sorties ornitho dans 30cm d'eau à la poursuite de cygnes chanteurs et ce magnifique saut au-dessus de ce petit ruisseau un jour de juin. Mathieu, pour nos randonnées (on a toujours le tour des 6 lacs à faire), nos discussions cuisine et chiffon (de rando), les ateliers bricolages de vélo et tout simplement pour ton amitié. Mathilde, Amandine, petites par la taille, grandes par le cœur. J'ai adoré partagé notre bureau, merci pour les fous-rires et les moments de folie, les attaques à la boulette de papier, le chocolat du tiroir du haut et pour votre soutien. Il doit en avoir des citations dans le petit cahier. Un merci tout particulier à maman Flo, merci pour ta franchise, ton soutien et

toutes nos discussions interminables sur GoT, la cuisine et un peu de tout. Même au pays du soleil levant, ton soutien m'a été très précieux au cours de cette thèse. Et promis, je prends soin du gourdin ;-)!

Val, I would love to tell you that in Portuguese (soon ;-)). The end of this thesis would not have been the same without you. Thank you for supporting me all along this process, for always being here, giving me motivation and inspiration. You have simply made my life easier and happier and I'm feeling so grateful.

Un merci tout particulier à Nico, pour ton amitié, les « vendredi, tout est permis », les sorties en vélos, les randonnées 5 étoiles avec réchaud et canard en boîte sur le dos, la bouteille de vendanges tardives sur le côté et nos missions geocaching.

Je souhaite également remercier toutes les personnes du DEPE pour leur aide tout au long de cette thèse et avant. En particulier, un grand merci à Thierry pour ton aide à la préparation du concours de l'école doctorale, nos discussions et la formation à la capture et la manipulation de manchots Adélie. Sylvie, je t'ai déjà remercié pour avoir accepté d'être dans mon jury de thèse, j'aimerais te remercier une seconde fois pour avoir accepté d'être dans mon comité de thèse, tes conseils, ta gentillesse et le fait de toujours être attentive pour nous. Merci à Yves pour les sorties ornitho et pour avoir partagé avec nous tes connaissances naturalistes. Bien entendu, merci à Claudine et Martine pour votre aide lorsqu'il s'agit de s'aventurer dans les méandres de l'administration française, mais surtout merci pour votre bonne humeur et votre gentillesse. Enfin, merci à tous ceux au DEPE qui m'ont aidé à préparer ma soutenance de thèse.

J'ai eu la chance de pouvoir enseigner en licence durant deux ans et j'aimerais pour cela remercier Sylvie Raison pour m'avoir fait confiance et m'avoir permis de découvrir le monde

de l'enseignement. J'ai adoré cette expérience et elle m'a ouvert de nouveaux horizons. Je tiens ainsi à remercier tous mes élèves de L2 (2014-2015, 2015-2016) mais également le super groupe de moniteurs/enseignants: Valentine, Séb, Evelyne, Mathieu, Emilio, Agnès et Anne. Merci Anne pour les sorties escalades au SUAPS et Rock & Stock durant cette dernière année de thèse. Comme j'en suis à l'escalade, je tenais à remercier l'ensemble des personnes du SUAPS-escalade pour m'avoir fait découvrir un nouveau sport qui m'a fait le plus grand bien durant cette thèse.

Avant et durant cette thèse, j'ai aussi pu compter sur le soutien de nombreuses personnes. Merci Barbara, Cathy et Bernard pour m'avoir aidé et soutenu lors de l'obtention de ma bourse de thèse. Un très grand merci à Fred, on se connaît maintenant depuis de nombreuses années et tu m'as toujours aidé à prendre du recul sur mon travail par nos discussions diverses et variées, nos randonnées/trek dans les Vosges et dans les Alpes. Merci pour ton soutien. Un très très très grand merci à Marion, pour nos discussions quotidiennes et m'avoir permis de m'évader dès que possible dans les Alpes pour des week-ends skis ou rando. Fred, Marion, merci pour votre présence, votre amitié et votre soutien, ma thèse n'aurait sans doute pas été la même sans vous.

Enfin et pour finir, j'aimerais remercier ceux sans qui je n'aurais pas réussi à arriver là où j'en suis aujourd'hui. Maman, Papa, je ne pense pas vous l'avoir souvent dit, même jamais, mais merci pour tout, pour votre soutien sans faille (même à l'autre bout de la planète) et pour m'avoir toujours aidé et encouragé à faire ce que je voulais. Vous m'avez transmis votre passion pour la nature et surtout la montagne, mais vous m'avez également donné toutes les clés pour réussir dans la vie. Aurel, Charlotte, je sais que votre grand frère vous a parfois paru bizarre (et oui faire peur à son frère ou sa sœur avec épervier en voie de

décomposition, ça fait de vous quelqu'un de bizarre ;-)), mais merci de m'avoir toujours accepté comme ça et soutenu. Enfin, je ne pouvais pas finir sans parler de mes grands-parents. Pour votre soutien sans faille, vos encouragements et votre amour, merci Mamie, merci Mamama, merci Papi, merci Papapa! Papi, Papapa, vous êtes partis avant la fin de cette thèse mais je sais que vous auriez été fiers de voir cet accomplissement auquel vous avez tant contribué. Merci !

Presque 6 pages de remerciements pourraient paraître un peu long, mais je pense que cela ne représente qu'un court résumé de toute l'aide reçue pendant cette thèse, mais aussi avant. Je ne pouvais pas finir ces remerciements sans évoquer toute la gratitude que j'ai envers mes modèles d'études : vous m'avez mordu, frappé, vous m'avez déféqué dessus, certains l'ont faites à la Gandalf (« You shall not pass ») pendant que d'autres l'ont faites à la Hannibal et à la Dexter, mais je vous ai aimé. Pour tout ça, merci les manchots!

Souvenir de la 2nd World Seabird Conference (2015), Le Cap, Afrique du Sud.


Articles et communications
Cape of Good Hope & Cape Point Lighthouse, South Africa
Xavier G. Meyer

Liste des études sur lesquelles ce travail est basé

Article A: Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species. Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, André Chiaradia et Yan Ropert-Coudert. **Publié dans Animal Biotelemetry**, 2015, 3:25, doi: 10.1186/s40317-015-0061-8

Article B: Shallow divers, deep waters, and the rise of behavioral stochasticity. Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, Andre Chiaradia, Thomas Mattern, Cédric Sueur et Yan Ropert-Coudert. **Soumis à Journal of Experimental Marine Biology and Ecology**.

Article C: Foraging behaviour organization variability in a seabird species highlights environmental changes. Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, Andre Chiaradia, Cédric Sueur et Yan Ropert-Coudert. **En préparation**.

Article présenté en annexe

A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. Yan Ropert-Coudert, Akiko Kato, Xavier Meyer, Marie Pellé, Andrew J.J. MacIntosh, Fréderic Angelier, Olivier Chastel, Michel Widmann, Ben Arthur, Ben Raymond et Thierry Raclot. Publié dans **Ecography**, 2015, 37:001-003, doi: 10.1111/ecog.01182

Autres études en cours

Multiyear analysis of diving activity of Adélie penguins: inter-annual changes and relation with sea-ice. *En collaboration avec Camille Le Guen, Akiko Kato et Yan Ropert-Coudert (see Annex 4).*

Communications orales présentées dans le cadre de la thèse

- "Fractal time series analysis: new insight into ecological processes". Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, André Chiaradia, Cédric Sueur et Yan Ropert-Coudert. 1^{eres} journées du GDR Ecostat, Lyon, France. 12-13 Mars 2015.
- "Hydrodynamic handicaps imposed by animal-attached recording devices alter structural complexity of penguin dive sequence". Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, André Chiaradia, Cédric Sueur et Yan Ropert-Coudert. 11th Ecology & Behaviour meeting, Toulouse, France. 18-21 Mai 2015.
- "Shallow divers in deep waters: does bathymetry lead to behavioural stochasticity?" Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, André Chiaradia, Thomas Mattern, Cédric Sueur et Yan Ropert-Coudert. 2nd World Seabird Conference, Le Cap, Afrique du Sud. 26-30 Octobre 2015.

Posters présentés dans le cadre de la thèse

- "Our iceberg may not be melting but the wind is definitely turning?" Yan Ropert-Coudert, Akiko Kato, Xavier Meyer*, Marie Pellé, Andrew J.J. MacIntosh, Fréderic Angelier, Olivier Chastel, Michel Widmann, Ben Arthur, Ben Raymond et Thierry Raclot. 2nd World Seabird Conference, Le Cap, Afrique du Sud. 26-30 Octobre 2015.

  * Présentateur

Vulgarisation scientifique

- "Walking on the wild side: should I stay or should I go". Vulgarisation de mes travaux de master et de thèse devant le personnel du Phillip Island Nature Parks, Australie, Novembre 2013.

- "Travailler la tête en bas: l'étude des manchots dans l'hémisphère sud ". Présentation lors de la journée des doctorants de l'IPHC en collaboration avec Quentin Schull. Nous y avons abordé les différentes espèces de manchots étudiés au laboratoire ainsi que les caractéristiques des sites d'études. Juin 2014.

- Vulgarisation des résultats d'une étude scientifique : une partie du travail que j'ai réalisé dans le cadre de ma campagne d'été à Dumont D'Urville, Terre Adélie a permis de mettre en évidence l'influence de conditions météorologiques inhabituelles sur un échec total de reproduction chez les manchots Adélie vivant sur l'île des Pétrels (Ropert-Coudert et al. 2015). Une brève de l'INEE a été publiée à l'occasion de la sortie de l'étude :

  http://www.cnrs.fr/inee/communication/breves/b073.html

- Participation à la conception et la présentation du stand du DEPE à la fête de la Science sur la thématique "Chasseurs de lumière". Octobre 2015.

- Participation au projet pédagogique "Embarquez en Antarctique" porté par la Maison de la Science Alsace, la Maison de la Science Bretagne, l'IPEV, l'EOST et le Muséum National d'Histoire Naturelle de Paris. Lors de l'inauguration du projet (novembre 2015), j'ai présenté le programme 1091 (IPEV) "l'AMMER: les manchots Adélie comme bioplateformes de l'environnement" dans le cadre duquel j'ai réalisé ma

campagne d'été en Antarctique. J'ai ensuite été impliqué dans le développement de ce projet en collaboration avec Corinne Walliang et Colette Schatz. Ainsi, je me suis rendu dans la classe de CM1-CM2 de Corinne Walliang à l'école primaire de Willer-sur-Thur afin d'y réaliser une intervention sur la thématique : "Travailler la tête en bas: un été en Antarctique" (Mai 2016).

- Participation au concours interne de ma thèse en 180 secondes de l'IPHC. Janvier 2016.

Table des matières

Adélie Land,
Antarctica

L

Table des matières

Figures et tables

Introduction

Summerland Peninsula,
Phillip Island, Australia

I. Introduction

I.1 Environmental changes

I.1.1 Living in a changing world

"Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, and sea level has risen." (IPCC, 2014)

It is with these words that the last Climate Change Synthesis Report begins (IPCC, 2014). Over the period 1880 to 2012, the globally-averaged combined land and ocean surface temperature has risen to 0.85°C (Figure I.1; IPCC, 2014). This increase of temperature has been attributed to the rise of atmospheric carbon dioxide (CO_2) levels, mainly caused by human activities (IPCC, 2014).

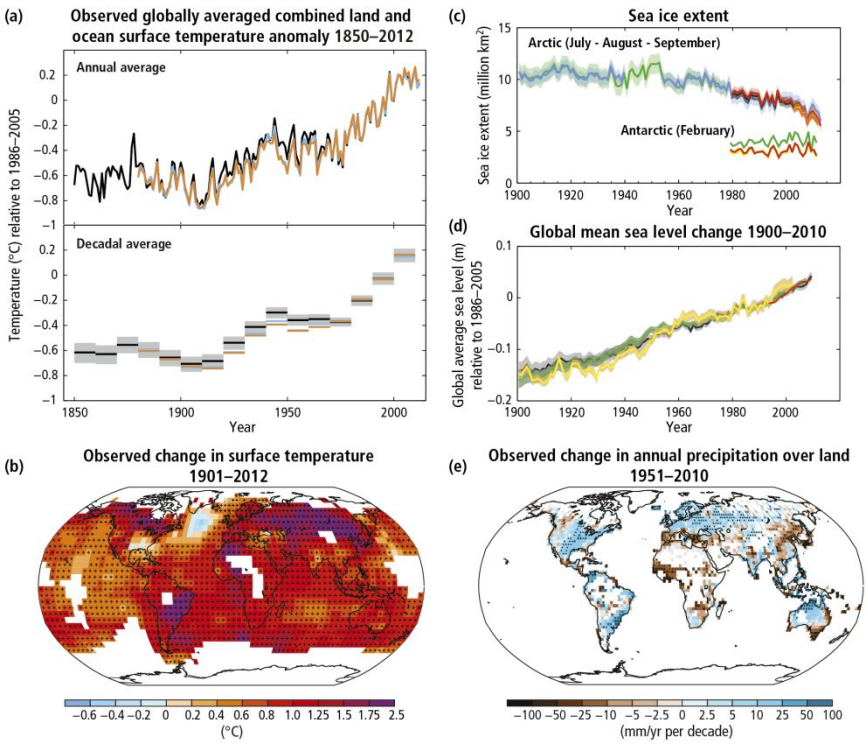


Figure I.1 : Multiple environmental indicators of a changing global climate system (from IPCC, 2014)

From polar to tropical environments, both in marine and terrestrial ecosystems, recent climate changes have induced various ecological responses over a broad range of organisms with diverse geographical distributions (Walther *et al.*, 2002; Walther, 2010). Biotic interactions, either at temporal or spatial levels, have been influenced by climatic parameters (Walther, 2010). For instance, phenological changes in plants and animals were reported with consequences on food webs, host-parasite webs and mutualistic webs (e.g. Barbraud & Weimerskirch, 2006; Chambers *et al.*, 2013). Simultaneously, climate change has induced shifts in species distribution ranges along altitudinal and latitudinal gradients, leading to the spatial reorganization of communities and finally modifications of trophic interactions and food webs.

However, the vast majority of studies examining climate change effects on ecosystems are concerned mainly with terrestrial ecosystems. Despite covering 71% of Earth's surface, the oceans are less studied than terrestrial ecosystems and it is even more surprising when one considers the major regulatory role marine ecosystems play at the climatic level (Richardson & Poloczanska, 2008). A reason might be the size, the complexity and the difficulty of conducting long-term monitoring studies in marine environments (Hoegh-Guldberg & Bruno, 2010). The IPCC Five Assessment Report (IPCC, 2014), however, indicates that marine ecosystems may be extremely vulnerable to climate change and changes can already be observed from polar marine to tropical marine ecosystems, highlighting the need to study them intensively in the future.

I.1.2 Physical and chemical changes affecting ocean ecosystems

The two major direct consequences of rising atmospheric carbon dioxide (CO_2) produced by human activities on oceans are an increase in water temperatures and acidity (Hoegh-

Guldberg & Bruno, 2010; Doney *et al.*, 2012). Most of the additional energy injected into the atmosphere through greenhouse effects is absorbed by oceans, which has led to a warming of the upper 75m layer of the oceans of 0.11°C per decade over the period 1971 to 2010. A recent estimate suggests that the oceans have absorbed approximately one-third of the CO_2 produced by human activities (Doney *et al.*, 2012). In turn, rising temperatures (i) increase ocean stratification, which in turn decreases oxygen concentrations (Keeling *et al.*, 2010; Rabalais *et al.*, 2010), (ii) modify sea-ice dynamics and extents (Stroeve *et al.*, 2012; Bintanja *et al.*, 2013), (iii) alter precipitation patterns and thus freshwater input, and iv) alter the patterns of ocean circulation (Hayward, 1997; Clark *et al.*, 2002). Currents indeed play a critical role in the dynamics of regional climates (e.g. major effects of the Atlantic Meridional Overturning Circulation on European climate (Pohlmann *et al.*, 2006)). Climate changes will also interact with natural variability of the ocean climate system, such as the El-Niño /Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO). In addition, these changes are interacting with other human activities, such as overfishing and eutrophication (Halpern *et al.*, 2008), which enhance the detrimental impact of climatic factors and have strong, negative consequences on the distribution and abundance of marine resources.

The ability of a given species to buffer environmental changes can be expressed at different levels of organization and different time scales. Over long time scales, adaptation to new conditions can occur at the molecular level though genotypic adaptation and the selection of tolerant genotypes over generations (Peñuelas *et al.*, 2013; Reusch, 2014). However, at short time scales, when a change occurs in the environment the most immediate responses are at the individual level (i.e. physiology and/or behavior). Species can eventually acclimatize through phenotypic adaptation and an adjustment of the

physiological characteristics of the individual. For example, a rise in ocean temperature is expected to lead to an increase in the metabolic rates of ectothermic organisms that would thus enhance primary production and growth rates in planktonic species (Kordas *et al.*, 2011; Doney *et al.*, 2012). Yet, the situation is not always so clear, and warmer waters are also characterized by lower oxygen and food availability, factors that would instead limit both growth and production of ectothermic species (Doney *et al.*, 2012). Besides physiological adaptations, changes in behavior can also allow species to cope with some of the new environmental conditions, for example by selecting preferential temperature ranges like in Atlantic Cod (*Gadus morhua*; Perry *et al.*, 2005). Alternatively, when changes become impossible to buffer, to escape from them altogether (e.g. the migration of birds in the UK (Thomas & Lennon, 1999), or changes in butterfly phenology (Roy & Sparks, 2000)). In the worst-case scenario, species are unable to adapt and environmental changes ultimately lead to death and local extinction (e.g. coral reefs (Carpenter *et al.*, 2008)).

I.1.3 Food web responses

As species interact via prey-predator relationships, food competition, etc., changes at the population (single species) level should have consequences at the community (multispecies) level, resulting in a decrease in species abundance and population productivity, and/or changes in the distribution and dispersion of species involved in the trophic network. In their review, Doney *et al.* (2012) mention that climate-related distribution shifts drive alterations in community composition across several species from rocky intertidal invertebrates to seabirds. These shifts lead finally to alteration in trophic interactions and structure at the ecosystem level. The ecosystem level will integrate physiological responses of organisms but also changes in the ecological interactions between all living organisms in the system.

Box 1: The California Current System: a case study of the effect of environmental changes on eco-indicators, such as seabirds, throughout the trophic chain.

The California current is flowing along the west coast of North America, carrying cold subarctic waters from the North which conjugate with wind-driven coastal upwelling flows that supply nutrients to the upper ocean. This is one of the four highest productive eastern boundary current in the world (Doney *et al.*, 2012). This current system is strongly influenced by natural climate variability: phenomenon like ENSO, PDO and the North Pacific Gyre Oscillation (Chavez *et al.*, 2011; Jacox *et al.*, 2015) play an important role in food web structure and productivity (figure I.2). In reaction to these climate variations, zooplankton communities vary in distribution and abundance (Doney *et al.*, 2012; Fisher *et al.*, 2015), impacting the upper-level predators like seabirds. Under warm-water conditions, seabirds present changes in abundance, distribution and behavior at sea but also changes in their diet, highlighting changes in the distribution and abundance of their prey communities (Oedekoven *et al.*, 2001; Hyrenbach & Veit, 2003; Sydeman *et al.*, 2006, 2014; Lyday *et al.*, 2014; Santora & Sydeman, 2015). This case study highlights the usefulness of seabirds as indicators of ocean productivity and prey availability.

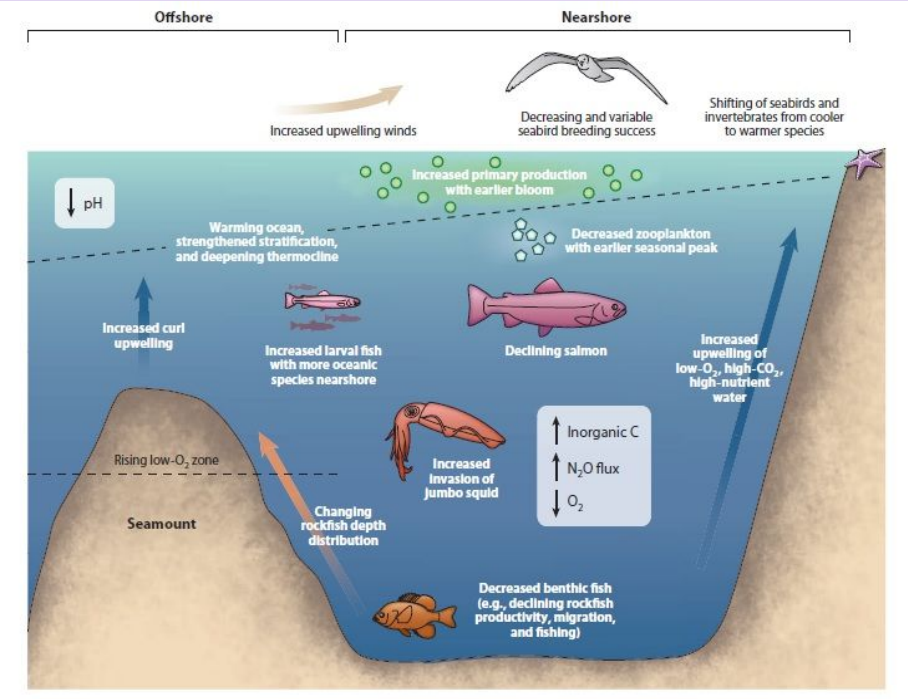


Figure I.2 : Summary of climate-dependent changes affecting the trophic web in the California Current system (from Doney et al., 2012)

Population and community levels are connected to ecosystem levels throughout the trophic structure, food-web dynamics, energy flow and biogeochemical cycle. Two main processes are thought to link changes in one trophic level to another, depending on the direction of the effect. On the one hand, if the changes are driven by declines at low trophic levels (e.g. declines in water column primary production), the process is described as a bottom-up process. On the other hand, if the changes are driven by declines at high trophic levels (e.g. decreases in the size of meso- or top-predator populations), the process is described as a top-down processes, which could be described as a cascade process from the losses or gains of ecologically dominant consumers. Monitoring these changes at each trophic level in an entire marine ecosystem long-term is complicated and economically costly. However, it has been shown that changes are amplified at higher trophic levels due to cascading effects and energy assimilation(Doney *et al.*, 2012). Consequently, responses of predators such as seabirds and marine mammals at upper trophic levels - from foraging strategies to demographic parameters - can indicate changes occurring at lower levels of the food web. Here, meso/top predators are used as "eco-indicators" of the entire ecosystem (See Box 1) (Furness & Camphuysen, 1997; Boyd & Murray, 2001; Frederiksen *et al.*, 2006).

I.2 Seabirds as eco-indicators of the environment

In order to qualify a species as a good eco-indicator of environmental changes, the species must respond in a sensitive and rapid way to environmental variability over multiple spatial and temporal scales (Briggs & Chu, 1986; Veit *et al.*, 1997; Hyrenbach & Veit, 2003; Springer *et al.*, 2003). In addition, mechanisms linking changes at lower trophic levels and changes in upper-level predators should preferably be well understood. Seabirds - with about 300 species in at least four different orders: Charadriiformes, Pelecaniformes,

Procellariiformes and Sphenisciformes (Gaston, 2004) - are perfect candidates for this eco-indicator status.

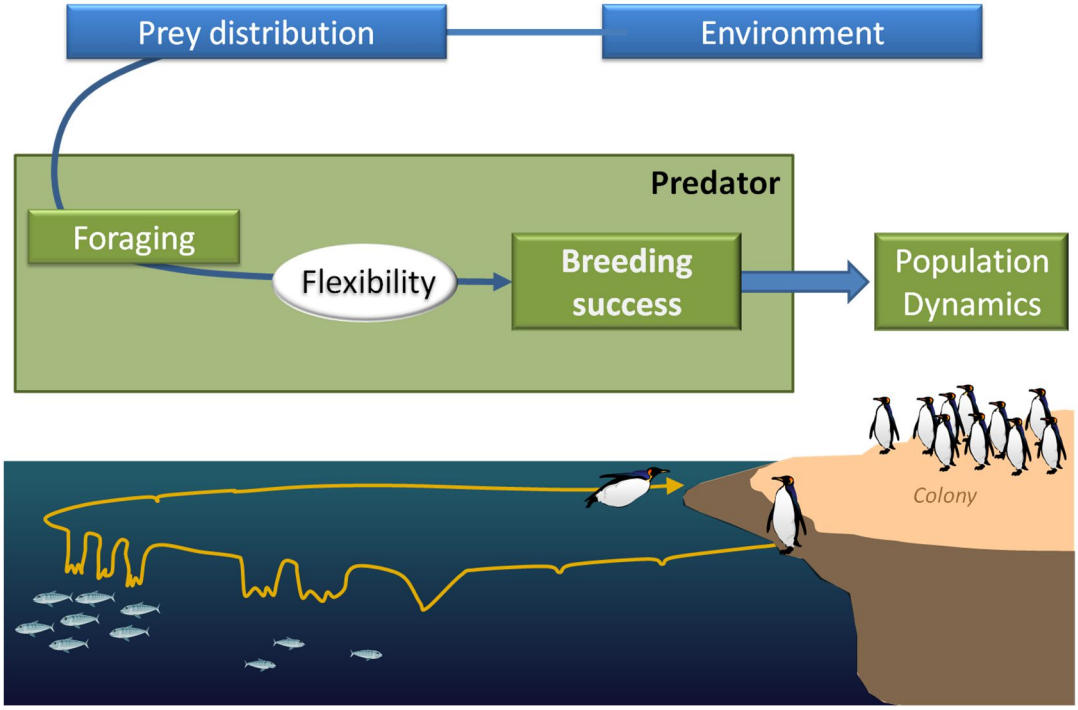


Figure I.3 : Schema showing the cascading effects of environmental changes on the population dynamic of central-place foragers and potential behavioral mechanism exhibited by the central-place foragers to buffer these changes. Environment changes induces different scenarios of prey distribution over time and space which will have multiple and complex effect on foraging behavior of predators, which will affect the breeding success and by extension dynamic of population. To buffer environment changes, marine predators would exhibit high flexibility in foraging behavior strategies in order to maximize their energy intakes.

Seabirds are widely distributed across the globe and have colonized almost all marine ecosystems. As meso-predators, they provide a way to monitor changes occurring at lower trophic levels in marine food chains, as they feed on prey from littoral to pelagic areas (Furness & Camphuysen, 1997; Ballance, 2007). They can especially inform us about the fluctuations in prey abundance and distribution linked to environmental changes (Frederiksen *et al.*, 2007). Finally, thanks to the development of animal-embarked monitoring methods like biotelemetry and bio-logging (e.g. Kooyman, 2004; Ropert-Coudert & Wilson, 2005; Ropert-Coudert *et al.*, 2012; Evans *et al.*, 2013; Wilmers *et al.*, 2015),

scientists are able to investigate in fine detail the foraging behavior of these birds even when it takes place remotely at-sea. While seabirds spend the majority of their time at sea, where they obtain their food, they must breed on land. Therefore, during their reproduction, birds are forced to commute between the colony and foraging sites, and are thus defined as 'central-place foragers'. Central-place foragers are constrained by a diverse set of physical parameters, such as sea-ice in polar regions (Watanuki *et al.*, 1997), bathymetry (Chiaradia *et al.*, 2007) and marine currents (Bost *et al.*, 2009). These constraints can impact the foraging and breeding success of individuals, and as consequence, the dynamics of seabird populations (Figure I.3). The costs of being a 'central-place forager' is further accentuated as the colony size increases due to intra- (but also inter-) specific competition at-sea (Lewis *et al.*, 2001; Ainley *et al.*, 2003). All these interacting factors make the foraging behavior of upper-level marine predators complex and diversified (Morrison *et al.*, 1990). For instance, seabirds require flexibility in their foraging behavior (i.e. altering their behavior) to catch mobile prey (Williams *et al.*, 1992; Hull, 2000) and are known to use a diverse array of hunting tactics, including plunge diving, dipping and pursuit diving (Schreiber & Burger, 2001). As such, seabirds can show a great variability in foraging behavior responses to environmental changes even within a homogeneous group like albatrosses (Weimerskirch, 1998; Weimerskirch & Guionnet, 2002), or even within a species, such as the highly variable within-species foraging (diving) behavior of rockhopper penguins (*Eudyptes chrysocome*) (Tremblay & Cherel, 2003), gentoo penguins (*Pygoscelis papua*) (Lescroël & Bost, 2005) and little penguins (*Eudyptula minor*) (Chiaradia *et al.*, 2007) when measured in different locations. This suggests that exposure to different environmental constraints results in differences in foraging behavior, which is itself comprised of a complex array of separate components. One illustration of such complexity can be found in the multiple variables that

are used to describe diving activity: dive depth, dive duration, bottom phase duration, post-dive duration, frequency of diving (e.g. Tremblay & Cherel, 2003; Chiaradia *et al.*, 2007; Ropert-Coudert *et al.*, 2009; Cook *et al.*, 2012; Pelletier *et al.*, 2012). A common approach to studying diving behavior consists of analyzing several of these diving variables in parallel. Although such classically-used diving variables undoubtedly provide useful quantitative information about behavior, variations observed in these numerous and often inter-related metrics can be difficult to interpret (Zimmer *et al.*, 2011a)(Box 2). In this context, researchers constantly explore novel analytical approaches that take advantage of methodologies developed in other fields and that might contribute to ours. From this perspective, the field of statistical physics has provided a particularly useful set of tools to improve our ability to evaluate foraging activity of seabirds. Borrowing from other fields of science (e.g. medicine, physics, economy), other approaches have been used in parallel, such as statistical clustering techniques or developing artificial neural networks to explore foraging behavior (e.g. (Schreer *et al.*, 1998; Sakamoto *et al.*, 2009). Recently, methods based on autocorrelation (Hart *et al.*, 2010) and fractal analysis (MacIntosh *et al.*, 2013) of foraging time series have increasingly been used to study the foraging behavior of multiple species, including seabirds.

Box 2: Disentangle the complex relationship between foraging parameters in diving seabirds.

Several attempts have been done to interpret foraging behavior data obtained through bio-loggers. For example, Zimmer *et al.* (2011) proposed a method based on the interpretation of primary output from Principal Component Analyses (PCA) to understand the relationship among several foraging parameters (Figure I.4). The authors used 6 diving variables summarized in 4 categories: (1) the diving frequency (number of dives), (2) the diving effort (total time spent underwater and mean bottom duration), (3) the prey distribution (median maximum dive depth) and (4) the hunting effort (percentage of prey encounter dives and the total time of prey pursuit). Then, they performed four PCA using each one of the following factors that are known to affect foraging behavior: body mass (PCA1), foraging date (PCA2), chicks' age (PCA3) and adult age (PCA4). Results suggest that the relationship between changes in prey availability and hunting effort could change at a fine scale within a breeding stage, but also that offspring age could be considered as a significant factor, while body mass, despite conditioning the amount of air that can be trapped, does not significantly affect most diving variables on the primary PCA axis. More specifically, this approach highlights the complex relationship between foraging parameters across time, and the need to disentangle these when dealing with foraging behavior across breeding seasons.

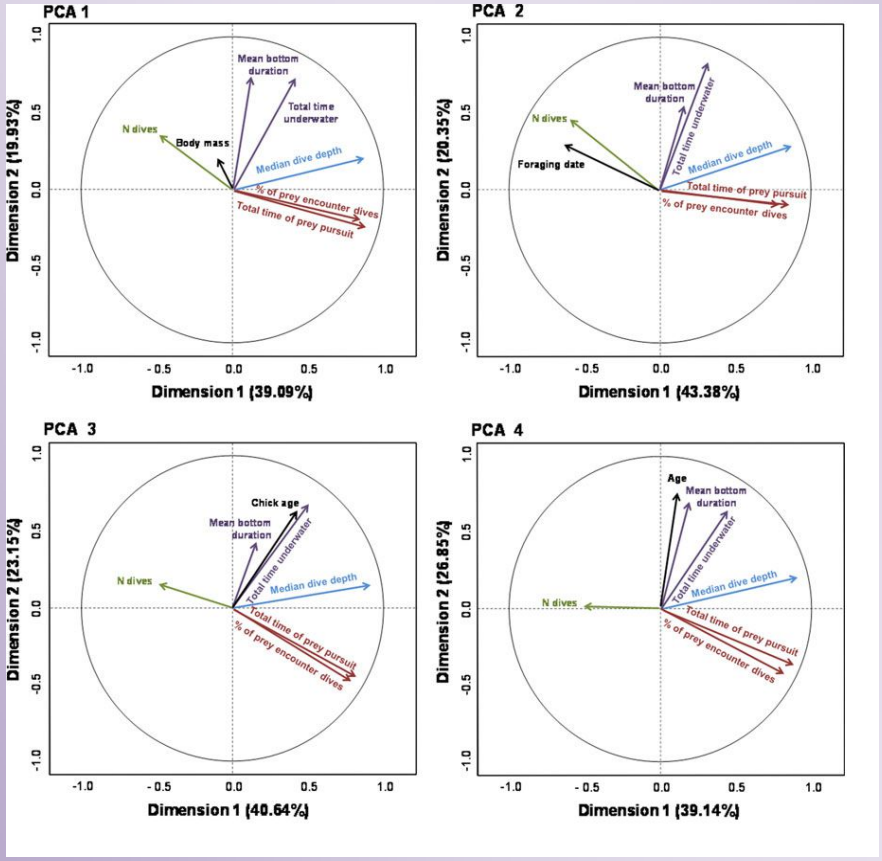


Figure I.4 : Principal Component Analysis used by Zimmer et al. (2011) to describe the complex interaction of intrinsic and extrinsic factors involved in the foraging activity of little penguin.

I.3 Diving into a fractal world

I.3.1 Fractals in Science

"*Clouds are not spheres, mountains are not cones, coastlines are not circles, and bark is not smooth, nor does lightning travel in a straight line*" (Benoît Mandelbrot, 1977)

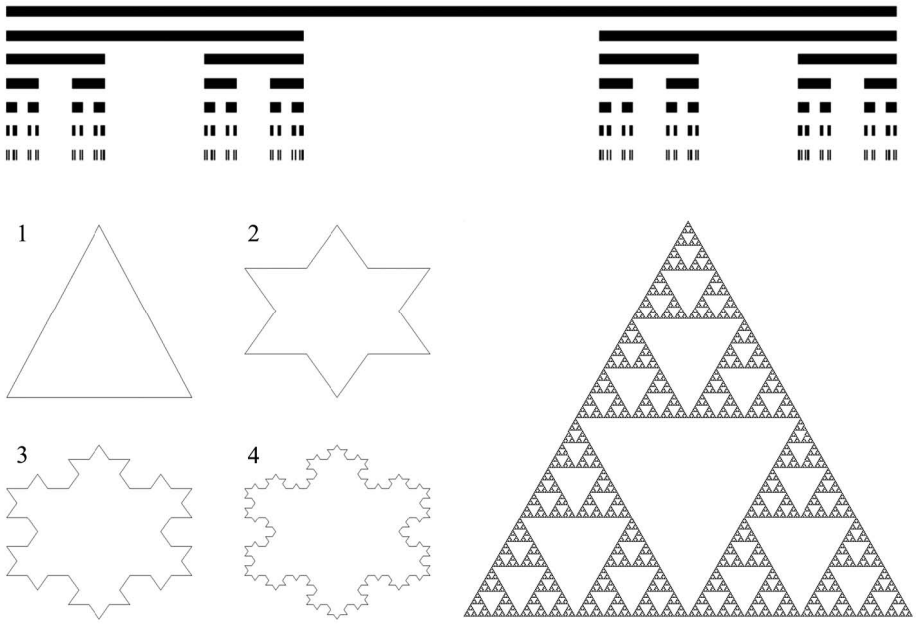


Figure I.5 : 'Mathematical monsters': on the top, the Cantor set which is formed by simply removing the middle third of each line recursively. On the bottom left, the construction of the Koch snowflake begins by dividing each line segment into three equal parts and adds an equilateral triangle with the removed middle segment acting as a base. On the bottom right left, the Sierpinski triangle's construction begins with a filled in equilateral triangle, place a point at the center of each of its three sides. Then, these three points are connected with new vertices while keeping the old vertices intact; four smaller triangles are produced among which the center triangle is removed. It results in three filled in equilateral triangles each with vertices half the length of the original and each touching both other triangles at a corner such that a triangle-shaped 'hole' is left in the center. The figure showed here is the result of many iterations of the process (from MacIntosh, 2014).

Before the seminal work of Benoit Mandelbrot (1977), scientists had difficulties characterizing mathematically natural objects and phenomena using Euclidian geometry. Various 'mathematical monsters' such as the Cantor set, Koch snowflake and Sierpinski triangle (Figure I.5), which were designed during the 19th century, eluded mathematical explanation (e.g. length, surface area, etc.) using Euclidian geometry. Mandelbrot's studies

on these ‘mathematical monsters’ led to the creation of a new field of mathematics, called fractal geometry. These patterns, known as fractal patterns, are characterized by the existence of self-similarity elements that appear recurrently at different scales. In other words, when one zooms on a global pattern, the same patterns are observable over and over again as reduced-scale images of the whole. In fractals, these recurrent patterns are linked through a common scaling exponent that describes the scaling relationship. In nature, fractal patterns are reproduced only with a statistical fidelity, but they remain close enough to the original ‘mathematical monsters’ to defy description by simple Euclidean geometry. In this context, Mandelbrot described fractal geometry as the geometry of nature.

Mathematically, the fractal concept can be characterized as having Haussdorff-Besicovitch (H-B) dimensions that exceed their topological (Euclidean) dimensions (Mandelbrot, 1977). Conversely, as explained by Peitgen *et al.* (2004), the H-B dimensions of non-fractal Euclidian shapes (e.g. points, lines, planes and spaces) are equal to their topological dimensions of 0, 1, 2 and 3, respectively. For example, for lines, squares and cubes, their scaling behavior will be governed by a strict power law which has an exponent equal to the topological dimension. To make it simpler, if you reduce a line by 1/3, you will have two copies of the reduced versions. Assembling them again will reproduce the original version. To estimate the relationship between the reduction factor and the number of pieces into which the object can be cut, self-similarity dimension, a type of fractal dimension estimate, can be used. In the example of the line, the self-similarity dimension is 1, the same as the line’s topological dimension. Analogously, the self-similarity dimension is 2 for squares and 3 for cubes, as indicated by the scaling exponent. These types of shapes and fractal shapes could be differentiated through 2 aspects: (a) the self-similarity dimension is an integer for Euclidean shapes, i.e. not fractional, and (b) the reduction factor can take

absolutely any value and the same power law will hold for Euclidean shapes. Even if statistical fractals observed in nature are more complicated, this description introduces two fundamental properties of fractal shapes: self-similarity (or self-affinity) and scaling. As defined by Mandelbrot (1967, 1977), fractal dimension will represent the relationship between patterns within a structure and the scale at which they are measured. As a consequence, it provides a quantitative measure of inherent structural complexity and describes the geometry of physical structures but also the correlation properties of temporal processes.

Since the seminal work of Mandelbrot in the 1960's through 1980's, there has been an explosion of interest in the development and use of fractal geometry in most of fields of study, including pure mathematics, statistical physics, computer science, economics, life and earth sciences. For example, fractal geometry has been used to characterize the coastline of Britain (Mandelbrot, 1967), Jackson Pollock's paintings (Taylor *et al.*, 1999), weather fluctuations (Koscielny-Bunde *et al.*, 1998; Meseguer-Ruiz *et al.*, 2016), city growth (Makse *et al.*, 1995), economics (Mantegna & Stanley, 1994, 1995; Stanley *et al.*, 1996, 1999), and biological processes from evolution (Raup, 1986; Kauffman & Johnsen, 1991; Bak & Sneppen, 1993; Chaline *et al.*, 1999; Solé *et al.*, 1999; Nottale *et al.*, 2002) to DNA nucleotide sequences (Peng *et al.*, 1992, 1994), heart rate variability (Havlin *et al.*, 1995; Peng *et al.*, 1995a; Perkiömäki *et al.*, 2005), stride patterns (Hausdorff *et al.*, 1995, 1996), neural activity (Abasolo *et al.*, 2008) and animal behavior (Wiens *et al.*, 1995; Alados *et al.*, 1996; Viswanathan *et al.*, 1996, 2008; Rutherford *et al.*, 2004, 2006, 2003; Boyer *et al.*, 2004; Bartumeus, 2007; Bartumeus & Levin, 2008; Seuront & Cribb, 2011; MacIntosh *et al.*, 2011, 2013; Humphries *et al.*, 2012; Wearmouth *et al.*, 2014; Cottin *et al.*, 2014; Cribb & Seuront, 2016). Despite this considerable interest in fractals in general, the fields of ecology and

evolution have paid less – yet growing – interest in fractal geometry over the last 30 years (Figure I.6).

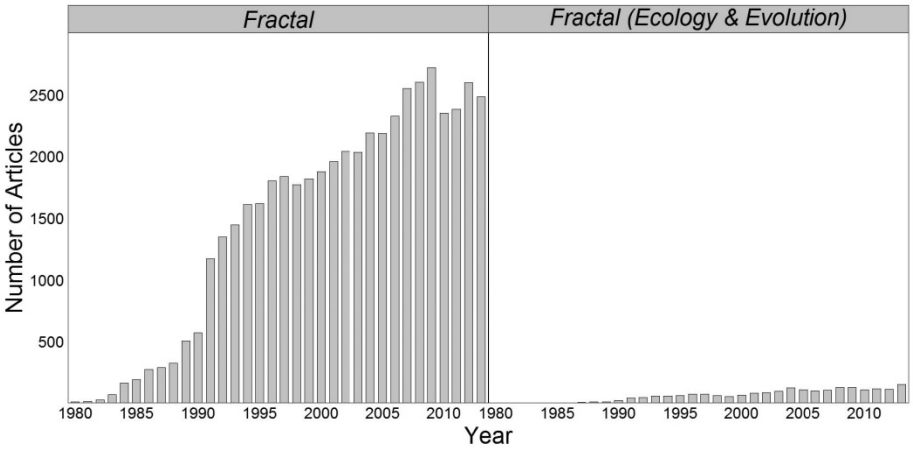


Figure I.6 : Evolution of numbers of articles published using fractal between 1980 & 2013 in all domains (at left) and in ecology and evolution (from MacIntosh, 2014)

I.3.2 Fractals in ecology

As reviewed in MacIntosh (2014), many fruitful applications of fractals in ecology have been identified and used to investigate phenomena such as structural hierarchies in coral reefs (Bradbury & Reichelt, 1983), succession dynamics in forest ecosystems (Hastings *et al.*, 1982), properties of food webs (Sugihara *et al.*, 1989) and variability in animal population densities (Pimm & Redfearn, 1988). Apart from these, the use of fractal statistics in the field of animal movement ecology has become commonplace. These applications of fractals in animal movement ecology are based on three hypotheses and/or approaches: 1) the Lévy Flight Foraging Hypothesis (LFFH), 2) the tortuosity for spatial analyses and 3) fractal time for temporal analysis.

I.3.2.a Animal movement: description of fractal applications

Movement can be described as a reaction-diffusion process centered around biological encounters (Einstein, 1956). Animals will diffuse in the environment via movements in order

to search for relevant encounters (e.g. food, mates) or avoid others, such as predators, before returning again to search (Viswanathan *et al.*, 2008, 2011). The mean squared displacement of a particle in normal diffusion processes is a linear function of time (Figure I.7 A). However, literature have actually highlighted in several species, such as primates (e.g: spider monkeys (*Ateles geoffroyi)*; Boyer *et al.*, 2004, 2006; Ramos-Fernandez *et al.*, 2004), marine predators (Viswanathan *et al.*, 1996; Sims *et al.*, 2008; Humphries *et al.*, 2012) and even humans (Bertrand *et al.*, 2005; Brown *et al.*, 2007; Raichlen *et al.*, 2013) that diffusion processes in animal movement is actually non-linear through time and exhibits a power law function (Figure I.7 B). The Lévy Flight Foraging Hypothesis (LFFH) is based on observations of such anomalous diffusion processes in animal movement and stipulates that the presence of such patterns may reflect, through the super-diffusive and fractal properties of these complex and non-linear movements (i.e. Lévy walks, which are random walks comprised of clusters of multiple short steps with longer steps between them (Reynolds, 2015)), an evolved strategy that optimizes resource encounters in both space and time, and thus energy balance, in heterogeneous environments (Bartumeus & Catalan, 2009; Viswanathan *et al.*, 2011).

The second approach to the study of fractal patterns in animal movement centers around tortuosity, and attempts to understand the importance of landscape scales on animal movement decisions, dispersion and distributions, as well as an animal's perception of habitat heterogeneity (Dicke & Burrough, 1988; Crist *et al.*, 1992; Johnson *et al.*, 1992; Wiens *et al.*, 1993, 1995). This approach is summarized by its key concept, tortuosity, which refers to the degree to which a curve consists of frequent turns with large turning angles (Dicke & Burrough, 1988). The two fractal hypotheses described above are concerned mostly with

spatial issues. Yet, there is a third approach that investigates the temporal characteristics of animal behavior and which is known as the 'fractal-time' approach.

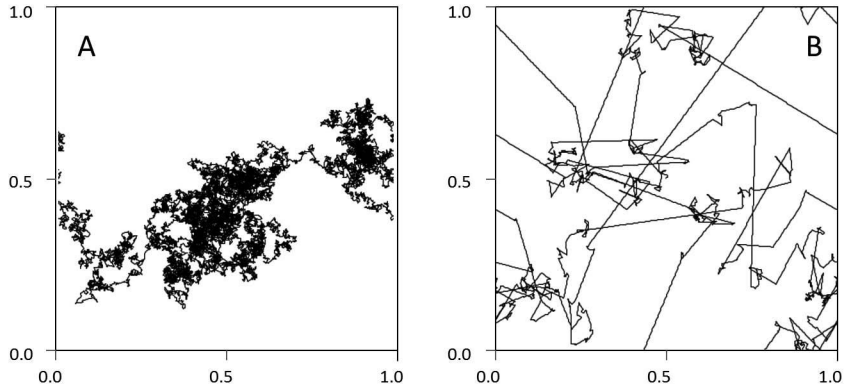


Figure I.7 : Typical trajectories taken by random walkers with step length distribution exhibiting (A) Gaussian versus (B) Lévy statistics.

The fractal time approach examines the sequential distribution of behaviors as they occur across time, i.e. behavioral time series. The pioneering studies of fractal time in animal behavior appeared in the 1990's, focusing on statistical properties in animal search behavior (Shimada *et al.*, 1993, 1995; Cole, 1995) or the effects of potential stressors on animal behavior in drug testing and animal welfare settings (Motohashi *et al.*, 1993; Escós *et al.*, 1995; Alados *et al.*, 1996; Alados & Weber, 1999). Borrowing from the field of complexity science, these studies adopted the term 'complexity' to refer to the correlation structure of the time series, which behave as nonlinear systems (Bradbury & Vehrencamp, 2014).

I.3.2.b Differences and contributions of each fractal approach

As presented above, we can highlight a dichotomy in application of fractal analysis to animal behavior. On the one hand, the two first approaches, one testing the LFFH and the other examining tortuosity, have been used in studies describing and interpreting animal movement patterns with respect to optimal foraging theory.

Studies testing LFFH have mostly used distributional characteristics of step lengths (distances between successive reorientations), turning angles and waiting times in order to see if animals show Lévy statistics in their movement patterns (see next section for a more extensive background). However, criticisms of the analytical approach and interpretation of the underlying causes of Lévy movements are numerous, and the validity of the LFFH remains a topic of hot debate in the literature (Benhamou, 2007; Edwards *et al.*, 2007; James *et al.*, 2011; Benhamou & Collet, 2015; Pyke, 2015; Reynolds, 2015).

One important point questions whether Lévy movements actually reflect an underlying Lévy process or simply emerge from typical animal-environment interactions, contesting the claim that Lévy movements are indeed an evolved strategy (Benhamou, 2007; Pyke, 2015; Reynolds, 2015). Recent works have demonstrated that Lévy movement patterns can emerge spontaneously and naturally from the interaction of innate behavior and innocuous responses to the environment (Benhamou, 2007; Reynolds, 2015). For example, Lévy patterns can arise from avoidance of conspecific odor trails (Reynolds, 2007), randomly reorienting at cues left by animals following more classical diffusion processes, such as correlated random walks (Reynolds, 2010) and use of chemotaxis in prey location (Reynolds, 2008). In dynamic marine environments, for example, Lévy walks emerged naturally in response to turbulence (Reynolds, 2014). The existence of Lévy movements should thus not be confused with the existence of Lévy processes underlying movement behavior (Benhamou, 2007).

In response, however, Reynolds (2015) has since speculated that while selection for Lévy search patterns seems unnecessary and may even be unlikely in the majority of cases, there may be selection against losing them if they subsequently prove adaptive and confer fitness

advantages (Reynolds, 2006, 2009, 2012; Humphries *et al.*, 2012). Lévy movements are particularly common in heterogeneous environments where resources are patchily distributed, i.e. the resources are themselves Lévy-distributed (Boyer *et al.*, 2006; Humphries *et al.*, 2012), and this may be one of the key factors governing the ubiquity of Lévy search patterns across the animal kingdom.

Fractal approaches to the study of tortuosity in animal movement have instead used global properties of the movement path itself to estimate fractal (or fractional) dimension, a metric originally described by Mandelbrot (1967) to describe the rate at which detail in a structure changes with changes in measurement scale. Fractal studies of tortuosity focus on multiple scaling regions in the spatial domain, and as such provide insight about the fundamental scales at which species operate, as well as their responses to changing scales, within or across landscapes (Fritz *et al.*, 2003; Nams & Bourgeois, 2004; Garcia *et al.*, 2005). As shown by Fritz *et al.*, (2003), fractal dimension estimates of wandering albatross (*Diomedea exulans*) behavior change according to the scale at which they are measured. At small scales, movement patterns of wandering albatross respond to wind currents, while at medium and large scales, they reflect food search and long-distance movement, respectively. Similarly, American marten (*Martes americana*) movements are influenced by microhabitat heterogeneity (Nams & Bourgeois, 2004) while grazing ewe movements are influenced by landscapes scales above a certain threshold (Garcia *et al.*, 2005).

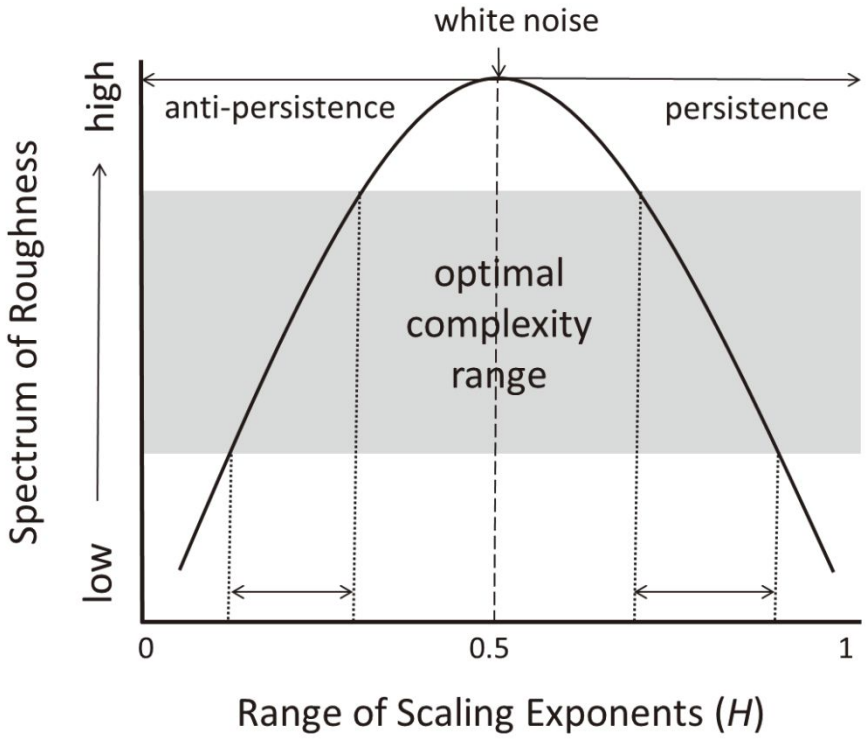


Figure I.8 : Schematic showing hypothetical optimal complexity range within which we expect to find scaling exponents (illustrated here with the Hurst estimator, a typical scaling exponent used to indicate fractal dimension) describing sequences of animal behavior. The y-axis illustrates here the deterministic-stochastic gradient and a deviation from this optimal scaling range toward more determinism or stochasticity may indicate underlying pathological conditions (from MacIntosh 2014)

On the other hand, fractal time studies have been more interested in utilization of fractal analysis as a diagnostic tool to differentiate between the behaviors of animals exposed to various physiological conditions (e.g. Motohashi *et al.*, 1993; Escós *et al.*, 1995; Alados *et al.*, 1996; Alados & Weber, 1999). These studies postulated that complexity in the temporal organization of animal behavior - defined as the degree to which behavioral time series are self-affine and long-range dependent (autocorrelated) - should converge on some optimal range in normally-functioning individuals. Deviations from this optimal range, when observed, might thus reveal an underlying challenging or pathological state. Given an optimal range, complexity in diverse biological phenomena is considered to be adaptive because it is error-tolerant, making it possible for biological systems to buffer changes

arising from both intrinsic (e.g. reproductive state and hormones) and extrinsic factors (e.g. environmental perturbations) (West, 1990). As described by (Goldberger *et al.*, 2002a, 2002b) and reviewed by (MacIntosh, 2014) (Figure I.8), a tendency toward either greater stochasticity (i.e. less long-range dependence or memory in a sequence) or greater determinism (i.e. greater long-range dependence or memory in a sequence) along a stochastic-deterministic gradient may indicate that the system (e.g. an animal) is operating in a potentially sub-optimal state. Fractal time analyses of heart inter-beat intervals and gait dynamics in humans have both shown deviations in fractal statistics, albeit in opposite directions, from the hypothesized optimal range in the case of heart disease (i.e. greater determinism; West & Goldberger, 1987; Goldberger *et al.*, 1990; Peng *et al.*, 1995b) and advanced neuromuscular disorder (i.e. greater stochasticity; Hausdorff *et al.*, 1995, 1997, 2001). In so doing, these studies introduced the idea of '*complexity loss*' into the literature, which simply describes the phenomenon that occurs when fractal scaling in a biological system diverges from its normal and presumed optimal range.

Further studies have provided evidence for the existence of optimal complexity ranges in several biological systems, such as neural circuitry (Abasolo *et al.*, 2008; Montez *et al.*, 2009), respiration (Peng *et al.*, 2002), the growth of plants and trees (Escós *et al.*, 1995; Alados *et al.*, 1999), and even animal behavior. Among the first to examine complexity in animal behavior via fractal time series analysis was a study investigating toxicological effects of chemical substances on rat locomotion behavior (Motohashi *et al.*, 1993). Similar analyses were later introduced as a new model of animal search behavior (Shimada *et al.*, 1993, 1995; Cole, 1995), and later still to assess the effects of potential stressors on animal behavior (Escós *et al.*, 1995; Alados *et al.*, 1996; Alados & Weber, 1999), including as a diagnostic tool in an animal welfare context (Rutherford *et al.*, 2004; Asher *et al.*, 2009). For example,

fractal analysis revealed subtle changes in behavioral organization of domestic hens during stress (i.e. change for a novel environment), changes that were not highlighted with traditional frequency-based approaches to behavioral analysis (Rutherford *et al.*, 2003). More generally, it has now been demonstrated repeatedly that the so-called '*complexity signatures*' of individual animals do indeed change in response to numerous and diverse stressors (Shimada *et al.*, 1993, 1995; Escós *et al.*, 1995; Alados & Huffman, 2000; Rutherford *et al.*, 2004; Hocking *et al.*, 2007; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011). These studies have set the stage for us to further investigate the role of complexity as an adaptive phenomenon in animal behavior.

I.3.3 Complexity in animal behavior and foraging strategies

The discovery that various biological systems exhibit complexity loss under pathological conditions provided some of the first evidence supporting the importance of deterministic chaos in their dynamics (i.e. error tolerance as noted above). However, further evidence comes from the marriage of fractal analyses in the spatial and temporal domains: if fractal movement patterns are predicted to outperform normally diffusive movements in heterogeneous environments as per the LFFH, then this must also be true for temporal dynamics in animal behavior sequences (MacIntosh, 2014). Indeed, studies on the foraging behavior of fruit flies (*Drosophila melanogaster*) (Shimada *et al.*, 1995) and Japanese quail (*Coturnix coturnix*)(Kembro *et al.*, 2009a) have suggested that animals motivated to explore their environments show higher levels of temporal complexity in their behavior, i.e. higher degrees of stochasticity in their foraging sequences as measured by alternations between active and inactive (or motile and non-motile) states. Similarly, MacIntosh and colleagues (2011) have shown that foraging behavior in Japanese macaques (*Macaca fuscata yakui*) is more stochastic in terrestrial than arboreal contexts, principally because food resources in

the former (e.g. fallen seeds and insects) are cryptic and more difficult to procure than in the latter, where the macaques primarily forage for more visible and predictably-distributed fruits and leaves, resulting in more deterministic behavior. Thus, in the temporal domain as well as the spatial domain, heterogeneous or otherwise less predictable environmental conditions appear to be associated with greater complexity (i.e. less determinism) in animal behavior.

However, despite an increasing body of literature using fractal time to understand animal behavior, few studies have examined the impacts of stressors on behavioral complexity in the area of wildlife health monitoring (Alados *et al.*, 1996; Alados & Huffman, 2000; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011; Cribb & Seuront, 2016) and even fewer involving environmental assessment. Seminal work in wild animal behavior was conducted on Spanish ibex (*Capra pyrenaica*) and showed that pregnancy and external parasitism were associated with complexity loss in foraging and vigilance behavior (i.e. animals becoming more stereotypic or deterministic in their behavioral sequences; Alados *et al.*, 1996). Later studies were interested in health monitoring of wild primates and marine predators, and investigated the effects of physiological and environmental parameters on behavioral complexity (Alados & Huffman, 2000; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011; Cottin *et al.*, 2014; Cribb & Seuront, 2016). Thus, there exists the need to now go beyond proof of concept for complexity loss and better understand how animal-environment interactions lead to the emergence of observed complexity signatures, and how these behavioral profiles might reflect behavioral adaptations to variable environmental conditions.

I.3.4 Temporal organization and fractals in penguin foraging behavior

One major constraint to assessing fractal time in behavioral sequences is the necessity to generate sufficiently long time series in order to perform meaningful analyses: this can be difficult under natural conditions when data collection is based on visual observations only. This issue can be solved using foraging behavior sequences collected via bio-logging, as described in MacIntosh *et al.* (2013) and Cottin *et al.* (2014) on penguins. This approach, where miniature data recording devices are attached to free-ranging animals, is indispensable for monitoring at fine time scales (e.g. at a rate of a point every second or even less) and over long periods (e.g. several days) the behaviors of animals that are impossible to directly observe systematically (e.g. penguins; Ropert-Coudert & Wilson, 2005; Ropert-Coudert *et al.*, 2012). The merger of bio-logging and fractal analysis in studies on little penguins, *Eudyptula minor* (MacIntosh *et al.*, 2013), and Adélie penguins, *Pygoscelis adeliae* (Cottin *et al.*, 2014), showed that penguin dive sequences exhibit a complex fractal structure through time. These studies further tried to relate the complexity of the penguin behavior to a combination of extrinsic and intrinsic factors, opening opportunities to better understand the interactions which occur between each animal's behavioral strategies and their environments, especially within the context of indicator species for climate and environmental change.

I.4 Objectives and Thesis Structure

My thesis aims at answering the following question:

"Does complexity in behavioral organization allow seabirds to adapt to changes in their environment?"

This driving research question echoes some of the questions that need to be addressed in the field of marine megafauna movement ecology as recently proposed by Hays *et al.*, 2016: (1) “How does the distribution of prey impact movement?”; (2) “How much does the physical environment influence movement?”; (3) “How will climate change impact animal movements”; but also, (4) “Are there simple rules underlying seemingly complex movement patterns and, hence, common drivers for movement across species?”. The studies that form the components of this thesis have been conducted on the two aforementioned species, little and Adélie penguins, considered as indicator species for climate and environmental change in their respective environments. The foraging activity of these species has been continuously monitored at-sea in different locations and across several years. These biological models give us the opportunity to study the impact of environmental variables on the complexity of foraging behavior and investigate whether and how seabirds buffer environmental changes through behavioral adjustments. In order to address my question, I need to understand first how the fractal-time based index, i.e. the value that defines the level of complexity of behavioral sequences, changes in response to various eco-physiological variables, including clear stressors. Using a situation where the animal is “handicapped” by a known stressor, I will determine how the fractal index will vary in response. After confirming the fractal index as an indicator of behavioral change, I will be able to test the influence of a set of environmental parameters (i.e. physical environment, prey distribution) on foraging behavior complexity. The specific aims of my thesis are thus to examine (i) how a known hydrodynamic handicap (i.e. caused by the attachment of bio-loggers of different sizes to the birds on different body locations) influences the temporal organization of little and Adélie penguin dive sequences; and (ii) how physical parameters of the ecosystem influence the temporal organization of little penguins foraging behavior in

different locations and across several years. In the first study (objective i), I predict that penguins carrying an added hydrodynamic handicap will show altered temporal organization (sensu '*complexity loss*'), i.e. more deterministic elements in their foraging sequences as evidenced by increases in the fractal index that characterizes them. Such information should also be important for future studies that use bio-loggers of different sizes. In this section, I will look more precisely at how the size and the position of bio-loggers attached to the backs of penguins – but also flipper bands – influence the temporal organization of foraging behavior (**Article A**).

Concerning the influence of the physical environment (objective ii), we expect penguins to differ in temporal organization of foraging behavior according to changes in the environment between different locations and/or between years. I will investigate how the temporal organization of little penguin foraging behavior is linked with characteristics of the physical environment (i.e. bathymetry) at four different colonies across their geographical range (**Article B**). I will then focus on how the temporal organization of little penguin foraging behavior changes within and between years during the breeding season, using an eleven year data set (2001-2012) from Phillip Island, Australia (**Article C**). Particularly, I will examine the link between behavioral changes, environmental changes (in sea-surface temperature, wind conditions) and population outputs (i.e. breeding success). Through physical changes in the environment I expect that differences in foraging complexity should reflect underlying changes in the availability of prey. The overarching aim is to test if a fractal time index can predict variables of ecological relevance, and thus be used as an indication of those variables.

I conclude this thesis with a general discussion that summarizes the results and places them in the global context of the adaptive value of foraging complexity in animals. I finish by enumerating some perspectives for future studies which aim to investigate deeper the behavioral mechanisms of foraging flexibility, the cost of exhibiting flexible foraging strategies, and how foraging strategies develop throughout the life of an individual..

Materials & Methods

Pétrels Island, Adélie land, Antarctica

II. Materials & Methods

II.1 Biological models

There are 18 penguin species, all living in the Southern Hemisphere, that compose the family Spheniscidae. The whole penguin breeding population is estimated at more than 24 million breeding pairs (Woehler *et al.*, 2001), widespread from the tropics to the Antarctic coast. This thesis will focus on two species, the little penguin and the Adélie penguin.

II.1.1 Little penguins

Little penguins, the smallest penguin species, are endemic to southern Australia and New-Zealand, breed in several colonies of various sizes with variable reproductive success, experiencing different environmental conditions across their geographic range (Chiaradia *et al.*, 2007). Males and females present a strong dimorphism in bill depth (Stahel & Gales, 1991), and penguins with a bill depth < 13.4mm are considered females, allowing us to discriminate their sex without genetic analyses (Arnould *et al.*, 2004). They are philopatric and tend to return every year not only in the same colony but also to the same area of the colony for reproduction.

Little penguin
- *Eudyptula minor* -
40 – 45cm
700 – 1700gr
2 eggs
Inshore species
Australia & New Zealand

However, the timing of breeding has been described as asynchronous between individuals (Chiaradia & Kerry, 1999) and early breeders are likely to lay a second clutch

(Reilly & Cullen, 1981; Chiaradia & Kerry, 1999). This timing is mostly influenced by local weather patterns and variations in ocean currents (Stahel & Gales, 1991; Reilly, 1994). For example, at Phillip Island, warmer temperatures in late summer and autumn have been linked with earlier nesting (Chambers, 2004; Cullen *et al.*, 2009), and both the number of chicks fledged per pair and their body mass at fledging has been positively correlated with the SST in early months of the year (Cullen *et al.*, 2009). Little penguins return to shore every year to breed, and this breeding cycle can be decomposed into five mains periods (Figure II.1).

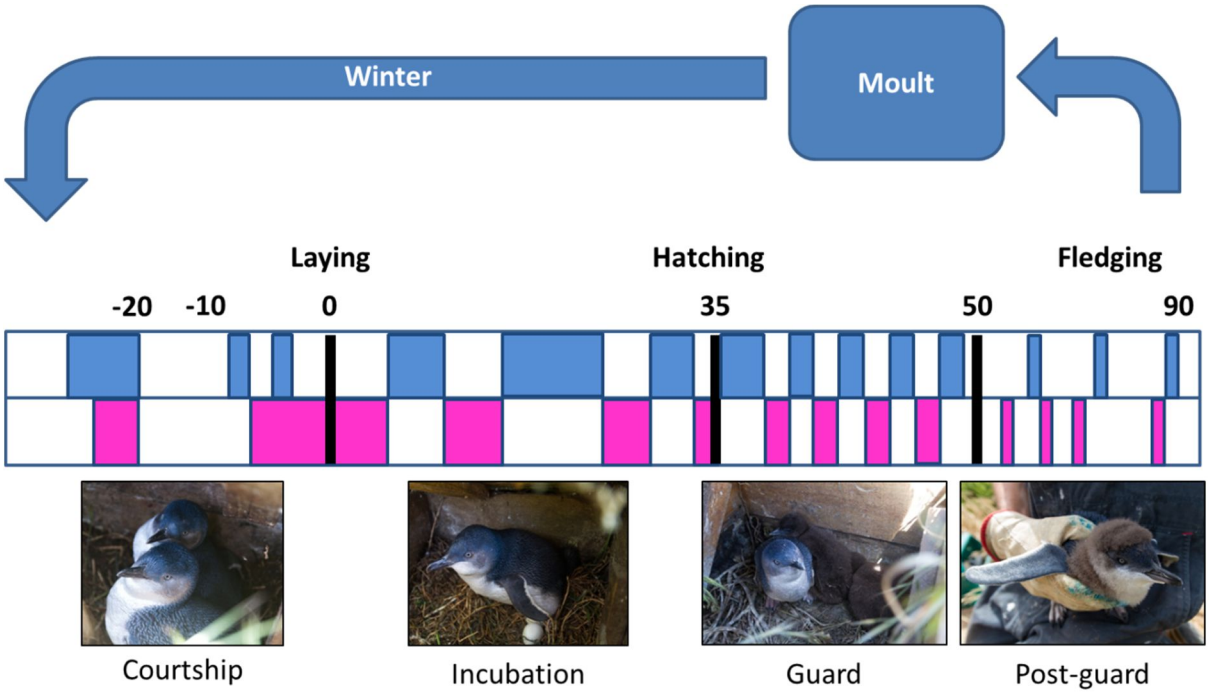


Figure II.1 : Schematic breeding cycle of the little penguin. Time scales are represented as days before and after laying date. Presence at the colony is represented in blue (for male) and pink (for female). Black lines represent the laying date, the hatching date and the end of guard period (modified from Chiaradia & Kerry 1999).

The breeding season is considered to begin with **courtship**, after which both males and females leave the colony for the pre-laying exodus that lasts 9.2±3.0 and 10.6±3.2 days, respectively (Chiaradia & Kerry, 1999). Then females remain at colony for a mean 5.6±3.1 days in order to lay two eggs in the burrow, which are laid at one-day inte(Chiaradia & Kerry,

1999). The laying triggers the **incubation** period, which lasts on average 35±2 days (Chiaradia & Kerry 1999). During this period, parents alternate to incubate the two eggs, i.e. one parent stays on nest to incubate while the other forages at-sea. These foraging trips last on average 3.4 days (±2.25 days for females and ±1.25 days for males) without difference between males and females, and partners made on average 5.6 (±2) shifts during incubation (Chiaradia & Kerry, 1999). However, foraging trips must be coordinated between both parents in order to provide food for the chicks just after hatching. This constraint involves shortening trip durations as incubation progresses until hatching, which marks the beginning of the chick-rearing period (Chiaradia & Kerry, 1999). This period, which lasts an average of 56 days (Stahel & Gales, 1991), finishes at the date of fledging of the last chick; this is the period in which most of the breeding failures occur.

The chick-rearing period is classically divided into two periods, guard and post-guard. The **guard** starts at the hatching of the first egg and finishes when both of parents leave the nest during the day (Chiaradia & Kerry, 1999; Chiaradia & Nisbet, 2006). Chicks are guarded until they become physically and thermally independent during 8-25 days for an average of 14.5 days (Chiaradia & Kerry, 1999). Usually, these foraging trips are no longer than 1 day and constrain the parents to forage within a radius of 20-25km (Collins *et al.*, 1999; Pelletier *et al.*, 2012). From the end of the guard to the fledging of the last chick (on average 6 weeks), **post-guard** is the period where both parents are at-sea and alternate short trips (to continue feeding the chicks) and long trips (to restore their body reserve) (Saraux *et al.*, 2011a). The length of the trip is mostly determined by the weight of the adult before the trip. Chicks become mature at 54 days and disperse at-sea widely during the first two years of their life (Stahel & Gales, 1991; Reilly, 1994), when the early breeders come back to the colony (Reilly, 1994; Nisbet & Dann, 2009).

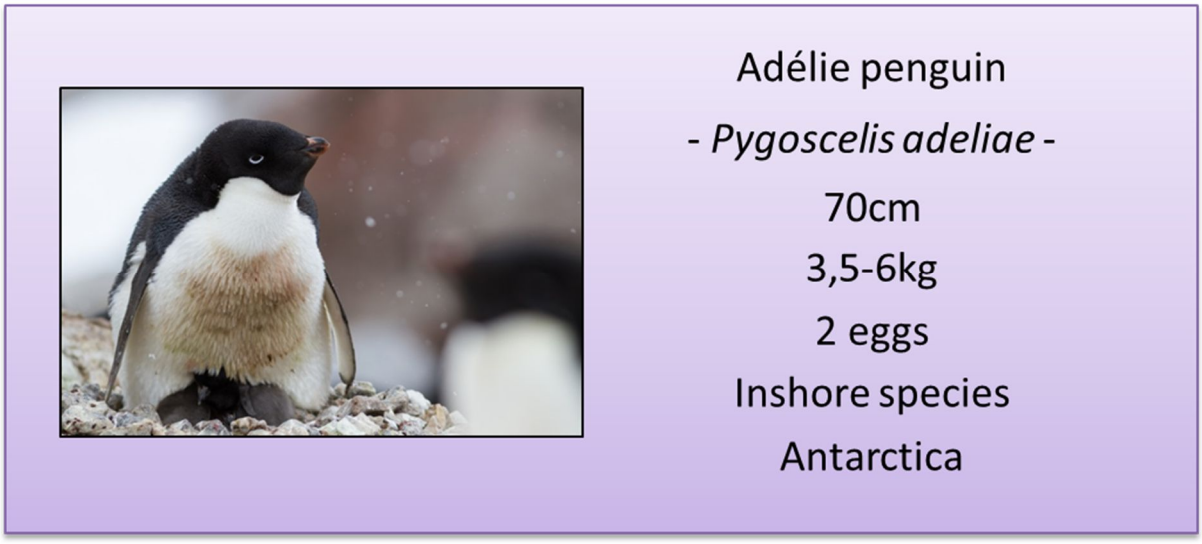
After chicks become independent and leave the colony, adults start to accumulate fat in preparation for their annual **moult** (Reilly, 1994), which lasts 2 weeks and happens between February and April (Reilly & Cullen, 1981). During this period, penguins are restricted to land in order to renew their waterproof feathers. At this stage, birds will reach almost twice their normal weight (≈2kg) and will lose half of it during moulting (Reilly, 1994). After renewing their feathers, little penguins leave the colony and remain mainly at-sea during the winter season to restore their body reserves for the next breeding season.

Little penguin's diet consists mainly of small, 3-12 cm clupeiformes fish (Cullen *et al.*, 1991), such as anchovies (*Engraulis australis*), pilchards (*Sardinops sagax*), barracudas (*Thyrsites atun*), blue warehouses (*Seriolella brama*) and red cods (*Pseudophycis bachus*), but also cephalopods (e.g. Gould's squid, *Nototodarus gouldi*) and crustaceans (i.e. krill, *Nyctiphanes australis*) (Chiaradia *et al.*, 2003).

Little penguins are visual predators and dive exclusively during the day (Cannell & Cullen, 2008). They can dive down to 66.8m for a maximum duration of 90s (Ropert-Coudert *et al.*, 2006a). However, most of the dives are concentrated between the surface and 40m (Ropert-Coudert *et al.*, 2006b; Chiaradia *et al.*, 2007). In this species, foraging behavior has been shown to be affected by Sea-Surface Temperature (SST) (Berlincourt & Arnould, 2015; Carroll *et al.*, 2016), wind (Berlincourt & Arnould, 2015; Saraux *et al.*, 2016) and water stratification (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012).

II.1.2 **Adélie penguins**

Adélie penguins are, with emperor penguins (*Aptenodytes forsteri*), one of the two species to breed only in Antarctica. Populations are estimated to be 3.79 million breeding pairs over 251 colonies on the Antarctic coast (Lynch & LaRue, 2014). However, driven by contrasted warming patterns and sea-ice dynamics, Adélie penguin population dynamics differ widely around the continent. Populations in the Ross Sea and East Antarctica are increasing (Taylor & Wilson, 1990; Emmerson & Southwell, 2008; LaRue *et al.*, 2013), while populations around the Antarctic Peninsula are decreasing, with Adélie penguins being replaced by Chinstrap (*Pygoscelis antarcticus*) and Gentoo penguins (*P. papua*) (Trivelpiece *et al.*, 1987; Forcada *et al.*, 2006; Hinke *et al.*, 2007; Schofield *et al.*, 2010). Adélie penguins are considered to be ice-dependent species, while Chinstrap and Gentoo penguins are considered to be ice-intolerant species.



Adélie penguins breed during the austral summer (from October to March) and the breeding cycle can be divided into 5 periods as described for little penguins above (Figure II.2) (Ainley, 2002). They are highly philopatric and tend to return every year not only to the same colony but also to the same area of the colony for reproduction. Males arrive at the

colony first in mid-October, followed by females a few days after. During the **courtship** period, partners build nests with small rocks and females lay two eggs before leaving the colony for re-supply, letting the male incubate the eggs. Males will fast for a few weeks (up to 50 days, Vleck & Vleck, 2002) until the female come back. Then males leave the colony for 10 days and return just before the hatching date. Afterwards, both parents conduct shorter foraging trips and alternate between trips at sea and staying at the colony to incubate the eggs and later raise the chicks. The **incubation** period lasts 30 to 39 days and finishes in mid-December when the two eggs hatch (Ainley, 2002). Hatching triggers the beginning of the **chick-rearing** period, when one parent stays on the nest while the other forages at-sea. After an average of 22 days, chicks become thermally independent and form a **crèche**. Parents still feed the chicks but less and less often until chicks fledge (Sladen, 1958; Ainley, 2002). Adults, after replenishing their reserves at-sea, will then come back to land to **moult** before their annual winter migration (Clarke *et al.*, 2003).

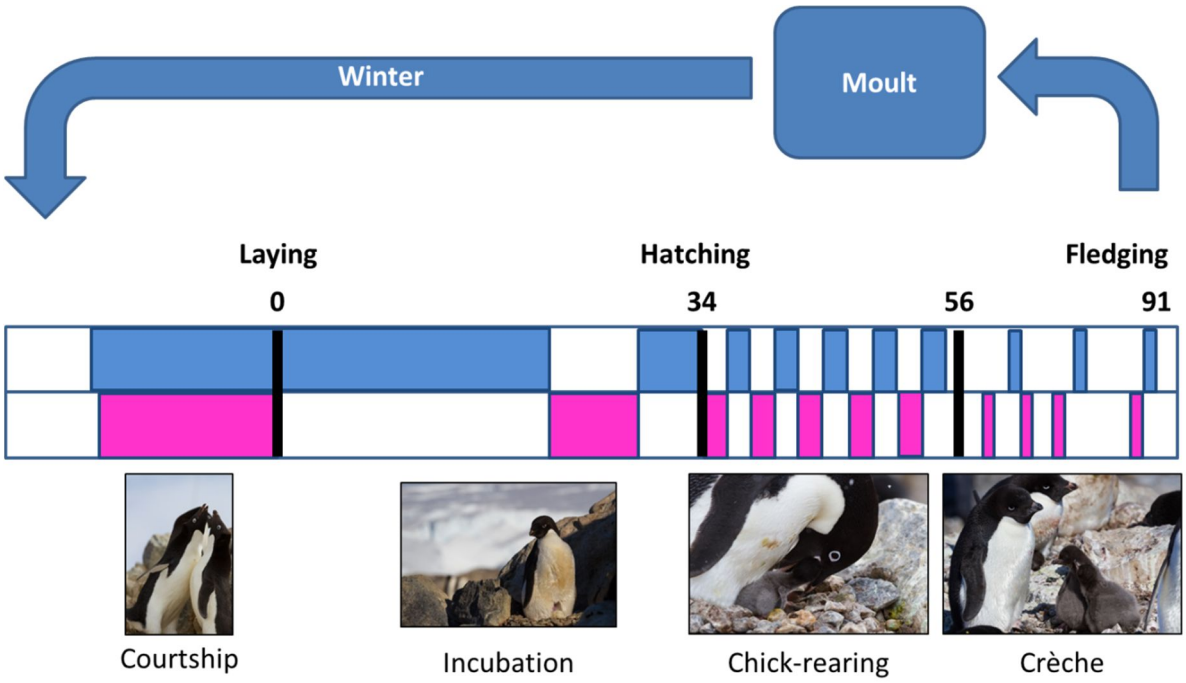


Figure II.2 : Schematic breeding cycle of the Adélie penguin. Time scales are represented as days before and after laying date. Presence at the colony is represented in blue (for male) and pink (for female). Black lines represent the laying date, the hatching date and the end of chick-rearing period (adapted from Ainley 2002).

The Adélie penguin diet consists mainly of krill (*Euphausia superba* and *E. chrystallorophias*), fish (*Pleuragramma antarcticum*) but also jellyfish(Nagy & Obst, 1992; Ainley *et al.*, 1998; Thiebot *et al.*, 2016). Adélie penguins' diets can be modified by sea-ice conditions, as are their foraging sites and diving patterns (Ainley *et al.*, 1998; Clarke *et al.*, 1998; Rodary *et al.*, 2000; Kato *et al.*, 2003; Widmann *et al.*, 2015). Adélie penguins forage both in open sea and under sea-ice, especially open-water areas surrounded by fast-ice (Watanuki *et al.*, 1993, 1999). They can dive down to 180m (Watanuki *et al.*, 1997) for a maximum duration of 354s (Norman & Ward, 1993).

II.2 Study sites

II.2.1 Temperate field site

II.2.1.a Phillip Island

Little penguins were studied mostly (see "other colonies" below for more information) at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (38°31'S, 145°09'E; Figure II.3, 4 & 5), where the breeding population is estimated to be between 26 100 and 28 400 individuals (Sutherland & Dann, 2012). This colony is located in the northwest of Bass Strait and has been surveyed for population trends with an automatic identification system since 1995 (Chiaradia & Kerry, 1999), and for the at-sea behavior of the penguins since 2003 by my supervisor's team and his collaborator, Dr. Andre Chiaradia. I participated in one season of fieldwork during the austral spring 2013 (October-November 2013), which included penguin handling and surveying, as well as logger programming, deployment on birds, recovery and data extraction.

The region of Bass Strait corresponds to the shallow continental shelf area between Tasmania and Australia mainland with an average bathymetry of 60 to 80m. On the crossroads of three different marine currents (Figure II.3), the oceanic region of south-

Figure II.3 : Location of the study site. Penguin colony studied marked with a yellow star. Summerland Peninsula marked with red circle (extracted from Google Earth).

Figure II.4 : The 'Penguin Parade' colony in the Summerland Peninsula, Phillip Island, Victoria, Australia. The colony is located next to the grandstand. Colony is composed of approximately 100 artificial burrows which were part of a series of measure of conservation to provide habitat at degraded areas. The 'Penguin Parade' is a place where people can come every night and enjoy the returns of little penguins crossing the beach. In order to avoid any disturbance from humans, the place is monitored by ranges. (Photo credit: Xavier Meyer)

eastern Australia is one of the fastest warming areas in the world (Hill *et al.*, 2008; Hobday & Pecl, 2013) and offers a great opportunity to study environmental change and its consequences on organisms such as little penguins. Bass Strait waters are influenced on the west side by the South Australian current (SAC), a tropical current characterized by warm waters, low salinity and poor nutrient levels (Gibbs, 1992), which comes from the Indian Ocean as a ramification of the Leeuwin current that flows along the west coast of Australia. According to Yamagata *et al.*, 2004, the Leeuwin current may entrain oceanographic anomalies of SST into the Bass Strait system, driven by the Indian Ocean Dipole. Coming from the south-west, the cold and nutrient-rich Flinders currents or sub-Antarctic Surface waters (SASW) (Gibbs, 1992) are highly influenced by the cold Antarctic Circumpolar Current (Middleton *et al.*, 2007), which flows from west to east around Antarctica. Finally, Bass Strait is influenced from the east by the East Australian Current (EAC) which comes from the Pacific Ocean. This current is characterized by warm and nutrient-poor waters flowing between Australia and New Zealand (Gibbs, 1992). This current apparently increases the SST to above 20°C in the Bass Strait in case of enhanced flow of warm waters (Cresswell, 1997), which causes shifts in the marine species distribution further south along the coast of Bass Strait (Poloczanska *et al.*, 2007; Ling *et al.*, 2009; Banks *et al.*, 2010). The contrasting oceanic regimes that Bass Strait is exposed to on an annual basis have strong influences on the foraging behavior of breeding little penguins in the area (e.g. Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012; Berlincourt & Arnould, 2015).

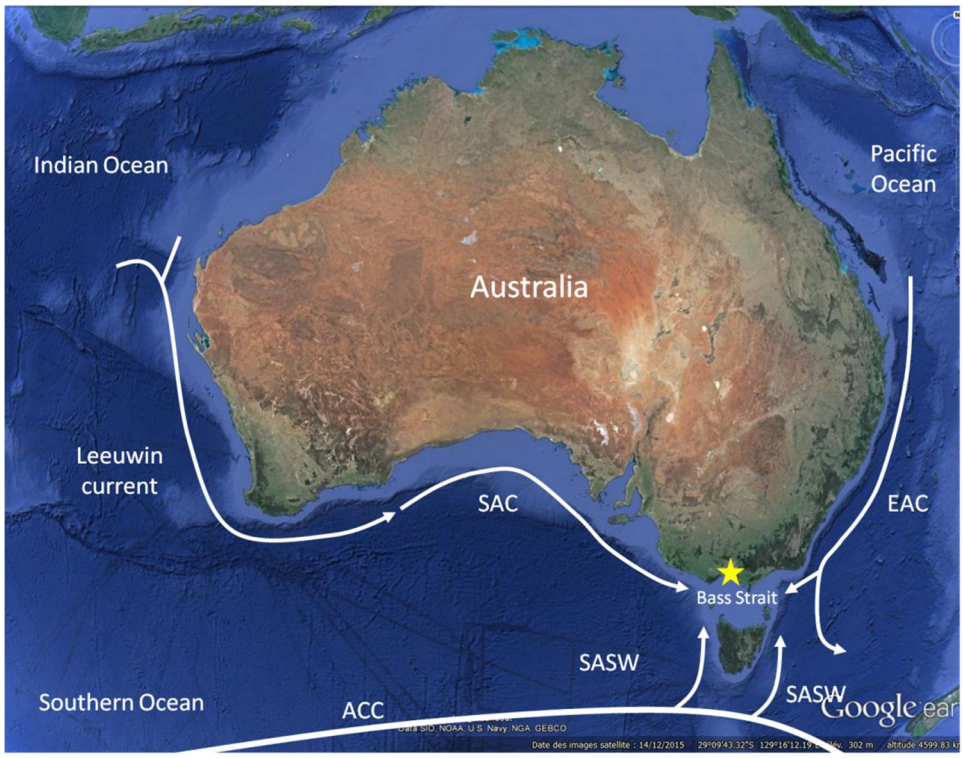


Figure II.5 : Simplified representation of the major currents which influenced the waters of the Bass Strait, localization of the study site (Phillip Island marked with a yellow star). SAC: South Australian Current; EAC: East Australian Current; SASW: Sub-Antarctic Surface Water; ACC: Antarctic Circumpolar Current (extracted from Google Earth).

I.1.1.a. Other colonies: Penguin Island, Motuara Island and Oamaru

While little penguins were mostly studied in Phillip Island, I also used datasets collected on birds from three other colonies across the species' geographical range (Figure II.6) in order to investigate the effect of the bathymetry on foraging organization (Article B).

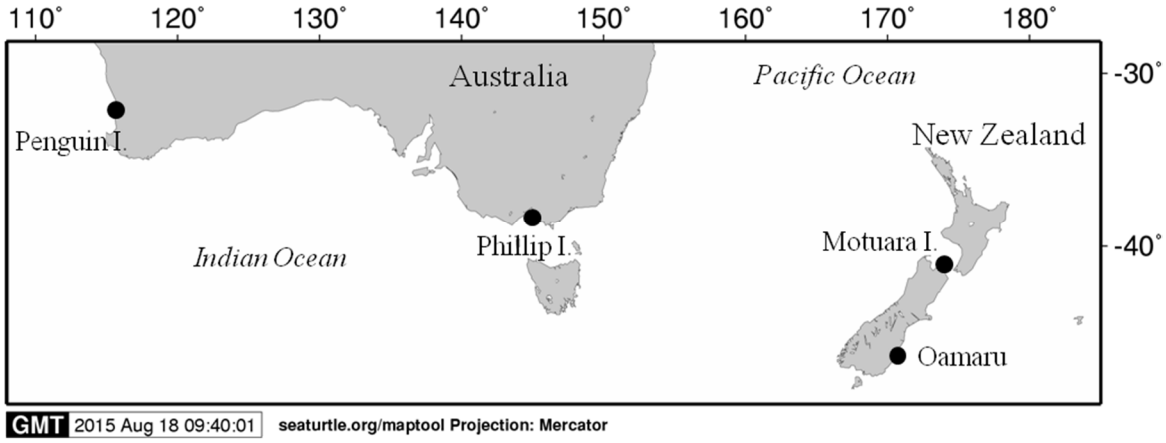


Figure II.6 : Location of the four colonies (black dots) of little penguins in Australia and New Zealand. Map was created using Maptool in Seaturtle.org

In the eastern part of the little penguins' geographical range, I used a diving dataset from the colony of Penguin Island (Figure II.6), Western Australia, Australia (32°16'S, 115°21'E) (Ropert-Coudert *et al.*, 2003). This colony of the Indian Ocean of approximately 1000 individuals is surrounded by shallower water than Phillip Island, with a maximum depth of approximately 35m and a substantial proportion of the birds' foraging area consisting of water depths between 0 and 20m. In the western part of the little penguins' geographical range, I used diving datasets collected on birds from the colonies of Motuara Island (600 individuals; 41°06'S, 170°59'E; Figure II.6) and Oamaru (6000 individuals; 41°06'S, 174°17'E; Figure II.6), both situated on New Zealand South Island (Mattern, 2001). Motuara Island and Oamaru are both surrounded by waters as deep as 55m, but Oamaru shows a greater proportion of shallower waters (between 10 and 20m) than Motuara Island where water depth in the foraging area of the birds is mostly between 20 and 55m.

II.2.2 Antarctic field site: Dumont d'Urville

Adélie penguins were studied at the colony around Dumont d'Urville Station, Adélie Land, Antarctica (66°40'S, 140°01'E, Figure II.7 & 8). I participated in one season of fieldwork

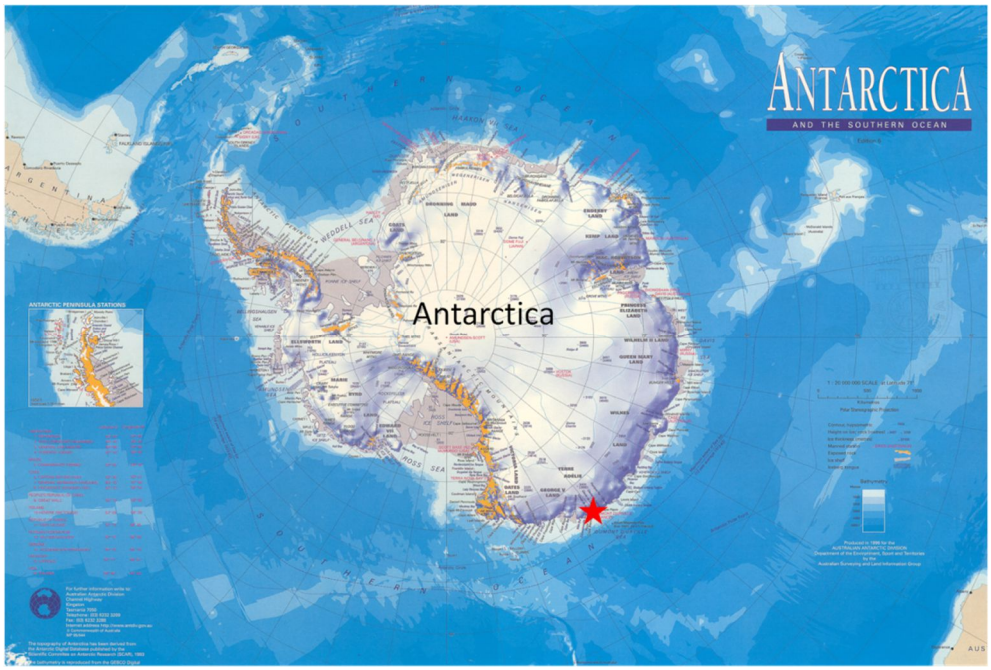


Figure II.7 : Location of the study site in Antarctica. Dumont d'Urville station marked with a red star (modified from the Australian Antarctic Division).

Figure II.8 : Aerial photography from Petrel Island. Buildings belong to Dumont D'Urville Station. Red circle marked the study site (photo credit: Christophe Sauser)

during the austral summer 2013-2014 (December 2013-February 2013) that included penguin handling and surveying, as well as logger programming, deployment on birds, recovery and data extraction. This colony of ca 34 000 Adélie penguins (Ropert-Coudert *et al.*, 2015, Annex 1) is located on Petrel Island, in the Pointe Géologie Archipelago, in the eastern part of Antarctica.

II.3 General methods

II.3.1 Long-term breeding season monitoring

II.3.1.a Phillip Island

Little penguins of Phillip Island, and more precisely in the 'Penguin Parade' colony (Figure II.4), have been monitored since 1978, with nests checked and birds banded as chicks or adults (Chiaradia & Kerry, 1999). In the study colony, there are approximately 100 artificial nest boxes (Figure II.9). Individuals have been surveyed with an Automated Penguin Monitoring System (APMS; Kerry *et al.*, 1993; Chiaradia & Kerry, 1999) since 1995, developed by the Australian Antarctic Division. Thanks to passive transponders (Allflex, Australia) associated with unique numbers and injected annually under the skin between the shoulders of chicks (Daniel *et al.*, 2007), the APMS can record the time, the direction, the weight and the ID of the birds crossing. The wounds caused by injection of transponders are closed with surgical glue (Vetbond™, 3M Worldwide) and manipulation lasts less than a minute. Artificial nests are visually checked every two days during the breeding season, allowing us to establish the breeding chronology every year (Annex 2).

Figure II.9 : Wooden nest boxes in the study area, partially covered by vegetation (in the center of photo) (photo credit: Xavier Meyer)

At-sea behavior of breeding penguins has been monitored since 2003 using a bio-logging approach (Ropert-Coudert & Wilson, 2005). At least 10 penguins (5 males, 5 females) have been equipped with data loggers (i.e. Time-Depth Recorder or GPS) during each period of the breeding season (i.e. incubation, guard, post-guard). Following literature recommendations (Bannasch *et al.*, 1994; Wilson *et al.*, 1997; Ropert-Coudert *et al.*, 2007a), loggers were attached to the feathers of the axis of the back of each animal near the tail with marine TESA® tape (Tesa Tape Incorporation) in order to minimize the drag effect during diving behavior (Figure II.10). Moreover, birds were weighed before logger attachment and after logger removal to the nearest 10g with a spring balance. Birds are finally released at the nest entrance.

Figure II.10 : Little penguin equipped with WACU logger (photo credit: Matt Simpson)

I.1.1.a. Dumont d'Urville

Sub-colonies of Adélie penguins (Figure II.11) at Petrel Island have been monitored sporadically between 1998 and 2010 (1998-1999; 2001-2002; 2009-2010; 2010-2011) and

extensively through Institut Paul-Emile Victor (IPEV, French polar institute) program 1091 since 2012-2013. Since the 2012 austral summer, approximately 100 pairs have been monitored visually from 6 to 14 times a day between November and mid-February (Ropert-Coudert *et al.*, 2015; Annex 1). This allows us to establish the breeding chronology every year (Annex 3).

Figure II.11 : Studied Sub-colony « le virage » of Adélie penguins on Petrel Island, Antarctica (photo credit : Xavier Meyer).

For all study years, at-sea behavior of breeding penguins has been monitored using a bio-logging approach (Ropert-Coudert & Wilson, 2005). Penguins were equipped with data

Figure II.12 : Adélie penguin equipped with GPS device CatLog™ (right) and WACU logger (left) (photo credit: Andrew J.J. MacIntosh)

loggers (i.e. Time-Depth Recorder or GPS) during each period of the breeding season (i.e. incubation, chick-rearing, crèche) and captured when they leave the colony. Similar to the case of little penguins and again following literature recommendations (Bannasch *et al.*, 1994; Wilson *et al.*, 1997; Ropert-Coudert *et al.*, 2007a), loggers were attached to the feathers of the axis of the lower back of animal with marine TESA® tape (Tesa Tape Incorporation) in order to minimize the drag effect during diving behavior (Figure II.12). Moreover, birds were weighed before logger attachment and after logger removal to the nearest 10g with a spring balance. During the birds' manipulation, which did not exceed five minutes, eggs were protected from predators at the nest with a cage while chicks were kept in a box and weighed.

Box 3: un été sur le terrain à Dumont d'Urville.

2 décembre 2013, départ pour l'Antarctique. Je suis arrivé la veille à Hobart, une dernière nuit à terre avant au minimum 6 jours et demi de mer et me voilà dans le taxi pour le dépôt de carburant du port d'Hobart. Au bout du quai, l'Astrolabe. Voilà le moment du départ qui arrive, moment émouvant au largage des amarres. L'ensemble de l'équipage est sur le pont arrière pour le passage sous le Tasman Bridge. Les cabines sont exigües et nous nous organisons comme nous pouvons pour y ranger toutes nos affaires. On s'habitue vite à la vie à bord et par chance, je m'aperçois que je suis peu sensible au mal de mer (en plus l'océan austral est relativement calme dans les premiers jours). Le bateau est suivi en permanence par de nombreux albatros, puffins, prions… et en tant qu'ornithologue, je m'en donne à cœur joie. Au petit matin du 6e jour, réveil matinal, le premier iceberg est en vue et on ne tarde pas à arriver dans le pack qui devient de plus en plus dense. Les premiers manchots ne tardent pas à montrer le bout de leurs becs et Dumont d'Urville se rapproche. Malheureusement la météo se dégrade, le pack se fait dense et l'Astrolabe se retrouve coincé. On restera à cette position jusqu'au 15 décembre pour finalement arriver à Dumont d'Urville 14 jours après notre départ d'Hobart. 20min d'hélicoptère et me voilà sur la base Dumont d'Urville. Thierry et Marie ont déjà commencé le travail de suivie des manchots adélie et nous les rejoignons dès le lendemain pour mettre en place la routine de travail des trois prochains mois : je m'occuperai donc des suivis des nids de manchots Adélie de 6h du matin à la fin d'après-midi, moment où Thierry prend le relais pour s'occuper du suivi jusqu'à 6h le lendemain matin. Le but de ce suivi est d'avoir un suivi de la phénologie de l'espèce mais également de capturer des individus partant en mer, d'effectuer une prise de sang et de les équiper de GPS et/ou enregistreurs de plongée afin de suivre leurs mouvements de recherche alimentaire. Malheureusement, le terrain se retrouvera quelque peu tronqué par la mortalité importante des poussins due à des conditions climatiques défavorables (Annex 1). Néanmoins, passer un été à Dumont d'Urville a été une expérience extraordinaire, professionnellement et humainement. Vivre 3 mois dans un lieu reculé, avec peu de connexion avec le monde extérieur, permet vraiment d'en apprendre beaucoup sur soi-même et la vie en générale.

II.3.2 **Monitoring at-sea foraging behavior**

II.3.2.a Time-Depth recorders/accelerometers

Several time-depth recorders/accelerometers have been used throughout Phillip Island's long-term study, including both two- and three-axis accelerometers.

In 2001-2002 and 2002-2003, the LTD 1200-100 (Lotek, Canada) were deployed. These loggers are cylindrical with 2-channel recording, and are 18 mm in diameter and 62 mm long with a weight of 17g in air (Ropert-Coudert *et al.*, 2007b). The logger records the depth at a resolution of 0.1m every second.

From 2004 to 2009, the M190-D2GT (Little Leonardo, Japan) were deployed. These loggers are cylindrical with 12-bit resolution and 4-channel recording, and are 15 mm in diameter and 52mm long with a weight of 16g in air (Ropert-Coudert *et al.*, 2006b). The logger records the depth at a resolution of 0.05m and the temperature at a resolution of 0.01°C each second. The M190-D2GT also records acceleration between -30 and 30 $m.s^{-2}$ at a frequency of 32 or 16Hz along two axes: the dorsoventral axis (*heave*) and the longitudinal axis (*surge*) of the bird. This logger was also used on Adélie penguins (Article A).

From 2010 to 2012, the ORI 400-D3GT (Little Leonardo, Japan) were deployed. These loggers are cylindrical with 4-channel recording, and are 12 mm in diameter and 45 mm long with a weight of 9g in air. The logger records the depth at a resolution of 0.1m and the temperature at a resolution of 0.1°C each second. This logger also records the acceleration between -40 and 40 $m.s^{-2}$ at a frequency of 50Hz along three axes: the dorsoventral axis (*heave*), the longitudinal axis (*surge*) and the lateral axis (*sway*) of the bird.

Moreover, additional loggers were used in Article B, such as the Mk7 (Wildlife Computers, USA). It is 12 mm large, 8 mm high and 65 mm long with a weight of 32g in air. It records the

depth at a resolution of 0.5m each second and the temperature at a resolution of 0.05°C each two seconds (Mattern, 2001 for details).

Finally, cylindrical, 3-channel recording W200-PDT (Little Leonardo, Japan) was also used on Adélie penguins (Article A, see details in Ropert-Coudert *et al.*, 2007a). These loggers have a diameter of 22m and a length of 102mm for a weight of 50g in air. This logger records depth and speed at 1 Hz resolutions.

II.3.2.b GPS loggers

Spatial information concerning foraging trips in both species has also been collected with CatTraQ™ GPS loggers (16 MB memory, 230mA lithium-ion battery, Catnip Technologies, USA) customized in my laboratory by the engineering team Métrologie et Instrumentation en Biologie et Environnement. Originally designed for tracking domestic cats, the original packaging was removed and the main switch button was replaced by a reed switch. Older versions were molded into a water-resistant resin but newer versions are kept 'naked' in order to be streamlined. During deployment, each unit was placed in a heat-shrink tube for waterproofing. Sampling intervals are dependent on the species and the breeding period (see details in Pelletier *et al.*, 2014; Widmann *et al.*, 2015).

II.3.3 Data processing and analysis

II.3.3.a Diving data

After collecting the data from time-depth recorders, the first step consists of correcting the drift of the pressure sensor with the temperature (i.e. when the bird is at the surface) with the program 'WaterSurface_D2GT' from the application 'Ethographer' (Sakamoto *et al.*, 2009) on IGOR pro software (Wavemetrics Inc., USA, 2008). This application is based on the linear regression between the depth and the temperature recorded by the same logger.

A foraging trip was defined as the period between the first dive and the last dive, and is comprised of several dive cycles. A dive cycle is divided into two periods: (1) the dive followed by (2) the post-dive surface period. The post-dive surface period is considered to have two main uses: (1) to recover from the dive and (2) to prepare for the next dive (Wilson et al. 2003). The dive period starts when the depth becomes greater than 1 m and ends when the depth becomes less than 1 m. It is characterized by three phases: the descent, the bottom and the ascent phases. The bottom phase characterizes the phase where the bird is around the maximum depth of the dive and where preys are predominantly encountered (Ropert-Coudert *et al.*, 2000, 2001, 2006b), but it is also characterized by vertical undulations or 'wiggles' in the dive profile (Le Boeuf *et al.*, 1992; Simeone & Wilson, 2003). According to Simeone & Wilson (2003), each wiggle can be considered as a prey capture attempt.

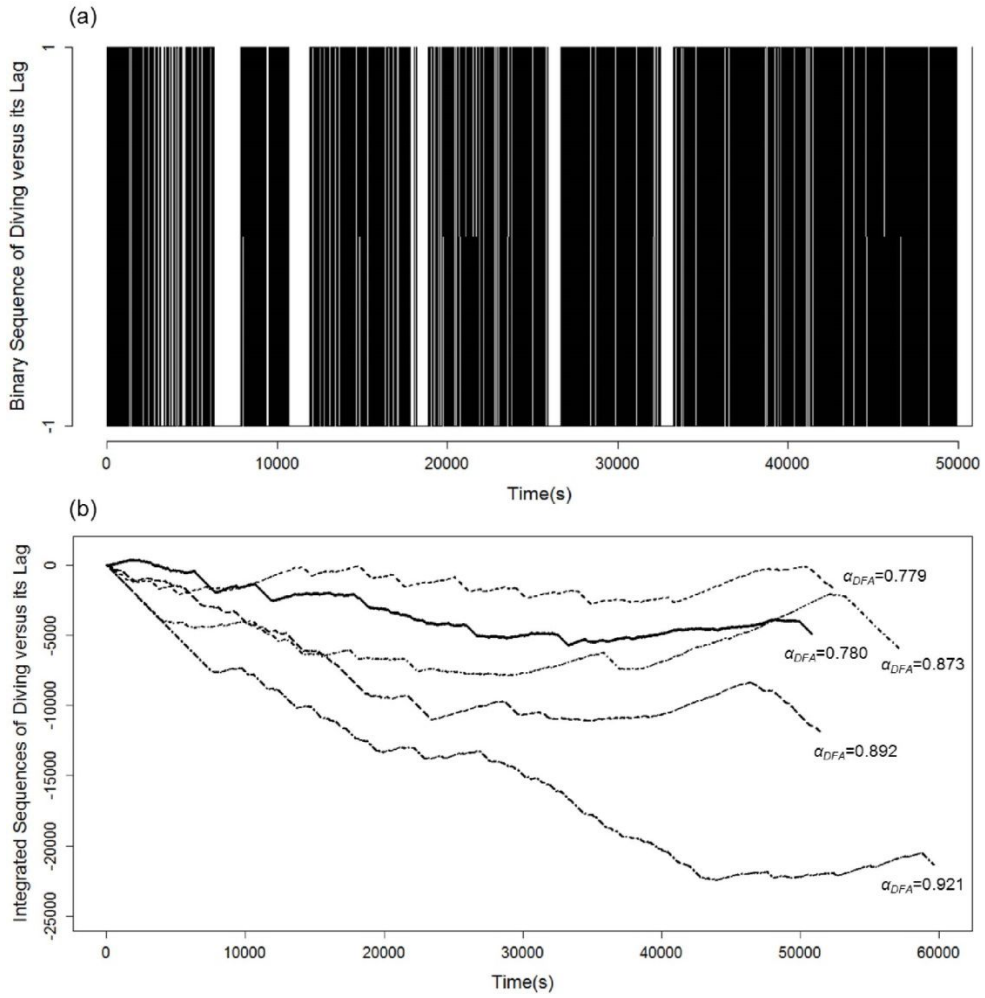


Figure II.13 : Example of (a) a little penguin's binary sequence denoted 1 for diving and -1 for post-surface period and (b) cumulatively summed dive sequences from 5 different little penguin (from MacIntosh et al. 2013).

In order to acquire these diving data, the script 'kaiseki' written by Dr. Katsufumi Sato and modified by Dr. Akiko Kato was used. This script is used among other things to automatically calculate the maximum depth (m), the total duration (sec), the duration of the dive period (and also the duration of descent, bottom, and ascent phases) (sec), the number of wiggles and the duration of the post-dive period (sec). The duration of dives and post-dives duration forms the basis of the fractal analytical approach used in this thesis.

I.1.1.a. Fractal analysis

We used Detrended Fluctuation Analysis (DFA) to measure long-range dependence as an index of temporal complexity in penguin diving sequences. This method was developed by

Peng *et al.* (1992) in order to study long-range correlations in nucleotide sequences. Indeed, DFA provides a robust estimate of the Hurst exponent (Hurst, 1951; Mandelbrot & Van Ness, 1968), which measures the degree to which time series are long-range dependent and statistically self-affine (Taqqu *et al.*, 1995; Cannon *et al.*, 1997).

The first step is to code dive sequences (i.e. succession of dives and post-dives surface periods) as binary time series [z(i)] (Figure II.13a). This series contains diving (denoted by 1) and post-surface events (denoted by -1) at n second intervals (according to the dataset) to length N. Next, the time series is cumulatively summed such that:

$$y(t) = \sum_{i=1}^{t} z(i)$$

where y(t) corresponds to the cumulative time series (Figure II.13b). Then, we divided sequences into non-overlapping boxes of length n. In order to remove local linear trends ($\hat{y}_n(t)$) (as mentioned in the name of the method), a least-squares regression was fit on each box and we repeated the process over all box sizes. Mathematically, these processes can be summarized as:

$$F(n) = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(y_n(t) - \hat{y}_n(t))^2}$$

where F(n) corresponds to the average fluctuation of the modified root-mean-square equation across all scales (2^2, 2^3,…, 2^n). *F* and *n* are related through the following equation:

$$F(n) \sim n^{\alpha}$$

where *α*, the scaling exponent, is the slope of the line on a double logarithmic plot of average fluctuation as a function of scale (Taqqu *et al.*, 1995; Cannon *et al.*, 1997). This

scaling exponent is bound to (0,1) for fractional Gaussian noises (fGn) and (1,2) for fractional Brownian motions (fBm) (Eke *et al.*, 2000; Delignières *et al.*, 2005). Values in the range (0.5, 1) and (1.5, 2) reflect persistent long-range dependence while those in the range (0, 0.5) and (1, 1.5) reflect antipersistent long-range dependence in the time series for fGn and fBm respectively, with 0.5 and 1.5 reflecting randomness (white noise). Theoretically, α_{DFA} is inversely related to the fractal dimension, which represents an index of structural complexity (Havlin *et al.*, 1999). The Hurst exponent will be equal to α_{DFA} for fGn and to α_{DFA}-1 for fBm. Hurst exponent is inversely related to fractal dimension (D_f) as described by the following equation:

$$D_f = 2 - H$$

As the smallest and the largest scales can introduce mathematical biases in the estimation of fractal scaling exponents (Cannon *et al.*, 1997), it is recommended to omit some of the smallest and the largest scales when performing DFA. To determine which scales should be removed, best-scaling regions are first calculated in order to maximize the fit of the regression line on the double logarithmic plot (Cannon *et al.*, 1997) using two different procedures described in Seuront, 2010: the **R^2-SSR procedure** and the **compensated-slope procedure**.

The R^2-SSR procedure (Figure II.14 A & B) involves using a series of regression windows in which the number of scales ranges from a minimum of 5 for valid regression analysis to the maximum number of scales considered. Then, each window was slid across the entire data set until the largest window is used to provide a unique regression for all scales. By plotting the coefficient of variation (R^2) and the sum of squared residuals (SSR), it should have points

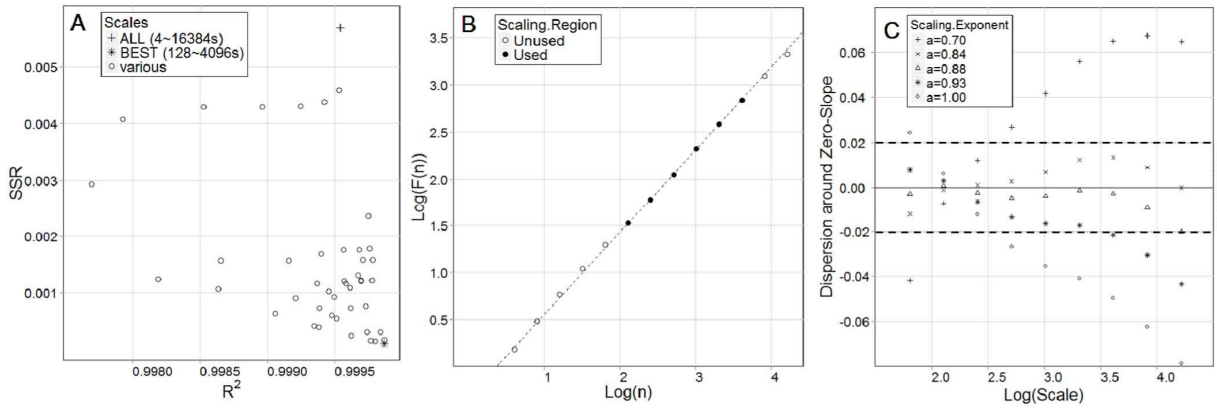


Figure II.14 : Illustrations of the two different procedures used to validate scaling regions in sequences of diving behavior from little penguins. (A) R^2-SSR procedure allows to determine the values of log(scale) that maximize the R^2 and minimize the SSR (*). This value, which corresponds to the range of scales within the date, reflects strong scaling behavior, represented as fill circles in (B). (C) Compensated-slope procedure aims to find the value at which our best range of scales (determined in (A)) and compensated-slope will converge to 0 on the plot of Log ($n^c * n^{-Df}$) versus Log(n) to produce a straight line in case of scaling is present with a zero slope. (From MacIntosh et al., 2013).

where the R^2 is maximized and the SSR minimized. These points allow us to identify the best scaling regions.

The second step to confirm the best scaling regions involves the compensated-slope procedure (Figure II.14 C). This procedure uses a scaling factor, named *c* with values ranging from $\in (0,1)$, to compensate the scaling behavior. In the case of DFA, it will be formalized by the following equation:

$$F(n) = n^c * n^{-Df}$$

As explained above, *F(n)* corresponds to the fluctuation about the box size *n*. The compensated-slope procedure aims to find the value at which our best range of scales (determined through R^2-SSR procedure) and compensated-slope will converge to 0 on the plot of Log ($n^c * n^{-Df}$) versus Log(n) to produce a straight line in the case where scaling is present with a zero slope. In this thesis, we used three values representing the minimum, best and maximum estimates of α_{DFA} obtained from the R^2-SSR procedure. Finally, by

bootstrapping 1000 simulations, we determine if variation from this zero slope in observed sequences could be explained by noise or if scaling was just an unlikely estimation of fractal dimension.

We then bootstrapped 1000 simulations to determine whether variation from this zero slope in observed sequences could be explained by noise, i.e. data points fall within the 95% confidence intervals, or whether scaling was simply unlikely given the fractal dimension estimate produced.

Chapter 1

Adélie penguin,
Adélie land, Antarctica

III. Chapter 1: Diving with a handicap: consequences of external devices on temporal organization of diving behavior of little penguins and Adélie Penguins

III.1 Article A: Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species

Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species

Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, André Chiaradia, Yan Ropert-Coudert

Animal Biotelemetry

2015

DOI: 10.1186/s40317-015-0061-8

Keywords: Fractal analysis, behavioral complexity, Adélie penguin, little penguin, flipper band, bio-logger, hydrodynamic handicap

III.1.1 Résumé (en français) – Article A

Les mouvements animaux présentent une autosimilarité rappelant les fractales statistiques, et ceci sur une série d'échelles tant spatiale que temporelle. Les facteurs de stress sont connus pour induire des changements dans ces motifs comportementaux mais tant la direction que l'interprétation de ces changements n'est pas toujours claire. Nous avons examiné ici comment des facteurs de stress hydrodynamique, comme des bio-loggers et des bagues alaires, induisent des changements dans l'organisation temporelle (complexité) des séquences de recherche alimentaire de deux espèces de manchots, la manchot pygmée (*Eudyptula minor*) et le manchot Adélie (*Pygoscelis adeliae*). Une detrended fluctuation analysis (DFA) a montré que les séquences de recherche alimentaire produites par les manchots pygmées portant des loggers large sont plus complexes, c'est-à-

dire tendant vers une plus grande stochasticité, que ceux portant des loggers plus petits. Au contraire, il apparaît que la taille de loggers n'affecte pas la complexité des séquences de recherche alimentaire chez le manchot Adélie et que la position du logger sur le dos du manchot pygmée est seulement associée faiblement avec une complexité comportementale altérée. Ainsi, les individus portant le logger au milieu du dos montrent que leur comportement de plongée est légèrement plus complexe que ceux portant le logger au bas du dos. Enfin, bien qu'on leur connaisse un effet délétère sur le succès reproducteur des manchots, les bagues alaires n'ont montré ici aucun effet sur la complexité des séquences de plongée chez le manchot pygmée. Malgré le fait que ces loggers et bagues alaires peuvent modifier certains paramètres comportement des oiseaux plongeurs, nous avons ici trouvé seulement des preuves contradictoires envers l'hypothèse que ces appareils peuvent significativement modifier l'organisation temporelle des séquences de recherche alimentaire chez les deux espèces de manchots ici étudiées. Cependant, des espèces de petite taille portant des loggers large, et peut-être aussi positionné plus haut sur le dos, peuvent subir du bruit supplémentaire dans leurs séquences comportementales. Ceci peut alors indiquer une déviation du comportement de recherche alimentaire observé sous des conditions normales.

III.1.2 **Abstract – Article A**

Animal movement exhibits self-similarity across a range of both spatial and temporal scales reminiscent of statistical fractals. Stressors are known to induce changes in these statistical patterns of behavior, although the direction and interpretation of such changes are not always clear. We examined whether the imposition of known hydrodynamic disruptors, bio-logging devices and flipper bands, induces changes in the temporal organization (complexity) of foraging sequences in two penguin species, little penguins

(*Eudyptula minor*) and Adélie penguins (*Pygoscelis adeliae*). Detrended Fluctuation Analysis (DFA) showed that foraging sequences produced by little penguins carrying larger loggers were more complex, i.e. were more erratic tending toward greater stochasticity, than those carrying smaller loggers. However, logger size did not affect complexity in foraging sequences of Adélie penguins. Logger position was associated only weakly with altered complexity in little penguins, with individuals carrying loggers in the middle of their backs displaying slightly more complex dive sequences than those carrying loggers lower on their backs. Finally, despite their known negative effects on penguin fitness, flipper bands were not associated with dive sequence complexity in little penguins. Despite that externally-attached devices can disrupt certain behavioral parameters in diving seabirds, we found mixed evidence in support of the hypothesis that such devices significantly disrupt the time-structured organizational properties of foraging sequences in the two penguin species investigated. However, smaller species carrying larger loggers, and perhaps those positioned higher on their backs, may experience an added element of noise in their behavioral sequences that may indicate a departure from foraging behavior observed under normal, unburdened conditions.

III.1.3 Introduction – Article A

Fractal patterns are found everywhere in nature, e.g. in the shapes of clouds, mountains and coastlines, or in plant structures such as those produced in the Romanesco broccoli (*Brassica oleracea* var. *botrytis*) (Mandelbrot, 1977). Such patterns are also known to emerge in spatial and temporal sequences of animal movement, which exhibits self-similarity across a range of measurement scales (Viswanathan *et al.*, 1996; Boyer *et al.*, 2004; Bartumeus & Levin, 2008; Sims *et al.*, 2008; MacIntosh *et al.*, 2011; Wearmouth *et al.*, 2014). Three approaches have used fractal geometry in the field of animal movement

ecology: (1) measuring step length distributions (*sensu* the Lévy flight foraging hypothesis) (Bartumeus, 2007; Sims *et al.*, 2008; Viswanathan *et al.*, 2008, 2011; Humphries *et al.*, 2012), (2) spatial fractal dimension estimation (Dicke & Burrough, 1988; Crist *et al.*, 1992; Johnson *et al.*, 1992; Wiens *et al.*, 1993, 1995), and (3) fractal time series analysis of behavior sequences (Asher *et al.*, 2009; MacIntosh, 2014). These studies highlight how highly irregular patterns of behavior may reflect an optimal strategy to facilitate resource encounters in heterogeneous environments.

Fractal time series analyses of animal behavior measure the structure of behavior as it occurs through time, which is linked to the concept of behavioral organization (Camazine *et al.*, 2001; Asher *et al.*, 2009). Borrowing from the field of complexity science, such studies have adopted the term 'complexity' to refer to the correlation structure of the time series, which behave as nonlinear systems (Bradbury & Vehrencamp, 2014). Complexity in diverse biological phenomena is considered to be adaptive because it is error-tolerant, making it possible to buffer changes arising from both intrinsic (e.g. reproductive state and hormones) and extrinsic factors (e.g. environmental perturbations) (West, 1990). On a temporal scale, physiological or behavioral changes can impact the complexity observed in time series data collected from diverse systems (MacIntosh, 2014). These deviations from normal behavioral patterns in nonlinear systems, known as 'complexity loss', were first observed in physiological systems producing heart rate variability (Peng *et al.*, 1995a), stride patterns (Hausdorff *et al.*, 1995) and neural activity (Abasolo *et al.*, 2008): pathological systems produce times series with altered complexity signatures. Complexity loss has now also been observed in various forms of animal behavior, such as foraging and movement but also vigilance, postural behavior and even social behavior, when animals are confronted with some or another stressor (Alados *et al.*, 1996; Rutherford *et al.*, 2003, 2004, 2006;

MacIntosh *et al.*, 2011; Seuront & Cribb, 2011; Cottin *et al.*, 2014). For example, Spanish ibex (*Capra pyrenaica*, Alados *et al.*, 1996) and Japanese macaques (*Macaca fuscata*, MacIntosh *et al.*, 2011) infected by parasites have showed a decrease in behavioral sequence complexity. Similarly, Adélie penguins (*Pygoscelis adeliae*, Cottin *et al.*, 2014) treated with corticosterone implants also exhibited reduced dive sequence complexity in comparison with untreated (control) birds. Moreover, Indo-Pacific bottlenose dolphins (*Tursiops aduncus,* Seuront & Cribb, 2011), exposed to the presence of motor boats also showed a decrease in the complexity of their dive sequences. Thus, complexity loss, as far as it has been detected in altered behavior sequences, is predicted to reduce an animal's fitness long term.

Altered complexity signatures may reflect changes toward either greater stereotypy or greater randomness, depending on the nature of the disruption (Rutherford *et al.*, 2003; Asher *et al.*, 2009; MacIntosh, 2014). Kembro *et al.* (2009b) for instance showed increased stochasticity in the movement behavior of mosquito larvae exposed to lethal and sub-lethal doses of essential oils. Similarly, greater stochasticity was also observed by Rutherford *et al.* (2003) in behavioral patterns of hens exposed to novel housing conditions. The contrasting responses to the presence of stressors appear to depend on the specific type of stressor faced by individuals, with greater stochasticity expected in cases of acute stress and greater stereotypy expected in cases of chronic stress (Rutherford *et al.*, 2004; MacIntosh, 2014). The concept of complexity loss was thus extended to allow for the fact that changes in both directions can equate to suboptimal complexity signatures, as both reflect a departure from optimal patterns of behavioral organization that can be detrimental over the long term (MacIntosh, 2014). We could easily hypothesize about the potential benefits of increased complexity in the vigilance behavior of animals exposed to novel environments in which the

location of potential resources, but also potential threats, cannot be *a priori* known. However, we would predict a return to normal, i.e. more deterministic behavior patterns over time, as animals familiarize with their surroundings, whereas the same might not be said of an animal exposed to a truly chronic stressor.

Here, we re-examined published datasets that found an effect of either external devices (Ropert-Coudert *et al.*, 2007a, 2007b) or flipper bands (Fallow *et al.*, 2009) on the foraging activities of penguins to determine whether hydrodynamic handicaps can induce altered complexity signatures in foraging (diving) sequences of two species of penguin: the Adélie penguin and the little penguin (*Eudyptula minor*). Indeed, previous studies of Adélie and little penguins have revealed short-term impacts of back-attached diving recorders on diving activities through comparisons of diving parameters in groups of birds equipped with devices of different sizes (Ropert-Coudert *et al.*, 2007a, 2007b). These experiments offer a good framework to test whether the attachment of such devices, which imposes a known hydrodynamic handicap (Culik & Wilson, 1991; Bannasch *et al.*, 1994), would also induce organizational changes in patterns of foraging behavior. Thus, we predicted the existence of variation in the organizational complexity of foraging behavior in relation to logger size (large versus small loggers) and logger position (higher versus lower on the penguin's back). Since large loggers and those positioned higher on the back should increase drag relative to smaller loggers and those positioned lower on the back (Culik & Wilson, 1991; Bannasch *et al.*, 1994), we assumed that the organizational properties of foraging sequences in birds under the latter conditions were more similar to those in birds under unburdened, control conditions. Following the results of Fallow *et al.* (2009), predictions about the impact of flipper bands should differ between short-term (acute stressor) and long-term (chronic

stressor) attachment experiments on little penguins. Thus, we predicted short-term effects on the organizational properties of foraging sequences but not long-term effects.

III.1.4 Material & Methods – Article A

We studied little penguins from the Penguin Parade colony at Phillip Island, Victoria, Australia (38°30'S, 145°09'E) and Adélie penguins in Dumont d'Urville, Adélie Land (66°39'S, 140°00'E).

III.1.4.a Little penguins

Studies were conducted on 15 males and 16 females from 9 to 26 November 2004 (logger size and position experiment) and 21 females between November and December 2005 (Flipper band experiment). In both cases, all birds were in the guard stage, raising 1 or 2 chicks. Further details on the colony and field protocol can be found in (Ropert-Coudert *et al.*, 2007b) and (Fallow *et al.*, 2009).

The effects of different logger sizes and positions of attachment were investigated using large and small loggers placed higher or lower on the backs of birds. Large loggers were cylindrical, two-channel depth data loggers (62mm x 18 mm, 17g, LTD 1200-100, Lotek, Canada) accounting for ca. 4.9% of the cross section area of little penguins, while small loggers were cylindrical (53 mm x 15 mm, 17g, M190-D2GT, Little Leonardo, Japan) accounting for ca. 3.4% of the cross section area of little penguins. All loggers sampled depth once per second with a 0.1m accuracy. Large and small devices were attached either to the lower (recommended to minimize drag (Bannasch *et al.*, 1994)) or middle back of the birds (where we expected the loggers to increase drag). The experimental design included four groups: birds with either small (n=21) or large loggers (n=15), placed either near the tail (n=17) or in the middle (n=19) of the back (See details in [32]). Birds were monitored for a

single trip at sea during the guard phase. All trips lasted one day only. Ropert-Coudert *et al.* (2007b) showed that birds carrying large loggers had shorter dives that were more frequent than penguins carrying small loggers. Logger position had no statistical effect on little penguin diving behavior.

The experiment testing the effect of flipper bands was conducted using three groups of individuals: an unbanded control group (n=7), a banded control group (n=6) that had been carrying bands for a number of years, and a treatment group of unbanded birds that were temporarily banded specifically for this experiment (n=7). Short-term effects (days) were examined in the treatment group by comparing the diving data from a first foraging trip when birds were not banded with the diving data obtained during the next foraging trip when birds had been banded. In parallel, long-term effects (years) were examined by comparing the diving data of the banded control group with the diving data of the unbanded control group. Diving activity was monitored using the M190-D2GT data loggers described above (see details in Fallow *et al.* (2009). Fallow *et al.* (2009) showed that birds in the treatment group dived deeper, longer, descended slower and ascended quicker with longer surface times after dives when banded but no long-term effect was found.

III.1.4.b Adélie penguins

The study was conducted on 14 birds from 18 December 2001 to 4 January 2002 during the guard phase. A logger size effect was investigated using two sizes of loggers: large loggers were cylindrical, 3-channel W200-PDT loggers (102 x 22 mm, 50g, Little Leonardo, Tokyo, Japan) which measured speed and depth at 1 Hz and accounted for 1.4% of the cross section area of Adélie penguins (n=7); small loggers were M190-D2GT loggers described above, which recorded depth at 1Hz and acceleration at 16 Hz, and accounted for 0.8% of

the cross section area of Adélie penguins (n=7). Diving data and swim speed (either measured directly via an anteriorly mounted propeller or reconstructed based on diving angle and depth changes) of two groups measured over a single foraging trip of 2-3 days were compared (see details in Ropert-Coudert *et al.* (2007a).

III.1.4.c Data analysis

Following the analytical approach described in MacIntosh *et al.* (2013), we used Detrended Fluctuation Analysis (DFA) to measure long-range dependence as an index of temporal complexity in penguin diving sequences. DFA was developed by Peng *et al.* (1992) to provide a more robust estimate of the Hurst exponent, which measures the degree to which time series are long-range dependent and statistically self-affine. The scaling exponent calculated by DFA (α_{DFA}) measures the slope of the line on a double logarithmic plot of average fluctuation as a function of scale (Taqqu *et al.*, 1995; Cannon *et al.*, 1997) and is bound to (0, 1) for fractional Gaussian noises (fGn) and (1, 2) for fractional Brownian motions (fBm) (Eke *et al.*, 2000; Delignières *et al.*, 2005). Values in the range (0.5, 1) and (1.5, 2) reflect persistence while those in the range (0, 0.5) and (1, 1.5) reflect antipersistence in the time series for fGn and fBm respectively, with 0.5 and 1.5 reflecting randomness (white noise). Theoretically, α_{DFA} is inversely related to the fractal dimension, which represents an index of structural complexity (Mandelbrot, 1977). Since its introduction, DFA has become widely used in a diverse array of biological systems (e.g. Peng *et al.*, 1995a; Kiraly & Janosi, 2005; Abasolo *et al.*, 2008), including animal behavior (Rutherford *et al.*, 2004; Asher *et al.*, 2009). DFA was previously shown to produce reliable estimates of scaling behavior in little penguin and Adélie penguin dive sequences (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014). Since including the smallest and largest scales in the estimation of fractal scaling exponents can introduce mathematical biases (Cannon *et al.*, 1997), we first calculated best-scaling

regions for each treatment group using methods provided in (Seuront, 2010) and used those rather than the full set of measurement scales available to estimate α_{DFA}. DFA was run using the package 'fractal' (Constantine & Percival, 2014) in R statistical software v.3.1.1 (R Development Core Team, 2016). Details of the analytical approach used here, including DFA calculation, the subsequent validation of scaling, and its relationship to other fractal dimension estimates are provided in (MacIntosh *et al.*, 2013). Example data set will be provided upon request to anyone wishing to reproduce our method.

All statistical analyses were conducted in R 3.1.1. We constructed General Linear Mixed effects models (GLMM) using the package 'nlme' (Pinheiro *et al.*, 2015) to investigate whether variation in α_{DFA} existed between groups in each experiment. In all models, we set individual identity and trip date as crossed random factors to account for pseudoreplication and temporal variation respectively, and trip duration as a covariate to control for the effects of sequence length on scaling exponents (MacIntosh *et al.*, 2013). In the logger size and/or position experiments we included the following factors in the models: logger size (for both species), logger position and sex of the individual (for little penguins only). For the flipper band experiments we added banded state (banded or not) as a fixed factor and trip duration as covariate. We also tested for interactions between logger size/position and sex via Likelihood ratio tests using the package 'lmtest' (Hothorn *et al.*, 2015) after first running the GLMM with and without these interaction terms. Values of α_{DFA} are presented as means ± SE, and we set the alpha level for all statistical analyses at 0.05.

III.1.5 **Results – Article A**

Fractal analyses showed values of α_{DFA} ranging between 0.74 and 0.94 (mean=0.86, SE=0.008) for little penguins during the logger experiment and values of α_{DFA} ranging

between 0.74 and 0.97 (mean=0.88, SE= 0.008) for little penguins during the flipper band experiment. Adélie penguins exhibited higher mean values of α_{DFA} ranging between 0.91 and 0.98 (mean=0.94, SE=0.005). These values indicate that dive sequences are long-range dependent and resemble persistent fractional Gaussian noise, as shown previously (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014). The likelihood ratio test showed no difference between statistical models with and without interaction terms (p=0.16), so we present

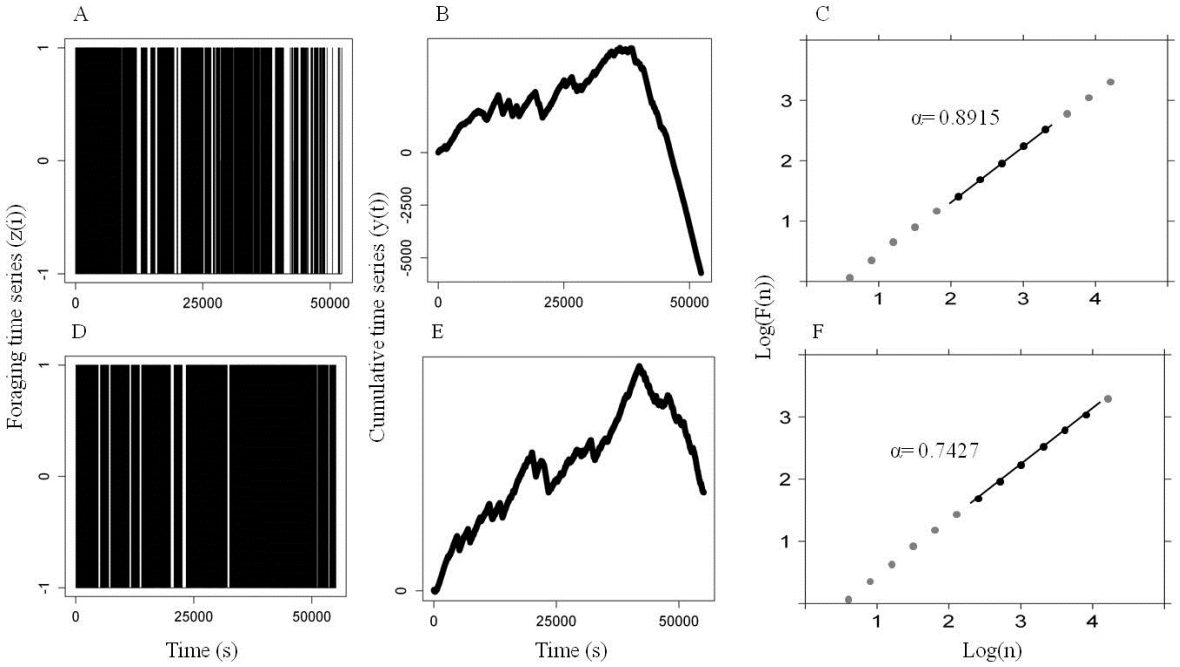


Figure III.1 : Detrented Fluctuation Analysis (DFA) of foraging sequences from a little penguin carrying a small logger (top row) and a little penguin carrying a large logger (bottom row). (A, D) Binary sequences (z(i)) generated from the diving (black bars) and not diving behavior at 1 s intervals. (B, E) Integrated sequences (y(t)) generated by the accumulation of z(i). (C, F) Log-log plots of the average fluctuation F(n) on the y-axes as a function of scale (n) on the x-axes. The αDFA is the slope of the regression line; the lower αDFA reflects greater complexity. Note that only the points in black were used to fit the regression line to avoid biases introduced at small (<10 s) and large (sequence length/10) scales.

results from the more parsimonious models without the interaction terms in which the main effects can be better interpreted.

We observed a significant difference between dive sequences produced by little penguins carrying loggers of different sizes (Table III.1; GLMM: α_{DFA}, df=21, t=2.22, p=0.04; mean α_{DFA} Large logger=0.85±0.008; mean α_{DFA} Small logger=0.94±0.008): little penguins carrying larger

loggers exhibited lower values of α_{DFA}, reflecting greater stochasticity in dive sequences than those carrying smaller loggers. Figure III.1 illustrates this difference as well as the process of DFA using representative little penguins equipped with a small and large logger, respectively. Logger position, on the other hand, was not significantly associated with complexity in dive sequences, although little penguins carrying loggers in middle positions showed a tendency towards lower α_{DFA} values compared with those carrying loggers in lower positions (Table III.1; GLMM: α_{DFA}, df=21, t=1.79, p=0.09; mean α_{DFA} middle position=0.85±0.015; mean α_{DFA} low position=0.87±0.008). Additionally, our statistical model showed that males displayed higher values of α_{DFA} than females (Table III.1; GLMM: α_{DFA}, df=21, t=-4.87, p=0.0001; mean α_{DFA} male=0.89±0.007; mean α_{DFA} female=0.84±0.009), whereas trip duration had no effect (Tab. 1; GLMM: α_{DFA}, df=21, t=-0.05, p=0.96).

We did not observe any effects of flipper banding on α_{DFA} values in either the short-term (Table III.1; GLMM: α_{DFA}, df=11, t=-0.91, p=0.38; mean α_{DFA} non-banded=0.88±0.021; mean α_{DFA} banded=0.86±0.013) or long-term (Tab. 1; GLMM: α_{DFA}, df=3, t=0.44, p=0.69; mean α_{DFA} non-banded=0.86±0.018; mean α_{DFA} banded=0. 88±0.014) experiments. Our covariate, trip duration, was also not associated with values of α_{DFA} in either experiment, respectively (Table III.1; GLMM: α_{DFA}, df=11, t=-057, p=0.58; GLMM: α_{DFA}, df=3, t=0.33, p=0.76).

Finally, logger size had no effect on the α_{DFA} values estimated for Adélie penguin diving sequences (Table III.1; GLMM: α_{DFA}, df=7, t=0.64, p=0.54; mean α_{DFA} large logger=0.938±0.008; mean α_{DFA} small=0. 937±0.008), but longer trip durations were negatively associated with α_{DFA} values (Table III.1; GLMM: α_{DFA}, df=7, t=-2.46, p=0.04), i.e. the longer the trip the greater the stochasticity of the dive sequence.

Experiment	Variable	Est.	SE	*df*	t-value	p-value
Little penguin logger size	Intercept	0.8733	0.1973	21	4.42	**0.0002**
	Size (Large vs Small)	0.0285	0.0128	21	2.22	**0.04**
	Position (Middle vs Low)	0.0232	0.013	21	1.79	0.09
	Trip duration	-0.0006	0.0132	21	-0.05	0.96
	Sex (male vs female)	-0.0623	0.0128	21	-4.87	**0.0001**
Adélie penguin logger size	Intercept	0.9628	0.0129	7	74.58	**0**
	Size (Small vs Big)	0.0053	0.0084	7	0.64	0.54
	Trip duration	-0.0008	0.0003	7	-2.46	**0.04**
Little penguin Flipper band short-term	Intercept	1.0824	0.344	11	3.15	**0.01**
	State (Non- banded vs banded)	-0.024	0.0265	11	-0.91	0.38
	Trip duration	-0.013	0.0226	11	-0.57	0.58
Little penguin Flipper band long-term	Intercept	0.7463	0.3493	14	2.14	0.05
	State (Non- banded vs banded)	0.011	0.025	3	0.44	0.69
	Trip duration	0.0076	0.0234	3	0.33	0.76

Table III-1 : Summary of GLMM statistics for all experiments. Bold text highlights significative p-value. Abbreviations include: Est= estimate, SE= Standard error, df= degree of freedom.

III.1.5.a Discussion – Article A

We demonstrate here that the size of back-mounted recording devices is associated with variation in the temporal organization of foraging behavior in little penguins. Unlike most previous studies of fractal time in animal behavior, which demonstrated alterations toward more stereotypical sequential patterns in the presence of various stressors (i.e. complexity loss), we show here that dive sequences were more complex, exhibiting greater stochasticity, in birds with larger loggers. The hydrodynamic handicaps imposed by large loggers, and by extrapolation perhaps loggers in general though studies of this nature necessarily lack true controls (i.e. birds without loggers), thus seem to add an extra element of noise into the diving sequences of little penguins. However, the lack of effects of logger position in little penguins, logger size in Adélie penguins and, surprisingly, flipper bands in little penguins suggest that animal-attached devices do not universally induce such organizational changes in seabird foraging behavior, despite having clear effects on other dive parameters and potentially, for flipper bands at least, fitness outcomes (Gauthier-Clerc *et al.*, 2004; Saraux *et al.*, 2011b; Dann *et al.*, 2014).

The use of back-mounted recording devices on penguins and other marine animals increases drag, which should increase swimming energy expenditure at a given velocity (Wilson *et al.*, 1986; Bannasch *et al.*, 1994). With increasing energy expenditures, air-breathing marine predators such as penguins may need to reduce dive durations as oxygen stores are depleted more rapidly than when they are not handicapped, and/or increase post-dive duration periods at the surface to replenish oxygen stores in provision of future dives. This may in part explain our results for little penguins; because of the increased foraging effort observed in little penguins with large loggers, evidenced by the greater numbers of dives per foraging trip, hourly dive rates, total time spent underwater and at least in males

longer foraging trips (Ropert-Coudert *et al.*, 2007b; see also Kato *et al.*, 2000), the between-dive durations were less variable (the mean standard deviations for individuals equipped with large loggers versus small loggers were 72.88 ± 10.11 seconds versus 105.13 ± 9.08 seconds, respectively), leading to more randomized sequences of behavior. All else being equal, surface durations are much freer to vary (diverge from a random distribution) than are dive durations due to the physiological constraints of diving activity (i.e. oxygen depletion, CO_2 and lactic acid accumulation; Kooyman, 1989). Given the small differences in body size between sexes (Arnould *et al.*, 2004), the sex differences observed here could be explained by variation in dietary preference, e.g. males having a different diet than females or perhaps feeding on same species but larger prey. Unfortunately we do not have any dietary information for the birds we monitored, though dietary differences between sexes have been shown to be minimal in little penguins (Chiaradia *et al.*, 2012).

Alternatively, rather than reducing dive durations and other frequency-based dive parameters, Adélie penguins equipped with large loggers are known to compensate for this handicap by reducing swim speeds, thereby maintaining similar per dive energy expenditures as birds equipped with small loggers (Ropert-Coudert *et al.*, 2007a). Both strategies would reduce achievable dive depths and time spent with prey, thus limiting foraging efficiency (Ropert-Coudert *et al.*, 2007a, 2007b), but such limitations would likely be far less detrimental to Adélie penguins, which feed on densely-packed, slow-moving prey (krill; Wilson *et al.*, 2002; Cherel, 2008). This effect should be stronger on little penguins that indeed showed organizational changes in their dives as they feed on fast-moving prey (fish, Chiaradia *et al.*, 2012). At a given position, the drag caused by back-mounted devices, and resultant effects on dive profiles, should depend primarily on the ratio of logger to body size. In the present study, large loggers accounted for a significantly larger cross-section of the

frontal area of little penguins (4.9%) than the much larger Adélie penguins (only 1.4%). Small body size already disadvantages diving seabirds, so little penguins may not have the option to decrease swim speeds to compensate for the extra drag as Adélie penguins seem to do (Ropert-Coudert *et al.*, 2007a), and must instead make organizational changes to their dive profiles. Interestingly, we detected an effect of trip duration on the sequential organization of foraging behavior in Adélie penguins and the direction of the effect may seem counter-intuitive when comparing with the results of MacIntosh *et al.* (2013). However, MacIntosh *et al.* (2013) conducted their analysis on little penguins during the guard stage where birds are restricted to a one-day trip. It is possible that variation in trip duration and the associated variation in foraging effort in Adélie penguins (Ropert-Coudert *et al.*, 2004) may have cause this statistical effect to appear. Future studies should investigate this as variable trip lengths could potentially influence the conclusions driven from the use of the DFA method. For the present analysis, we note that the effect should be limited as the estimate value only changes by 0.0008.

Despite that logger position was not significantly associated with foraging sequence complexity in little penguins, we hesitate to reject this possibility outright for two reasons: (i) that the results showed a statistical trend and (ii) that the difference exhibited consistency with the effect of logger size in that the sign of the difference was the same, i.e. toward greater stochasticity in the middle position, which we predicted would impose a greater hydrodynamic handicap than loggers placed lower on the back. Still, that the effect of logger position was weaker than that of logger size also mirrors the original study, in which the former had little impact on the dive parameters examined (Ropert-Coudert *et al.*, 2007b). However, penguins with small loggers positioned middle on their backs did dive to significantly greater depths than those with large loggers on the same position and displayed

a tendency toward increased dive durations as well, while no difference was observed when the loggers were positioned lower (Ropert-Coudert *et al.*, 2007b). As discussed above, resultant changes in the sequential distributions of dive and between-dive times may account for the tendency toward greater stochasticity observed here in penguins equipped with loggers in the middle of their backs as well, however marginal these differences may be. Since the change in drag is expected to be less dramatic for the two logger positions than the two logger sizes (Ropert-Coudert *et al.*, 2007b), the weaker influence of position on dive sequence complexity is not surprising.

What is perhaps most surprising in our study is the lack of effect of flipper bands on observed dive sequences. Using the same dataset, Fallow *et al.*, 2009 highlighted the immediate effects of flipper banding on the diving behavior of little penguins using conventional measures; notably, dive durations increased significantly while dive efficiency, defined as bottom phase duration/(dive duration + post dive duration), decreased significantly in newly banded birds. Apparently, these differences are not necessarily associated with organizational changes in dive sequences. One major difference between the previously observed flipper band and large logger effects is that increased logger size induced significant increases in overall diving effort, defined as the cumulative time spent underwater during the trip, and total numbers of dives performed, neither of which differed in the flipper band experiment (Ropert-Coudert *et al.*, 2007b; Fallow *et al.*, 2009). Indeed, dive durations and between-dive durations increased in the flipper band experiment, meaning that the sequential distribution and variance of both dive and surface durations may not have changed, leaving the global structure of the foraging trip unchanged as well. This also suggests that global structural changes in the organizational complexity of dive sequences need not be associated with other changes in foraging behavior, e.g. those

induced by flipper bands, that are known to significantly affect survival and reproduction (e.g. Gauthier-Clerc *et al.*, 2004; Saraux *et al.*, 2011b; Dann *et al.*, 2014).

While variation in performance outcomes (e.g. body mass gain) was not measured in the original study (Ropert-Coudert *et al.*, 2007b), the alterations in the organizational structure of foraging sequences we observed in little penguins equipped with large loggers, and potentially those placed in positions that further increase drag, can theoretically affect the overall performance of birds in their ability to detect and capture prey. Emergent fractal patterns in the movement behavior of numerous animal species are thought to reflect an underlying strategy aimed at maximizing prey encounters, particularly with heterogeneous prey fields (Bartumeus, 2007; Sims *et al.*, 2008; Viswanathan *et al.*, 2008, 2011; Humphries *et al.*, 2012). Observed complexity signatures under normal conditions are thus predicted to reflect theoretical optimal behavior patterns (Johnson et al., 1992; Alados et al., 1996), while deviations from such theoretical optimal patterns have been associated on numerous occasions with pathological or otherwise challenging intrinsic conditions, such as intense parasitic infection (Alados *et al.*, 1996; MacIntosh *et al.*, 2011), increased physiological stress (Cottin *et al.*, 2014), anthropogenic disturbance (Seuront & Cribb, 2011) and even advanced reproductive state (Alados *et al.*, 1996; MacIntosh *et al.*, 2011). While increased complexity might approximate an optimal solution to some imposed stressors, e.g. the increased vigilance sequences observed in hens moved to novel enclosures (Rutherford *et al.*, 2003), these tendencies toward stochasticity also appear to be associated with decreased energetic efficiency. Thus, hens in novel environments also significantly increased their total vigilance behavior, which would interfere with normal feeding patterns (Rutherford *et al.*, 2003). Here, little penguins carrying large loggers were probably forced to compensate with more-

frequent dives and longer foraging trips, presumably to achieve baseline energy gains. These compensatory behavior patterns are unlikely to be optimal in the long term.

III.1.6 **Conclusions**

Hydrodynamic handicaps caused by carrying externally-attached devices exhibited variable influence on the organizational properties of penguin foraging sequences. Relative drag caused by back-mounted devices is likely an important component of dive sequence complexity for smaller species, decreasing variability in the alternation between diving and surface intervals and thus creating greater stochasticity in patterns of foraging behavior. It is also important to remember that there was no true control in this experiment, since all birds were equipped with loggers of variable sizes and positions. Given our results, it seems likely at least for little penguins that unequipped birds might exhibit a different set of fractal properties altogether, with even less noise in their dive sequences. This might even have confounded our flipper band experiment, for which there was a true control, if the effects of loggers interacted in some way with or overshadowed the effects of flipper bands, but this cannot be tested. Ultimately, we show here that increased noise in dive sequences, as opposed to the more commonly observed increased stereotypy (Alados *et al.*, 1996; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011; Cottin *et al.*, 2014), is a potential outcome of coping with an added stressor. Further application of fractal tools to temporal sequences of behavior is needed to examine how animals cope with various realizations of environmental change, particularly organisms used as indicator species for environmental change.

Competing interests

The authors declare that they have no competing interests.

Author contributions

YRC, AK and AC conceived of the experiment, collected the data and analysed the frequency-based measures presented. YRC and AK arranged the data set for fractal analysis. XM and AM conducted all fractal analyses and wrote the manuscript. All authors contributed to manuscript discussion and revision.

Acknowledgements

The authors thank P. Fallow, K. Yoda, the staff of Phillip Island Nature Parks and all members of the 52nd over-wintering party at Dumont d'Urville for their help in the field. We thank B. Class and M. Widmann for their help with R software. This work was financially supported by grants from BHP-Billiton (Australia), Sasakawa Foundation (Japan), Australian Academy of Science, the Japan Society for the Promotion of Science, and the Ministère de l'Enseignement Supérieur et de la Recherche (France). The study on Adélie penguins was approved by the ethics committee of and supported logistically by the French Institute Paul-Emile Victor (IPEV). Little penguin research was approved by the Phillip Island Nature Parks Ethics Committee, with research permission from the Department of Sustainability and Environment of Victoria, Australia.


Chapter 2
Cape Woolamai
Phillip Island, Australia

IV. Chapter 2: Influence of environment on temporal organization of foraging behavior of little penguin

IV.1 Article B: Shallow divers, deep waters, and the rise of behavioral stochasticity

Shallow divers, deep waters, and the rise of behavioral stochasticity

Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, Andre Chiaradia, Thomas Mattern, Cédric Sueur & Yan Ropert-Coudert

To be submitted in Journal of Experimental Marine Biology and Ecology

Keywords: fractal analysis, behavioral complexity, little penguin, environmental constraints, diving behavior, foraging.

IV.1.1 Résumé (en français) – Article B

Le manchot pygmée (*Eudyptula minor*) a une des plus large distribution parmi les manchots, les exposant ainsi à différentes contraintes écologiques au sein de leur aire de distribution. En réaction, les animaux vont présenter des variations dans leur comportement de recherche alimentaire. En théorie, cette flexibilité comportementale permet aux animaux de s'adapter aux conditions environnementales locales. Nous avons examiné comment la complexité de l'organisation temporelle des séquences de recherche alimentaire correspond aux caractéristiques de la zone de recherche alimentaire au sein des quatre différentes colonies. Complexité et dimension fractale dans les distributions du comportement de recherche alimentaire aux échelles tant spatiale que temporelle ont été théoriquement liées à l'efficacité de recherche alimentaire dans des environnements hétérogènes. Utilisant des méthodes d'analyses des séries temporelles fractales (Detentred Fluctuation Analysis), nous avons trouvé que la complexité de la recherche alimentaire sur un gradient de stochasticité-determinisme était associée avec la bathymétrie dans les zones de recherche alimentaire ; les manchots pygmées plongeant en eaux plus profondes présentent des séquences de

recherche alimentaire plus stochastique/moins déterministique que les individus plongeant en eaux moins profondes. Les données de succès d'envol correspondantes suggèrent également que les manchots recherchant leur nourriture en eaux plus profondes ont un succès reproducteur réduit. Une analyse par composante principale a montré que notre index de dimension fractal, mesurant spécifiquement la dépendance à long-terme dans les séquences de comportement (un phénomène déterministique), se charge positivement avec l'efficacité de recherche alimentaire dans PC1 alors que l'effort de recherche alimentaire s'y charge négativement. Les modèles statistiques corroborent ces relations. La production de séquence de recherche alimentaire complexe avec un haut degré de stochasticité semble avoir un coût énergétique, bien que nous ne sommes pas en capacité ici de déterminer quelle stratégie maximisera le succès de recherche alimentaire, une variable que nous ne pouvons mesurer ici, sous les conditions observées. Nous proposons que l'augmentation des éléments stochastiques dans le comportement de recherche alimentaire est nécessaire en cas de conditions environnementales difficiles mais peut-être pas suffisant pour atteindre les gains de fitness réalisés sous des conditions plus favorables.

IV.1.2 **Abstract - Article B**

Little penguins (*Eudyptula minor*) have one of the widest distribution among penguins, exposing them to variable ecological constraints across their geographic range, which in turn can affect variation in foraging behavior. In theory, behavioral flexibility allows animals to adapt locally to prevailing environmental conditions. Here, we examined whether complexity in the temporal organization of foraging sequences corresponded to characteristics of the foraging area across four geographically structured colonies. Complexity and fractal scaling in the spatial and temporal distribution of foraging behavior have been theoretically linked to foraging efficiency in heterogeneous environments. Using fractal time series methods

(Detrended Fluctuation Analysis), we found that foraging complexity along a stochastic-deterministic gradient was associated with bathymetry in the local foraging areas; little penguins foraging in deeper waters produced more stochastic/less deterministic foraging sequences than those foraging in shallower waters. Corresponding data on fledging success suggest that little penguins foraging in deeper waters also experience reduced reproductive success. A Principal Component Analysis showed that our fractal scaling index, which specifically measures long-range dependence (a deterministic phenomenon), loaded positively onto PC1 along with foraging efficiency (catch per unit time), whereas foraging effort (total time underwater) loaded negatively. Statistical models corroborated these relationships. The production of complex foraging sequences with high degrees of stochasticity thus appears to be highly energy intensive, though we cannot determine which strategy would have maximized foraging success, a variable we could not measure here, under the conditions observed. We propose that increasing stochastic elements in foraging behavior is necessary under challenging environmental conditions, but may not be sufficient to match fitness gains attained under more favourable conditions.

Highlights:

- We measured foraging complexity in little penguins via fractal analysis.
- Bathymetry may drive variability in foraging complexity across little penguins.
- More stochastic foraging was linked to increased effort and decreased efficiency.
- Less deterministic foraging sequences thus appear highly energy intensive.
- Greater stochasticity may buffer penguins against challenging foraging conditions.

IV.1.3 **Introduction – Article B**

Diversity in marine habitats induces variability in prey distributions across time and space (Weimerskirch, 2007). This has multiple and complex effects on the foraging behavior of marine predators, including seabirds (Morrison *et al.*, 1990). For instance, seabirds require flexibility in their foraging behavior to catch mobile prey (Williams *et al.*, 1992; Hull, 2000), and are known to use a variety of hunting tactics to pursue their prey, including plunge diving, dipping and pursuit diving (Schreiber & Burger, 2001). Among diving seabirds, penguins occupy diverse habitats across their range and attempts have been made to determine how they cope with such diversity. Breeding penguins, like other central place foragers, are restricted to certain foraging zones and are constrained by a diverse set of physical parameters, such as sea ice (Watanuki *et al.*, 1997), bathymetry (Chiaradia *et al.*, 2007) and marine currents (Bost *et al.*, 2009). For example, the foraging (diving) behavior of rockhopper penguins (*Eudyptes chrysocome*) varies significantly among populations breeding on three subantarctic archipelagos in the Indian Ocean (Tremblay & Cherel, 2003). Similarly, gentoo penguins (*Pygoscelis papua*) exhibit extensive variation in foraging behavior between colonies, even within the same archipelago when they have variable access to open sea (Lescroël & Bost, 2005). These examples suggest that colonies across a given geographic range are exposed to different ecological constraints, and this might explain the observed differences in their foraging behavior.

Advances in bio-logging (see Ropert-Coudert & Wilson, 2005; Ropert-Coudert *et al.*, 2012) have allowed scientists to simultaneously measure a suite of foraging parameters at fine spatiotemporal scales, which can then be examined in parallel to fitness indicators, such as survival and reproductive success. Bio-logging has thus facilitated a new era in the study of foraging behavior of seabirds, but also necessitated the development of new ways to

manage and analyse large datasets (Rutz & Hays, 2009). A common approach to studying diving behavior consists of analysing several diving variables in parallel, such as dive depths, durations and frequencies, or the numbers of undulations at the bottom phase of the dives, and so on. While such classically-used diving variables undoubtedly provide useful quantitative information about behavior, these numerous and often inter-related metrics can be difficult to interpret (Zimmer *et al.*, 2011a), so researchers have begun to explore novel analytical approaches that take advantage of methodologies from the field of statistical physics and treat animal behavior as part of an adaptive system aimed at mediating biological encounters.

Optimal foraging theory, as originally developed by MacArthur & Pianka (1966), stipulates that animals adopt foraging patterns that maximize their rates of energy intake. This idea was up-to-dated with the development of the Lévy flight foraging hypothesis. This hypothesis stipulates that the super-diffusive and fractal properties of Lévy movements performed by numerous animals from slime moulds to humans, may reflect an evolved strategy that optimizes resource encounters, and thus energy balance, in heterogeneous environments (Viswanathan *et al.*, 1999, 2008; Bartumeus *et al.*, 2005; Bartumeus, 2007, 2009; Sims *et al.*, 2008; Humphries *et al.*, 2010). At the same time, however, recent work has demonstrated that Lévy movements can emerge spontaneously and naturally from the interaction of innate behavior and innocuous responses to the environment (Reynolds, 2015). In dynamic marine environments, for example, Lévy flights emerged naturally in response to turbulence (Reynolds, 2014). The existence of Lévy movement patterns should thus not be confused with the existence of Lévy processes underlying movement behavior (Benhamou, 2007). Reynolds (2015) has since speculated that, while selection for Lévy

search patterns seems unnecessary and may even be unlikely in the majority of cases, there may be selection against losing them if they subsequently prove adaptive.

Since its inception, the Lévy flight foraging hypothesis has fuelled numerous works conducting spatial fractal analysis of animal movement data. An alternative approach uses fractal time-series analyses to measure scaling (complexity) in sequences of animal behavior, where behavior is modeled as a stochastic-deterministic process in which the degree of stochasticity or determinism can be linked to factors both intrinsic and extrinsic to the animal (MacIntosh, 2014). Using this framework, several studies have showed that certain complexity signatures should optimize foraging efficiency with respect to biological encounters (Shimada *et al.*, 1993, 1995; Cole, 1995; Escós *et al.*, 1995; Rutherford *et al.*, 2004; Hocking *et al.*, 2007; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011). These complexity signatures are analogous to the Lévy flight foraging hypothesis, and they can arise in animals experiencing stress or disease (reviewed in MacIntosh, 2014). Such altered complexity or '*complexity loss*' was first observed in fractal patterns in stressed physiological systems, such as those producing human heart rate (Peng *et al.*, 1995a) and gait dynamics (Hausdorff *et al.*, 1995), respiration (Peng *et al.*, 2002) and neuronal activity (Abasolo *et al.*, 2008). Complexity loss has now also been found in the behavior of animals under various physiologically challenging conditions, including in parasitized Spanish ibex (*Capra pyrenaica*: Alados *et al.*, 1996), health-challenged chimpanzees (*Pan troglodytes*: Alados & Huffman, 2000) and Japanese macaques (*Macaca fuscata*: MacIntosh *et al.*, 2011), and corticosterone-treated Adélie penguins (*Pygoscelis adeliae*: Cottin *et al.*, 2014). This means that complexity signatures have the capacity to act as behavioral indicators of animal condition and performance (Rutherford *et al.*, 2004; Asher *et al.*, 2009; MacIntosh, 2014). Moreover, priority-based decision-making and the inherent competition between stochastic and

deterministic elements of behavior may be critical in the emergence and maintenance of behavioral flexibility (MacIntosh, 2015; Reynolds *et al.*, 2015), and this may be further linked to chaotic neurobiological dynamics which also appear variable with respects to internal and external conditions (Reynolds *et al.*, 2016).

As such, complexity measures can complement current methods used to investigate diving behavior and its flexibility in diving seabirds. Fractal tools directly measure fundamental organizational/structural properties of behavior, rather than using derived statistics such as means and durations of behavioral variables. Detrended Fluctuation Analysis (DFA) is a commonly used fractal method that was developed to measure long-range dependence (autocorrelation) in physical and temporal sequences (Peng *et al.*, 1992, 1995a). DFA has since been used and validated in multiple studies of animal behavior (Alados & Huffman, 2000; Kembro *et al.*, 2009a, 2013; MacIntosh *et al.*, 2011, 2013).

Here, we applied DFA to diving sequences collected via time-depth recorders attached to little penguins (*Eudyptula minor*) at four colonies located across the species' geographic range (Chiaradia *et al.*, 2007) to test the influence of the environment on the foraging ecology of this marine predator. Factors commonly expected to influence diving behavior, such as bathymetry and primary production (Chiaradia *et al.*, 2007; Afán *et al.*, 2015), vary across colonies, thereby allowing us to examine their effects on the behavioral organization of chick-rearing adult little penguins foraging at sea. For example, primary productivity, as reflected by sea-surface chlorophyll-a, is a known arbiter of prey availability (Tynan, 1998; Afán *et al.*, 2015). Bathymetry is another determinant of prey availability as it can mediate the distribution of prey within the water column (Hunt *et al.*, 1998; Russell *et al.*, 1999; Ladd *et al.*, 2005). In these four colonies, little penguins feed on similar types of small, schooling

pelagic prey, mainly clupeiformes (Klomp & Wooller, 1988; Cullen *et al.*, 1991; Stahel & Gales, 1991; Chiaradia *et al.*, 2003, 2010, 2015; Fraser & Lalas, 2004), which can be distributed from the surface to depths of 200m (Kailola *et al.*, 1993). We hypothesized that penguins foraging in habitats characterized by deeper waters (i.e. where individual prey are more difficult to locate and capture) and/or less productive waters (i.e. where prey patches should be more dispersed and less numerous (Kowalczyk *et al.*, 2015a, 2015b)) will show increased elements of stochasticity in their foraging sequences, as evidenced by decreased long-range dependence, to account for such challenging environmental conditions.

IV.1.4 Materials & Methods – Article B

IV.1.4.a Study subjects and colonies

The study was conducted on little penguins from four different breeding colonies located across their entire geographic range. Data come from different years and have different sample sizes, both concerning the number of individuals sampled and the number of foraging trips recorded (Figure II.6). Data were collected in two colonies in Australia sampled in both 2001 and 2002 (Penguin Island: 32°18'S, 115°41'E; $N_{individuals}$=8, n_{trips}=9 trips, 4 males and 4 females; Phillip Island: 38°21', 145°09'E; $N_{individuals}$=21, n_{trips}=28 trips, 11 males and 10 females), and two colonies in New Zealand, both sampled in 2000 (Oamaru: 45°07'S, 170°59'E; $N_{individuals}$=4, n_{trips}=7 trips, 2 males and 2 females; and Motuara Island: 41°06'S, 174°17'E; $N_{individuals}$=4, n_{trips}=9 trips, 3 males and 1 female) (see details in Chiaradia *et al.*, 2007). Sampling at all colonies occurred during the guard stage with penguins rearing either 1 or 2 chicks, where absence from the nest (foraging trips) lasted one day only. This means that birds from all colonies faced similar constraints on foraging trip duration and maximum foraging range. Diving activity was monitored using three different data loggers at 2sec sampling intervals (Table 1 in Chiaradia *et al.*, 2007). Loggers used in Phillip Island and

Penguin Island had a bigger frontal area (accounting for 4.9% and 3.4% of the penguins' frontal area, respectively) than the loggers used in Motuara Island and Oamaru (both at 1.8%). It is known that loggers of different sizes exhibit some influence on diving behavior in little penguins (Ropert-Coudert *et al.*, 2007b). In fact, using the same analytical approach as that used here, larger loggers were recently shown to coincide with more stochastic dive sequences in little penguins (Meyer *et al.*, 2015). Unfortunately, because logger size varied as a function of colony, or more accurately as a function of the study design within each colony, we were unable to separate logger size effects from inter-colony effects in this study (see discussion).

The four colonies differed in the area of water available for penguin foraging, based on the proportion of water/land found within a 20km radius of the breeding sites (Chiaradia *et al.*, 2007). This radius corresponds to the mean maximum distance that a little penguin can travel in a one-day trip, ca. 25 km (Collins *et al.*, 1999; Pelletier *et al.*, 2014). Phillip Island displayed the highest proportion of foraging area available (89%), followed by Penguin Island (65%), Motuara Island (62%) and Oamaru (51%). More than 90% of the foraging zone around Penguin Island and Oamaru are in waters shallower than 50m, where the penguins' mean dive depths are 6±3.5 m and 5±0.9 m, respectively (Chiaradia *et al.*, 2007). Both colonies also have a high fledging success, with 0.7 and 0.8 chicks fledged per pair, respectively. Despite having 95% of waters shallower than 50m, very shallow waters (e.g. <20m) are rare around Motuara Island, where the mean dive depth is 11±2.7m and the fledging success is low at 0.5 (Chiaradia *et al.*, 2007). Like Motuara Island, the Phillip Island colony has a low fledging success at 0.5. However, the Phillip Island colony is surrounded by deeper waters than that on Motuara, with only 42% of its waters shallower than 50m and a mean dive depth of 13±3.9m (Chiaradia *et al.*, 2007). Fledging success for Phillip Island, Motuara Island and

Oamaru was based on contemporaneous data (Chiaradia *et al.*, 2007), while that for Penguin Island was based on historical data (Wienecke *et al.*, 1995). Chlorophyll-*a* concentrations were obtained by averaging chlorophyll-a data on an 8-day composite basis in each foraging area from satellite Orbiew-2 SeaWiFS measurements (National Oceanic and Atmospheric Administration, 2000; 2001; 2002). Mean chlorophyll-a concentrations were 0.49 $mg.m^{-3}$ around Motuara Island, 0.46 $mg.m^{-3}$ around Oamaru, 0.6 $mg.m^{-3}$ in 2001 and 0.98 $mg.m^{-3}$ in 2002 around Penguin Island and 0.44 $mg.m^{-3}$ in 2001 and 0.68 $mg.m^{-3}$ in 2002 around Phillip Island. Further details on colonies, field protocols and loggers can be found in Mattern, (2001; Oamaru and Motuara Island), Ropert-Coudert *et al.* (2003; Penguin Island) and Chiaradia *et al.* (2007; Phillip Island). The study was approved by the respective ethics committees of Phillip Island Nature Parks, Murdoch University and Otago University, and permits were acquired from all relevant regional conservation departments at each study site.

IV.1.4.b Fractal analyses

We used detrended fluctuation analysis (DFA; Peng *et al.*, 1992) to investigate long-range dependence in the sequential distribution of little penguin dives and surface times during foraging (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014; Meyer *et al.*, 2015). DFA is one of the more robust estimators of the Hurst exponent (Cannon *et al.*, 1997), a scaling exponent that measures self-affinity across scales in time series data. Briefly, we first converted dive sequences into binary time series (z(i)) containing diving periods (denoted by 1) and recovery periods at the surface (denoted by -1) at 1s intervals to length N (Alados *et al.*, 1996; Alados & Weber, 1999). We then integrated (cumulatively summed) the binary time series and estimated the scaling exponents (α_{DFA}) of these sequences using DFA. Sequences were divided after integration into non-overlapping boxes of length n and we fitted a least-square

regression line on data from each box in order to remove local linear trends. We repeated this process over all box sizes and measured the scaling exponent (α_{DFA}), which is the slope of the line on a double logarithmic plot of average fluctuation as a function of scale (Taqqu *et al.*, 1995; Cannon *et al.*, 1997). This exponent takes values between 0 and 1 for fractional Gaussian noises (fGn) and between 1 and 2 for fractional Brownian motions (fBm) (Eke *et al.*, 2000; Delignières *et al.*, 2005). Values in the range (0.5, 1) and (1.5, 2) reflect persistence (positive long-range autocorrelation) while those in the range (0, 0.5) and (1, 1.5) reflect antipersistence (negative long-range autocorrelation) in the time series for fGn and fBm, respectively, with 0.5 and 1.5 reflecting randomness (white noise) (Eke *et al.*, 2000; Delignières *et al.*, 2005). Theoretically, α_{DFA} is inversely related to the fractal dimension, which represents an index of structural complexity (Mandelbrot, 1977). DFA was previously shown to produce reliable estimates of scaling behavior in little penguin and Adélie penguin dive sequences (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014). To reduce bias in scaling exponent estimation, we first calculated best-scaling regions and used those to estimate α_{DFA} rather than the full set of measurement scales available (Cannon *et al.*, 1997; Seuront, 2010; MacIntosh *et al.*, 2013). DFA was run using the package 'fractal' (Constantine & Percival, 2014) in R statistical software v.3.1.3 (R Development Core Team, 2016). Details of the analytical approach used, including DFA calculation, validation of scaling and its relationship to other fractal dimension estimates and illustrations are provided in MacIntosh *et al.*, 2013 and Meyer *et al.*, 2015.

IV.1.4.c Statistics

All statistical analyses were conducted in R 3.1.3 (R Development Core Team, 2016). We constructed Linear Mixed-effects Models (LMMs, 'lme4' package in R, Bates *et al.*, 2015) to investigate variation in α_{DFA} across colonies. We set individual identity and trip date as

random factors to account for pseudoreplication caused by re-sampling a small number of individuals and temporal variation in sampling, respectively. Trip duration (in hours) was set as a covariate to control for the effects of sequence length on scaling exponents (MacIntosh *et al.*, 2013). We included the following predictor variables in the model: colony, chlorophyll-a concentration at the time of the trip and sex of the individual. In order to compare all colonies with one another, we re-leveled this factor in our statistical models so that each colony was used as the baseline intercept value once, allowing all pairwise comparisons to be made.

We then conducted a Principal Component Analysis (PCA) to aid interpretation of the relationships between α_{DFA} and various other commonly-presented foraging parameters, including (1) diving frequency (number of dives), (2) foraging effort (total time spent underwater; (Takahashi *et al.*, 2003)), (3) trip duration, (4) mean dive depth and (5) foraging efficiency (taken here as estimated Catch Per Unit Time (CPUT) as determined from vertical undulations in the dive profile during a dive's bottom phase divided by the total time spent underwater during foraging; for details see Sala *et al.*, 2012). PCA reduces a set of variables that exhibit some degree of multicollinearity into a smaller set of linearly uncorrelated variables (principal components), and is commonly used to reduce dimensionality in data sets but also to understand at once the relationships between multiple variables of interest (Zimmer *et al.*, 2011a). When the first two dimensions or principal components explain most of the variance in the data (using the highest eigenvalue), the relationships between parameters within these two dimensions provide information about their relative importance to the observed dimensions, their similarities with one another, and their differences. PCA was run using the prcomp function of the 'stats' package in R (R Development Core Team, 2016).

Because we were interested in relating our complexity signatures to these other important parameters measuring aspects of diving performance, particularly effort and efficiency, we constructed separate LMMs to investigate whether α_{DFA} covaries with CPUT, as a proxy of foraging efficiency, and the total time spent underwater, as a proxy of foraging effort. We again set individual identity and trip date as random factors in our models.

Descriptive results are presented as means and standard errors (SE), and we set the alpha level for all statistical analyses at 0.05.

IV.1.5 Results – Article B

Detrended fluctuation analysis produced values of α_{DFA} ranging between 0.79 and 0.99 (mean=0.89, S.E.=0.005, Figure IV.1), indicating that binary dive sequences from foraging little penguins are best characterized as persistent, long-range dependent fractional Gaussian noise, as was shown previously for Spheniscidae (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014; Meyer *et al.*, 2015). In other words, dives and surface times of a given length are typically followed by dives and surface times of a similar length, with such patterns of fluctuation between behavioral states persisting across a range of measurement scales;

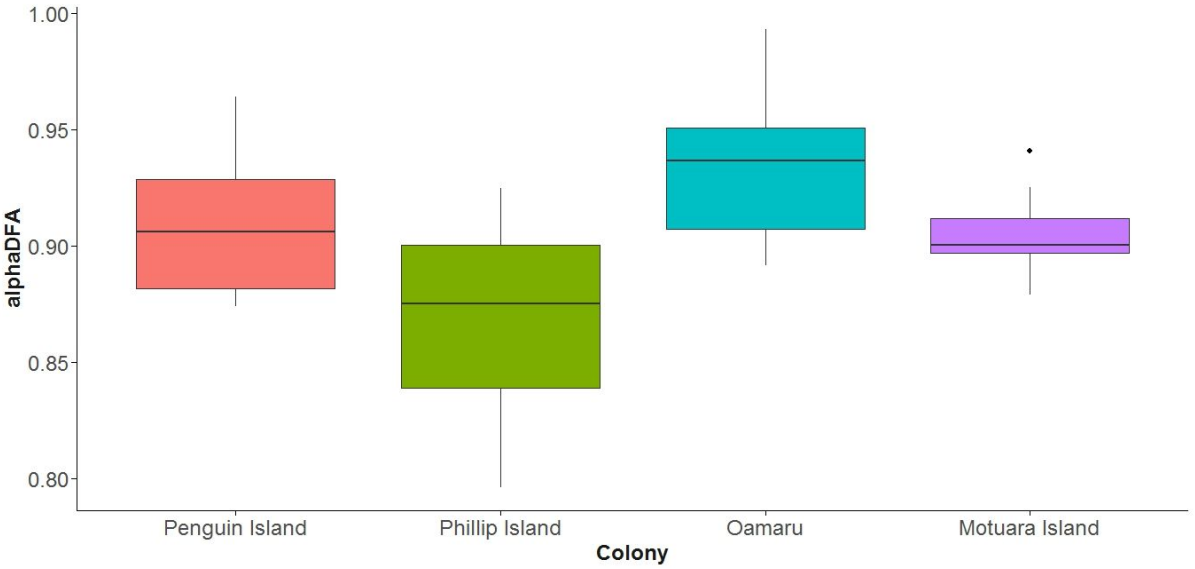


Figure IV.1 : Results of fractal analysis of binary sequences of diving behaviour of little penguins showing scaling exponent for each colony.

observed best scaling regions included the scales 2^7-2^{13}, or 128-8192 seconds.

Our statistical model (Table IV.1) showed that foraging sequences from Penguin Island, Motuara Island and Oamaru were characterized by higher values of α_{DFA}, reflecting higher degrees of long-range dependence (determinism) in dive sequences than those from Phillip Island (Figure IV.1). In other words, little penguins from Phillip Island exhibited greater stochasticity in the temporal organization of their foraging behavior compared with penguins from the three others colonies. There were no clear differences amongst the three other colonies. Finally, we observed no effects of sex, trip duration or chlorophyll-a concentration on complexity in foraging sequences.

Variable		*Est.*	*SE*	*Df*	*t-value*	*p-value*
Intercept		0.910	0.109	42	8.336	>0.0002
Chlorophyll-a		-0.0018	0.047	40	-0.038	0.97
Sex (female)		-0.010	0.01	28	-1.049	0.30
Trip duration		0.0005	0.007	40	0.080	0.94
site 1	site 2	0.026	0.019	21	1.376	0.18
Motuara Island	Oamaru					
Motuara Island	Penguin Island	0.006	0.022	24	0.301	0.76
Motuara Island	Phillip Island	-0.040	0.016	19	-2.5	**0.019**
Phillip Island	Oamaru	0.066	0.015	21	4.279	**0.0003**
Phillip Island	Penguin Island	0.047	0.022	26	2.145	**0.041**
Oamaru	Penguin Island	-0.019	0.025	28	-0.763	0.45

Table IV-1 : Effects of colonies, chlorophyll-a concentration at the time of the trip and sex on αDFA using LMM statistics. Bold text highlights significant p-values. Abbreviations: Est=estimate, SE= Standard error, Df=degree of freedom.

Variable	Est.	SE	Df	t-value	p-value
Intercept	0.891	0.005	17	162.145	$<2.10^{-16}$
CPUT	0.011	0.006	28	1.912	0.066
Foraging effort	-0.014	0.006	25	-2.524	**0.018**

Table IV-2 : Effects of CPUT (Catch per Unit Time, foraging efficiency) and foraging effort (total time spent underwater) on αDFA using LMM statistics. Bold text highlights significant p-values. Abbreviations: Est=estimate, SE= Standard error, df=degree of freedom.

The two first principal components of the PCA explained 72% of the variance in the data (Figure IV.2a). The variables α_{DFA}, CPUT, foraging effort and mean dive depth all loaded into PC1, which explained 49.2% of the variance in the data. However, while α_{DFA} (0.40) and CPUT (0.50) loaded positively onto PC1, foraging effort (-0.42) and mean dive depth (-0.52) loaded negatively. Generalized linear models showed that α_{DFA} correlated positively with CPUT, the proxy for foraging efficiency (Figure IV.2b, Table IV-2) and negatively with time spent underwater, the proxy for foraging effort (Figure IV.2c, Table IV-2). These results suggest that more efficient foraging sequences are also more deterministic (higher α_{DFA}), while more stochastic sequences (lower α_{DFA}) are associated with greater foraging effort. The number of

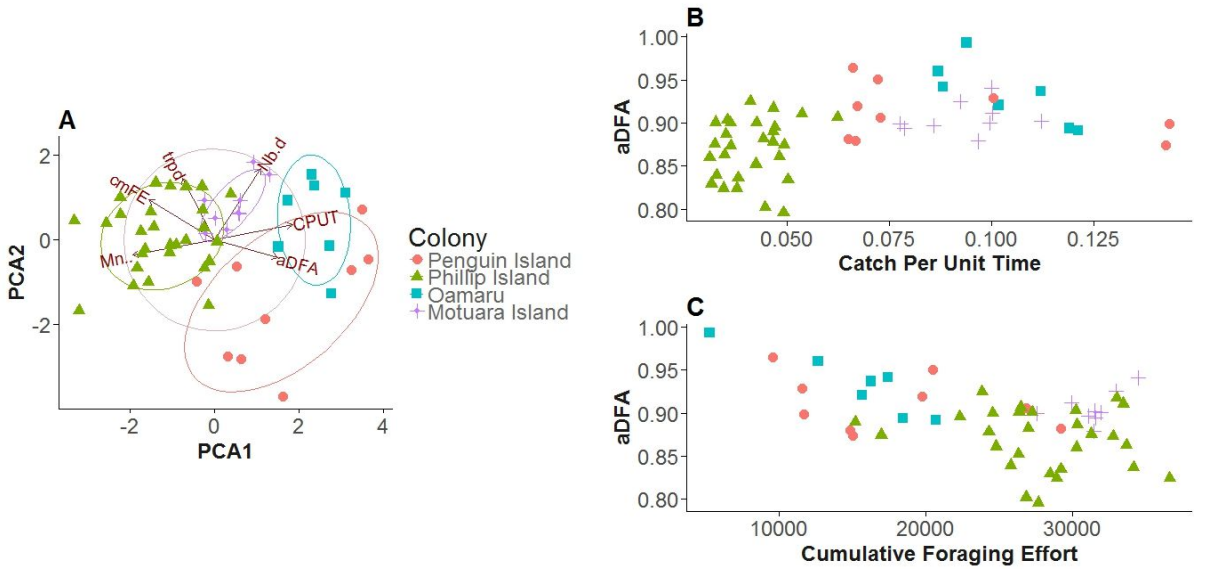


Figure IV.2 : (A) Principal Component Analysis presented by their first two component loadings. This PCA compiles a selection of foraging parameters that represent (1) the diving frequency (number of dives, Nb.d), (2) the foraging effort (total time spent underwater, cmFE), (3) the trip duration (trpd), (4) the mean dive depth (Mn.) and (5) the foraging efficiency (Catch Per Unit Time, CPUT), and their relationship with αDFA. Representation of αDFA as a function of (B) the CPUT and (C) the foraging effort.

dives performed and trip duration both loaded positively onto PC2 (0.67 and 0.58, respectively), which explained 22.8% of the variance in the data.

IV.1.6 **Discussion – Article B**

The greater stochasticity observed in the foraging activity of penguins from Phillip Island corroborates our prediction that individuals from colonies surrounded by relatively deeper waters would produce less deterministic foraging sequences than those from colonies surrounded by shallower waters. We propose that in deeper waters, where prey are presumably harder to catch as they may escape to deeper depths than that reachable by penguins, reductions in long-range dependent or deterministic patterns of foraging behavior may improve the probability of prey encounters. In contrast, shallower waters such as those surrounding Penguin Island and Oamaru may have more predictable prey fields, leading to the emergence of more deterministic foraging sequences in little penguins. Given that fledging success was also significantly higher in these colonies than at Phillip Island, further attests to the presence of challenging foraging conditions around Phillip Island. Shifting to a more stochastic pattern of foraging may thus represent a strategy that may allow little penguins to cope with environmental heterogeneity.

Following Reynolds *et al.* (2015), greater determinism in sequences of foraging behavior may result from an underlying decision-based queuing process favouring exploitation over exploration, which is likely to occur when the prey field is more homogeneous or otherwise highly predictable. During periods of heavy prey exploitation within patches, penguins are physiologically constrained by oxygen reserves (Wilson, 2003) and lactic acid build-up (Butler, 2006). Patterns of alternation between dives and surface times are thus highly regulated in a way that would produce persistent and more or less periodic behavior. If the

need for more exploratory modes of behavior is limited due to environmental homogeneity, such behavioral determinism may persist throughout the foraging trip. Conversely, under less predictable environmental conditions, individuals are expected to increase their performance of exploratory dives, which would then be interspersed with foraging dives in an attempt to maximize prey encounters. For example, greater stochasticity in foraging behavior in deeper waters (e.g. Phillip Island) could be explained by greater heterogeneity in the vertical distribution of prey (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012). As a consequence, birds may drastically augment their target depths from one dive to the next, inducing variability in both dive durations and the subsequent post-dive durations, which serve as recovery periods from previous dives and for anticipating the next dive based on prey availability (Wilson, 2003). Such alternation between foraging modes may 'interrupt' dive sequences and thus lead to reduced long-range dependence.

Diving behavior is affected by resource availability (Mori & Boyd, 2004), which could be summarized by two major components: abundance of prey (patch size) and prey distribution in the water column. Abundance of prey seems to be the main driver of behavior and foraging success among air-breathing diving predators (Mori & Boyd, 2004; Cook *et al.*, 2008; Elliott *et al.*, 2008; Doniol-Valcroze *et al.*, 2011; Goundie *et al.*, 2015). In response to heterogeneity in the abundance and distribution of food resources, animals are hypothesized to have evolved a scale-invariant foraging strategy that allows them to maximize the success of prey search (Viswanathan *et al.*, 1999, 2008; Bartumeus *et al.*, 2005; Bartumeus, 2007, 2009; Sims *et al.*, 2008; Humphries *et al.*, 2010). Behavioral scale-invariance, through its super-diffusive and fractal properties, allows animals to reduce "oversampling" by avoiding revisitation of previously visited areas (Shlesinger *et al.*, 1986). While there is currently ample debate in the literature about the validity of the Levy Flight

Foraging Hypothesis (Benhamou, 2014; Benhamou & Collet, 2015; Pyke, 2015; Reynolds, 2015; Patterson *et al.*, 2016), our study does show that the degree to which such behavioral scale-invariance can vary within species depends strongly on physical characteristics of the environment that are known to mediate the abundance and distribution of food resources. Indeed, studies on the temporal structure of behavior in wild Japanese macaques (*Macaca fuscata*: MacIntosh *et al.*, 2011) suggest that animals in more structurally complex environments (i.e. arboreal versus terrestrial) or those exploiting resources that are harder to procure (i.e. mobile invertebrates versus immobile fruits) both moved and foraged in a less deterministic manner. Moreover, controlled studies on fruit flies (*Drosophila melanogaster*: Cole, 1995; Shimada *et al.*, 1995) showed greater complexity in the dwelling time in relation to a new environment and inferior food quality, while studies on hens (*Gallus gallus domesticus*: Rutherford *et al.*, 2003) showed that vigilance time series become more stochastic when animals are moved to novel environments. Taken together, these and our own results suggest that more stochastic behavioral sequences coincide with more structurally complex (e.g. bathymetry) or otherwise less predictable environments (e.g. resource type, abundance and distribution), offering a possible mechanism to enhance fitness in heterogeneous or otherwise more complex or challenging environments.

If our suggestion is correct, it is also significant that the more stochastic sequences observed at Phillip Island were also characterized by lower foraging efficiency and higher foraging effort, and that the colony as a whole exhibits significantly lower breeding success than those at Penguin Island and Oamaru (Chiaradia *et al.*, 2007). At the small scale of a single, short trip, foraging in shallow waters, where prey are easily captured, in a deterministic manner may be more efficient than using a more stochastic strategy, which may not substantially increase prey encounters per unit time. In addition, all else being

equal, foraging in shallow waters should allow penguins to allocate a greater amount of underwater time to the bottom phase of dives, wherein penguins predominantly feed (Ropert-Coudert *et al.*, 2000, 2001, 2003; Takahashi *et al.*, 2003). Similar to blue whales (*Balaenoptera musculus*, Doniol-Valcroze *et al.*, 2011) and Steller sea lions (*Eumetopias jubatus*, Goundie *et al.*, 2015), little penguins present a higher foraging efficiency when diving shallow and also forage less efficiently in areas with more complex prey fields such as deeper waters. We found no association between primary production, a proxy of prey availability, and the temporal organization of diving behavior, which suggests that foraging conditions arising from divergent bathymetric conditions are likely to be the main factor driving the temporal organization of diving behavior. Thus, even under the hypothesis that stochasticity is expected to enhance prey encounters in more heterogeneous environments (e.g. Phillip Island), it may not be sufficient to match fitness gains attained under more homogeneous and favourable conditions (e.g. in Oamaru and Penguin Island).

Interestingly, Motuara Island presents an intermediary case: greater determinism in the temporal organization of foraging sequences and high foraging efficiency, as was the case at Penguin Island and Oamaru, but also greater foraging effort and a fledging success similar to that at Phillip Island. We can propose two mutually non-exclusive explanations for this discrepancy. On the one hand, foraging trip durations of Motuara birds are longer during incubation (Numata *et al.*, 2000). During this period, penguins left Queen Charlotte Sound and foraged northwards towards the South Taranaki Bight (North Island) and crossed Cook Strait waters which are deeper than 150m. In contrast, during the guard stage, all penguins stayed within a spatially-restricted, shallow region of Queen Charlotte Sound north of Motuara Island (Mattern, 2001; Te Papa, pers. comm.). This suggests that the foraging grounds visited during incubation are too far away for parents that need to provision their

chicks frequently. Thus, instead of extending their foraging ranges to increase their likelihood of prey encounters, the penguins increased their foraging effort (longer dive times and greater depths) in order to increase their foraging efficiency. This constraint on foraging area might have led to greater determinism through constraints imposed by diving physiology of penguins. On the other hand, a recent study (Grosser *et al.*, 2015) suggests that the *Eudyptula* genus could include one species distributed across Australia and the south-eastern coast of New Zealand's South Island (including Oamaru), and a second species distributed elsewhere in New Zealand (including Motuara). Hence, there may also be a species-specific component determining organizational structure in dive sequences. Yet, even if these new species were confirmed, this would not fundamentally change our results because three of our colonies consisted of the "Australian" species with different conditions of bathymetry.

As shown above, our results were in line with our prediction and fit theoretical expectations derived from the literature on optimal search strategies under divergent environmental conditions. Nonetheless, we stress the need for caution here because of the small sample size of two of the four colonies considered: 4 individuals and 9 trips at Motuara Island and 4 individuals and 7 trips at Oamaru. Low statistical power can at once enhance the likelihood of both Type I and Type II errors (Button *et al.*, 2013). Moreover, while we did not find a sex effect in the present study, the number of sampled males and females were not always equivalent, especially at Motuara where the sex ratio was biased in favour of males. We previously described a sex effect in the complexity signatures of little penguins at Phillip Island (Meyer et al., 2015), although in that case males produced more stochastic sequences than females, and thus cannot explain the reverse trend we observed here between Motuara and Phillip Island. Finally, loggers themselves affect the swimming

performance (e.g. Ropert-Coudert *et al.*, 2007b) and temporal organization of diving activity (Meyer *et al.*, 2015) in little penguins. In the latter case, the authors showed that little penguins carrying loggers that covered a larger cross-sectional area of the penguins (4.9% vs 3.4%) produce more stochastic sequences. The present study shows that individuals from the colony equipped with the biggest loggers (Phillip Island) also produced the most stochastic foraging sequences among the four colonies studied, which is consistent with what we would predict given differences in logger size alone. That said, the size of the effect of colony in the present study is much greater than that observed in relation to logger size in Meyer *et al.* (2015), so it is unlikely that this difference reflects an artefact of our methodology. Furthermore, the fact that we did not observe differences between either Motuara Island or Oamaru and Penguin Island where devices were almost twice the size, indicates that logger size cannot sufficiently explain our results. Thus, while all of these factors may have played a role in our study, it is unlikely that they could explain our findings on their own.

Temporal fractal analysis of behavior provides new avenues in which to study the finer points of seabird foraging behavior and how it might change in response to prevailing environmental conditions. Our study suggests that the performance of complex foraging sequences characterized by higher degrees of stochasticity, which are predicted to outperform more deterministic sequences in heterogeneous environments, may in fact be more energy intensive and as a consequence, may not be sufficient to match fitness gains observed in animals foraging under more favourable conditions. However, we were unable to directly test this possibility on an individual basis here, and thus cannot currently determine whether links exist between complexity signatures, foraging success and fitness

within colonies. These aspects should be a key focal point for future studies dealing with the adaptive value of foraging complexity in animals.

Acknowledgments

The authors thank the staff and students of Phillip Island Nature Parks, in particular P. Dann, L. Renwick, P. Waziak, J. Yorke and also the support of B. Cannell, D. Houston, Y. Naito, S. Ward, the staff and rangers at Penguin Island and Oamaru Blue Penguin Colony. We also thank Timothée Poupart and Te Papa Tongarewa for sharing with us foraging area location use by Motuara's penguin in incubation. This work was financially supported by grants from the Japan Society for the Promotion of Science, Phillip Island Nature Parks, Penguin Foundation, Australian Academy of Science, Murdoch University, Otago University Research Grant, Sasakawa Scientific Research Grant from the Japan Science Society, and the Ministère de l'Enseignement Supérieur et de la Recherche (France).

IV.2 Article C: Temporal organization variability of foraging behaviour in a seabird species highlights environmental changes.

Temporal organization variability of foraging behaviour in a seabird species highlights environmental changes.

Xavier Meyer, Andrew J.J. MacIntosh, Akiko Kato, Andre Chiaradia, Cédric Sueur & Yan Ropert-Coudert

Article in preparation to be submitted to Global Change Biology

IV.2.1 Résume (en français) – Article C

Les océans sont vulnérables au changement global actuellement à l'œuvre. Ces changements ont des conséquences majeures sur la distribution et l'abondance des espèces marines. Il est ainsi essentiel de comprendre comment les réseaux trophiques sont affectés par les changements environnementaux. Les manchots pygmées (*Eudyptula minor*) sont des méso-prédateurs se nourrissant d'espèces du premier niveau trophique et sont ainsi très sensibles aux changements environnementaux. Nous avons examiné dans cet article comment la complexité de l'organisation temporelle des séquences de recherche alimentaire des manchots pygmées est affectée par la température de surface de l'océan, la concentration en chlorophylle-a, la force et la direction du vent dans le détroit de Bass entre 2001 et 2012. De plus, nous avons également examiné comment cette complexité est liée à l'efficacité de recherche alimentaire et à l'effort de recherche alimentaire sur cette même période. En théorie, certaines signatures de complexité, mesurées à travers la dimension fractale de la distribution temporelle des séquences de recherche alimentaire, peuvent optimiser l'efficacité de recherche alimentaire en fonction des rencontres biologiques. Utilisant des analyses fractales des séries temporelles, nous avons trouvé que la complexité de recherche alimentaire sur un gradient de stochasticité-déterminisme était associée avec

la température de la surface de l'eau mais pas avec la vitesse du vent, la direction du vent et la concentration en chlorophylle-a. Les manchots pygmées cherchant leur nourriture dans des eaux plus chaudes ont des séquences de recherche alimentaire plus déterministiques et montrent une efficacité de recherche alimentaire supérieure et un effort de recherche alimentaire inférieure que ceux recherchant leur nourriture en eaux plus froides. Comme prédit, les animaux cherchant leur nourriture dans des conditions environnementales plus difficiles, comme par exemple des eaux plus froides et des patchs de proies moins prédictibles, vont présenter une plus grande stochasticité dans leur séquence de plongée.

IV.2.2 **Abstract – Article C**

Oceans are highly vulnerable to ongoing global change, which have major consequences for the distribution and abundance of species. It is thus essential to understand how food webs are affected by these environmental changes. Little penguins (*Eudyptula minor*) are meso-predators that feed on low trophic-level species and are very sensitive to environmental change. Here, we examined whether complexity in the temporal organization of foraging sequences is affected by sea-surface temperature, chlorophyll-a concentration, wind speed and wind direction in the Bass Strait between 2001 and 2012, and how it related to foraging efficiency and foraging effort over this period. In theory, certain complexity signatures, as measured by fractal scaling in the temporal distribution of foraging sequences, may optimize foraging efficiency with respect to biological encounters. Using fractal time series analysis, we found that foraging complexity along a stochastic-deterministic gradient was associated with prevailing sea-surface temperatures but not with wind speed, wind direction or chlorophyll-a concentration. Little penguins foraging in warmer waters produced more deterministic foraging sequences and showed higher foraging efficiency and lower foraging effort than those foraging in colder waters. As predicted, animals foraging in more

challenging conditions, i.e. cooler waters with less predictable prey patches, exhibited greater stochasticity in dive sequences.

I.1.1. Introduction – Article C

Understanding the responses and adaptations of organisms to environmental change has received a growing interest in ecology, especially in the context of ongoing global change (Walther, 2010; Doney *et al.*, 2012; Poloczanska *et al.*, 2016). Among all ecosystems, the last IPCC Synthesis Report (2014) noted that marine ecosystems may be one of the most vulnerable to climate change, and that these changes can already be observed from polar to tropical marine ecosystems, such as increases in sea surface temperatures (SST) and interactions with the natural variability of ocean climate systems (e.g. El-Nino Southern Oscillation) (Doney *et al.*, 2012). These changes in the physical properties of oceans are associated with decreases in species abundances and/or changes in the distribution and dispersion of organisms, all of which affect trophic interactions and by extension the structure of ecosystems (Doney *et al.*, 2012; Constable *et al.*, 2014).

To monitor changes affecting the marine food chain, a good eco-indicator should respond in a sensitive and rapid way to environmental variability over multiple spatial and temporal scales, which is the case for upper-level predators such as seabirds (Briggs & Chu, 1986; Hyrenbach & Veit, 2003; Ballance, 2007; Frederiksen *et al.*, 2007). Occupying the upper levels of their respective food chains, seabirds also synthesize changes occurring at lower levels. Among the parameters used to monitor seabirds (e.g. breeding success, populations dynamics, etc.), foraging behavior has been shown to be capable of rapidly assessing about drivers of population change (Lewis *et al.*, 2006a). Because seabirds forage for resources that are distributed patchily across space and time in the marine environment (Weimerskirch,

2007), they require flexibility in foraging behaviour to meet their own energy requirements but also to provision their offspring (Weimerskirch *et al.*, 1997; Burke & Montevecchi, 2009; Saraux *et al.*, 2011a; Welcker *et al.*, 2012). This is especially true for central-place foragers who are constrained in terms of foraging range and duration (Orians & Pearson, 1979). Among seabirds, penguins are affected by a diverse set of physical parameters, such as sea-ice (Watanuki *et al.*, 1997), bathymetry (Chiaradia *et al.*, 2007), marine currents (Bost *et al.*, 2009), water stratification (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012), wind (Dehnhard *et al.*, 2013; Saraux *et al.*, 2016) and SST (Carroll *et al.*, 2016). In response to the aforementioned environmental changes, penguins exhibit variability in several foraging parameters, including myriad diving parameters. However, interpreting variation in these numerous diving parameters can be difficult because they are often inter-related (Zimmer *et al.*, 2011a).

Recently, considering animal behavior as part of a complex adaptive system aimed at mediating biological encounters has fueled numerous works focusing on animal movement data at a the spatial level, such as the myriad works testing facets of the Lévy flight foraging hypothesis (LFFH; Viswanathan *et al.*, 1999, 2008; Humphries *et al.*, 2013) and those examining movement tortuosity (Fritz *et al.*, 2003; Nams & Bourgeois, 2004; Garcia *et al.*, 2005). In the temporal domain, studies have also begun to explore the fractal properties of animal-derived time-series data (see review in MacIntosh, 2014). Regarding the latter, the aim is to measure to what degree behavioral patterns are related across time scales, or more precisely, to model animal behavior as a complex process falling along a gradient from purely stochastic, uncorrelated behavior to highly deterministic, long-range dependent (autocorrelated) behavior. This has been used as an index of complexity in animal behavior, and variability in the complexity signatures of individual animals has been linked to both

intrinsic (e.g. stress, disease) and extrinsic (e.g. environmental) factors (MacIntosh, 2014). Moreover, in the same way that fractal spatial statistics are predicted by the LFFH to optimize animal search (Bartumeus & Catalan, 2009; Viswanathan *et al.*, 2011), certain complexity signatures are predicted to optimize foraging efficiency with respect to biological encounters (Shimada *et al.*, 1993, 1995; Cole, 1995; Escós *et al.*, 1995; Rutherford *et al.*, 2004; Hocking *et al.*, 2007; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011). As a result, the fact that complexity signatures are linked to behavioral optimization and known to vary when animals are stressed, diseased or challenged in other ways (Alados *et al.*, 1996; Alados & Huffman, 2000; MacIntosh *et al.*, 2011; Cottin *et al.*, 2014; Meyer *et al.*, 2015), a phenomenon now known as '*complexity loss'*, such information can be used as a behavioral indicator of animal condition and performance (Rutherford *et al.*, 2004; Asher *et al.*, 2009; MacIntosh, 2014) and consequently offers the opportunity to act as a noninvasive diagnostic tool for monitoring wildlife health and/or environmental change, and also to explore the potential behavioral mechanisms that animals might employ to buffer environmental variability.

Identified as one of the fastest warming marine areas in the world (Hill *et al.*, 2008; Hobday & Pecl, 2013), south-eastern Australia is expected to experience significant changes in both oceanographic features and species distributions (Ridgway, 2007). The region of Bass Strait resides in the shallow continental shelf area located between Tasmania and the Australian mainland, and lies at the crossroads of three different marine currents: (1) the warm, nutrient-poor South Australian Current (SAC) from the west; (2) the cold, nutrient-rich sub-Antarctic Surface Water (SASW) from the south; and, (3) the warm, nutrient-poor East Australian Current (EAC) from the east. Changes in these current intensities are likely to alter species distributions and thus trophic interactions in the Bass Strait area, as shown

previously for the EAC (Poloczanska *et al.*, 2007; Ling *et al.*, 2009; Banks *et al.*, 2010) and in the Bonney upwelling. These changes seem to entrain cascading effects throughout the Bass Strait region's upper-level predators, including little penguins (*Eudyptula minor*) (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012; Hoskins & Arnould, 2014; Afán *et al.*, 2015; Angel *et al.*, 2015; Berlincourt & Arnould, 2015).

Little penguins are known to be sensitive to fluctuations in prey availability, which are driven by environmental changes associated with SST (Berlincourt & Arnould, 2015; Carroll *et al.*, 2016), wind (Berlincourt & Arnould, 2015; Saraux *et al.*, 2016) or water stratification (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012). Interestingly, little penguin showed a lower prey capture success, an indicator of less predictable prey patches, at both low and high SST for an temperature optimum including between 19 and 21°C. Thus, little penguins are good models for investigating the relationship between environmental change and complexity in foraging behavior, and for studying how animals might cope with environmental variability through flexibility in foraging behavior. Previous study (Article B) has shown that little penguins exhibited greater stochasticity in their temporal organization of foraging in deeper waters, where prey field are less predictable than in shallower waters. Measuring complexity in penguin at-sea foraging behavior also offers a parsimonious, sensitive fractal-based index that can serve as a rapid measure of environmental change. In this study, we examined changes in the temporal organization of diving behavior of little penguins over 11 years, in all cases during the guard phase, which is a critical period of the breeding season (Gales & Greenberg, 1990) where penguins are constrained in time as they must return on a daily basis to the colony to feed their chicks. During this phase, birds are capable of varying their at-sea behavior to match environmental conditions in order to address the needs of their growing chicks, as well as their own needs (e.g. in Cory's

shearwater *Calonectris diomedea*, Granadeiro *et al.*, 1998; or masked booby, *Sula dactylatra*, Sommerfeld *et al.*, 2015). We hypothesized that under challenging environmental conditions (e.g. lower or higher SST, strong wind) little penguins should exhibit greater stochasticity in their diving behavior than under less challenging conditions if they are to match their energetic needs.

I.1.1. Material & Methods – Article C

The study was conducted on the little penguin colony of the western end of Phillip Island, Australia (38°15'S, 143°30'E). This colony contains 28 000-32 000 breeding adults (Sutherland & Dann, 2012). Data were collected over 11 breeding seasons (2001/2002-2002/2003 and 2004/2005-2012/2013). We deployed data loggers on 141 adult penguins (n=141 trips) during the guard phase, when birds were raising chicks aged 1 to 2 weeks. This phase is characterized by 1 day-trips over less than 20-25km from the colony (Collins *et al.*, 1999; Pelletier *et al.*, 2014). We used three different data-loggers throughout the 11 years. In 2001-2002 and 2002-2003 we used the LTD 1200-100 (Lotek, Canada), a cylindrical depth recorder with a diameter of 18mm, a length of 62mm and a weight in the air of 17g. Depth was recorded at a resolution of 0.1m every second. From 2004-2005 to 2009-2010 we used M190-D2GT (Little Leonardo, Japan) data-loggers. They are also cylindrical with a diameter of 15mm, a length of 52mm and a weight in the air of 16g. Depth was recorded at a resolution of 0.05m every second. Finally, from 2010-2011 to 2012-2013, we used the ORI400-D3GT (Little Leonardo, Japan). These loggers are also cylindrical with a diameter of 12mm, a length of 45mm and a weight in the air of 9g. Depth was recorded at a resolution of 0.1m every second. Birds were captured in their nest boxes and loggers were attached to their lower backs with TESA tape (Wilson et al. 1997). Attachment and removal of the logger were both completed in less than 5 min. The breeding activity of each bird was monitored

over the whole of the breeding season. The fieldwork protocol across all years was approved by the Animal Experimentation Ethics Committee, Phillip Island Nature Park, with a research permit issued by the Department of Sustainability and Environment, Flora and Fauna of Victoria, Australia. Upon the return of each bird from a single trip at sea, data were downloaded from the loggers onto a computer and analyzed using Igor Pro (Wavemetrics Inc., USA, 2008). A purpose-written macro included in this software semi-automatically adjusted the diving signal to zero when birds were at the surface between two dives and automatically calculated diving parameters, including but not limited to depth, dive and post-dive duration, and the number of vertical undulations in the bottom phase of the dive, which are largely indicative of prey pursuit (see Kato *et al.*, 2006; Ropert-Coudert *et al.*, 2006b). Foraging efficiency, taken here as estimated Catch Per Unit Time (CPUT), was calculated as the sum of vertical undulations in the dive profile during a dive's bottom phase divided by the total time spent underwater during foraging (for details see Sala *et al.*, 2012).

We used Detrended Fluctuation Analysis (DFA; Peng *et al.*, 1992) to investigate long-range dependence in the sequential distribution of little penguin dives and surface times during foraging. DFA is one of the more robust estimators of the Hurst exponent (Cannon *et al.*, 1997), a scaling exponent that measures self-affinity across scales in time series data. This method was previously shown to produce reliable estimates of scaling behavior in little penguin and Adélie penguin *Pygoscelis adeliae* dive sequences (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014). Theoretically, αDFA is inversely related to the fractal dimension, which represents an index of structural complexity (Mandelbrot, 1977). DFA was run using the package 'fractal' (Constantine & Percival, 2014) in R statistical software v.3.2.5 (R Development Core Team, 2016). A thorough description of this method, including DFA

calculation, validation of best scaling region and its relationship to other fractal dimension estimates and illustrations are provided in MacIntosh *et al.* (2013) and Meyer *et al.* (2015).

In order to assess the influence of environmental variables, we obtained measurements of satellite-derived daily High Resolution SST data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site (http://www.esrl.noaa.gov/psd/) (Reynolds *et al.*, 2007). Weekly Chlorophyll *a* (SeaWiFS and MODIS) and daily sea wind (QuikStat and ASCAT) measurements, constitute by u-wind (wind towards east on a west-east axis) and v-wind (wind towards north on a south-north axis), were obtained through Xtractomatic R package (http://coastwatch.pfel.noaa.gov/xtracto/) sourced on the ERD/CoastWatch ERDDAP Server. These environmental variables were averaged over the penguin foraging area, i.e. 20-25km during the guard period (Collins *et al.*, 1999; Pelletier *et al.*, 2014).

All statistical analyses were conducted in R v3.2.5 (R Development Core Team, 2016). We constructed Linear Mixed-effects Models (LMMs, 'lme4' package in R, Bates *et al.* (2015)) to investigate variation in αDFA as a function of environmental variables. Year was nested within logger type as random factors since in any given year, we used only one logger type, whereas each logger was used across multiple years. We included the following predictor variables in the model: SST at the time of trip, chlorophyll-*a* concentration over the week (8 days) during which the trip occurred, u-wind (wind towards east) and v-wind (wind towards north) kept separate following Dehnhard *et al.* (2013), and sex of the individual. Numeric predictor variables were scaled and centered (z-transformed) to simplify interpretation of the parameter estimates in the statistical model. Models were validated by visual examination of histograms of the residuals to ensure homogeneity and plots of residuals

versus fitted values to ensure homoscedasticity. We also found no evidence (e.g. via measurement of Cook's distance) of overly influential data points in our models. To test for multicollinearity, variance inflation factors (VIF) were calculated for each predictor variable with the package 'car': all showed values lower than 2 and were thus retained in the model (Zuur *et al.*, 2010). Because we were interested in relating our complexity signatures to those other parameters measuring aspects of diving performance, particularly effort and efficiency, we constructed generalized additive models (GAMs, 'mgcv' package in R, Wood, 2016) with Gaussian error distributions to estimate whether α_{DFA} covaries with CPUT, as a proxy for foraging efficiency, and the total time spent underwater, as a proxy for foraging effort. Descriptive results are presented as means and standard errors (SE), and we set the alpha level for all statistical analyses at 0.05.

IV.2.3 **Results – Article C**

Detrended fluctuation analysis produced values of αDFA ranging between 0.72 and 0.97 (mean=0.86, SE=0.004, Fig. IV.3), indicating that binary dive sequences from foraging little penguins are best characterized as persistent, long-range dependent fractional Gaussian noise, as was shown previously for Spheniscidae (MacIntosh *et al.*, 2013; Cottin *et al.*, 2014; Meyer *et al.*, 2015). In other words, dives and surface times of a given length are typically followed by dives and surface times of a similar length, with such patterns of fluctuation between behavioral states persisting across a range of measurement scales; observed best scaling regions included the scales 2^7-2^{11}, or 128-2048 seconds.

Variable	*Est.*	*Std.Error*	*Df*	*t-value*	*p-value*
Intercept	0.859	0.008	18	108.7	**<0.0.1**
SST	0.017	0.007	15	2.371	**0.03**
SexM	-0.0002	0.095	80	-0.023	0.98
Chla8d	-0.016	0.010	22	-1.559	0.13
u-wind	-0.0007	0.0005	85	-1.498	0.14
v-wind	0.0005	0.0005	68	1.070	0.29

Table IV-3 : Results of LMM examining variation in α_{DFA} in relation to Sea-Surface Temperature (SST), u-wind and v-wind at the time of the trip, weekly chlorophyll-a concentration and sex on α_{DFA} using LMM statistics. Bold text highlights significant p-values. Abbreviations: *Est*= estimate, *SE*= Standard error, *Df*=degree of freedom.

Our statistical model (Table IV-3) showed that an increase in sea-surface temperature (SST) was linked with higher values of α_{DFA}, reflecting higher degrees of long-range dependence (determinism) in dive sequences. Conversely, dive sequences of little penguins foraging in colder waters exhibited greater stochasticity than those of birds foraging in warmer waters (Figure IV.4). Finally, we observed no effects of sex, chlorophyll-*a*, or both u- and v-wind on complexity in foraging sequences.

Generalized additive models (GAMs) also showed that α_{DFA} correlated positively with CPUT as proxy for foraging efficiency (GAM R^2 = 0.22, F=15.16, p<0.001; Figure IV.5A) and negatively with time spent underwater, the proxy for foraging effort (GAM R^2=0.38, F=20.63, p<0.001; Figure IV.5B). These results suggest that more efficient foraging sequences are also more deterministic (higher α_{DFA}), while more stochastic sequences (lower α_{DFA}) are associated with greater foraging effort.

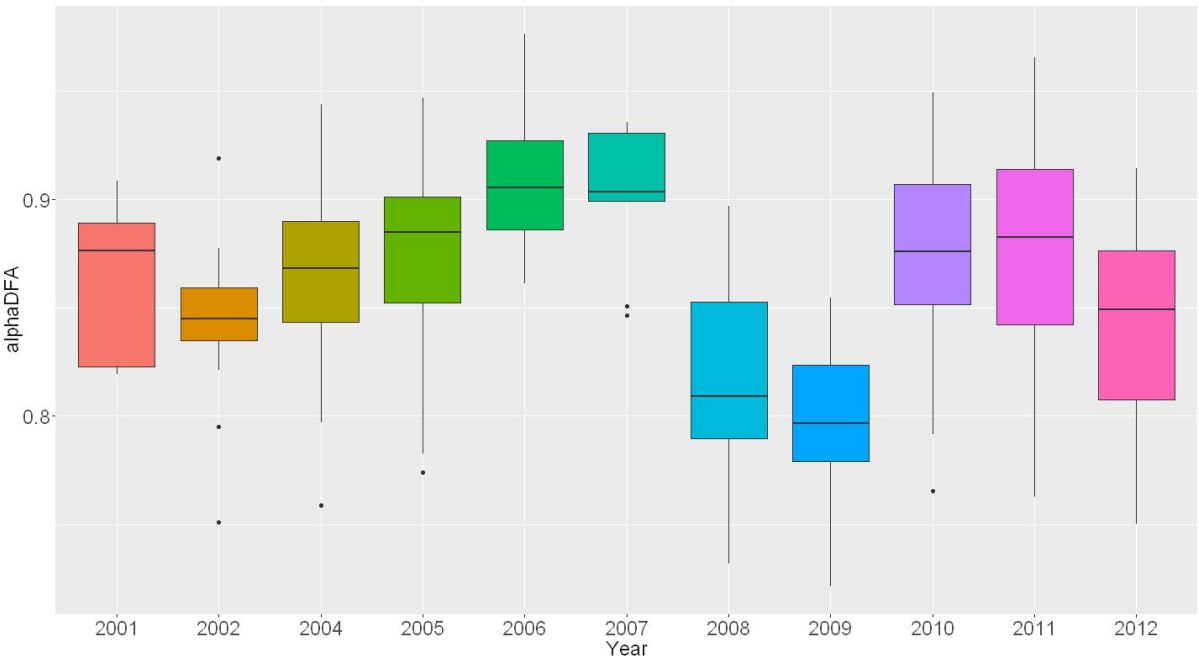


Figure IV.3 : Results of fractal analysis of binary sequences of diving behavior of little penguins showing scaling exponent for each years.

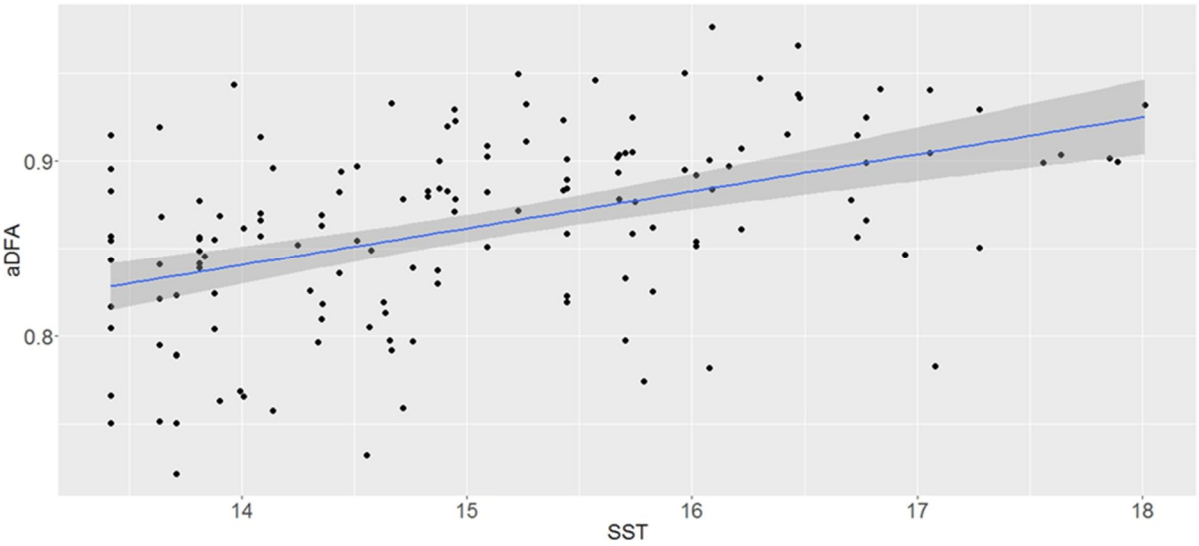


Figure IV.4 : Linear representation of αDFA as a function of SST

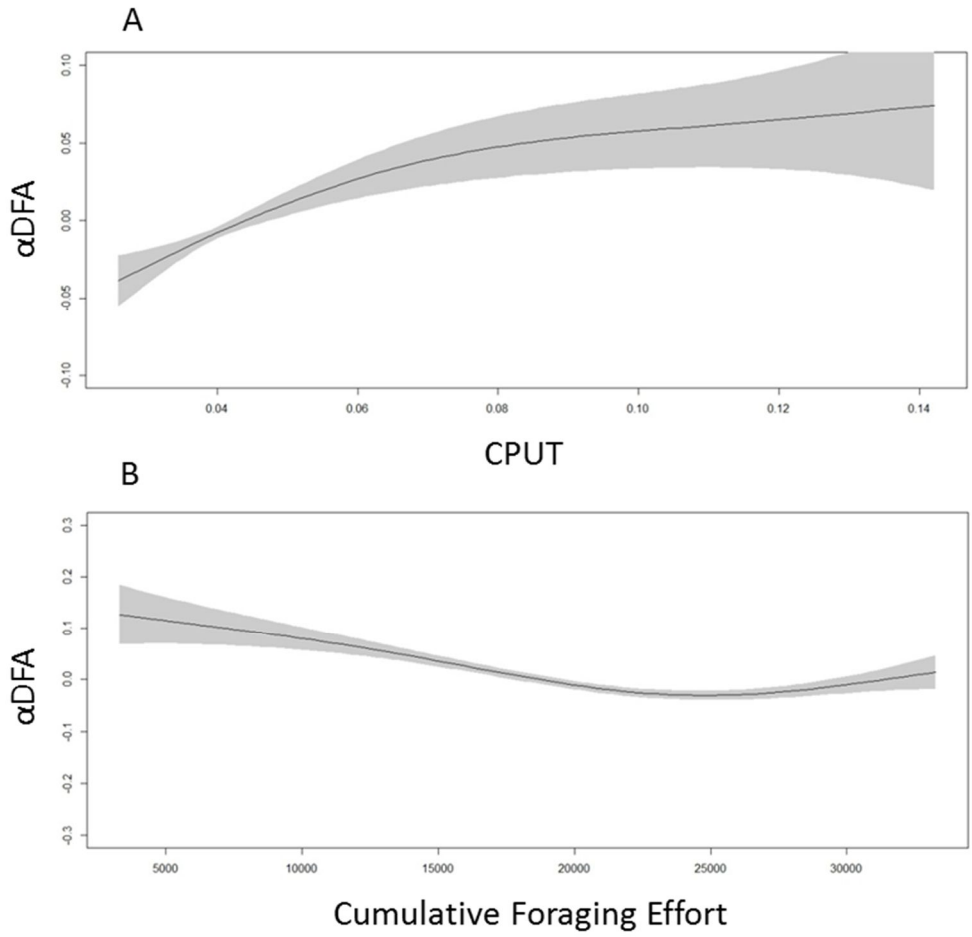


Figure IV.5 : GAMs representation of αDFA as a function of (A) the CPUT and (B) the foraging effort.

IV.2.4 **Discussion – Article C**

To monitor how changes in the Bass Strait affect one of its top predators, we investigated how the temporal organization of diving behavior of a foraging marine predator, the little penguin, is linked to environmental variables. We observed a significant positive relationship between temporal organization of foraging behavior of little penguins and SST, e.g. more deterministic temporal organization of foraging behavior when SST increases.

Fish populations are highly sensitive to environmental conditions, especially temperature, as they are cold-blooded and depend on ambient temperature to perform optimally at a physiological level. As such, fish can exhibit “boom-bust” dynamics (Chavez *et al.*, 2003). These fluctuations in fish populations are known to have a significant effect on the

productivity of marine predators (Cury *et al.*, 2011), including little penguins (Dann *et al.*, 2000). High SST has been correlated with a reduction in the abundance of fish species, e.g. sardine and anchovy in the Sea of Japan (Yasuda *et al.*, 1999; Thayer *et al.*, 2008). In our study, an increase in SST would thus represent a challenging situation for little penguins. Surprisingly, while we predicted that individuals in a challenging situation should show a higher stochasticity in their behavior, we actually observe the opposite as an increase in SST led to a greater determinism in the foraging activity (Fig. 3A & B). Yet, this greater determinism was also linked with higher CPUT (catch per unit time), our proxy for foraging efficiency, and lower total time spent underwater, our proxy for foraging effort. These results also echo those of Article B that linked greater determinism, higher foraging efficiency and lower foraging effort. We can propose three mutually non-exclusive explanations about the link between lower SST, higher stochasticity in foraging activity of little penguin and less predictable prey patches: i) colder waters in some years simply might not be warm enough to drive a high phytoplankton bloom at the beginning of the season (Berlincourt & Arnould, 2015), which would lead to a low abundance of planktivorous fish (Nevárez-Martínez *et al.*, 2001); ii) colder waters could also influence the distribution of prey, as each fish species have to live in a specific optimal temperature range, like sardines (*Sardinops sagax*) in Australia, South Africa and in the Gulf of California (Agenbag *et al.*, 2003; Lanz *et al.*, 2009; O'Donoghue *et al.*, 2010; Doubell *et al.*, 2015). In contrast, maximum SST recorded in our study (i.e. 18°C) is much lower than the maximum SST (i.e. 23°C) recorded in Montague Island (New South Wales, Australia) by (Carroll *et al.*, 2016), who showed that little penguin's optimal temperature range for prey capture is around 19°C to 21°C, which suggests that prey availability should be more predictable in this SST range; iii) SST differences (measured at the surface of the ocean) actually reflect differences in the

thermal structure of the water column. An increase in SST can lead to the formation of a thermocline as the rapid warming up of the surface waters provoke a separation from the colder deep waters (Gaspar, 1988). Fish are known to concentrate around thermoclines (Sogard & Olla, 1993; Hansen *et al.*, 2001), an important cue for prey localization by fish predators (Boyd & Arnbom, 1991; Kokubun *et al.*, 2010) including little penguins (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012). When this thermocline is absent, little penguins indeed showed lower foraging efficiency than in the presence of a thermocline (Ropert-Coudert *et al.*, 2009), and we hypothesize that birds will show here more stochastic temporal organization of foraging behavior. Such a shift to a more stochastic pattern of foraging could happen in reaction to environmental heterogeneity and may allow little penguins to cope with environmental variability.

Our model showed no effect of wind, whether it is for u-wind (winds towards north) or v-wind (wind towards east), on temporal organization of foraging behavior of little penguins. Previous studies showed effect of wind on foraging effort and foraging duration, which lead to decrease in body mass of foraging individuals (Berlincourt & Arnould, 2015; Saraux *et al.*, 2016). However, daily u-wind and v-wind speeds registered during foraging trips of our penguins in Phillip Island showed lower means (mean u-wind speed= 2.07 m/s ± 0.48; mean v-wind speed= 1.40m/s ± 0.32) than mean wind speed presented in Gabo Island (mean wind speed= 8.46 m/s) and London Bridge (mean wind speed= 8.1 m/s) (Berlincourt & Arnould, 2015), two colonies located at both extremities of the Bass Strait. In addition, oceanographic mixing models applied to the Bass Strait have shown a relative resilience of thermocline to wind (Jones, 1980; Fandry, 1982). Low wind speed observed in our study and resilience of thermocline to wind could explain why wind speed did not affect temporal organization of foraging behavior of little penguins in our study. Our model also showed no effect of Chl-*a*

concentration on temporal organization of foraging behavior. Moreover, even if Chl-*a* concentration is considered as a proxy of primary production, little penguins are not eating phytoplankton but small fishes. An increase in fish population is expected to happen with a time lag after a phytoplankton bloom (Ward *et al.*, 2006; Keane & Neira, 2008) which could explain why Chl-*a* at the period of trip was not linked with temporal organization of foraging behavior.

Variability in the temporal organization of foraging behavior provides a novel way to investigate and interpret how foraging behavior of seabirds might change according to environmental conditions. This approach might aid future studies aiming to understand the responses and adaptations of organisms in the context of ongoing global change. More stochastic foraging sequences may reflect a more challenging environmental situation, where prey patches are less predictable. This observation is also confirmed by the lower foraging efficiency and higher foraging effort that characterized more stochastic foraging sequences. According to theory, certain complexity signatures may optimize foraging efficiency with respect to biological encounters. However, we were unable to test directly the effect of biological encounters and this aspect should be an important point in future studies investigating the adaptive value of variability in temporal organization of foraging behavior.


Discussion
Adélie Land
Antarctica

V. General discussion & conclusion

In this thesis, my aim was to explore complexity in the temporal organization of foraging behavior in two species of seabirds, little penguins and Adélie penguins. These biological models give us the opportunity to study the impact of environmental variables on the complexity of foraging behavior and investigate whether and how seabirds buffer environmental changes through behavioral flexibility. These species are also considered as eco-indicating species. My analyses therefore aimed to understand animal-environment interactions under certain conditions and make predictions about future irreversible change. The first part of my PhD was dedicated to studying how a fractal index (i.e. the value that defines the level of complexity observed in a behavioral sequence) changes when the animal is facing a constraint, in this case the attachment of data recording devices, which imposes a known hydrodynamic handicap. In these experiments, the two study species responded differently. In response to wearing larger versus smaller loggers, little penguins showed more stochastic foraging behavior while Adélie penguins showed no difference in their temporal organization of foraging behavior. Other hydrodynamic stressors, such as logger position and the presence of flipper bands showed no effect on temporal organization of foraging behavior in little penguins (Article A). The second part of my PhD aimed at investigating the influence of a set of environmental parameters on the temporal organization of foraging behavior of little penguins. Penguins exhibited more stochastic foraging behavior when foraging in deeper waters than those foraging in shallower waters (Article B). Similarly, little penguins foraging in waters characterized by colder sea-surface temperatures exhibited more stochastic foraging behavior than those foraging in warmer waters where prey are less accessible and prey fields less predictable due to a potential thermal disorganization of the water column (Article C). More stochastic foraging behavior

was also linked to lower foraging efficiency and higher foraging effort, which in turn provides cues about foraging success.

V.1 Using fractal index as a diagnostic tool of environmental changes

Eco-indicators allow us to summarize large quantities of information about the health of ecosystems into few but relevant signals for users, such as decision-makers (Durant *et al.*, 2009). Climate variability has been shown to have direct effects on animals (e.g. physiology), as well as indirect effects that impact the biological and physical environment of the animals. Previous studies showed that seabirds are good eco-indicators of environmental changes through their ability to respond in a sensitive and rapid way to environmental variability over multiple spatial and temporal scales (Briggs & Chu, 1986; Hyrenbach & Veit, 2003; Ballance, 2007; Frederiksen *et al.*, 2007). The most accessible parameters on which researchers focus at first are demographic and population parameters, but it has been shown later than variation in demographic parameters may reflect not only environmental variability at-sea but also changes in several variables, such as extreme weather (Annex 1), predation and parasites (Durant *et al.*, 2009). Moreover, several studies highlighted temporal lags in the response of seabird populations to broad-scale climate indices (Durant *et al.*, 2009), and changes in the environment can thus only become apparent at the population level several years later (Thompson & Ollason, 2001). As mentioned above, environmental changes have direct effects on animal physiology, and endocrine mechanisms are known to mediate behavioral responses to changes in the environment. More specifically, the "stress hormone" corticosterone should be a good candidate for a hormonal index of environmental change through its role in governing locomotor activities; a role that led to it being termed the "environmental hormone" (Angelier *et al.*, 2007a). However, Angelier and collaborators

(2009) showed later that the influence of foraging success and food intake on corticosterone levels is complex and that more studies are needed to better understand how corticosterone can be used as an eco-indicating parameter. In the light of these restrictions, behavioral parameters may be the key as they have been described as being more sensitive to change than demographic parameters (Durant *et al.*, 2009). Among all behavioral parameters available, foraging behavior seems to be an excellent candidate, as not only is it informative about drivers of population change, it also provides a rapid assessment of causes of population change (Lewis *et al.*, 2006b). For example, little penguin foraging behavior is influenced by the structure of the water column (Ropert-Coudert *et al.*, 2009; Pelletier *et al.*, 2012), bathymetry (Chiaradia *et al.*, 2007), wind (Berlincourt & Arnould, 2015; Saraux *et al.*, 2016) and SST (Berlincourt & Arnould, 2015; Carroll *et al.*, 2016). This sensitivity to environmental conditions makes little penguins an interesting model to study how animals may cope with environmental variability through temporal organization of foraging behavior.

Yet, how useful would such an index of temporal organization be in comparison with other, more classical, parameters of foraging behavior? Previous studies have used several dive characteristics (e.g. number of dives, mean dive depth, mean dive duration, trip duration) in order to monitor environmental changes in seabirds (e.g. Watanuki *et al.*, 1993; Charrassin *et al.*, 2002; Kato *et al.*, 2003; Ropert-Coudert *et al.*, 2009; Kokubun *et al.*, 2010; Pelletier *et al.*, 2012; Rey *et al.*, 2012; Ramírez *et al.*, 2014; Berlincourt & Arnould, 2015). However, using several diving parameters leads to a complex study framework that could slow the analysis and complicate the interpretation of changes observed in one (or several) of the parameters defining the foraging behavior. Moreover, interpretation of such changes is further complicated because diving parameters are often inter-related and their relations

could change from individual to individual or as the season advances (Zimmer *et al.*, 2011a). As mentioned above, our index of temporal organization of foraging behavior improves this situation by allowing scientists to have one integrated value of the organization of diving behavior per trip, along a stochastic-deterministic gradient in association with environmental change. Moreover, studies based on more classical parameters often used averages of diving characteristics, which may not be sensitive enough to detect changes in the distribution patterns of behavioral sequences, as shown in Seuront & Cribb (2011). On the contrary, these authors showed that fractal analyses, applied to the same dataset, were sensitive enough to highlight changes in the distribution patterns of behavioral sequences and, as such, may provide an objective and quantitative framework to investigate such changes.

I highlighted in this thesis that penguins exhibited greater stochasticity in the temporal organization of foraging behavior when individuals were exposed to non-optimal conditions (e.g. hydrodynamic handicap, Article A; bathymetry, Article B; lower sea-surface temperature, Article C). Bathymetry determines prey availability as it can mediate the distribution of prey within the water column (Hunt *et al.*, 1998; Russell *et al.*, 1999; Ladd *et al.*, 2005), while SST has been correlated with the abundance and distribution of fish species that comprise the prey field of foraging penguins (Yasuda *et al.*, 1999; Agenbag *et al.*, 2003; Thayer *et al.*, 2008; Lanz *et al.*, 2009; O'Donoghue *et al.*, 2010; Doubell *et al.*, 2015). It seems that higher SST in Article C is not reflecting a more challenging condition, and this has further support because CPUT was also higher with increasing SST, just like behavioral determinism. In the situations where prey fields are less predictable, little penguins showed a tendency towards an increase in the complexity of foraging sequences, suggesting that this index could be used as an eco-indicator of environmental changes. At the scale of foraging trip that

last several days, I think that our fractal index cannot be used as we did here in the case of trips lasting only one day. Indeed, little penguins are visual predators (Cannell & Cullen, 2008): they forage exclusively during the day and rest during the night. Such day-night cycles will drive the appearance of a strong determinism in the temporal organization of foraging behavior and our index would reflect, in this specific case, an emergent property of their natural circadian rhythm. Further study will need to focus on this issue and perhaps should consider analyzing independently each day of the trip. Rhythms linked to physical parameters, mostly rhythms that are highly predictable, such as the aforementioned day-night cycles, should thus be considered in the design of any future studies.

A limit in the use of seabirds as eco-indicators resides in the inconstancy of individual responses to the environment and its effects at the population level (Durant *et al.*, 2009). This individual plasticity could be explained by several factors, i.e. age, personality, sex, body mass, individual quality and physiology. Yet, in little penguins, age, sex and body mass do not affect the temporal organization of foraging behavior (MacIntosh *et al.*, 2013), a result which was partially confirmed in my thesis as Articles B and C did not show any effect of sex, although Article A included a sex effect so this cannot be ruled out entirely. As mentioned above, age does not seem to influence the temporal organization of foraging behavior but it was only tested in little penguins over one breeding season. As some studies showed that the age structure of the population can interact with environmental change in different ways (e.g. in Atlantic puffins *Fratercula arctica*, Durant *et al.*, 2004; in wandering albatross, Lecomte *et al.*, 2010), studies investigating relationships between environmental changes, age and temporal organization of foraging behavior over several years will be needed. Finally, two last traits, animal personality traits (e.g. boldness, shyness...) and individual quality, are considered to be highly plastic among individuals, but their effects on foraging

complexity remain unknown. Animal personality traits have been suggested to influence foraging activity, spatial aspects of foraging and physiological drivers of foraging (Toscano *et al.*, 2016). Individual quality is a concept difficult to define (Wilson & Nussey, 2010) and numerous traits have been used to measure it, such as reproductive traits (Côté & Festa-Bianchet, 2001; Blackmer *et al.*, 2005; Lewis *et al.*, 2006c; Lescroël *et al.*, 2010; Moyes *et al.*, 2011) or physiological traits (Magee *et al.*, 2006; Angelier *et al.*, 2007b; Bauch *et al.*, 2012; Le Vaillant *et al.*, 2015). For example, telomere length, a proxy of individual quality, has been shown to influence foraging activity in king penguins (*Aptenodytes patagonicus*, Le Vaillant *et al.*, 2016). In my results, individuals differed in their responses to environmental conditions and this may cause difficulties in using seabirds as eco-indicators. This problem is large and concerns all parameters used as eco-indicators, not just which presented in this thesis.

Even if fractal analysis is not very difficult to perform and can give us a parsimonious and integrated value about environmental changes, the interpretation of the mechanism that leads to variation in temporal organization of foraging behavior are more challenging. As such, fractal analysis does not replace other more traditional approaches and it should be used in conjunction with classical foraging variables. Moreover, additional works are needed to understand how generative mechanism of decision-making processes according to the environment during foraging could lead to complex behavior patterns. Finally, I think it is important to highlight the fact that utilization of fractal analysis in behavior and ecology are highly debated and critiques are focusing both on the analytical tool and interpretation of the underlying cause of such patterns (Mercik *et al.*, 2003; Benhamou, 2004, 2007; Edwards *et al.*, 2007; Turchin, 2007; James *et al.*, 2011; Bryce & Sprague, 2012; Benhamou & Collet, 2015; Pyke, 2015), although several of the critiques concerned with the analytical tool have

already been rebutted persuasively (Seuront *et al.*, 2004; Seuront, 2010, 2015). This stresses out the need for not applying straightforwardly the fractal index without following a series of both conceptual and practical steps at first to avoid biases in the results, which was the case for this thesis (see II.3.3.a, fractal analysis). I believe the utilization of fractal analysis could provide useful insights about output of mechanisms that allow animal to cope with environmental changes and that this tool can be used as an index of environment changes. Fractal approach starts to have widespread applications and has been also used in a context of biodiversity conservation, wildlife health monitoring (MacIntosh *et al.*, 2011; Seuront & Cribb, 2011; Cribb & Seuront, 2016), captive care and management (Rutherford et al., 2003). Following on Motohashi *et al.* (1993) I would like to suggest this approach to be used in tests-batteries, for example in which animals are used in gene knockout or drug testing research.

V.2 Complexity signatures in foraging behavior: adaptive value or not?

Previous works showed fractal scaling in the temporal organization of foraging behavior in little penguins (MacIntosh *et al.*, 2013), and highlighted transient alterations towards more determinism in foraging complexity among Adélie penguins exposed to artificially-implanted corticosterone time-released capsules (Cottin *et al.*, 2014). In this thesis, I investigated further how certain complex signatures in foraging behavior may allow seabirds to adapt to changes in their environment, and for this purpose, I tackled the potential adaptive value of certain complexity signatures. In theory, those anomalous processes may reflect, through the super-diffusive and fractal properties of complex and non-linear movements (i.e. Lévy movements), an evolved strategy that optimizes resource encounters in both space and time, and thus energy balance, in heterogeneous environments

(Bartumeus & Catalan, 2009; Viswanathan *et al.*, 2011). Indeed, several studies have shown that specific complexity signatures should optimize foraging efficiency with respect to biological encounters as a function of time spent foraging (Shimada *et al.*, 1993, 1995; Escós *et al.*, 1995; Alados & Huffman, 2000; Rutherford *et al.*, 2004; Hocking *et al.*, 2007; MacIntosh *et al.*, 2011; Seuront & Cribb, 2011). MacIntosh *et al.* (2011), for instance, showed that more structurally complex environments (i.e. arboreal versus terrestrial) and also resources that are harder to obtain (i.e. mobile invertebrates versus immobile fruits) led to a more stochastic temporal organization of foraging and movement behavior in Japanese macaques. In others words, from a complex environment (i.e. less predictable food resources, more discontinuous substrates) seems to emerge more complex foraging and search behavior. Moreover, controlled studies on fruit flies (*Drosophila melanogaster*: Cole, 1995; Shimada *et al.*, 1995) showed greater complexity in dwelling time in relation to a new environment and inferior food quality, while studies on hens (*Gallus gallus domesticus*: Rutherford *et al.*, 2003) showed that vigilance time series become more stochastic when animals are moved to novel environments. Variability in complexity signatures, then, in particular through alterations in the degree to which behavior sequences are long-range dependent, may provide a mechanism whereby animals can adapt to prevailing environmental conditions.

These set of studies found echoes with my thesis work, where I showed that more complex foraging behavior in little penguins was associated with more complex situations, i.e. regarding the hydrodynamic handicap or less predictable prey patches due to bathymetry and lower SST (Article A, B & C). As specific complexity signatures should optimize foraging efficiency with respect to biological encounters and allow animals to cope with environmental heterogeneity, it opens an important question: do specific complexity

signatures really emerge simply from interactions with the environment or are they actually adaptive?

Resource availability (i.e. abundance and distribution of prey in the water column) has been described as one the main drivers of diving behavior and foraging success in air-breathing diving predators, such as Antarctic fur seals (*Arctocephalus gazella*, Mori & Boyd, 2014), blue-eyed shags (*Phalacrocorax spp*, Cook *et al.*, 2008), thick-billed murres (*Uria lomvia*, Elliott *et al.*, 2008), blue whales (*Balaenoptera musculus,* Doniol-Valcroze *et al.*, 2011) and Steller sea lions (*Eumetopias jubatus*, Goundie *et al.*, 2015). The performance of complex foraging behavior in more complex situations (e.g. less predictable prey patches) might be linked to a priority-based queuing process favoring exploration over exploitation under such circumstances (Reynolds *et al.*, 2015). When prey are heterogeneously distributed, i.e. when the environment is challenging, birds should increase the occurrence of exploratory dives in an attempt to maximize prey encounters, which would then be interspersed with foraging dives, breaking up the structure of the diving bout and rendering the behavioral sequence more stochastic. Following this hypothesis, specific complexity signatures might emerge from the distribution of exploratory versus prey-pursuit dives. In articles B & C, as mentioned above, little penguins exhibiting complex foraging signatures with greater stochasticity also exhibited lower foraging efficiency and higher foraging effort than penguins foraging under more profitable conditions such as shallower waters or higher SST. The lower foraging efficiency and higher effort suggests that in our specific case, more stochastic foraging behavior is linked with more challenging environmental conditions (e.g. bathymetry, lower SST) and does not always increase prey encounters per unit time to the same level of efficiency observed with a more deterministic foraging behavior organization under less challenging conditions. Even under this interpretation, however, whether more

stochastic foraging behavior is a consequence of the environment or an adaptation to it cannot be easily determined.

However, the difficulty with this assessment is that we did not compare the same thing, as the scale is different. For example, in a complex environment characterized by less predictable food patches, what would be the consequence of an animal performing a more deterministic sequence of foraging behavior relative to others performing more stochastic behavior? Will that individual have a lower foraging success than the others? Moreover, on the broader scale of the breeding season, which individual will perform better? The individual able to change its foraging behavior or the individual that is more constrained to narrower range around its own hard-wired complexity signature? I think these questions are more likely to inform us about the potential adaptive value associated with complexity in the temporal organization of foraging behavior. Unfortunately, I was unable to test this hypothesis directly on an individual level in this thesis, and further studies are thus needed to understand better the potential adaptive advantages of specific complexity signatures, and their variability.

V.3 Perspectives

V.3.1 From juvenile to senescent: effect of ageing on temporal organization of foraging behavior in long-lived species.

Foraging behavior has been shown to be influenced by age in several long-lived species of seabirds, such as king penguins (Le Vaillant *et al.*, 2012) or wandering albatrosses (Lecomte *et al.*, 2010). Behavior of juveniles in long-lived seabirds is mostly unknown and only a few studies have started to investigate the problem (de Grissac *et al.*, 2016). Learning processes involved in foraging behavior have been listed as a priority for research (Hazen *et al.*, 2012), and studies combining questions on the learning process of foraging behavior with fractal

analysis could provide unprecedented information about how individuals learn to forage and buffer environmental changes.

At the other end of the spectrum of life, older birds will be subject to senescence, which can be defined as the gradual deterioration of functional characteristics of animals over time, and is characterized by an increasing rate of mortality with age (Ricklefs, 2008, 2010; Turbill & Ruf, 2010). Long-lived species are a good model to examine senescence, as a higher proportion of mortality is attributable to senescence than in short-lived species (Ricklefs, 2008, 2010; Turbill & Ruf, 2010). Fractal analysis has been described as more sensitive than more classical parameters used to measure behavior (Seuront & Cribb, 2011), and thus provide a new way to investigate the effects of senescence on the behavior of long-lived species. How useful this approach might be remains to be seen, although MacIntosh *et al.* (2011) do provide some evidence that behavior sequences become more deterministic with age in primates. Returning to seabirds, using thick-billed murres (*Uria lomvia*) as model, Elliott and collaborators (2015) recently showed that physiological markers (e.g. blood oxygen stores, resting metabolism and thyroid hormone) decrease with advancing age, but no changes were recorded in foraging behavior (e.g. dive depth, dive shape and dive effort). Given its alleged sensitivity, applying fractal analysis to the thick-billed murre case (among others) might reveal a previously undetected behavioral adjustment to the effects of senescence in old individuals.

V.3.2 Differences across the reproductive cycle

Studies have shown differences in foraging behavior across the reproductive cycle in several species, such little penguins (Kato *et al.*, 2008; Zimmer *et al.*, 2011b), Cape gannets (*Morus capensis*, Rishworth *et al.*, 2014), wandering albatrosses (Shaffer *et al.*, 2003) and

Adélie penguins (Takahashi *et al.*, 2003; Widmann *et al.*, 2015). For example, little penguins perform longer trips during the incubation and post-guard phases (Kato *et al.*, 2008; Saraux *et al.*, 2011a), which allows them to target more distant foraging areas. In order to understand how individuals breed successfully, it is important to understand how they buffer changes in the environment that occur across their reproductive cycle, especially given that reproductive constraints (increasing food demand as chicks grows, for instance) are also changing over the reproductive cycle. I hypothesize that animals will in turn exhibit differences in foraging complexity following these changes. However, as mentioned above, temporal organization of foraging behavior in long trips may be affected by some periodical rhythms (e.g. alternation day-night) according to species, and this methodological limit should be addressed prior to future studies on this topic.

V.3.3 Behavioral complexity, prey capture success, energy expenditure and breeding success

As developed above, behavioral complexity may have adaptive value in allowing seabirds to cope with challenging environmental conditions. To investigate further the adaptive value of behavioral complexity and its link with breeding success, I suggest studying temporal organization of foraging organization of both breeding partners over the complete breeding season and investigate how birds might buffer a challenging breeding season by adjusting – or not – their temporal organization of foraging behavior. It has been shown in several seabird species that an unequal parental investment is associated with compensatory behaviors (e.g. Velando & Alonso-Alvarez, 2003; Paredes *et al.*, 2005; Beaulieu *et al.*, 2009), including in little penguins (Saraux *et al.*, 2011c). Taken together, it will give us invaluable information about behavioral mechanisms partners may exhibit to buffer challenging situations and successfully raise their progeny.

Finally, to investigate in greater details the link between behavioral complexity and breeding success, future studies should consider using finer proxies for prey capture success, such as those that can be obtained using animal-borne video-recording devices coupled with accelerometers (Watanabe & Takahashi, 2013; Carroll *et al.*, 2016), an approach which was only recently allowed thanks to the latest advances in data logger miniaturization. In order to measure the energetic costs of different foraging strategies, it is also possible to use accelerometers to obtain a proxy of energy consumption based on the Overall Dynamic Body Acceleration (ODBA, *sensu* Wilson *et al.*, 2006). However, it is necessary to calibrate this method via an indirect measurement of energy expenditure, such as doubly-labeled water (DLW, Speakman, 1997; Fort *et al.*, 2011; Elliott *et al.*, 2013). Comparison of energy expenditure between individuals exhibiting different foraging complexity signatures but exposed to the same environmental conditions should provide new avenues to study the adaptive value of behavioral complexity.

V.4 Conclusion

My thesis revealed the influence of challenging situations, artificial and environmental, on the complexity of the foraging behavior of two species of seabirds, little penguins and Adélie penguins. Greater stochasticity in the temporal organization of foraging behavior might be a way for birds to buffer environmental changes. I also highlighted the opportunity to use fractal analysis to investigate the behavior of upper-level predators and use it as an eco-indicator of environmental changes.

In a global context of rapid environmental change (IPCC, 2014), it has become essential to develop tools that allow us to rapidly diagnose environmental change and its incumbent consequences for wildlife. It can help the scientific community but also policy-makers to get

a quick, sensitive and integrative diagnostic about changes happening in the environment and affecting wildlife. Moreover, utilization of fractal analysis to investigate temporal organization in behavior as a diagnostic tool could be extended to numerous contexts, such as biodiversity conservation, wildlife health monitoring, captive care and management, and test-batteries. This approach could indeed be a powerful tool in the setup of conservation measures to protect an environment, but also to see if conservation measures have the expected effects on animals.

In addition to this direct application of fractal analysis as an index of environmental change, my thesis also opens up new ways to investigate flexibility in foraging behavior and the adaptive value associated with it. Unfortunately, I was unable to test within the frame of my PhD the hypothesis about the energetic costs of exhibiting foraging flexibility to buffer environmental changes and its consequences on fitness. Future studies should focus more particularly on links between complexity signatures, foraging success, energy expenditure and fitness.


Bibliography
Summerland Peninsula
Phillip Island, Australia

VI. Bibliography

-A-

Abasolo D, Hornero R, Escudero J, Espino P (2008) A Study on the Possible Usefulness of Detrended Fluctuation Analysis of the Electroencephalogram Background Activity in Alzheimer 's Disease. *IEEE Transactions on Biomedical engineering*, **55**, 2171–2179.

Afán I, Chiaradia A, Forero MG, Dann P, Ramírez F (2015) A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator. *Proceedings Biological sciences / The Royal Society*, **282**, 20150721.

Agenbag JJ, Richardson AJ, Demarcq H, Fréon P, Weeks S, Shillington FA (2003) Estimating environmental preferences of South African pelagic fish species using catch size- and remote sensing data. *Progress in Oceanography*, **59**, 275–300.

Ainley DG (2002) *The Adélie penguin: bellwether of climate change*. Columbia University Press, New York, 310 pp.

Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology*, **20**, 311–319.

Ainley DG, Ford RG, Brown ED, Suryan RM, Irons DB (2003) Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology*, **84**, 709–723.

Alados CL, Huffman MA (2000) Fractal long-range correlations in behavioural sequences of wild chimpanzees: A non-invasive analytical tool for the evaluation of health. *Ethology*, **106**, 105–116.

Alados CL, Weber DN (1999) Lead effects on the precitability of reproductive behavior in fathead minnows (*Pmephales promelas*): A mathematical model. *Environmental Toxicology and Chemistry*, **18**, 2392–2399.

Alados CL, Escos JM, Emlen JM (1996) Fractal structure of sequential behaviour patterns: an indicator of stress. *Animal Behaviour*, **51**, 437–443.

Alados CL, Escos J, Emlen JM, Freeman DC (1999) Characterization of branch complexity by fractal analyses. *International Journal of Plant Science*, **160**.

Angel LP, Barker S, Berlincourt M, Tew E, Warwick-Evans V, Arnould JPY (2015) Eating locally: Australasian gannets increase their foraging effort in a restricted range. *Biology Open*, 1–8.

Angelier F, Clément-Chastel C, Gabrielsen GW, Chastel O (2007a) Corticosterone and time-activity budget: An experiment with Black-legged kittiwakes. *Hormones and Behavior*, **52**, 482–491.

Angelier F, Moe B, Weimerskirch H, Chastel O (2007b) Age-specific reproductive success in a long-lived bird: Do older parents resist stress better? *Journal of Animal Ecology*, **76**,

1181–1191.

Angelier F, Clément-Chastel C, Welcker J, Gabrielsen GW, Chastel O (2009) How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. *Functional Ecology*, **23**, 784–793.

Arnould JPY, Dann P, Cullen JM (2004) Determining the sex of Little Penguins (*Eudyptula minor*) in northern Bass Strait using morphometric measurements. *Emu*, **104**, 261–265.

Asher L, Collins LM, Ortiz-Pelaez A, Drewe JA, Nicol CJ, Pfeiffer DU (2009) Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of the Royal Society, Interface / the Royal Society*, **6**, 1103–1119.

-B-

Bak P, Sneppen K (1993) Punctuated Equilibrium and Criticality in a Simple Model of Evolution. *Physical Review*, **71**, 4083–4086.

Ballance LT (2007) Understanding seabirds at sea: Why and how? *Marine Ornithology*, **35**, 127–135.

Banks SC, Ling SD, Johnson CR, Piggott MP, Williamson JE, Beheregaray LB (2010) Genetic structure of a recent climate change-driven range extension. *Molecular Ecology*, **19**, 2011–2024.

Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic Aspects of Design and Attachment of a Back-Mounted Device in Penguins. *The Journal of experimental biology*, **194**, 83–96.

Barbraud C, Weimerskirch H (2006) Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 6248–6251.

Bartumeus F (2007) Lévy Processes in Animal Movement: an Evolutionary Hypothesis. *Fractals*, **15**, 151–162.

Bartumeus F (2009) Behavioral intermittence, Lévy patterns, and randomness in animal movement. *Oikos*, **118**, 488–494.

Bartumeus F, Catalan J (2009) Optimal search behavior and classic foraging theory. *Journal of Physics A: Mathematical and Theoretical*, **42**, 434002.

Bartumeus F, Levin SA (2008) Fractal reorientation clocks: Linking animal behavior to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19072–7.

Bartumeus F, da Luz MGE, Viswanathan GM, Catalan J (2005) Animal Search Strategies: a Quantitative Random-Walk Analysis. *Ecology*, **86**, 3078–3087.

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: Linear mixed-effects models using Eigen and S4 version 1.1-9.

Bauch C, Becker PH, Verhulst S (2012) Telomere length reflects phenotypic quality and costs

of reproduction in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122540–20122540.

Beaulieu M, Raclot T, Dervaux A, Le Maho Y, Ropert-Coudert Y, Ancel A (2009) Can a handicapped parent rely on its partner? An experimental study within Adélie penguin pairs. *Animal Behaviour*, **78**, 313–320.

Benhamou S (2004) How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, **229**, 209–220.

Benhamou S (2007) How Many Animals Really Do the Lévy Walk? *Ecology*, **88**, 1962–1969.

Benhamou S (2014) Of scales and stationarity in animal movements. *Ecology Letters*, **17**, 261–272.

Benhamou S, Collet J (2015) Ultimate failure of the Lévy Foraging Hypothesis: Two-scale searching strategies outperform scale-free ones even when prey are scarce and cryptic. *Journal of Theoretical Biology*, **387**, 221–227.

Berlincourt M, Arnould JPY (2015) Influence of environmental conditions on foraging behaviour and its consequences on reproductive performance in little penguins. *Marine Biology*, **162**, 1485–1501.

Bertrand S, Burgos JM, Gerlotto F, Atiquipa J (2005) Lévy trajectories of Peruvian purse-seiners as an indicator of the spatial distribution of anchovy (*Engraulis ringens*). *ICES Journal of Marine Science*, **62**, 477–482.

Bintanja R, van Oldenborgh GJ, Drijfhout SS, Wouters B, Katsman C a. (2013) Important role for ocean warming and increased ice-shelf melt in Antarctic sea-ice expansion. *Nature Geoscience*, **6**, 376–379.

Blackmer AL, Mauck RA, Ackerman JT, Huntington CE, Nevitt GA, Williams JB (2005) Exploring individual quality: Basal metabolic rate and reproductive performance in storm-petrels. *Behavioral Ecology*, **16**, 906–913.

Le Boeuf BJ, Naito Y, Asaga T, Crocker D, Costa DP (1992) Swim speed in a female northern elephant seal: metabolic and foraging implications. *Canadian Journal of Zoology*, **70**, 786–795.

Bost CA, Cotté C, Bailleul F et al. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, **78**, 363–376.

Boyd IL, Arnbom T (1991) Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology*, **11**, 259–266.

Boyd IL, Murray AWA (2001) Monitoring a marine ecosystem using upper trophic level predators. *Journal of Animal Ecology*, **70**, 747–760.

Boyer D, Miramontes O, Ramos-Fernández G, Mateos JL, Cocho G (2004) Modeling the searching behavior of social monkeys. *Physica A: Statistical Mechanics and its Applications*, **342**, 329–335.

Boyer D, Ramos-Fernández G, Miramontes O et al. (2006) Scale-free foraging by primates emerges from their interaction with a complex environment. *Proceedings. Biological sciences / The Royal Society*, **273**, 1743–50.

Bradbury RH, Reichelt E (1983) Fractal Dimension of a Coral Reef at Ecological Scales. *Marine Ecology Progress Series*, **10**, 169–171.

Bradbury JW, Vehrencamp SL (2014) Complexity and behavioral ecology. *Behavioral Ecology*, **25**, 435–442.

Briggs KT, Chu EW (1986) Sooty Shearwaters off California: distribution, abundance and habitat use. *Condor*, **88**, 355–364.

Brown CT, Liebovitch LS, Glendon R (2007) Lévy flights in dobe Ju/'hoansi foraging patterns. *Human Ecology*, **35**, 129–138.

Bryce RM, Sprague KB (2012) Revisiting detrended fluctuation analysis. *Scientific reports*, **2**, 315.

Burke CM, Montevecchi WA (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*, **278**, 354–361.

Butler PJ (2006) Aerobic dive limit. What is it and is it always used appropriately? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **145**, 1–6.

Button KS, Ioannidis JP a, Mokrysz C, Nosek B a, Flint J, Robinson ESJ, Munafò MR (2013) Power failure: why small sample size undermines the reliability of neuroscience. *Nature reviews. Neuroscience*, **14**, 365–76.

-C-

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) *Self-organization in biological systems*. Princeton University Press, Princeton.

Cannell B, Cullen JM (2008) The foraging behaviour of Little Penguins *Eudyptula minor* at different light levels. *Ibis*, **140**, 467–471.

Cannon MJ, Percival DB, Caccia DC, Raymond GM, Bassingthwaighte JB (1997) Evaluating scaled windowed variance methods for estimating the Hurst coefficient of time series. *Physica A*, **241**, 606–626.

Carpenter KE, Abrar M, Aeby G et al. (2008) One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. *Science*, **321**, 560–563.

Carroll G, Everett JD, Harcourt R, Slip D, Jonsen I (2016) High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. *Scientific Reports*, **6**, 22236.

Chaline J, Nottale L, Grou P (1999) Is the evolutionary tree a fractal structure? *Comptes rendus de l'Académie des Sciences-Séries IIA-Earth and Planetary Science*, 717–726.

Chambers LE (2004) Delayed breeding in little penguins - evidence of climate change? *Australian Meteorological Magazine*, **53**, 13–19.

Chambers LE, Altwegg R, Barbraud C et al. (2013) Phenological Changes in the Southern Hemisphere. *PLoS ONE*, **8**.

Charrassin JB, Park YH, Maho Y Le, Bost CA (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters*, **5**, 317–319.

Chavez FP, Ryan J, Lluch-Cota SE, Niquen C M (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, **299**, 217–221.

Chavez FP, Messie M, Pennington JT (2011) Marine Primary Production in Relation to Climate Variability and Change. *Annual review of marine science*, **3**, 227–260.

Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. *Marine Biology*, **154**, 813–821.

Chiaradia A, Kerry KR (1999) Daily nest attendance and breeding performance in the little penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology*, **27**, 19–20.

Chiaradia A, Nisbet ICT (2006) Plasticity in parental provisioning and chick growth in little penguins *Eudyptula minor* in years of high and low breeding success. *Ardea*, **94**, 257–270.

Chiaradia A, Costalunga A, Kerry K (2003) The diet of Little Penguins (*Eudyptula minor*) at Phillip Island, Victoria, in the absence of a major prey - Pilchard (*Sardinops sagax*). *Emu*, **103**, 43–48.

Chiaradia A, Ropert-Coudert Y, Kato A, Mattern T, Yorke J (2007) Diving behaviour of Little Penguins from four colonies across their whole distribution range: Bathymetry affecting diving effort and fledging success. *Marine Biology*, **151**, 1535–1542.

Chiaradia A, Forero MG, Hobson KA, Cullen JM (2010) Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science*, **67**, 1710–1720.

Chiaradia A, Forero MG, Hobson KA, Swearer SE, Hume F, Renwick L, Dann P (2012) Diet segregation between two colonies of little penguins *Eudyptula minor* in southeast Australia. *Austral Ecology*, **37**, 610–619.

Chiaradia A, Ramirez F, Forero MG, Hobson KA (2015) Stable Isotopes (δ13C, δ15N) Combined with Conventional Dietary Approaches Reveal Plasticity in Central-Place Foraging Behavior of Little Penguins *Eudyptula minor*. *Frontiers in Ecology and Evolution*, **3**, 154.

Clark PU, Pisias NG, Stocker TF, Weaver AJ (2002) The role of the thermohaline circulation in abrupt climate change. *Nature*, **415**, 863–869.

Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. *Polar Biology*, **20**, 248–258.

Clarke J, Kerry K, Fowler C, Lawless R, Eberhard S, Murphy R (2003) Post-fledging and winter migration of Adélie penguins *Pygoscelis adeliae* in the Mawson region of East Antarctica. *Marine Ecology Progress Series*, **248**, 267–278.

Cole BJ (1995) Fractal time in animal behavior: the moment activity of Drosophila. *Animal Behaviour*, **50**, 1317–1324.

Collins M, Cullen JM, Dann P (1999) Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. *Wildlife Research*, **26**, 705–721.

Constable AJ, Melbourne-Thomas J, Corney SP et al. (2014) Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology*, **20**, 3004–3025.

Constantine W, Percival D (2014) Fractal Time Series Modeling and Analysis version 2.0-0. Accessed 10 Oct. 2014.

Cook TR, Lescroël A, Tremblay Y, Bost CA (2008) To breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags. *Animal Behaviour*, **76**, 565–576.

Cook TR, Hamann M, Pichegru L, Bonadonna F, Grémillet D, Ryan PG (2012) GPS and time-depth loggers reveal underwater foraging plasticity in a flying diver, the Cape Cormorant. *Marine Biology*, **159**, 373–387.

Côté SD, Festa-Bianchet M (2001) Reproductive success in female mountain goats: the influence of age and social rank. *Animal Behaviour*, **62**, 173–181.

Cottin M, MacIntosh AJJ, Kato A, Takahashi A, Debin M, Raclot T, Ropert-Coudert Y (2014) Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. *Marine Ecology Progress Series*, **496**, 249–262.

Cresswell G (1997) Sea surface Temperature and drifter buoy movements around Tasmania: compiled SST images for 1990 to 1997. *CSIRO Marine Research Piscator production*.

Cribb N, Seuront L (2016) Changes in the behavioural complexity of bottlenose dolphins along a gradient of anthropogenically-impacted environments in South Australian coastal waters: Implications for conservation and management strategies. *Journal of Experimental Marine Biology and Ecology*, **482**, 118–127.

Crist TO, Guertin DS, Wiens J a, Milne BT (1992) Animal Movement in Heterogeneous Landscapes - an Experiment with Eleodes Beetles in Shortgrass Prairie. *Functional Ecology*, **6**, 536–544.

Culik BM, Wilson RP (1991) Swimming energetics and performance of instrumented Adélie Penguins (*Pygoscelis adeliae*). *Journal of Experimental Biology*, **158**, 355–368.

Cullen JM, Montague TL, Hull C (1991) Food of Little penguin *Edyptula minor* in Victoria: comparison of three localities between 1985 and 1988. *Emu*, **91**, 318–341.

Cullen J, Chambers L, Coutin P, Dann P (2009) Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Marine Ecology Progress*

Series, **378**, 269–278.

Cury PM, Boyd IL, Bonhommeau S et al. (2011) Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. *Science*, **334**, 1703–1706.

-D-

Daniel TA, Chiaradia A, Logan M, Quinn GP, Reina RD (2007) Synchronized group association in little penguins, *Eudyptula minor*. *Animal Behaviour*, **74**, 1241–1248.

Dann P, Norman FI, Cullen JM, Neira FJ, Chiaradia A (2000) Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995-96, following a widespread mortality of pilchard, *Sardinops sagax*. *Marine and freshwater research*, **51**, 355–362.

Dann P, Sidhu LA, Jessop R et al. (2014) Effects of flipper bands and injected transponders on the survival of adult Little Penguins *Eudyptula minor*. *Ibis*, **156**, 73–83.

Dehnhard N, Ludynia K, Poisbleau M, Demongin L, Quillfeldt P (2013) Good days, bad days: Wind as a driver of foraging success in a flightless seabird, the southern rockhopper penguin. *PLoS ONE*, **8**.

Delignières D, Torre K, Lemoine L (2005) Methodological issues in the application of monofractal analyses in psychological and behavioral research. *Nonlinear dynamics, psychology, and life sciences*, **9**, 435–461.

Dicke M, Burrough PA (1988) Using fractal dimensions for characterizing tortuosity of animal trails. *Physiological Entomology*, **13**, 393–398.

Doney SC, Ruckelshaus M, Duffy JE et al. (2012) Climate change impacts on marine ecosystems. *Ann Rev Mar Sci*, **4**, 11–37.

Doniol-Valcroze T, Lesage V, Giard J, Michaud R (2011) Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology*, **22**, 880–888.

Doubell M, Ward T, Watson P, James C, Carroll J, Redondo Rodriguez A (2015) *Optimising the size and quality of Sardines through real-time harvest monitoring*. Prepared by the South Australian Research and Development Institute (Aquatic Science), Adelaide, CRC Project No. 2013/746, 47 pp.

Durant JM, Anker-Nilssen T, Hjermann DØ, Stenseth NC (2004) Regime shifts in the breeding of an Atlantic puffin population. *Ecology Letters*, **7**, 388–394.

Durant JM, Hjermann D, Frederiksen M et al. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research*, **39**, 115–129.

-E-

Edwards AM, Phillips RA, Watkins NW et al. (2007) Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature*, **449**, 1044–1048.

Einstein A (1956) *Investigations on the Theory of the Brownian Movement* (ed Fürth R).

Dover publications, Mineola, 121pp.

Eke A, Herman P, Bassingthwaighte JB et al. (2000) Physiological time series: Distinguishing fractal noises from motions. *Pflugers Archiv European Journal of Physiology*, **439**, 403–415.

Elliott KH, Davoren GK, Gaston AJ (2008) Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour*, **75**, 1301–1310.

Elliott KH, Le Vaillant M, Kato A, Speakman JR, Ropert-Coudert Y (2013) Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology letters*, **9**, 20120919.

Elliott KH, Hare JF, Le Vaillant M, Gaston AJ, Ropert-Coudert Y, Anderson WG (2015) Ageing gracefully: Physiology but not behaviour declines with age in a diving seabird. *Functional Ecology*, **29**, 219–228.

Emmerson L, Southwell C (2008) Sea ice cover and its influence on Adélie penguin reproductive performance. *Ecology*, **89**, 2096–2102.

Escós JM, Alados CL, Emlen JM (1995) Fractal Structures and Fractal Functions as Disease Indicators. *Oikos*, **74**, 310–314.

Evans K, Lea MA, Patterson TA (2013) Recent advances in bio-logging science: Technologies and methods for understanding animal behaviour and physiology and their environments. *Deep-Sea Research Part II: Topical Studies in Oceanography*, **88-89**, 1–6.

-F-

Fallow PM, Chiaradia A, Ropert-Coudert Y, Kato A, Reina RD, Sciences B (2009) Flipper Bands Modify the Short-Term Diving Behavior of Little Penguins. *Journal of Wildlife Management*, **73**, 1348–1354.

Fandry CB (1982) A numerical model of the wind-driven transient motion in Bass strait. *Journal of Geophysical Research: Oceans*, **87**, 499–517.

Fisher JAD, Casini M, Frank KT, Moellmann C, Leggett WC, Daskalov G (2015) The importance of within-system spatial variation in drivers of marine ecosystem regime shifts. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **370**, 20130271.

Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology*, **12**, 411–423.

Fort J, Porter WP, Grémillet D (2011) Energetic modelling: A comparison of the different approaches used in seabirds. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **158**, 358–365.

Fraser MM, Lalas C (2004) Seasonal variation in the diet of blue penguins (*Eudyptula minor*) at Oamaru, New Zealand. *Notornis*, **51**, 7–15.

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to

top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, **75**, 1259–1268.

Frederiksen M, Edwards M, Mavor RA, Wanless S (2007) Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series*, **350**, 137–143.

Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings. Biological sciences / The Royal Society*, **270**, 1143–8.

Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, **54**, 726–737.

-G-

Gales R, Greenberg B (1990) The annual energetics cycle of little penguins (Eudyptula minor). *Ecology*, **71**, 2297–2313.

Garcia F, Carrère P, Soussana JF, Baumont R (2005) Characterisation by fractal analysis of foraging paths of ewes grazing heterogeneous swards. *Applied Animal Behaviour Science*, **93**, 19–37.

Gaspar P (1988) Modeling the Seasonal Cycle of the Upper Ocean. *Journal of Physical Oceanography*, **18**, 161–180.

Gaston AJ (2004) *Seabirds: A Natural History*. Yale University Press, New Haven.

Gauthier-Clerc M, Gendner JP, Ribic C a et al. (2004) Long-term effects of flipper bands on penguins. *Proceedings. Biological sciences / The Royal Society*, **271 Suppl** , S423–S426.

Gibbs CF (1992) Oceanography of Bass Strait: implications for the food supply of little penguins *Eudyptula minor*. *Emu*, **91**, 395–401.

Goldberger AL, Rigney DR, West BJ (1990) Chaos and fractals in human physiology. *Scientific American*, **262**, 42–49.

Goldberger AL, Peng CK, Lipsitz LA (2002a) What is physiologic complexity and how does it change with aging and disease? *Neurobiology of Aging*, **23**, 23–26.

Goldberger AL, Amaral LAN, Hausdorff JM, Ivanov PC, Peng C-K, Stanley HE (2002b) Fractal dynamics in physiology: Alterations with disease and aging. *Proceedings of the National Academy of Sciences*, **99**, 2466–2472.

Goundie ET, Rosen DAS, Trites AW (2015) Low prey abundance leads to less efficient foraging behavior in Steller sea lions. *Journal of Experimental Marine Biology and Ecology*, **470**, 70–77.

Granadeiro J, Nunes M, Silva M, Furness R (1998) Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal behaviour*, **56**, 1169–1176.

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. *Scientific Reports*, **6**, 26103.

Grosser S, Burridge CP, Peucker AJ, Waters JM (2015) Coalescent Modelling Suggests Recent Secondary-Contact of Cryptic Penguin Species. *PLoS one*, **10**, 1–17.

-H-

Halpern BS, Walbridge S, Selkoe KA et al. (2008) A Global Map of Human Impact on Marine Ecosystems. *Science*, **319**, 948–952.

Hansen JE, Martos P, Madirolas A (2001) Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fish. Oceanogr.*, **10**, 193–206.

Hart T, Coulson T, Trathan PN (2010) Time series analysis of biologging data: autocorrelation reveals periodicity of diving behaviour in macaroni penguins. *Animal Behaviour*, **79**, 845–855.

Hastings HM, Pekelney R, Monticciolo R, vun Kannon D, Del Monte D (1982) Time scale, persistence, and patchiness. *Biosystems*, **15**, 281–289.

Hausdorff JM, Peng CK, Ladin Z, Wei JY, Goldberger a L (1995) Is walking a random walk? Evidence for long-range correlations in stride interval of human gait. *Journal of applied physiology*, **78**, 349–358.

Hausdorff JM, Purdon PL, Peng CK, Ladin Z, Wei JY, Goldberger A (1996) Fractal dynamics of human gait-stability of long-range correlations in stride interval fluctuations. *Journal of applied physiology*, **80**, 1448–1457.

Hausdorff JM, Mitchell SL, Firtion R, Peng CK, Cudkowicz ME, Wei JY, Goldberger a L (1997) Altered fractal dynamics of gait: reduced stride-interval correlations with aging and Huntington's disease. *Journal of applied physiology*, **82**, 262–269.

Hausdorff JM, Ashkenazy Y, Peng CK, Ivanov PC, Stanley HE, Goldberger AL (2001) When human walking becomes random walking: Fractal analysis and modeling of gait rhythm fluctuations. *Physica A: Statistical Mechanics and its Applications*, **302**, 138–147.

Havlin S, Buldyrev S V, Goldberger a L et al. (1995) Fractals in biology and medicine. *Chaos, solitons, and fractals*, **6**, 171–201.

Havlin S, Buldyrev S V, Bunde a, Goldberger a L, Ivanov PCh, Peng CK, Stanley HE (1999) Scaling in nature: from DNA through heartbeats to weather. *Physica A*, **273**, 46–69.

Hays GC, Ferreira LC, Sequeira AMM et al. (2016) Key Questions in Marine Megafauna Movement Ecology. *Trends in Ecology & Evolution*, **31**, 463–475.

Hayward TL (1997) Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. *Tree*, **12**, 150–154.

Hazen EL, Jorgensen S, Rykaczewski RR et al. (2012) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **3**, 234–238.

Hill KL, Rintoul SR, Coleman R, Ridgway KR (2008) Wind forced low frequency variability of the East Australia Current. *Geophysical Research Letters*, **35**, 1–5.

Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ (2007) Divergent responses of Pygoscelis penguins reveal a common environmental driver. *Oecologia*, **153**, 845–855.

Hobday AJ, Pecl GT (2013) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Reviews in Fish Biology and Fisheries*, **24**, 415–425.

Hocking PM, Rutherford KMD, Picard M (2007) Comparison of time-based frequencies, fractal analysis and T-patterns for assessing behavioural changes in broiler breeders fed on two diets at two levels of feed restriction: A case study. *Applied Animal Behaviour Science*, **104**, 37–48.

Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World's Marine Ecosystem. *Science*, **19604**, 1523–1528.

Hoskins AJ, Arnould JPY (2014) Relationship between long-term environmental fluctuations and diving effort of female Australian fur seals. *Marine Ecology Progress Series*, **511**, 285–295.

Hothorn T, Zeilis A, Farebrother RW, Cummins C, Millo G, Mitchell D (2015) Testing linear regression models versions 0.9-33.

Hull CL (2000) Comparative diving behaviour and segregation of the marine habitat by breeding Royal Penguins, *Eudyptes schlegeli*, and eastern Rockhopper Penguins, *Eudyptes chrysocome filholi*, at Macquarie Island. *Canadian Journal of Zoology*, **78**, 333–345.

Humphries NE, Queiroz N, Dyer JRM et al. (2010) Environmental context explains Levy and Brownian movement patterns of marine predators. *Nature*, **465**, 1066–1069.

Humphries NE, Weimerskirch H, Queiroz N, Southall EJ, Sims DW (2012) Foraging success of biological Lévy flights recorded in situ. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 7169–74.

Humphries NE, Weimerskirch H, Sims DW (2013) A new approach for objective identification of turns and steps in organism movement data relevant to random walk modelling. *Methods in Ecology and Evolution*, **4**, 930–938.

Hunt GL, Russell RW, Coyle KO, Weingartner T (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series*, **167**, 241–259.

Hurst HE (1951) Long-term storage capacity of reservoirs. *Transactions of the American Society of Civil Engineers*, **116**, 770–799.

Hyrenbach K, Veit R (2003) Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. *Deep Sea Research Part II: Topical Studies in Oceanography*, **50**, 2537–2565.

-I-

IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. 151 pp.

-J-

Jacox MG, Bograd SJ, Hazen EL, Fiechter J (2015) Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. *Geophysical Research Letters*, **42**, 5950–5957.

James A, Plank MJ, Edwards AM (2011) Assessing Lévy walks as models of animal foraging. *Journal of the Royal Society, Interface / the Royal Society*, **8**, 1233–47.

Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal Movements and Population-Dynamics in Heterogeneous Landscapes. *Landscape Ecology*, **7**, 63–75.

Jones ISF (1980) Tidal and wind-driven currents in Bass strait. *Australian Journal of Marine and Freshwater Research*, **31**, 109–117.

-K-

Kailola PJ (1993) *Australian fisheries resources*. Bureau of Resources Sciences and the Fisheries Research and Development Corporation, Canberra, A.C.T., 422 pp.

Kato A, Watanuki Y, Nishumi I, Kuroki M, Shaugnessy P, Naito Y (2000) Variation in foraging and parental behavior of King cormorants. *The Auk*, **117**, 718–730.

Kato A, Watanuki Y, Naito Y (2003) Annual and seasonal changes in foraging site and diving behavior in Adélie penguins. *Polar Biology*, **26**, 389–395.

Kato A, Ropert-Coudert Y, Grémillet D, Cannell B (2006) Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series*, **308**, 293–301.

Kato A, Ropert-Coudert Y, Chiaradia A (2008) Regulation of trip duration by an inshore forager, the little penguin (*Eudyptula Minor*), during incubation. *The Auk*, **125**, 588–593.

Kauffman SA, Johnsen S (1991) Coevolution to the edge of chaos: Coupled fitness landscapes, poised states, and coevolutionary avalanches. *Journal of Theoretical Biology*, **149**, 467–505.

Keane JP, Neira FJ (2008) Larval fish assemblages along the south-eastern Australian shelf: Linking mesoscale non-depth-discriminate structure and water masses. *Fisheries Oceanography*, **17**, 263–280.

Keeling RE, Körtzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. *Annual review of marine science*, **2**, 199–229.

Kembro J. M, Perillo MA, Pury PA, Satterlee DG, Marín RH (2009a) Fractal analysis of the

ambulation pattern of Japanese quail. *British poultry science*, **50**, 161–70.

Kembro JM, Marin RH, Zygadlo JA, Gleiser RM (2009b) Effects of the essential oils of *Lippia turbinata* and *Lippia polystachya* (Verbenaceae) on the temporal pattern of locomotion of the mosquito *Culex quinquefasciatus* larvae. *Parasitology Research*, **104**, 1119–1127.

Kembro JM, Flesia AG, Gleiser RM, Perillo MA, Marin RH (2013) Assessment of long-range correlation in animal behavior time series: The temporal pattern of locomotor activity of Japanese quail (*Coturnix coturnix*) and mosquito larva (*Culex quinquefasciatus*). *Physica A: Statistical Mechanics and its Applications*, **392**, 6400–6413.

Kerry K, Clarke J, Else G (1993) the Use of an Automated Weighing and Recording System for the study of the biology of Adélie penguins (*Pygoscelis Adeliae*). In: *Proceedings of the NIPR symposium in Polar Biology*, pp. 62–75.

Kiraly A, Janosi IM (2005) Detrended fluctuation analysis of daily temperature records: geographic dependence over Australia. *Meteorology and Atmospheric Physics*, **88**, 119–128.

Klomp NI, Wooller RD (1988) Diet of little penguins, *Eudyptula minor*, from Penguin Island, Western Australia. *Australian Journal of Marine and Freshwater Research*, **39**, 633–639.

Kokubun N, Takahashi A, Ito M, Matsumoto K, Kitaysky A, Watanuki Y (2010) Annual variation in the foraging behaviour of thick-billed murres in relation to upper-ocean thermal structure around St. George Island, Bering Sea. *Aquatic Biology*, **8**, 289–298.

Kooyman GL (1989) *Diverse divers. Physiology and behaviour*. Springer-Verlag, Berlin, 200 pp.

Kooyman GL (2004) Genesis and evolution of bio-logging devices: 1963--2002. *Memoirs Nat Inst Polar Res Special Issue*, **58**, 15–22.

Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*, **400**, 218–226.

Koscielny-Bunde E, Bunde A, Havlin S, Roman H, Goldreich Y, Schellnhuber H-J (1998) Indication of a Universal Persistence Law Governing Atmospheric Variability. *Physical Review Letters*, **81**, 729–732.

Kowalczyk ND, Chiaradia A, Preston TJ, Reina RD (2015a) Fine-scale dietary changes between the breeding and non-breeding diet of a resident seabird. *Royal Society Open Science*, **2**, 140291.

Kowalczyk ND, Reina RD, Preston TJ, Chiaradia A (2015b) Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia*, **178**, 967–979.

-L-

Ladd C, Jahncke J, Hunt GL, Coyle KO, Stabeno PJ (2005) Hydrographic features and seabird

foraging in Aleutian Passes. *Fisheries Oceanography*, **14**, 178–195.

Lanz E, López-Martínez J, Nevárez-Martínez M, Dworak JA (2009) Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. *California Cooperative Oceanic Fisheries Investigations Reports*, **50**, 134–146.

LaRue MA, Ainley DG, Swanson M, Dugger KM, Lyver POB, Barton K, Ballard G (2013) Climate Change Winners: Receding Ice Fields Facilitate Colony Expansion and Altered Dynamics in an Adélie Penguin Metapopulation. *PLoS ONE*, **8**, 2–8.

Lecomte VJ, Sorci G, Cornet S et al. (2010) Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 6370–5.

Lescroël A, Bost CA (2005) Foraging under contrasting oceanographic conditions: The gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series*, **302**, 245–261.

Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG (2010) Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology*, **91**, 2044–2055.

Le Vaillant M, Wilson RP, Kato A et al. (2012) King penguins adjust their diving behaviour with age. *The Journal of Experimental Biology*, **215**, 3685–92.

Le Vaillant M, Viblanc VA, Saraux C et al. (2015) Telomere length reflects individual quality in free-living adult king penguins. *Polar Biology*, **38**, 2059–2067.

Le Vaillant M, Ropert-Coudert Y, Le Maho Y, Le Bohec C (2016) Individual parameters shape foraging activity in breeding king penguins. *Behavioral Ecology*, **27**, 352–362.

Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, **412**, 816–818.

Lewis S, Grémillet D, Daunt F, Ryan PG, Crawford RJM, Wanless S (2006a) Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia*, **147**, 606–614.

Lewis S, Grémillet D, Daunt F, Ryan PG, Crawford RJM, Wanless S (2006b) Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia*, **147**, 606–614.

Lewis S, Wanless S, Elston DA et al. (2006c) Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology*, **75**, 1304–1312.

Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon M (2009) Climate-driven range extension of a sea urchin: Inferring future trends by analysis of recent population dynamics. *Global Change Biology*, **15**, 719–731.

Lyday SE, Ballance LT, Field DB, David Hyrenbach K (2014) Shearwaters as ecosystem indicators: Towards fishery-independent metrics of fish abundance in the California Current. *Journal of Marine Systems*, **146**, 109–120.

Lynch HJ, LaRue MA (2014) First global census of the Adélie Penguin. *The Auk*, **131**, 457–466.

-M-

MacArthur RH, Pianka ER (1966) On Optimal Use of a Patchy Environment. *The American Naturalist*, **100**, 603–609.

MacIntosh AJJ (2014) The Fractal Primate: Interdisciplinary Science and the Math behind the Monkey. *Primate Research*, **30**, 95–119.

MacIntosh AJJ (2015) At the edge of chaos – error tolerance and the maintenance of Lévy statistics in animal movement. *Physics of Life Reviews*, **14**, 105–107.

MacIntosh AJJ, Alados CL, Huffman MA (2011) Fractal analysis of behaviour in a wild primate: behavioural complexity in health and disease. *Journal of the Royal Society, Interface / the Royal Society*, **8**, 1497–509.

MacIntosh AJJ, Pelletier L, Chiaradia A, Kato A, Ropert-Coudert Y (2013) Temporal fractals in seabird foraging behaviour: diving through the scales of time. *Scientific reports*, **3**, 1884.

Magee SE, Neff BD, Knapp R (2006) Plasma levels of androgens and cortisol in relation to breeding behavior in parental male bluegill sunfish, *Lepomis macrochirus*. *Hormones and Behavior*, **49**, 598–609.

Makse HAHA, Havlin S, Stanley HE (1995) Modelling urban growth patterns. *Nature*, **377**, 608–612.

Mandelbrot B (1967) How Long Is the Coast of Britain? Statistical Self-Similarity and Fractional Dimension. *Science*, **156**, 636–638.

Mandelbrot BB (1977) *The fractal geometry of nature*. W.H. Freeman and Company, New York.

Mandelbrot BB, Van Ness JW (1968) Fractional Brownian motions, fractional noises and applications. *SIAM Review*, **10**, 422–437.

Mantegna RN, Stanley HE (1994) Stochastic Process with Ultraslow Convergence to a Gaussian: The Truncated Lévy Flight. *Physical Review Letters*, **73**, 2946–2949.

Mantegna RN, Stanley HE (1995) Scaling behaviour in the dynamics of an economic index. *Nature*, **376**, 46–49.

Mattern T (2001) *Foraging strategies and breeding success in the Little Penguin, Eudyptula minor: a comparative study between different habitats*. University of Otago, Dunedin, New Zealand.

Mercik S, Weron K, Burnecki K, Weron A (2003) Enigma of self-similarity of fractional Lévy stable motions. *Acta Physica Polonica B*, **34**, 3773–3791.

Meseguer-Ruiz O, Olcina Cantos J, Sarricolea P, Martín-Vide J (2016) The temporal fractality of precipitation in mainland Spain and the Balearic Islands and its relation to other precipitation variability indices. *International Journal of Climatology*.

Meyer X, MacIntosh AJJ, Kato A, Chiaradia A, Ropert-Coudert Y (2015) Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species. *Animal Biotelemetry*, **3**, 25.

Middleton JF, Arthur C, Van Ruth P et al. (2007) El Niño effects and upwelling off south Australia. *Journal of Physical Oceanography*, **37**, 2458–2477.

Montez T, Poil S-S, Jones BF et al. (2009) Altered temporal correlations in parietal alpha and prefrontal theta oscillations in early-stage Alzheimer disease. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 1614–9.

Mori Y, Boyd IL (2004) Segregation of foraging between two sympatric penguin species: Does rate maximisation make the difference? *Marine Ecology Progress Series*, **275**, 241–249.

Mori Y, Boyd IL (2014) The Behavioral Basis for Nonlinear Functional Responses and Optimal Foraging in Antarctic Fur Seals. *Ecology*, **85**, 398–410.

Morrison M, Ralph J, Verner J, Jehl J (1990) Avian Foraging: Theory , Methodology , and Applications. *Studies in Avian Biology*, **13**, 515.

Motohashi Y, Miyazaki Y, Takano T (1993) Assement of behavioral effects of tetrachloroethylene using a set of time-series analyses. *Neurotoxicology and teratology*, **15**, 3–10.

Moyes K, Morgan B, Morris A, Morris S, Clutton-Brock T, Coulson T (2011) Individual differences in reproductive costs examined using multi-state methods. *Journal of Animal Ecology*, **80**, 456–465.

-N-

Nagy KA, Obst BS (1992) Food and energy requirements of Adelie penguins *Pygoscelis adeliae* on the Antarctic peninsula. *Physiological Zoology*, **65**, 1271–1284.

Nams VO, Bourgeois M (2004) Fractal analysis measures habitat use at different spatial scales: an example with American marten. *Canadian Journal of Zoology*, **82**, 1738–1747.

Nevárez-Martínez MO, Lluch-Belda D, Cisneros-Mata MA, Pablo Santos-Molina J, De los Angeles Martínez-Zavala M, Lluch-Cota SE (2001) Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. *Progress in Oceanography*, **49**, 565–580.

Nisbet ICT, Dann P (2009) Reproductive performance of little penguins *Eudyptula minor* in relation to year, age pair-bond duration, breeding date and individual quality. *Journal of Avian Biology*, **40**, 296–308.

Norman FI, Ward SJ (1993) Foraging group size and dive duration of Adelie penguins *Pygoscelis adeliae* at sea off Hop Island, Rauer Group, East Antarctica. *Marine Ornithology*, **21**, 37–47.

Nottale L, Chaline J, Grou P (2002) On the fractal structure of evolutionary trees. In: *Fractals in biology and medicine*, Vol. 3 (eds Losa G, Merlini D, Nommenmacher T, Weibel E), pp.

247–258. Birkhäuser, Basel.

Numata M, Davis LS, Renner M (2000) Prolonged foraging trips and egg desertion in little penguins (*Eudyptula minor*). *New Zealand Journal of Zoology*, **27**, 277–289.

-O-

O'Donoghue SH, Drapeau L, Dudley SF, Peddemors VM (2010) The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *African Journal of Marine Science*, **32**, 293–307.

Oedekoven CS, Ainley DG, Spear LB (2001) Variable responses of seabirds to change in marine climate: California Current, 1985-1994. *Marine Ecology Progress Series*, **212**, 265–281.

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: *Analysis of Ecological Systems* (eds Horn DJ, Mitchell RD, Stairs GR), pp. 154–177. The Ohio State University Press, Colombus.

-P-

Paredes R, Jones IL, Boness DJ (2005) Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour*, **69**, 197–208.

Patterson TA, Parton A, Langrock R, Blackwell PG, Thomas L, King R (2016) Statistical modelling of animal movement: a myopic review and a discussion of good practice. *arXiv*, 1603.07511.

Peitgen H-O, Jürgens H, Saupe D (2004) *Chaos and Fractals*. Springer New York, New York, NY.

Pelletier L, Kato A, Chiaradia A, Ropert-Coudert Y (2012) Can thermoclines be a cue to prey distribution for marine top predators? a case study with little penguins. *PLoS ONE*, **7**, 4–8.

Pelletier L, Chiaradia A, Kato A, Ropert-Coudert Y (2014) Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia*, **176**, 399–408.

Peng CK, Buldyrev S V, Goldberger a L, Havlin S, Sciortino F, Simons M, Stanley HE (1992) Long-range correlations in nucleotide sequences. *Nature*, **356**, 168–70.

Peng CK, Buldyrev S V, Havlin S, Simons M, Stanley HE, Goldberger AL (1994) Mosaic Organization of DNA Nucleotides. *Physical Review E*, **49**, 1685–1689.

Peng C-K, Havlin S, Stanley HE, Goldberger AL (1995a) Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. *Chaos*, **5**, 82–87.

Peng C, Hausdorff J, Mietus J (1995b) Fractals in physiological control: From heart beat to gait. *Lévy Flights and Related …*.

Peng CK, Mietus JE, Liu Y et al. (2002) Quantifying fractal dynamics of human respiration: Age and gender effects. *Annals of Biomedical Engineering*, **30**, 683–692.

Peñuelas J, Sardans J, Estiarte M et al. (2013) Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Global Change Biology*, **19**, 2303–2338.

Perkiömäki JS, Mäkikallio T, Huikuri H (2005) Fractal and Complexity Measures of Heart Rate Variability. *Clinical and Experimental Hypertension*, **27**, 149–158.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pimm SL, Redfearn A (1988) The variability of population densities. *Nature*, **334**, 613–614.

Pinheiro J, Bates D, DebRoy S, Sarkar D (2015) nlme: linear and nonlinear mixed effects models version 3.1-118.

Pohlmann H, Sienz F, Latif M (2006) Influence of the multidecadal Atlantic meridional overturning circulation variability on European climate. *Journal of Climate*, **19**, 6062–6067.

Poloczanska ES, Babcock RC, Butler A et al. (2007) *Climate change and Australian marine life*, Vol. 45. 407–478 pp.

Poloczanska ES, Burrows MT, Brown CJ et al. (2016) Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, **3**, 1–21.

Pyke GH (2015) Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis. *Methods in Ecology and Evolution*, **6**, 1–16.

-R-

R Development Core Team (2016) A language and environment for statistical computing.

Rabalais NN, Díaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, **7**, 585–619.

Raichlen DA, Wood BM, Gordon AD, Mabulla AZP, Marlowe FW (2013) Evidence of Lévy walk foraging patterns in human hunter-gatherers. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 728–733.

Ramírez F, Afán I, Hobson K a. KK a., Bertellotti M, Blanco G, Forero MGM (2014) Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin. *Ecosphere*, **5**, art38.

Ramos-Fernandez G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B (2004) Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*, **55**, 223–230.

Raup DM (1986) Biological Extinction in Earth History. *Science*, **231**, 1528–1533.

Reilly P (1994) *Penguins of the world*. Melbourne: Oxford University Press, Oxford, 164p. pp.

Reilly PN, Cullen JM (1981) The Little Penguin Eudyptula minor in Victoria, II: Breeding. *Emu*, **81**, 1–19.

Reusch TBH (2014) Climate change in the oceans: Evolutionary versus phenotypically plastic responses of marine animals and plants. *Evolutionary Applications*, **7**, 104–122.

Rey AR, Pütz K, Scioscia G, Lüthi B, Schiavini A (2012) Sexual differences in the foraging behaviour of Magellanic Penguins related to stage of breeding. *Emu*, **112**, 90.

Reynolds AM (2006) Optimal scale-free searching strategies for the location of moving targets: New insights on visually cued mate location behaviour in insects. *Physics Letters, Section A: General, Atomic and Solid State Physics*, **360**, 224–227.

Reynolds a. M (2007) Avoidance of conspecific odour trails results in scale-free movement patterns and the execution of an optimal searching strategy. *Europhysics Letters (EPL)*, **79**, 30006.

Reynolds AM (2008) Deterministic walks with inverse-square power-law scaling are an emergent property of predators that use chemotaxis to locate randomly distributed prey. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, **78**, 1–5.

Reynolds AM (2009) Scale-free animal movement patterns: Lévy walks outperform fractional Brownian motions and fractional Lévy motions in random search scenarios. *Journal of Physics A: Mathematical and Theoretical*, **42**, 434006.

Reynolds AM (2010) Animals That Randomly Reorient at Cues Left by Correlated Random Walkers Do the Lévy Walk. *The American Naturalist*, **175**, 607–613.

Reynolds AM (2012) Fitness-maximizing foragers can use information about patch quality to decide how to search for and within patches: optimal Levy walk searching patterns from optimal foraging theory. *Journal of The Royal Society Interface*, **9**, 1568–1575.

Reynolds AM (2014) Lévy flight movement patterns in marine predators may derive from turbulence cues. *Proceedings. Mathematical, physical, and engineering sciences / the Royal Society*, **470**, 20140408.

Reynolds AM (2015) Liberating Lévy walk research from the shackles of optimal foraging. *Physics of Life Reviews*, **14**, 59–83.

Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, **20**, 5473–5496.

Reynolds AM, Ropert-Coudert Y, Kato A, Chiaradia A, MacIntosh AJJ (2015) A priority-based queuing process explanation for scale-free foraging behaviours. *Animal Behaviour*, **108**, 67–71.

Reynolds AM, Bartumeus F, Kölzsch A, van de Koppel J (2016) Signatures of chaos in animal search patterns. *Scientific Reports*, **6**, 23492.

Richardson AJ, Poloczanska ES (2008) Under-resourced, under threat. *Multiple values selected*, **320**, 1294–1295.

Ricklefs RE (2008) The evolution of senescence from a comparative perspective. *Functional Ecology*, **22**, 379–392.

Ricklefs RE (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences*, **107**, 1265–1272.

Ridgway KR (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters*, **34**, 1–5.

Rishworth GM, Tremblay Y, Green DB, Connan M, Pistorius PA (2014) Drivers of time-activity budget variability during breeding in a pelagic seabird. *PLoS ONE*, **9**, 1–17.

Rodary D, Bonneau W, Le Maho Y, Bost CA (2000) Benthic diving in male emperor penguins Aptenodytes forsteri foraging in winter. *Marine Ecology Progress Series*, **207**, 171–181.

Ropert-Coudert Y, Wilson R (2005) Trends and perspectives in animal- attached remote sensing. *Front Ecol Environ*, **3**, 437–444.

Ropert-Coudert Y, Sato K, Kato A, Charrassin J-B, Bost C-A, Le Maho Y, Naito Y (2000) Preliminary investigations of prey pursuit and capture by king penguins at sea. *Polar Bioscience*, **13**, 101–112.

Ropert-Coudert Y, Kato A, Baudat J, Bost CA, Le Maho Y, Naito Y (2001) Feeding strategies of free-ranging Adélie penguins Pygoscelis adeliae analysed by multiple data recording. *Polar Biology*, **24**, 460–466.

Ropert-Coudert Y, Kato A, Naito Y, Cannell B (2003) Individual Diving Strategies in the Little Penguin. *Waterbirds*, **26**, 403–408.

Ropert-Coudert Y, Wilson RP, Daunt F, Kato A (2004) Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. *Behavioral Ecology*, **15**, 824–830.

Ropert-Coudert Y, Chiaradia A, Kato A (2006a) An exceptionnally deep dive by a little penguin *Eudyptula minor*. *Marine Ornithology*, **2005**, 71–74.

Ropert-Coudert Y, Kato A, Wilson RP, Cannell B (2006b) Foraging strategies and prey encounter rate of free-ranging Little Penguins. *Marine Biology*, **149**, 139–148.

Ropert-Coudert Y, Wilson RP, Yoda K, Kato A (2007a) Assessing performance constraints in penguins with externally-attached devices. *Marine Ecology Progress Series*, **333**, 281–289.

Ropert-Coudert Y, Knott N, Chiaradia A, Kato A (2007b) How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep-Sea Research Part II: Topical Studies in Oceanography*, **54**, 415–423.

Ropert-Coudert Y, Kato A, Chiaradia A (2009) Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. *Proceedings. Biological sciences / The Royal Society*, **276**, 4105–9.

Ropert-Coudert Y, Kato A, Grémillet D, Crenner F (2012) Bio-logging: recording the ecophysiology and behavior of animals moving freely in their environment. In: *Sensors for Ecology: Towards integrated knowledge of ecosystems* (eds Le Galliard JF, Guarinia JM, Gaill F), pp. 17–41. CNRS, INEE, Paris.

Ropert-Coudert Y, Kato A, Meyer X et al. (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography*, **38**, 111–113.

Roy DB, Sparks TH (2000) Phenology of British butterfies and climate change. *Global Change Biology*, **6**, 407–416.

Russell RW, Harrison NM, Hunt GL (1999) Foraging at a front: Hydrography, zooplankton, and avian planktivory in the northern Bering Sea. *Marine Ecology Progress Series*, **182**, 77–93.

Rutherford KMD, Haskell MJ, Glasbey C, Jones RB, Lawrence AB (2003) Detrended fluctuation analysis of behavioural responses to mild acute stressors in domestic hens. *Applied Animal Behaviour Science*, **83**, 125–139.

Rutherford K, Haskell M, Glasbey C, Jones RB, Lawrence A (2004) Fractal analysis of animal behaviour as an indicator of animal welfare. *Animal Welfare*, **13**, 99–103.

Rutherford KMD, Haskell MJ, Glasbey C, Lawrence AB (2006) The responses of growing pigs to a chronic-intermittent stress treatment. *Physiology and Behavior*, **89**, 670–680.

Rutz C, Hays GC (2009) New frontiers in biologging science. *Biology Letters*, rsbl.2009.0089.

-S-

Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE*, **4**.

Sala JE, Wilson RP, Quintana F (2012) How Much Is Too Much? Assessment of Prey Consumption by Magellanic Penguins in Patagonian Colonies. *PLoS ONE*, **7**, 21–25.

Santora JA, Sydeman WJ (2015) Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. *Ecosphere*, **6**, art214.

Saraux C, Robinson-Laverick SM, Maho Y Le, Ropert-Coudert Y, Chiaradia A (2011a) Plasticity in foraging strategies of inshore birds: How little penguins maintain body reserves while feeding offspring. *Ecology*, **92**, 1909–1916.

Saraux C, Le Bohec C, Durant JM et al. (2011b) Reliability of flipper-banded penguins as indicators of climate change. *Nature*, **469**, 203–206.

Saraux C, Chiaradia A, Le Maho Y, Ropert-Coudert Y (2011c) Everybody needs somebody: Unequal parental effort in little penguins. *Behavioral Ecology*, **22**, 837–845.

Saraux C, Chiaradia A, Salton M, Dann P, Viblanc VA (2016) Negative effects of wind speed on individual foraging performance and breeding success in little penguins. *Ecological*

Monographs, **86**, 61–77.

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How Do Polar Marine Ecosystems Respond to Rapid Climate Change? *Science*, **328**, 1520–1523.

Schreer JF, Hines ROH, Kovas KM (1998) Classification of dive profiles: A comparison of statistical clustering techniques and unsupervised artifical neural networks. *Journal of Agriculture, Biological, and Environmental Statistics*, **3**, 383–404.

Schreiber EA, Burger J (2001) *Biology of marine birds* (eds Schreiber EA, Burger J). CRC Press, Tampa, 744 pp.

Seuront L (2010) *Fractals and multifractals in ecology and aquatic science*. CRC Press, Boca Raton.

Seuront L (2015) On uses, misuses and potential abuses of fractal analysis in zooplankton behavioral studies: A review, a critique and a few recommendations. *Physica A: Statistical Mechanics and its Applications*, **432**, 410–434.

Seuront L, Cribb N (2011) Fractal analysis reveals pernicious stress levels related to boat presence and type in the IndoPacific bottlenose dolphin, *Tursiops aduncus*. *Physica A: Statistical Mechanics and its Applications*, **390**, 2333–2339.

Seuront L, Hwang JS, Tseng LC, Schmitt FG, Souissi S, Wong CK (2004) Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta*. *Marine Ecology Progress Series*, **283**, 199–217.

Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology*, **17**, 66–74.

Shimada I, Kawazoe Y, Hara H (1993) A temporal model of animal behavior based on a fractality in the feeding of *Drosophila melanogaster*. *Biological Cybernetics*, **68**, 477–481.

Shimada I, Minesaki Y, Hara H (1995) Temporal fractal in the feeding behavior of D*rosophila melanogaster*. *Journal of Ethology*, **13**, 153–158.

Shlesinger MF, Klafter J, J. West B (1986) Levy walks with applications to turbulence and chaos. *Physica A: Statistical Mechanics and its Applications*, **140**, 212–218.

Simeone A, Wilson RP (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: Can we estimate prey consumption by perturbations in the dive profile? *Marine Biology*, **143**, 825–831.

Sims DW, Southall EJ, Humphries NE et al. (2008) Scaling laws of marine predator search behaviour. *Nature*, **451**, 1098–1102.

Sladen WJL (1958) The Pygoscelid penguins. *Falkland Island Dependencies survey scientific reports*, **17**, 1–122.

Sogard SM, Olla BL (1993) Effects of light, thermoclines and predator presence on vertical

distribution and behavioral interactions of juvenile walleye pollock, *Theragra chalcogramma Pallas*. *Journal of Experimental Marine Biology and Ecology*, **167**, 179–195.

Solé R V., Manrubia SC, Benton M, Kauffman S, Per B (1999) Criticality and scaling in evolutionary ecology. *Trends in Ecology and Evolution*, **14**, 156–160.

Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Wilcox C, Hindell MA (2015) Flexible foraging behaviour in a marine predator, the Masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions. *Journal of Experimental Marine Biology and Ecology*, **463**, 79–86.

Speakman JR (1997) *Doubly labelled water: theory and practive*. Springer Science & bussiness media.

Springer AM, Estes JA, van Vliet GB et al. (2003) Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12223–12228.

Stahel C, Gales R (1991) *Little Penguins: fairy penguins in Australia*. UNSW Press, Kensington.

Stanley HE, Afanasyev V, Amaral LAN et al. (1996) Anomalous fluctuations in the dynamics of complex systems: from DNA and physiology to econophysics. *Physica A*, **224**, 302–321.

Stanley HE, Amaral LAN, Canning D, Gopikrishnan P, Lee Y, Liu Y (1999) Econophysics: Can physicists contribute to the science of economics? *Physica A: Statistical Mechanics and its Applications*, **269**, 156–169.

Stroeve JC, Serreze MC, Holland MM, Kay JE, Malanik J, Barrett AP (2012) The Arctic's rapidly shrinking sea ice cover: A research synthesis. *Climatic Change*, **110**, 1005–1027.

Sugihara G, Schoenly K, Trombla A (1989) Scale invariance in food web properties. *Science*, **245**, 48–52.

Sutherland DR, Dann P (2012) Improving the accuracy of population size estimates for burrow-nesting seabirds. *Ibis*, **154**, 488–498.

Sydeman WJ, Bradley RW, Warzybok P et al. (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters*, **33**, 1–5.

Sydeman WJ, Thompson SA, Garcia-Reyes M, Kahru M, Peterson WT, Largier JL (2014) Multivariate ocean-climate indicators (MOCI) for the central California Current: Environmental change, 1990-2010. *Progress in Oceanography*, **120**, 352–369.

-T-

Takahashi A, Watanuki Y, Sato K, Kato A, Arai N, Nishikawa J, Naito Y (2003) Parental foraging effort and offspring growth in Adélie Penguins: Does working hard improve reproductive success? *Functional Ecology*, **17**, 590–597.

Taqqu MS, Teverovsky V, Willinger W (1995) Estimators for long-range dependance: an

empirical study. *Fractals*, **3**, 785–798.

Taylor RH, Wilson PR (1990) Recent increase and southern expansion of Adelie penguin populations in the Ross Sea, Antarctica, related to climatic warming. *New Zealand Journal of Ecology*, **14**, 25–29.

Taylor RP, Micolich AP, Jonas D (1999) Fractal analysis of Pollock ' s drip paintings. *Nature*, **399**, 422–423.

Thayer JA, Bertram DF, Hatch SA, Hipfner MJ, Slater L, Sydeman WJ, Watanuki Y (2008) Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1610–1622.

Thiebot J-B, Ito K, Raclot T, Poupart T, Kato A, Ropert-Coudert Y, Takahashi A (2016) On the significance of Antarctic jellyfish as food for Adélie penguins, as revealed by video loggers. *Marine Biology*, **163**, 1–8.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, **413**, 417–420.

Toscano BJ, Gownaris NJ, Heerhartz SM, Monaco CJ (2016) Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*.

Tremblay Y, Cherel Y (2003) Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Marine Ecology Progress Series*, **251**, 279–297.

Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie, Gentoo, and Chinstrap penguins at King George Island, Antarctica. *Ecology*, **68**, 351–361.

Turbill C, Ruf T (2010) Senescence is more important in the natural lives of long- than short-lived mammals. *PLoS ONE*, **5**.

Turchin P (2007) Fractal Analyses of Animal Movement: A Critique. *Landscape Ecology*, **77**, 2086–2090.

Tynan CT (1998) Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature*, **392**, 708–710.

-V-

Veit RR, McGowan JA, Ainley DG, Wahls TR, Pyle P (1997) Apex marine predator declines ninety percent in association with changing oceanic climate. *Global Change Biology*, **3**, 23–28.

Velando A, Alonso-Alvarez C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology*, **72**, 846–856.

-W-

Viswanathan GM, Afanasyev V, Buldyrev S V, Murphy EJ, Prince PA, Stanley HE (1996) Lévy flight search patterns of wandering albatrosses. *Nature*, **381**, 413–415.

Viswanathan GM, Buldyrev S V, Havlin S, da Luz MGE, Raposo EP, Stanley HE (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.

Viswanathan GM, Raposo EP, da Luz MGE (2008) Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews*, **5**, 133–150.

Viswanathan GM, da Luz MGE, Raposo EP, Stanley HE (2011) *The physics of foraging*. Cambridge University Press, Cambridge, 178 pp.

Vleck D, Vleck CM (2002) Physiological Condition and Reproductive Consequences in Ade. *Comparative and General Pharmacology*, **83**, 76–83.

Walther G-R (2010) Community and ecosystem responses to recent climate change. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2019–24.

Walther G-R, Post E, Convey P et al. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Ward TM, McLeay LJ, Dimmlich WF et al. (2006) Pelagic ecology of a northern boundary current system: Effects of upwelling on the production and distribution of sardine (*Sardinops sagax*), anchovy (*Engraulis australis*) and southern bluefin tuna (Thunnus maccoyii) in the Great Australian Bight. *Fisheries Oceanography*, **15**, 191–207.

Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 2199–2204.

Watanuki Y, Kato a, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. *Journal of Animal Ecology*, **62**, 634–646.

Watanuki Y, Kato A, Naito Y, Robertson G, Robinson S (1997) Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biology*, **17**, 296–304.

Watanuki Y, Miyamoto Y, Kato A (1999) Dive bouts and feeding sites of Adélie penguins rearing chicks in an area with fast sea-ice. *Waterbirds*, **22**, 120–129.

Wearmouth VJ, McHugh MJ, Humphries NE et al. (2014) Scaling laws of ambush predator "waiting" behaviour are tuned to a common ecology. *Proceedings. Biological sciences / The Royal Society*, **281**, 20132997.

Weimerskirch H (1998) Foraging strategies of southern albatrosses and their relationship with fisheries. In: *Albatross Biology and Conservation* (eds Roberston G, Gales R), pp. 168–179. Surrey Beatty & Sons, Chipping Norton.

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II: Topical Studies in Oceanography*, **54**, 211–223.

Weimerskirch H, Guionnet T (2002) Comparative activity pattern during foraging of four albatross species. *Ibis*, **144**, 40–50.

Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V (1997) Alternative Foraging Strategies and Resource Allocation by Male and Female Wandering Albatrosses. *Ecology*, **78**, 2051–2063.

Welcker J, Beiersdorf A, Varpe Ø, Steen H (2012) Mass fluctuations suggest different functions of bimodal foraging trips in a central-place forager. *Behavioral Ecology*, **23**, 1372–1378.

West BJ (1990) Physiology in fractal dimensions: Error tolerance. *Annals of Biomedical Engineering*, **18**, 135–149.

West BJ, Goldberger A (1987) Physiology in fractal dimensions. *American Scientist1*, **4**, 354–365.

Widmann M, Kato A, Raymond B et al. (2015) Habitat use and sex-specific foraging behaviour of Adélie penguins throughout the breeding season in Adélie Land, East Antarctica. *Movement Ecology*, **3**, 30.

Wienecke BC, Wooler RD, Klomp NI (1995) The ecology and management of Little penguins on Penguin Island, Western Australia. In: *The penguins: ecology and management* (eds Dann P, Norman FI, Reilly P). Surrey Beatty & Sons, Melbourne.

Wiens JA, Crist TO, Milne BT (1993) On Quantifying Insect Movements. *Environmental Entomology*, **22**, 709–715.

Wiens JA, Crist TO, With KA, Milne BT (1995) Fractal patterns of insect movement in microlandscape mosaics. *Ecology*, **76**, 663–666.

Williams TD, Briggs DR, Croxall JP, Naito Y, Kato A (1992) Diving pattern and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *Journal of Zoology*, **227**, 211–230.

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V, Hebblewhite M (2015) The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, **96**, 1741–1753.

Wilson R (2003) Penguins predict their own dive performance. *Marine Ecology Progress Series*, **249**, 305–310.

Wilson AJ, Nussey DH (2010) What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution*, **25**, 207–214.

Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology*, **67**, 1091–1093.

Wilson RP, Pütz K, Peters G, Culik BM, Scolaro JA, Charrassin J-B, Ropert-Coudert Y (1997)

Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin*, **25**, 101–106.

Wilson RP, Ropert-coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. 85–95.

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, **75**, 1081–1090.

Woehler EJ, Cooper J, Croxall JP et al. (2001) a Statistical Assessment of the Status and Trends of a Statistical Assessment of the Status and Trends of Antarctic and Subantarctic Seabirds. *Report on SCAR BBS Workshop on Southern Ocean seabird populations*.

Wood S (2016) Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation.

-Y-

Yamagata T, Behera SK, Luo J-J, Masson S, Jury MR, Rao SA (2004) Coupled ocean-atmosphere variability in the tropical Indian Ocean. In: *Earth's Climate* (eds Wang C, Xie SP, Carton JA), pp. 189–211. American Geophysical Union, Washington, D.C.

Yasuda I, Sugisaki H, Watanabe Y, Minobe SS, Oozeki Y (1999) Interdecadal variations in Japanese sardine and ocean/climate. *Fisheries Oceanography*, **8**, 18–24.

-Z-

Zimmer I, Ropert-Coudert Y, Poulin N, Kato A, Chiaradia A (2011a) Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: A case study on female little penguins. *Marine Biology*, **158**, 715–722.

Zimmer I, Ropert-Coudert Y, Kato A, Ancel A, Chiaradia A (2011b) Does foraging performance change with age in female little penguins (*Eudyptula minor*)? *PLoS ONE*, **6**.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

Annexes

Adélie Land
Antarctica

VII. Annexes

VII.1 Annex 1: A complete breeding failure in an Adélie penguin correlates with unusual and extreme environmental events

A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events

Yan Ropert-Coudert, Akiko Kato, Xavier Meyer, Marie Pellé, Andrew J.J. MacIntosh, Frédéric Angelier, Olivier Chastel, Michel Widmann, Ben Arthur, Ben Raymond and Thierry Raclot

Ecography

2014

DOI: 10.1111/ecog.01182

Brevia

Ecography 37: 001–003, 2014
doi: 10.1111/ecog.01182

Subject Editor: Eric Post. Editor-in-Chief: Miguel Araújo. Accepted 21 August 2014

A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events

Yan Ropert-Coudert, Akiko Kato, Xavier Meyer, Marie Pellé, Andrew J. J. MacIntosh, Frédéric Angelier, Olivier Chastel, Michel Widmann, Ben Arthur, Ben Raymond and Thierry Raclot

Y. Ropert-Coudert (docyaounde@gmail.com), A. Kato, X. Meyer, M. Pellé, M. Widmann and T. Raclot, CNRS and Univ. de Strasbourg, UMR7178, IPHC, 23 rue Becquerel, FR-67087 Strasbourg, France. – A. J. J. MacIntosh, Center for International Collaboration and Advanced Studies in Primatology, Kyoto Univ. Primate Research Inst., Kanrin 41-2, Inuyama, Aichi, 484–8506, Japan. – F. Angelier and O. Chastel, Centre d'Etudes Biologiques de Chizé, FR-79360 Villiers-en-Bois, France. – B. Arthur and B. Raymond, Inst. for Marine and Antarctic Studies, Univ. of Tasmania, Hobart 7001, Australia. BR also at: Australian Antarctic Division, Dept of the Environment, Australian Government, Channel Highway, Kingston 7050, Australia.

Among the outcomes of the drastic changes affecting the Earth's ecosystems, nothing is more telling than a complete failure in the reproductive success of a sentinel species: a 'zero' year. Here, we found that unusual environmental conditions in the Terre Adélie sector of Antarctica disrupted the breeding activity of Adélie penguins *Pygoscelis adeliae* on land – but also their foraging activity at sea – to such a degree that no chicks survived in the 2013/2014 breeding season. Uncommonly heavy precipitation for this normally dry desert killed chicks en masse, while weak katabatic winds maintained a persistent sea ice around the colony, thereby impacting chick provisioning by adults. Extreme events such as this have direct repercussions for the species in question, and may also affect the wider sea-ice dependent food web. Understanding the nature, frequency, and consequences of such events are central to the management and conservation of this remote yet crucial ecosystem.

Adélie penguins are one of the most important predators in Antarctic sea-ice ecosystems, totalling up to 3.79 million pairs (Lynch and LaRue 2014). Their foraging and breeding ecology is highly related to the status of the sea ice (Ainley 2002), and increasing (Ross Sea, Smith et al. 1999) or decreasing (Antarctic Peninsula, Wilson et al. 2001) population trends have been related to winter sea-ice conditions or occurrence of polynia in the vicinity of colonies. While the populations in the Terre Adélie sector of east Antarctica are generally increasing, the colony of ca 34 000 Adélie penguins from Pétrels Island (66°40′S, 140°01′E) has experienced a complete breeding failure for the first time since the early monitoring began in the 1950s. Not a single chick on this island survived the summer, despite a 55% hatching success (relative to e.g. a 77% hatching success and a total of 0.65 chicks per breeding pair in 2012/2013, Centre d'Etudes Biologiques de Chizé unpubl.). To put this into perspective, the lowest breeding success recorded between 1992 and 2003 on Pétrels Island before the 2013/2014 season was ca 30% in 2001 (Jenouvrier et al. 2006). Zero – or near zero – breeding success years have been reported on other high latitude species, like in black-browed albatrosses *Thalassarche melanophris* in the Sub Antarctic (Xavier et al. 2003, and papers cited therein) but they remain rare events. Similarly, such events for Adélie penguins have been recorded occasionally in other regions of the Antarctic continent (e.g. at Béchervaise Island, Irvine et al. 2000) but the causes for these events appear to be diverse according to the study site and season considered.

The year 2013 saw the greatest sea-ice extent around the Antarctic continent since 1979 (ca 19.5 million km^2 in 2013 for an 18.0–19.4 million km^2 range between 1979–2012, NOAA: < http://earthobservatory.nasa.gov/IOTD/view.php?id=82160 >), which was also observed in the Adélie Land region (IFREMER: < wwz.ifremer.fr/institut >). Monthly data from the Dumont d'Urville meteorological station (< www.antarctica.ac.uk/met/READER/ >) showed that autumn and winter 2013 were among the coldest since recording started in 1956 (Supplementary material, Appendix 1). However, the trend reversed completely in August 2013 so that air temperatures in spring and summer became warmer than usual. Perhaps more importantly, the wind direction was predominantly and unusually blowing from the east throughout the year and wind strength was low at the start of the breeding season. Normally, strong katabatic winds blow from the continent towards the north in this region, helping to push the sea ice away from the coast (Adolphs and Wendler 1995) and create access to open water, usually polynyas, which is critical to penguin breeding success (Massom et al. 1998).

Thus, in the 2013/2014 season penguins suffered from two contrasting plagues: an extensive sea-ice cover that forced them to walk more often on compact ice, hampering their efforts to forage for themselves and their

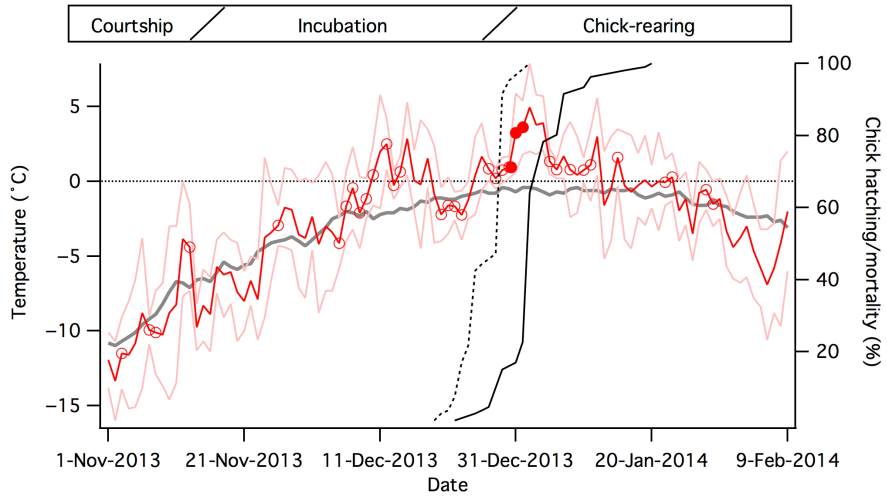


Figure 1. Daily temperature (average, maximum and minimum in red and pink lines, respectively) and snow/rainy episodes (open and filled red circles, respectively) at Dumont d'Urville during the 2013/2014 breeding season show a progressive deterioration of the weather around the turn of the year that culminated into intensive rainfall on 31 December and 1 January. Average temperature evolution over 1981–2010 is shown in grey for comparison. Finally, cumulative Adélie penguin hatching success (dotted black line) and chick mortality (solid black line) are also indicated.

chicks, and a warm and wet summer with alternating periods of snowfall and especially rain – an extremely rare feature in east Antarctica (Fig. 1). GPS devices (Cottin et al. 2012) attached to chick-rearing birds revealed that the extreme sea-ice extent affected foraging behaviour and success in a variety of ways. Penguins were forced to travel twice the distance they covered in the previous season (217.5 ± 56.1 km, n = 35 birds in 2013/2014; 117.7 ± 73.0 km, n = 38 birds in 2012/2013, student t-test t = –6.91, $p < 0.001$). Adults started their foraging trips with a lower body mass (4.0 ± 0.4 kg, n = 40 birds in 2013/2014; 4.3 ± 0.5 kg, n = 42 birds in 2012/2013, t = 3.0, p = 0.004) and they also spent longer at sea (5.3 ± 3.3 d, n = 41 birds in 2013/2014; 3.3 ± 3.7 d, n = 43 birds in 2012/2013, t = –2.60, p = 0.011). As a result, the chicks were not adequately provisioned and emaciated chicks were a common sight throughout the summer. Yet, extensive sea-ice cover was perhaps the lesser of two evils: relatively warm temperatures in the summer provoked unprecedented rainy episodes and snowmelt. Small chicks are covered with a downy plumage that has little – if any – waterproofing ability (Duchamp et al. 2002). With unusual rain in this normally dry and cold desert, the chicks' thermoregulation capacities weakened rapidly and the rainy episode that took place just around the turn of the year led to the death of 49% of the chicks in the colony we monitored (Fig. 1). The rest of the chicks were taken by starvation, additional precipitation and predators/scavengers.

This complete breeding failure was a result of multiple factors: several temporal and spatial scales need to be considered to understand its ramifications. This clearly highlights the need to monitor the breeding and foraging activity of polar species both on land and at sea simultaneously. What ecophysiological mechanisms are triggered in response to such a catastrophic year, especially at the hormonal level where the endocrine responses to stressors are known to affect foraging performances and/or parental care? Although a zero year has relatively little immediate impact on the survival of long-lived species, we can wonder how population dynamics may be affected by the absence of an entire cohort over the long term? What will be the long-term effects on other species and trophic levels of the regional ecosystem? Extreme events like those reported here are indeed likely to have direct repercussions on other levels of the sea-ice dependent food web. These fundamental questions echo those voiced at the 1st Horizon Scan (Kennicutt et al. 2014) of the Scientific Committee on Antarctic Research (SCAR). These are research priorities for SCAR, as well as for the Antarctic Treaty Consultative Meetings and the Commission for the Conservation of Antarctic Marine Living Resources, especially since predictions from the Intergovernmental Panel on Climate Change announce the coming of an era with more frequent extreme events (IPCC 2007). In this context, the recent breakdown of a giant iceberg in Antarctica and the resultant havoc it created for the ecosystem (Lescroël et al. 2014), the increasing frequency of storms and rainfall (Dee Boersma and Rebstock 2014), or the extreme event reported here bode ominously for the future of these remote and fragile ecosystems.

Acknowledgements – This project was supported by the French Polar Inst. (IPEV, prog. 1091, YR-C, and partly prog. 109, H. Weimerskirch), the WWF and the zone atelier Antarctique at CNRS. The meteorological team of TA64 at Dumont d'Urville, especially D. Lacoste, gave us access to a wealth of data. M. Bruecker, N. Chatelain and F. Crenner at the IPHC customized the GPS devices used in this study. The study was authorized by IPEV and the Terres Australes et Antarctiques Françaises through the Arrêté no. 2013-79 from the 29 October 2013.

References

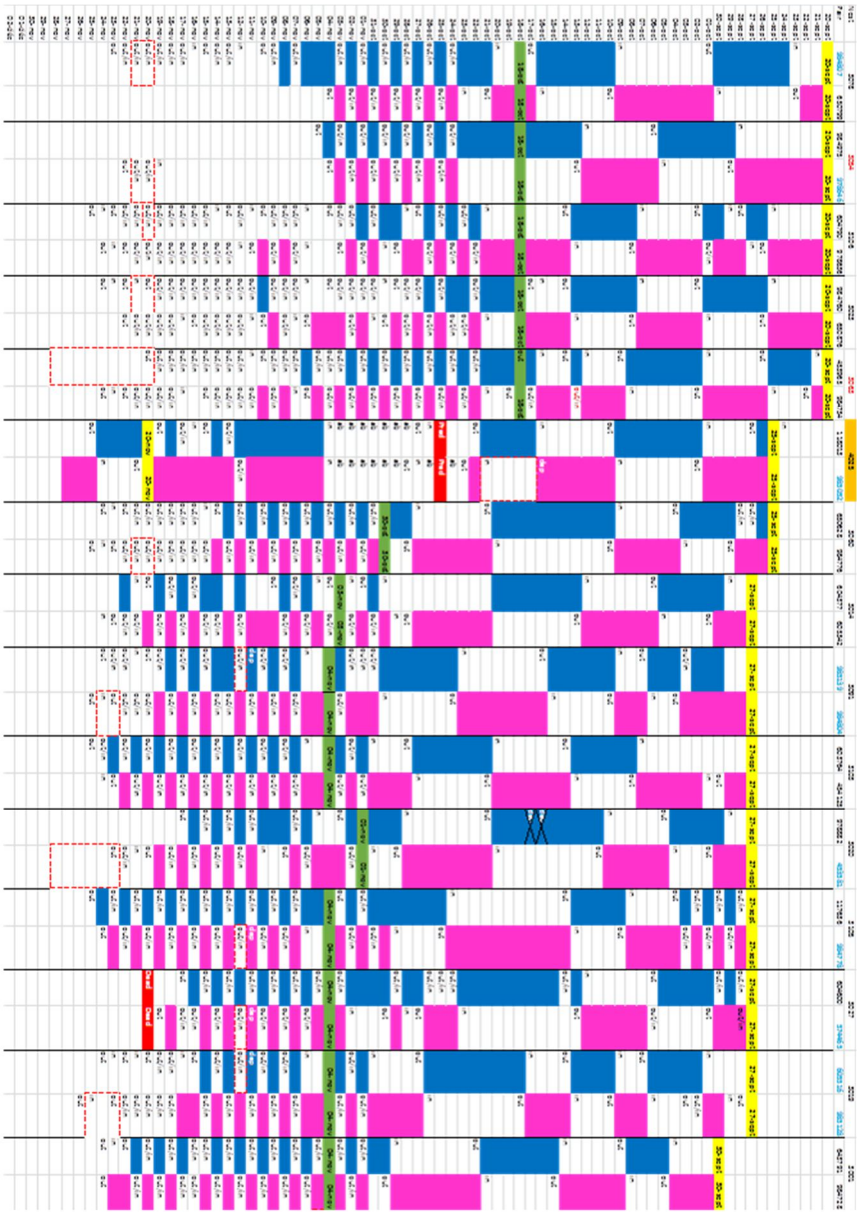
Adolphs, U. and Wendler, G. 1995. A pilot study on the interactions between katabatic winds and polynyas at the Adélie Coast, eastern Antarctica. – Antarct. Sci. 7: 307–314.

Ainley, D. G. 2002. The Adélie penguin. Bellwether of climate change. – Columbia Univ. Press.
Cottin, M. et al. 2012. Foraging strategies of male Adélie penguins during their first incubation trip in relation to environmental condition. – Mar. Biol. 159: 1843–1852.
Dee Boersma, P. and Rebstock, G. A. 2014. Climate change increases reproductive failure in Magellanic Penguins. – PLoS One 9: e85602.
Duchamp, C. et al. 2002. Ontogeny of thermoregulatory mechanisms in king penguin chicks (*Aptenodytes patagonicus*). – Comp. Biochem. Physiol. A 131: 765–773.
IPCC 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. – Cambridge Univ. Press.
Irvine, L. G. et al. 2000. Low breeding success of the Adélie penguin at Béchervaise Island in the 1998/99 season. – CCAMLR Sci. 7: 151–167.
Jenouvrier, S. et al. 2006. Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. – Polar Biol. 29: 413–423.

Supplementary material (Appendix ECOG-01182 at <www.ecography.org/readers/appendix>). Appendix 1.

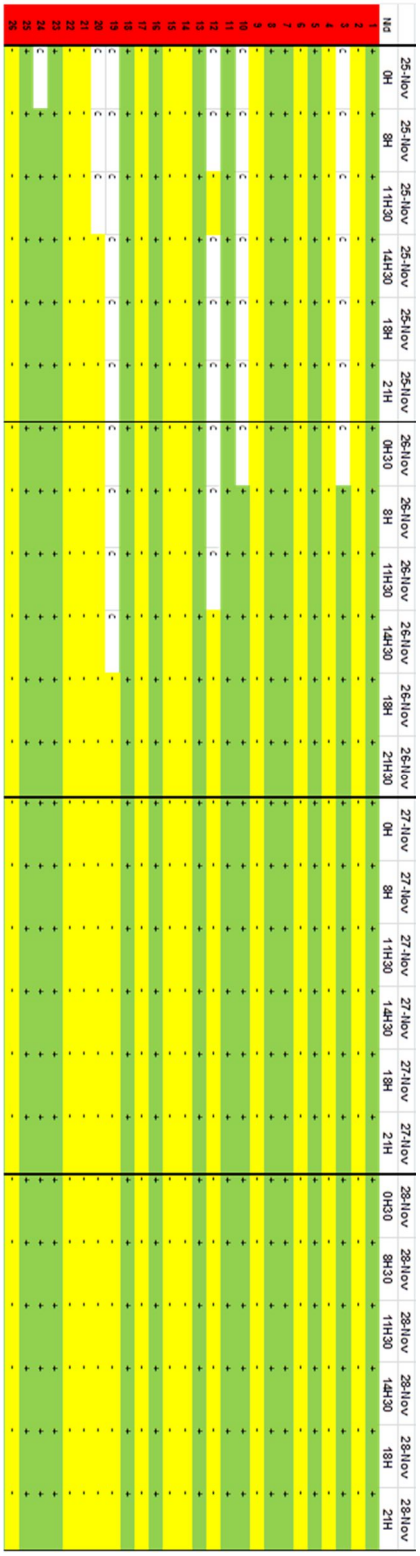
Kennicutt, M. C. I. et al. 2014. Polar research: six priorities for Antarctic science. – Nature 512: 23–25.
Lescroël, A. et al. 2014. Antarctic climate change: extreme events disrupt plastic phenotypic response in Adélie penguins. – PLoS One 9: e85291.
Lynch, H. J. and LaRue, M. A. 2014. First global census of the Adélie penguin. – Auk 131: 457–466.
Massom, R. A. et al. 1998. The distribution and formative processes of latent-heat polynyas in east Antarctica. – Ann. Glaciol. 27: 420–426.
Smith, R. C. et al. 1999. Marine ecosystem sensitivity to climate change. – BioScience 49: 393–404.
Wilson, P. R. et al. 2001. Adélie penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic circumpolar current. – Mar. Ecol. Prog. Ser. 213: 301–309.
Xavier, J. C. et al. 2003. Interannual variation in the diets of two albatross species breeding at South Georgia: implications for breeding performance. – Ibis 145: 593–610.

VII.2 Annex 2: Graphical representation of the reproductive cycle of some little penguins in the colony with data from the APMS and the visual checking of the colony.



In yellow the laying date. In colour (blue for male, pink for female) period spent in the nest by the birds. In red dotted line, bird at sea equipped by a logger.

VII.3 Annex 3: Extract from the graphical representation of the reproductive cycle of some Adélie penguins in the colony with data from visual checking of the colony.



Yellow (-) and green (+) represent members of the pair, c the time when both members of the pair were on the nest. This table is extract from the incubation period.

VII.4 Annex 4: Influence of sea-ice conditions on the diving activity of a marine predator: the Adélie penguin (*Pygoscelis adeliae*). Camille le Guen internship report (2016).

AGROCAMPUS OUEST

☐ **CFR Angers**

☑ **CFR Rennes**

Année universitaire : 2015 – 2016 Spécialité : Halieutique Spécialisation (et option éventuelle) : REA (Ressources et Ecosystèmes Aquatiques)	**Mémoire de fin d'études** ☐ d'Ingénieur de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage ☐ de Master de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage ☑ d'un autre établissement (étudiant arrivé en M2)

Influence of sea-ice conditions on the diving activity of a marine predator: The Adélie penguin (*Pygoscelis adeliae*)

Par: Camille LE GUEN

Soutenu à Rennes le 09/09/2016

Devant le jury composé de :

Président : Elodie Réveillac (Agrocampus Ouest)

Maître de stage : Yan Ropert-Coudert (CEBC)

Enseignant référent : Elodie Réveillac

Autres membres du jury :

Etienne Rivot (Agrocampus Ouest)

Marie Nevoux (INRA Rennes)

Fiche de confidentialité et de diffusion du mémoire

Confidentialité

☑ Non ☐ Oui si oui : ☐ 1 an ☐ 5 ans ☐ 10 ans

Pendant toute la durée de confidentialité, aucune diffusion du mémoire n'est possible [1].

Date et signature du maître de stage [2] : le 24/08/2016

A la fin de la période de confidentialité, sa diffusion est soumise aux règles ci-dessous (droits d'auteur et autorisation de diffusion par l'enseignant à renseigner).

Droits d'auteur

L'auteur[3] LE GUEN Camille
autorise la diffusion de son travail (immédiatement ou à la fin de la période de confidentialité)

☑ Oui ☐ Non

Si oui, il autorise

☐ la diffusion papier du mémoire uniquement(4)

☐ la diffusion papier du mémoire et la diffusion électronique du résumé

☐ la diffusion papier et électronique du mémoire (joindre dans ce cas la fiche de conformité du mémoire numérique et le contrat de diffusion)

(Facultatif) ☐ accepte de placer son mémoire sous licence Creative commons CC-By-Nc-Nd (voir Guide du mémoire Chap 1.4 page 6)

Date et signature de l'auteur :

Autorisation de diffusion par le responsable de spécialisation ou son représentant

L'enseignant juge le mémoire de qualité suffisante pour être diffusé (immédiatement ou à la fin de la période de confidentialité)

☐ Oui ☐ Non

Si non, seul le titre du mémoire apparaîtra dans les bases de données.
Si oui, il autorise

☐ la diffusion papier du mémoire uniquement(4)

☐ la diffusion papier du mémoire et la diffusion électronique du résumé

☐ la diffusion papier et électronique du mémoire

Date et signature de l'enseignant :

(1) L'administration, les enseignants et les différents services de documentation d'AGROCAMPUS OUEST s'engagent à respecter cette confidentialité. (2) Signature et cachet de l'organisme (3).Auteur = étudiant qui réalise son mémoire de fin d'études (4) La référence bibliographique (= Nom de l'auteur, titre du mémoire, année de soutenance, diplôme, spécialité et spécialisation/Option)) sera signalée dans les bases de données documentaires sans le résumé

Acknowledgements

I would like to gratefully thank my supervisor, Yan Ropert-Coudert, for allowing me to do this amazing internship with him, but also for his helpful advice and guidance. Thank you for the way you supervised me, being available when needed and always nice and full of humour. I also sincerely thank Akiko Kato, for her explanations, advice and co-supervision. It was a real pleasure to work with both of you.

I gratefully acknowledge Michael Sumner and Ben Raymond for their collaboration in data processing and analysis; and Xavier Meyer, for his help with the fractal analysis.

I would like to thank the program 1091 supported by the "Institut polaire français Paul-Emile Victor" (IPEV) and WWF that have permitted this long-term monitoring. Some data were collected through the program 137 of IPEV and through collaboration with the National Institute of Polar Research of Japan.

Thanks to Jean-Roger, Jonathan, Maxime, Quentin, Antoine, Marieke, Lauren, Domitille and Aurélie, for your support, for our board game nights, for the moments shared doing some ornithology, potery or playing tennis.

I also thank and give special recognition to my parents for supporting my projects all these years and for always being there for me.

To finish, to the birds, that made this project possible. Learning things about you is always fascinating.

Synthèse étendue

L'océan Austral fait l'objet de changements environnementaux majeurs affectant notamment la couverture de glace de mer. La formation de la glace de mer conduit au piégeage d'une quantité non négligeable de nutriments, affectant ainsi les cycles biogéochimiques (Sedwick and DiTullio, 1997; Wang et al., 2014) mais elle constitue un habitat favorable pour les microalgues, proies majoritaires du krill (Knox, 2006). Le krill étant un maillon essentiel de la chaîne alimentaire dans l'océan Austral, consommé par la plupart des meso-prédateurs, la glace de mer a donc des conséquences majeures sur le fonctionnement d'un tel écosystème, depuis les producteurs primaires jusqu'aux hauts niveaux trophiques. Pour étudier de tels écosystèmes, les oiseaux marins apparaissent comme de bons eco-indicateurs (Furness and Camphuysen, 1997; Boyd and Murray, 2001; Frederiksen et al., 2007) puisqu'ils sont relativement accessibles, qu'ils intègrent et amplifient les effets survenant aux niveaux trophiques inférieurs (Hindell et al., 2003) et qu'ils sont connus pour être particulièrement sensibles aux pressions anthropiques et aux variations environnementales (Croxall et al., 2002; Smith et al., 1999; Bost et al., 2009). De par son abondance et sa distribution circumpolaire, le manchot Adélie constitue un modèle biologique pertinent pour cette étude, suspecté d'être particulièrement touché par les changements affectant la glace de mer (Woehler and Johnstone, 1991; Ainley, 2002). Cette variable environnementale influence notamment la survie et la reproduction des oiseaux (Croxall et al., 2002; Barbraud and Weimerskirch, 2003; Gaston et al., 2005), en conditionnant la disponibilité et l'accès à la ressource et en étant à l'interface entre les colonies et les zones d'alimentation (Knox, 2006). Comprendre la relation entre la glace de mer et le succès reproducteur des manchots Adélie nécessite d'étudier l'activité de plongée des adultes puisque leur efficacité alimentaire conditionne la survie et la croissance des poussins, facteurs à l'origine du bon déroulement du cycle de reproduction (Wilson, 1995). Le stade de garde des poussins est notamment intéressant puisqu'il s'agit d'une période où les parents alternent voyages en mer et soins apportés aux poussins, et ce jusqu'à leur indépendance thermique (Ainley, 2002). A cette période, l'effort alimentaire est donc déterminé par les propres besoins énergétiques des parents et par ceux des poussins (Charrassin et al., 1998).

L'objectif de cette étude consiste à mieux comprendre comment les variations de couverture de glace de mer affectent les stratégies alimentaires des manchots Adélie. Nous nous sommes donc intéressés à l'activité de plongée d'une centaine d'individus au stade de garde de la colonie de Dumont D'Urville (Terre Adélie, Antarctique) échantillonnés sur 9 années contrastées en termes de glace de mer entre 1995 et 2014. Nous nous sommes notamment intéressés à l'existence d'une gamme optimale de couverture de glace en termes d'efficacité alimentaire et de succès reproducteur, l'objectif ultime de cette étude étant de savoir si le manchot Adélie constitue réellement un eco-indicateur pertinent concernant les changements de glace de mer, dans un contexte de changement climatique.

Pour tenter de répondre à ces questions, des données de concentration de glace de mer ont été collectées auprès de l' « Australian and Antarctic Division » (AAD) et ont permis de calculer pour chaque jour de la saison la concentration moyenne (en %) et l'étendue de glace de mer (en km^2), la distance entre la colonie et l'eau libre et celle entre la colonie et les polynies (zones libres de glace au milieu de la banquise conférant un accès à la ressource). Ces données ont pu être confrontées aux données de plongée de 121 manchots Adélie échantillonnés sur 9 années, issues du Programme 1091 soutenu par l'Institut polaire français Paul-Emile Victor et WWF). Différents paramètres de plongée ont été explorés dans cette étude tels que la profondeur maximale, le temps passé au fond, le temps de récupération ou encore le temps de descente et de remontée. L'organisation des plongées dans le temps (analyse des séquences de plongées, rythme journalier et complexité comportementale) a également pu être étudiée. En outre, nous avons intégré des données de succès reproducteur, nous permettant d'identifier les années les plus favorables, afin de mieux comprendre les mécanismes impliqués dans cette relation entre la glace de mer et l'activité de plongée.

Pour modéliser la relation entre le succès reproducteur et la glace de mer, nous avons utilisé un Modèle Additif Généralisé (GAM), permettant un ajustement souple aux données. Le GAM a révélé la présence d'un seuil de glace de mer (autour de 20%) en dessous et au-dessus duquel le succès reproducteur s'effondre, suggérant notamment l'existence d'une gamme optimale de glace pour ce trait d'histoire de vie. Deux arguments majeurs peuvent potentiellement expliquer cette tendance. D'une part, il s'avère que le krill, proie majoritaire des manchots Adélie, est peu abondant lorsque la couverture de glace est faible puisqu'il se nourrit sur des communautés vivant sous la glace (Knox, 2006; Nicol, 2006). L'efficacité alimentaire des parents est par conséquent affectée, faisant chuter le succès reproducteur. A l'inverse, lorsque la couverture de glace est très importante, les adultes doivent parcourir de longues distances pour atteindre les zones d'alimentation. L'effort à terre étant plus coûteux que l'effort en mer chez cette espèce, cela impacte la condition corporelle des parents qui doivent alors prioriser leurs propres besoins, impliquant un espacement des épisodes de nourrissage des poussins ou dans le pire des cas la désertion des nids (Davis, 1982).

Compte-tenu du lien étroit entre succès reproducteur et efficacité alimentaire (i.e. la croissance des poussins est directement dépendante du succès alimentaire des parents), nous supposions également l'existence d'un optimum de glace concernant les paramètres de plongée. La relation entre ces derniers et la glace de mer a été étudiée grâce à des Modèles Linéaires Mixtes (LMM) dans le cas d'une loi gaussienne et à des Modèles Linéaires Mixtes Généralisés (GLMM) sinon, avec un effet aléatoire placé sur l'identifiant des individus. Les résultats ont montré que les années intermédiaires en termes de conditions de glace de mer avaient des profils de plongée bien différents des autres années, marqués par des individus qui exploitent moins la phase de fond au profit des phases de descente et de remontée. En outre, ils effectuent des plongées plus profondes, nécessitant un temps de récupération plus important. Ainsi, une certaine flexibilité comportementale a pu être mise en évidence selon les

différentes conditions de glace. Lors des années extrêmes, les individus exploitent davantage la phase au fond sans pour autant que la plongée soit efficace (Viviant et al., 2016). Ces variations interannuelles peuvent éventuellement s'expliquer par des différences de qualité et/ou de quantité de proies rencontrées selon les années. Il semblerait alors que lors des années intermédiaires, les oiseaux se nourrissent sur des bancs plus gros, plus denses ou plus énergétiques (variations du ratio krill/poisson).

En parallèle, l'étude de l'organisation des plongées dans le temps a montré que lors des années intermédiaires, les individus ont un rythme d'activité plus faible, marqué par un nombre de plongées par jour et un nombre de séquences de plongées par jour (regroupement de plongées très rapprochées dans le temps) moins importants. En outre, les résultats de l'analyse jour/nuit des fréquences de plongée suggèrent un rythme de plongée plus régulier lors des années intermédiaires (plongées réparties de façon homogène tout au long de la journée); suggérant probablement un rythme d'activité moins contraint, en lien avec des conditions environnementales plus favorables. L'analyse des fractales, quant à elle, a permis de mettre en évidence une augmentation de la complexité du comportement de plongée selon un gradient décroissant de concentration de glace de mer, suggérant que lors des années de forte couverture de glace, les oiseaux sont davantage contraints dans leur comportement (révélant notamment l'importance des polynies dans ces conditions).

La confrontation des données de plongée, de succès reproducteur et de glace de mer dans une analyse à long-terme a permis de mettre en évidence des différences de stratégies alimentaires à différentes échelles (saison de reproduction, voyage alimentaire, journée, plongée). Les résultats ayant montré qu'il semble y avoir une gamme optimale de glace de mer en termes d'efficacité alimentaire et de succès reproducteur chez le manchot Adélie, cette étude fournit des arguments supplémentaires pour conforter l'idée qu'il s'agit certainement d'une bonne espèce eco-indicatrice concernant les conditions de glace. En outre, les arguments avancés n'auraient pu être possibles sans la multiplicité des approches utilisées dans cette étude. Une étude à plus long terme permettrait de mieux caractériser cette gamme optimale. En outre, il serait intéressant d'avoir plus d'informations sur les individus, notamment concernant leur efficacité alimentaire (données de condition corporelle, de régime alimentaire, de localisation avec GPS) afin de mieux comprendre les mécanismes impliqués dans cette plasticité comportementale.

Table of content

List of appendices

Glossary

Bout: sequence of multiple dives over a certain period of time.

Central-place forager: animal that must return to its central place (e.g. nest) regularly during the breeding season

Colony: large congregation of breeding birds.

Eco-indicator: indicator which refers to ecological processes and which is used to communicate information about ecosystems and anthropogenic impacts on ecosystems.

Fledging: characteristic of a chick that has grown enough to acquire its adult plumage.

Foraging: act of searching for food

Polynya: area of unfrozen sea within the ice pack.

School: aggregation of individuals with polarized orientation, all moving in the same way at the same time.

List of abbreviations

BCI: Bout Criterion Interval

CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources

DFA: Detrended Fluctuation Analysis

GAM: Generalized Additive Model

LMM: Linear Mixed Model

PCA: Principal Component Analysis

SIC: Sea-Ice Concentration

SIE: Sea-Ice Extent

TCPUE: Attempts of Catch per Unit Effort

List of figures

List of tables

1. Introduction

Marine ecosystems are experiencing different types of disturbances such as climate change, overfishing or invasion of exotic species, yet they remain understudied (Richardson and Poloczanska, 2008). If we are willing to protect marine ecosystems, it is fundamental to determine how and to what extent organisms are able to cope with environmental changes. This is especially true in polar regions, where the effects of climate change are the strongest (Clarke and Harris, 2003; Gaston et al., 2005). For instance, the Southern Ocean experiences regional changes in air and water temperatures that cause a cascade of changes in oceanic currents, water column thermal stratification and sea-ice cover, which consequently affect food availability and trophic network structure (Trathan and Agnew, 2010; Constable et al., 2014). Sea-ice dynamics are particularly important as they can affect the stability of the Antarctic ecosystem by turning from solid to liquid easily, making it more fragile. Sea ice forms at the surface once the temperature drops to the freezing point, which is about -1.9°C for a salinity of 35 (Weeks and Ackley, 1982; Ainley, 2002). During austral summer (from October to March), the -1.9°C isotherm retreats toward the pole with rising temperatures, reducing the sea-ice extent. At its maximal extent (in September), the Antarctic pack ice covers 40% of the Southern ocean (between 17.5 and 19 million square kilometres), which corresponds to 6% of the world's oceans (Ainley, 2002; Meier et al., 2013).

Sea ice has strong impacts on biogeochemical cycles and marine ecosystems (Sedwick and DiTullio, 1997; Wang et al., 2014). Sea ice removes nutrients from seawater during its formation (Wang et al., 2014) so that changes in sea-ice cover alter the nutrient cycling, inducing seasonal variations of nutrients availability (Wang et al., 2014). The Southern Ocean is considered as a High Nutrients, Low Chlorophyll area (HNLC) meaning that the concentration of nutrients is sufficient but that the primary production observed is lower than expected. Productivity is actually limited by low iron availability (Martin et al., 1990; Wang et al., 2014) and sea-ice melting represents a non-negligible iron resource (Aguilar-Islas et al., 2008). In addition, as sea ice reduces the amount of light available, limiting phytoplankton growth rate (Buckley and Trodahl, 1987; Knox, 2006), phytoplankton blooms are always observed where there is recent melting of sea ice (Smith and Nelson, 1985; Wang et al., 2014). Yet, sea ice provides a highly favourable habitat for microalgae and bacteria that are well adapted to a dynamic salinity regime and have the potential to photosynthesize even in low light conditions (Knox, 2006). As krill is known to feed on sea-ice microalgae (Brierley et al., 2002), marine predators take advantage of this association between sea ice and krill to feed on concentrated prey within a small volume (Knox, 2006). In other words, sea ice has major consequences on the Southern Ocean ecosystem structure and functioning, from grazers up to the highest trophic levels. At a time when climate is prone to abrupt changes, this ecosystem deserves a close monitoring.

However, monitoring an entire ecosystem is logistically challenging, especially in the Antarctic region. To address this difficulty, ecologists often use meso and top-predators, like seabirds and marine mammals, as eco-indicators of their ecosystem (Furness and

Camphuysen, 1997; Boyd and Murray, 2001; Frederiksen et al., 2007). Predators at high levels of the trophic network are indeed expected to integrate and amplify the effects occurring at lower trophic levels (Hindell et al., 2003). Predators have to face two major constraints: to find prey before starving and to make sure that the energetic cost of pursuit, catch and ingestion is not too high so that it, at minimum, balances the cost of acquiring the food (Sinervo, 1997). As prey distribution is often patchy, predators search for prey over extensive areas and travel long distances (Weimerskirch et al., 2005).

Seabirds are abundant wide-ranging predators (Cairns, 1987) and major consumers of marine food resources. In 2004, the annual food consumption of all the world's seabirds amounted 70 million tons, which was similar to the global fisheries landings, reaching 80 million tons the same year (Brooke, 2004). They are also widely used as environmental indicators because they are sensitive to human pressure and environmental variability (Croxall et al., 2002; Smith et al., 1999; Bost et al., 2009). Changes in sea-ice cover and distribution are major determinants of seabirds' survival and reproduction in the Southern Ocean (Croxall et al., 2002; Barbraud and Weimerskirch, 2003; Gaston et al., 2005). Sea ice is actually at the interface between nesting grounds and foraging areas (Knox, 2006), making this parameter a primary factor affecting populations (Fraser et al., 1992; Kato et al., 2002). As such, understanding the relationship between sea ice and breeding success cannot be achieved without assessing the feeding activity of parents foraging at sea (Wilson, 1995). The breeding success is indeed linked to the chick's growth, which is directly depending on the successful foraging activity of parents. This highlights the necessity to investigate the relationship between sea ice and diving behaviour. In addition, seabirds are central place foragers (Orians and Pearson, 1979) meaning that individuals return regularly to land to breed; making them easily accessible to researchers (Piatt et al., 2007). Finally, the miniaturization of electronic devices has allowed researchers to develop animal-embarked data recording loggers to track the fine-scale activity of seabirds at sea, an approach known as bio-logging (Ropert-Coudert and Wilson, 2005; Ropert-Coudert et al., 2012).

Among seabirds, penguins represent up to 90% of the total avian biomass in the Southern Ocean (Woehler, 1995; Knox, 2006; Halsey et al., 2007) and the Adélie penguin (*Pygoscelis adeliae*) is one of only two species of penguins found in Adélie land (with the Emperor penguin, *Aptenodytes forsteri*) (Woehler, 1995). They play a fundamental role in the southern part of the Southern Ocean's trophic network, with breeding adults estimated to consume 24% of the fish and 90% of the crustaceans of the area (Woehler, 1995). The biomass of Adélie penguins' prey is strongly dependent on primary production and sea-ice conditions (Jenouvrier et al., 2006). As such, and because of its abundance reaching 3.79 million of breeding pairs (Lynch and Larue, 2014) and its circumpolar distribution, the Adélie penguin appears as a relevant eco-indicator of the Southern Ocean ecosystem. This is particularly the case for marine Antarctic habitats that are sensitive to changes affecting the sea ice (Woehler and Johnstone, 1991; Ainley, 2002).

The Adélie penguin is a colonial and mainly monogamous species (Schwartz et al., 1999), which can live up to 20 years. The age of first breeding averages 5 years for females and 6.2 years for males (Ainley, 2002). The species breeds during the austral summer

(October - March), gathering in colonies located on shores around the Antarctic continent. Despite its lifespan and its abundance, the IUCN status of this species has been upgraded to Near Threatened (NT) in 2012 because its population is expected to undergo a rapid decline in the forthcoming years in relation with global change (BirdLife International, 2012). The annual cycle of Adélie penguins includes a pre-migratory phase of feeding and fattening, a spring migration towards the different colonies, nesting, and moult (Ainley, 2002) (Fig. 1).

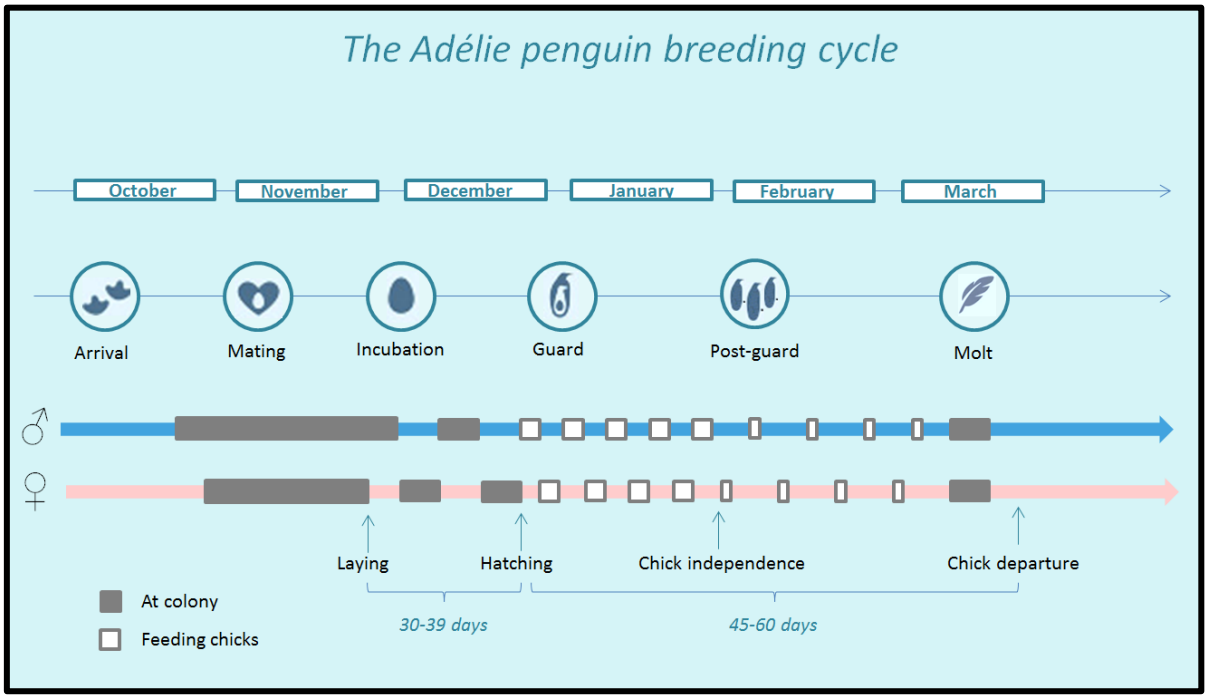


Figure 1: Illustration of the Adélie penguin's breeding cycle.

Birds arrive at their breeding sites around mid-October to form pairs (end of October – beginning of November) and build nests (Southwell et al., 2010) (Fig. 1). After laying one or two eggs, the incubation period, which ranges from 30 to 39 days for this species, follows with a single adult at a time incubating (Southwell et al., 2010; Ainley, 2002). Indeed, as soon as the second egg is laid, the female leaves the nest for the sea in order to replenish its body reserves and then return from foraging to relieve the male from its duties which in turn leaves the colony to forage (Ainley, 2002) (Fig. 1). During the whole incubation period, the eggs are alternately guarded by a single parent while the other one is at sea (Southwell et al., 2010; Ainley, 2002). Over the next stage, the « guard stage », both parents keep alternating foraging at sea with chick attendance at the nest until the chicks reach thermal independence (Ainley, 2002) (Fig. 1). Guard stage lasts 22 days on average and parents change roles every 1-3 days (Ainley, 2002). In central place foragers, such as Adélie penguins, the foraging effort at this stage is determined by the energetic requirement to forage, the energy required to restore body condition and the energy demand of the chicks (see an example for king penguins *Aptenodytes patagonicus* in Charrassin et al., 1998). As the chicks grow and their food requirements increase, both parents undertake foraging trips simultaneously. Because chicks still need protection from predators, they form groups known as crèches (Ainley, 2002) (Fig. 1). The chicks moult, fledge and leave the colony when they are around 60 days old. After

moulting, adult Adélie penguins embark on a winter migration, which takes them away from the breeding site for 8 months (Knox, 2006). With the coming of spring, birds start to migrate towards land where they will engage in a new breeding attempt.

The Adélie penguin feeds essentially on krill, a tiny shrimp living in schools (Hardy and Gunther, 1935; Stretch et al., 1988). Their main prey are the Antarctic krill (*Euphausia superba*), which is the dominant species of krill in the Southern ocean, and the ice krill (*E. crystallorophias*), but they also occasionally feed on Antarctic silverfish (*Pleuragramma antarcticum*) and jellyfish (Cherel, 2008; Libertelli et al., 2003; Croxall and Lishman, 1987; Volkman et al., 1980; Thiebot et al. 2016). Stomach content studies in Dumont D'Urville have shown that the Antarctic krill seems to occur in much lower number than the ice krill but contributed slightly more by biomass (41% vs 38%) (Ridoux and Offredo, 1989). However, this may vary annually and seasonally. Adélie penguins spend more than 90% of their time at sea (Ainley, 2002). They are visual predators, feeding as deep as the penetration of light into the water allows, but spending most of their time diving to depths considerably less than they are capable of, where there is sufficient light to be able to see their prey (Wilson, 1993). They are highly capable swimmers, with a mean swim speed measured around 2.03m/s and can reach up to 4m/s (~15.8km/h) (Ropert-Coudert et al., 2002).

The quality of a given habitat can be associated with the matching between the predators' requirements and the prey availability in terms of period, biomass and accessibility (Durant et al., 2007). In the Southern Ocean, the quality of the habitat seems to be highly correlated with the annual primary production, which is known to depend on sea-ice conditions (Quetin and Ross, 2001). In this context, studying the foraging activity, and in the case of diving predators, the diving behaviour appears to be crucial because it reflects both the availability of prey and sea-ice conditions. In addition, the use of the 3D habitat provides a better understanding of the impact of climate variability on ecosystems (Hooker and Baird, 2001; Hickmott, 2005).

Several studies have already investigated the relationship between Adélie penguins' foraging behaviour and sea ice. They all converged towards the idea that sea ice plays a fundamental role in foraging strategies and success. Habitat use in relation with sea-ice distribution was especially examined but it was exclusively spatial analyses. For example, in Widmann et al. (2015), authors have shown that in the Dumont D'Urville Sea, foraging areas could differ according to changes in sea-ice extent, highlighting the strong dependence of birds on the access to polynyas (areas of unfrozen sea within the ice pack) during guard stage. In parallel, Cottin et al. (2012) also investigated foraging strategies of Adélie penguins in relation with sea ice. Findings revealed a positive relationship between body condition and the maximum distance reached during the foraging trip, both linked to sea ice. Then, comparing two different situations enabled scientists to discover the potential impacts of differences in sea-ice conditions. In Watanuki et al. (1997), differences in at-sea behaviour (dive depth, dive duration and walking/swimming ratio) were observed between two colonies: Lützom-Holm Bay, where sea ice remained during summer and Magnetic Island, where sea ice disappeared in January. These behavioral variations probably reflect differences in the availability of feeding sites in relation to the contrasted sea-ice distributions. However, comparisons between

sites can be biased by other potential factors that can be responsible for the differences observed between two locations. Comparisons have also been done between two periods for the same colony. Indeed, binary results were obtained from Rodary et al. (2000) concerning Adélie penguins' diving behaviour in relation to sea ice at Dumont D'Urville. Authors have shown that differences in diving metrics previously occurring in different locations could also be observed for a single colony over two consecutive years. In addition, Beaulieu et al. (2010) monitored responses of Adélie penguins in terms of diving metrics, diet, foraging range and breeding success during two seasons of contrasting timing of sea-ice retreat. Findings revealed that birds seem to be able to adjust their behaviour while at-sea for survival and reproduction purposes. On the other side, in Bost et al. (2015), authors underlined that the analysis of a long-term dataset could be a powerful approach in order to identify the mechanisms involved in the relationship between environmental variables and king penguin's population dynamics. Long term studies performed on a single colony could clearly enable us to have gradations of the impact of sea ice on populations.

With the objective of understanding how sea ice influences the ecology of Adélie penguins in a context of global warming, the main research question is: How changes in sea-ice parameters affect the diving activity and the breeding success of this marine predator? At first, we were interested in investigating the effect of changes in sea-ice conditions on breeding success. Then, we examined the influence of sea ice on the diving behavior of Adélie penguins at different scales, meaning that we studied both the diving parameters and the temporal organisation of dives. To this end, we compared the breeding success and the diving behavior of chick-rearing Adélie penguins from a single colony in Adélie Land over nine austral summers with contrasted sea-ice conditions. In relation with the ecological theory, the underlying assumption that we were especially interested in was: Is there an optimal range of sea-ice cover in terms of foraging efficiency and breeding success? The ultimate aim of the present study was to investigate if Adélie penguins are relevant eco-indicators of sea ice.

2. Material and Methods

2.1. Study site and period

The study was conducted on Adélie penguins breeding near the Dumont D'Urville scientific station (66°40'S, 140°01'E), Adélie Land, Antarctica (Fig. 2) over nine austral summers (October-March) between 1995 and 2014 (Program 1091 of IPEV and WWF).

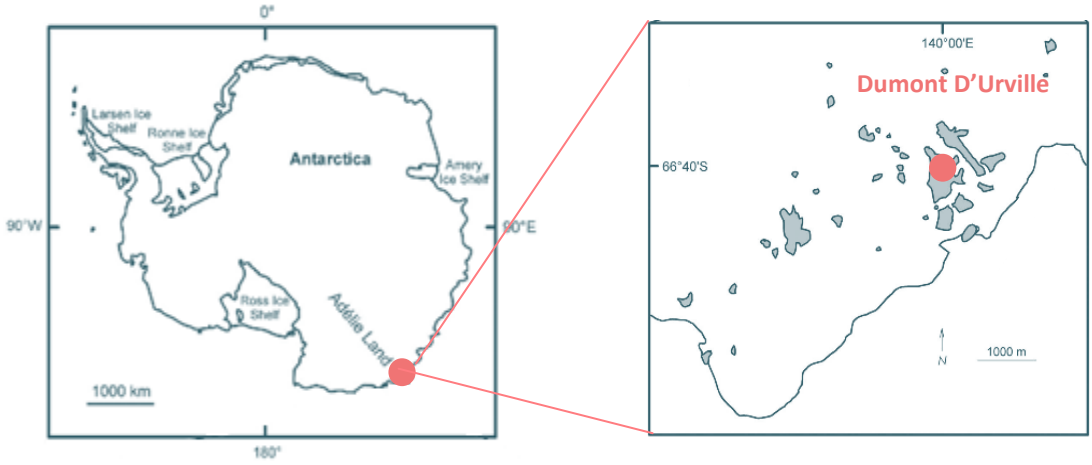


Figure 2: Location of the Dumont D'Urville scientific station, Adélie Land, Antarctica.

Three different types of data were used in this study: (i) sea-ice data, (ii) breeding success data and (iii) diving data.

2.2. Sea-ice parameters at different scales

We used satellites' passive microwaved measurements of daily sea-ice concentration (SIC) downloaded from the Australian and Antarctic Division website (https://github.com/AustralianAntarcticDivision/raadtools) to characterize the sea-ice conditions encountered by the studied individuals. Two different temporal scales were considered in this study: (i) the period concerned by diving data (daily scale) and (ii) the period corresponding to both incubation and guard-stage (global scale). As the foraging trips of Adélie penguins at the Dumont D'Urville colony extend from 63.7°S to 66.6°S and from 134.7°E to 142.3°E for the whole breeding season, corresponding to an area of 119 389 km^2 (Widmann et al., 2015; Cottin et al., 2012), we considered a slightly larger area to extract the sea-ice data at the global scale (from 62°S to 68°S, and from 134°E to 144°E). For the days concerned by diving data, a shorter area was chosen because during guard stage, the foraging extent is smaller than during incubation (Widmann et al., 2015). We defined the guard phase foraging zone as 139-141°E and 67-65.5°S. Sea-ice data were processed using the R package 'raster' (Hijmans et al., 2016) with a resolution of 25 km (Appendix I).

Basically, daily maps were created with a single value of sea-ice concentration in each cell of the raster. Sea-ice concentration describes how much percentage of a 25 km by 25 km box is covered by ice (compared to a reference established on a 1981-2010 baseline), 0% being open water and 100% full ice coverage (NSDIC, 2016). Four sea-ice parameters were calculated from these maps: the mean sea-ice concentration (SIC), the sea-ice extent (SIE), the distance between the colony and the open-water and finally the distance between the colony and the polynyas. The sea-ice extent corresponds to the total area covered by sea ice in square kilometres. For each cell, we defined a binary term according to the typical threshold of 15% chosen by NASA which determines if a cell has ice or not: pixels with more than 15% of sea-ice concentration are considered as "ice-covered" (value of 1) and pixels with less than 15% of sea-ice concentration are considered as "open water" (value of 0) (Meier et al., 2015).

Sea-ice extent was calculated by summing the area of all grid cells that contained sea ice (i.e. cells with a value of 1). In addition, the distance between the colony and the open water was also calculated using the threshold of 15%. Polynyas were defined as a cell or a group of cells with less than 15% of sea-ice concentration surrounded by cells of more than15% of sea-ice concentration. The presence of polynyas was taken into account because birds are known to rely on the opening of polynyas during chick-rearing in order to improve prey accessibility and breeding success (Kato et al., 2002;Widmann et al., 2015).

2.3. Breeding success data analysis

Breeding success data for Adélie penguins in Dumont D'Urville were provided by the Programme IPEV 109 and are available for 20 years from 1995 to 2014 (Barbraud et al., 2015). Breeding success is defined here as the ratio of the number of chicks counted in the area in February (end of the breeding season) to the number of incubating pairs in December. We investigated the relationship between Adélie penguins' breeding success and sea-ice concentration using a non-parametric smoothing regression technique. A generalized additive model (GAM) was fitted to the time series of breeding success. GAMs are the preferred approach for modelling the nonlinear relationships between predators and environmental parameters (Redfern et al., 2006). A GAM corresponds to a flexible extension of a Generalized Linear Model that can combine parametric forms along with nonparametric smoothers. Therefore, this model is more sensitive to nonlinear patterns (Wood, 2006).

In this study, the GAM was specified with a Gaussian family to investigate temporal variations in breeding success. We used the 'mgcv' package from R (version 3.2.3) to fit the GAM to our data (Wood, 2006) (Appendix II). In 'mgcv', the smooth functions are represented as spline functions (polynomial functions often used to represent smoothed and nonlinear relationships). In the present study, a cubic regression spline was used, which means that the predictor X (sea-ice parameter) is divided into a certain number of intervals and in each segment, a cubic polynomial is fitted ($Y=\alpha+\beta X+\mu X^2+\varkappa X^3$). The fitted values per interval are then joined together to create the smoothing curve. The cubic regression spline ensures that the curve will look smooth at the knots (points between intervals) using first order and second order derivatives. The problem with modelling GAMs with spline functions is to make sure that the model does not overfit but approximates the patterns in the data. Indeed, the objective is to have a smooth connection at the knots. The optimal amount of smoothing was estimated using knots recommendations from Zuur et al. (2009). Authors suggest using 3 knots if there are less than 30 observations and 5 knots if there are more than a hundred observations. In this study, the dataset was quite small (around 20 values) and the SIC values were not evenly spaced (with a lot of values between 17% and 22%). As a consequence, the model, which used 10 knots by default, placed multiple knots in this segment, tending to overfit in this region and giving a wiggly curve, which was ecologically meaningless. This is the reason why a smaller number of knots has been chosen, following Zuur et al. (2009).

2.4. Diving data collection and processing

In order to reduce the variability due to the differences in foraging strategies at the different breeding stages, we decided to focus our study to a single breeding stage. We selected the guard stage (end of December - beginning of January) because as sea ice is known to constraint birds in terms of trip duration and foraging range, the behaviour reflects local conditions. A total of 121 birds were considered in this study (Table 1).

Table 1: Number of birds studied over the nine austral summers.

Year	Males	Females	Unknown	Total
1995	8	-	-	8
1998	-	-	13	13
2001	-	-	21	21
2007	5	5	-	10
2009	5	-	-	5
2010	6	-	-	6
2011	13	-	-	13
2012	17	18	-	35
2014	5	5	-	10
Total	**59**	**28**	**34**	**121**

2.4.1. Field procedure

Diving behaviour of adult Adélie penguins was recorded by miniature data loggers attached to the birds. Birds were captured while leaving for a foraging trip and equipped with Time-Depth Recorders (TDRs). These devices record time-series of depth readings taken regularly at pre-determined intervals (1s or 5s) (Table 2) (Luque, 2007). Loggers were attached to the lower back of penguins using waterproof tape (Wilson and Wilson, 1989) except LUL type, which was attached to a leg band. After one foraging trip that lasted a few days, birds were recaptured upon their return to the colony, and the loggers were retrieved. In addition to recording depth as a function of time, TDRs also recorded water temperature data. Loggers were cylindrical or box-shaped and had different characteristics (Table 2).

Table 2: Table of loggers' characteristics.

Year	***Loggers' characteristics***				
	Logger type	Provider	Size	Sampling interval	Depth accuracy (m)
1995	mk5	Wildlife computer, USA	57*13mm	5 s	2
1998	UWE-PDT	Little Leonardo, Japan	102*20 mm	1 s	0.5
2001	M190-D2GT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2007	mk9	Wildlife computer, USA	68*17 mm	5 s	0.5
2009	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2010	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2011	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2012	M190-DT	Little Leonardo, Japan	53*15 mm	1 s	0.1
2014	LUL	IPHC, France	20*10mm	1 s	0.3

2.4.2. Extracting diving data

Upon recovery, depth data were downloaded onto a computer and analysed using IGOR Pro (WaveMetrics, 2015, Version 6.3, Oregon, USA) with the WaterSurface function of the Ethographer (Sakamoto et al., 2009). IGOR Pro is an integrated program to visualize, analyse, transform and represent experimental data (WaveMetrics 2015). Pressure transducers in TDRs may drift over time because of temperature changes, inducing deviations in recorded depth. Zero offset correction (ZOC) of the measured depth is thus required in order to remove artefacts (Luque and Fried, 2011). Identification of the points corresponding to depth of 0 m (water surface) is easy in seabirds as they must return to the surface regularly to breathe, providing a reference point for calibration (Luque and Fried, 2011).

The idea is to calculate the histogram for the raw depth data. As the data concern animals which stay at the water surface for a certain time, the mode corresponds approximately to a depth of 0 m. Then, the procedure fits a Gaussian distribution to the histogram of raw depth data and extracts the depth data in the range of mean ± 3SD, which represents water surface. The next step consists in performing a regression analysis for the extracted data in order to examine the relationship between depth and temperature, by giving the degree of temperature drift of pressure sensor (because these data points are supposed to indicate water surface). Raw data are then corrected using the regression line. To finish, the procedure updates the histogram by using the corrected depth data and fits a Gaussian distribution to the histogram again (Sakamoto, 2012). This process permits to have the dive profile of each bird (Fig. 3).

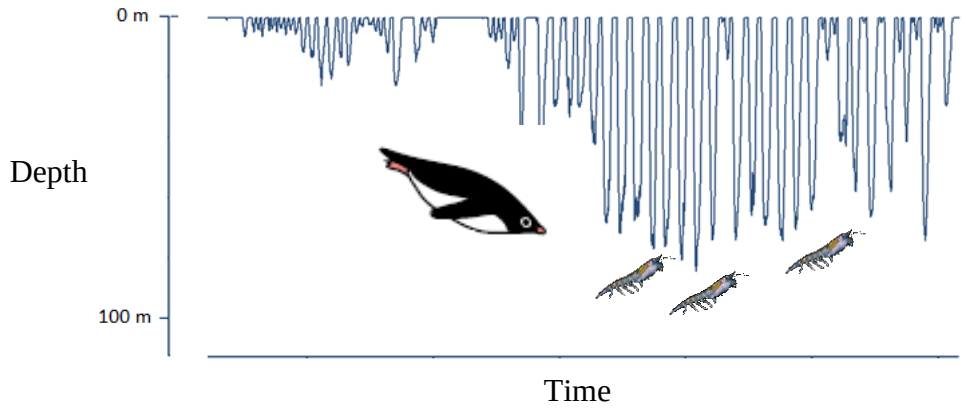


Figure 3: Diving profile of an Adélie penguin of the present study after ZOC.

2.4.3. Temporal organisation of dives : analyses of bouts, daily patterns and fractals

Marine mammals and seabirds dive in bouts, which correspond to sequences of multiple dives succeeding to each other over a certain period of time (Le Boeuf and Laws, 1994). Between two bouts, individuals can rest at the surface, on land, on sea ice or transit to other foraging areas (Le Boeuf and Laws, 1994). Bouts were defined here by a quantitative criterion based on post-dive intervals. A commonly used technique is the log survivorship analysis, which corresponds to a graphical method to specify the minimum interval separating bouts, also called the bout criterion interval (BCI) (Martin and Bateson, 1993).

Any gap less than BCI in length (short gaps) correspond to gaps between dives in a bout and all gaps greater than BCI are treated as between bouts intervals. In order to estimate the BCI, we plotted the cumulative frequency of gap lengths (surface duration) on a logarithmic scale against gap length. This technique is based on the assumption that both types of intervals are generated by two random processes with different rate constants. Basically, the log survivorship curve is supposed to have two portions: a rapidly declining part corresponding to the short gaps (between dives) and a slowly declining one representing longer gaps (between bouts). The point where these portions join can be considered as an objective quantitative criterion to specify the BCI (Martin and Bateson, 1993). To estimate the breakpoints, we used the 'segmented' package on R (Muggeo, 2015). From this bout definition, we could consider, for complete days only, the number of dives per day, the number of dives per bout, the number of bouts per day, the bout duration and the mean bottom duration per bout for each bird. Boxplots were firstly produced for each parameter of the bout analysis (number of bouts per day, number of dives per bout, mean bout duration, mean bout bottom duration, and number of dives per day). In order to compare the means for each parameter, as all samples were independent and come from normally distributed populations (Shapiro-Wilk test: p-value>0.05), Student tests were used to compare the means of each parameter knowing that samples' variances were unknown but equal (Fisher test: p-value>0.05) and Welch tests were used in case of non-equal variances. The Bonferroni correction was applied to correct the level of significance because multiple comparisons were performed simultaneously. If an experimenter wants to do n comparisons and if the desired level of significance for the entire study is α, then the Bonferroni correction tests each comparison at a significance level of α/n (Bonferroni, 1935). Performing a bout analysis over the years permits to investigate changes in the organisation of the diving activity. In addition, some bout parameters have already been related to prey patch size and density and prey encounter rates (Boyd, 1996; Sommerfeld et al., 2015). Authors assumed that the prey patch is bigger when the number of dives within a bout increases. In the same way, small distances between dives within a bout are likely to reflect a higher prey patch density and the distance between bouts (i.e. the distance between two prey patches) can be linked to the prey encounter rate of the bird (Sommerfeld et al., 2015).

In parallel, we also examined the percentage of the number of dives and the mean depth reached during the day for each year using complete days only in order to investigate day/night patterns in diving behaviour. With diel migration, krill is known to come close to the surface at night (Kalinowski and Witek, 1980). Therefore, dives might be deeper during the day if they are targeting krill in open water. So, if the birds are foraging around ice, perhaps they might show shallower dives (targeting the krill near the underside of the ice), and maybe not show so much diurnal variation in their dive depth (because they are targeting krill at relatively constant depth under ice).

In addition, we used a fractal approach to measure the temporal complexity of dive sequences in relation with sea-ice conditions as an indicator of diving performance. A fractal is defined as a phenomenon that exhibits a repeating pattern at several scales (Mandelbrot, 1977). It is different from the other geometric figures because of the way in which it scales.

When zooming in, the same pattern appears over and over again as a reduced picture of the whole and each picture is connected to it by a scaling exponent, which is not necessarily an integer. Fractals are largely used in medical sciences (lungs and heart diseases, e.g. Shlesinger and West, 1991; Peng et al., 1993), geology (coastlines and rivers, e.g. Mandelbrot, 1977; Tarboton et al., 1988), astronomy (e.g. Heck and Perdang, 1991), meteorology (clouds and thunder structures, e.g. Lovejoy, 1985), but also in biology (plants, bacteria, e.g. Smith, 1984) and in various fields of ecology (study of corals, movement ecology and organization of behaviour, e.g. Bradbury and Reichelt, 1983; Riley and Turvey, 2002; Alados and Huffman, 2000). Fractal time series analyses concerning animal behaviour aim to describe the structure of behaviour as it occurs through time (Asher et al., 2009; MacIntosh, 2014). The resulting fractal index will be linked to the complexity of this behaviour. This approach helps to understand how interactions occurring between animal's behavioural strategies and their environmental conditions lead to the emergence of observed complexity signatures, which might reflect behavioural adaptations to environmental changes (Cribb and Seuront, 2016). We assume that when the environment changes towards greater heterogeneity, flexibility appears in the patterns of behaviour inducing a greater irregularity or stochasticity. This trend could show some adaptability of foraging strategies in relation with prey availability.

Following the method described by MacIntosh et al. (2013), we used the Detrended Fluctuation Analysis (DFA) approach to measure long-range dependence as an indicator of complexity in birds' diving sequences. We performed DFA using the 'fractal' package (Constantine and Percival, 2011) in R and this has been done in five main steps (Fig. 4).

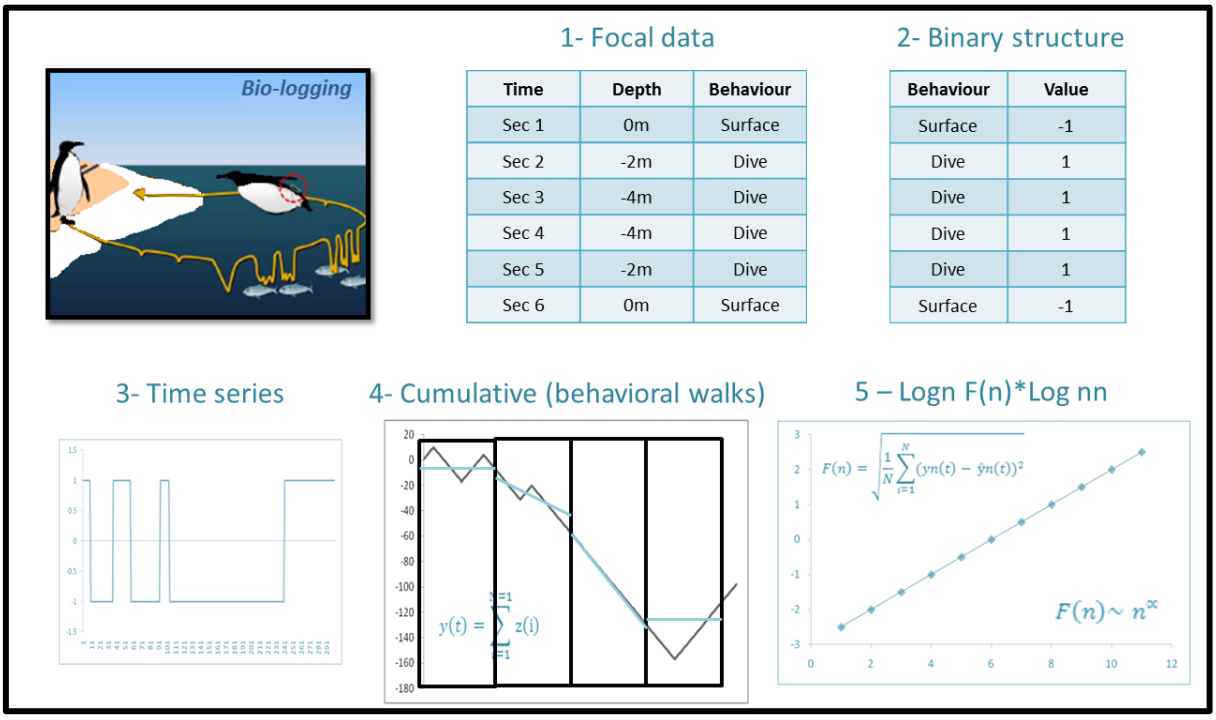


Figure 4: The calculation of the fractal index with the DFA method in five steps.

At first, dive sequences were coded as binary time series (z(i)) containing diving events (for which a value of 1 is attributed) and surface events (for which a value of −1 is attributed) (Fig. 4). Then, series were cumulatively summed (y(t)) (Fig. 4) meaning that for each second, we added +1 or -1 to the previous value. The next step consisted in estimating the scaling exponents (αDFA) of these sequences (Peng et al., 1992), which measures the degree to which time series are long-range dependent and statistically self-similar (Taqqu et al., 1995). In order to calculate this exponent, the cumulative curve of each bird was first divided into several time windows and for each segment, a local least-square regression line was fitted to the data by minimising the squared error (Fig. 4). Then the root-mean-square deviation (RMSE), the fluctuation, is calculated over each window (difference between predicted values and values actually observed). Different box sizes have been chosen and the previous process has been repeated over all window sizes. Then, a log-log graph of the fluctuation against the scale is constructed (Fig. 4). With the first scale (4s-window), the error is lower than with the next scale (8s-window) because the regression line best fits the data. This is why the relationship between the fluctuation F and the scale n is of the form: $F(n) \sim n^{\alpha}$, where α is the slope of the line on the double logarithmic plot of average fluctuation as a function of scale. When αDFA equals 0.5, this indicates a non-correlated, random sequence. As αDFA increases above 0.5, the diving sequence becomes more self-similar (indicating persistent long-range dependence) and the patterns over time are more predictable (Peng and Havlin, 1995). Theoretically, smaller values reflect greater complexity.

Values of αDFA are presented as mean ± SE and a GAM was also performed to investigate the temporal variations in αDFA. The GAM was specified with a Gaussian family and 5 knots (121 values of αDFA).

2.4.4. Analysis of the diving parameters

From the dive profile, each dive was identified and different metrics were automatically calculated with a purpose-written macro in Igor Pro, for each dive deeper than 1m. Dives were cut into a descent phase, a bottom phase, where most of the prey hunting activity is known to occur in penguins (Kirkwood and Robertson, 1997; Ropert-Coudert et al., 2000; Ropert-Coudert et al., 2006), and an ascent phase (Fig. 5). Among the parameters automatically extracted by the macro, we principally investigated dive depth and duration, the two most basic parameters to study diving behaviour (Womble et al., 2013). However, other metrics were also calculated. The number of undulations, also called wiggles, is defined as the number of vertical undulations higher than 2m. Then, the bottom phase duration corresponds to the time spent between the first and the last time the depth change rate became <0.25 m/s during a dive (i.e. the time spent between the first and last wiggle). The post dive duration was also calculated, defined as the time at the surface (Fig. 5). The number of wiggles occurring during the bottom phase can be considered as a proxy of prey pursuit (Kirkwood and Robertson, 1997; Ropert-Coudert et al., 2001; Bost et al., 2007). This metric has been linked to foraging success and mass gain for king penguins (Hanuise et al., 2010).

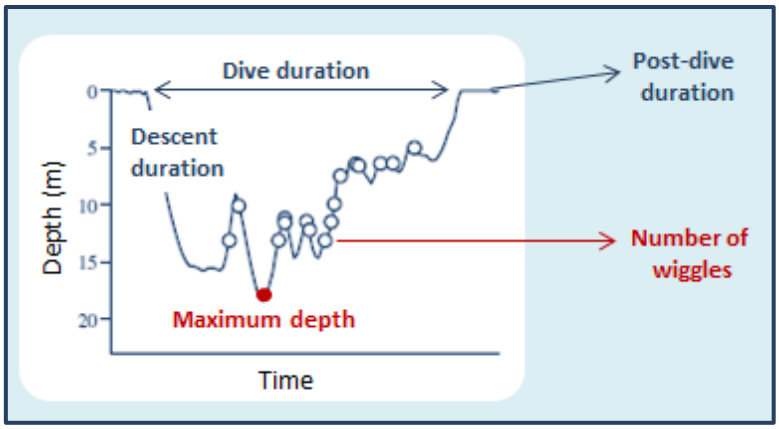


Figure 5: Presentation of the major diving metrics automatically extracted with IGOR Pro.

Indices can be developed as a combination of several of the basic, aforementioned diving metrics. A typical index, classically used in the literature, is the "diving efficiency" (Ydenberg and Clark, 1989) (Eq. 1). A second indicator was added, that we termed "TCPUE (Attempts of catch per unit effort)", corresponding to pursuits per unit effort, an index which is close to the Catch per Unit Effort often used in fisheries science (Schaefer, 1954) (Eq. 2).

$$\text{Diving efficiency} = \frac{\text{Bottom duration}}{\text{Dive duration+Surface duration}} \qquad \text{(Eq. 1)}$$

$$\text{TCPUE} = \frac{\text{Number of wiggles}}{\text{Bottom duration}} \qquad \text{(Eq. 2)}$$

At first, a Principal Component Analysis (PCA) was performed to describe the relationships among diving parameters (Zimmer et al., 2011). PCA reduces the recorded variables to fewer ones in order to investigate the effects of sea ice only on these remaining variables. PCA corresponds to a multivariate technique in which observations are described by correlated quantitative variables (Husson et al., 2009). A principal axis corresponds to a linear combination of variables built on their correlation coefficients. On the variables factor map (variables represented by arrows), when the angle between variables is 180°, they are highly and negatively correlated, when it is ± 90°, the variables are totally independent from each other and when the angle is near 0°, they are highly and positively correlated. In addition, the higher a coordinate is (the closest to the circle), the better the variable is explained by the corresponding dimension. For all axes, the quality of representation of each variable can be assessed with the $\cos^2$ values, being higher with increasing $\cos^2$ values (in absolute values) (Husson et al., 2009). Diving metrics were analysed using the R package 'FactoMineR' with the function 'PCA' (Husson et al., 2009) on a dive-by-dive basis. The first thing to do was to decide which variable would be active or supplementary. Supplementary variables don't take part in the distance calculations between individuals. They are included to illustrate the factorial axes. All the basic diving metrics were considered as active in this study as we are interested in diving profiles. The diving efficiency and the TCPUE indicators were set as supplementary variables but they indirectly take part in the construction of axes because they are a combination of basic metrics which are active. Sea-ice parameters truly constitute supplementary variables. All data were standardized because all variables were not stated in the same unit of measurement.

Then, boxplots were realized for each remaining diving parameters (maximum depth, descent rate, number of wiggles, post-dive duration, diving efficiency and TCPUE) and mean comparisons were performed using Welch tests (with the Bonferroni correction). Welch tests can also be used to compare the means of two groups under the assumption that both samples present a lot of observations (n>>100) and are random, independent and come from non-normally distributed populations (checked with a Shapiro-Wilk test). For all results, only the first trip of each bird was used and the overall significance level was set at 0.05.

In addition, linear mixed models (LMMs) were also performed on the diving metrics. The aim of a LMM is to study the connection between a dependent variable (response Y) and a set of explanatory variables (predictors X_1 .... X_k) (Eq. 3).

$$Y = X.\beta + Z.\alpha + \varepsilon \qquad \text{(Eq. 3)}$$

where Y is the response vector, X is the matrix of covariates, β is a vector of unknown regression coefficients called the fixed effects, Z is a known matrix, α is the vector of random effects, and ε is a vector of errors (Jiang, 2007). Fixed effects factors have a finite number of levels that are well represented and random effects factors correspond to factors that include data which represent only a sampling of the possible levels of the factor (Zuur et al., 2007). A mixed model combines both fixed and random effects.

LMMs are particularly useful when the data have a hierarchical form, such as in longitudinal data, involving repeated observations of the same variables over long periods of time, with the possibility to include both fixed and random coefficients together with multiple error terms (Zuur et al., 2007). Longitudinal data have a hierarchical structure that can introduce correlations for the observations within a subject. Indeed, when measures are repeated for each individual, there might be some dependence between each observation. Random effects determine the structure of these correlations. The model offers the possibility to choose between a random intercept model (same slope for all birds) or a random intercept and slope model (both can vary among birds). For all diving parameters, a random intercept and slope model was performed assuming that the relationship between each metric and sea ice is different for each bird. Therefore, the effects of sea-ice parameters on each diving parameter could have been tested including the identification number of each bird in the random effect.

Several correlation structures could have been tested for each model in relation with the idea that a dive can impact the following ones, but R memory limitations prevented us from testing this. The compound symmetry and the first order auto-regressive (AR1) structures could have been chosen here, even if the first order auto-regressive structure seems more adapted to longitudinal data (Zuur et al., 2007). Compound symmetry refers to a special case of a variance covariance matrix (uniform correlation), assuming constant variance and that all within-subjects correlations are equal, and the AR1 structure is a model in which we use a linear model to predict the value at the present time using the values at previous time points: x(t)= phi1*x(t-1) + delta + w (Appendix III).

When data were normally distributed, which was the case for most of the metrics, the estimation of the different parameters was done using the Maximum Likelihood method (ML) and the Restricted Maximum Likelihood method (REML). The method adopted here was: (i) search for the optimal random structure between a random intercept model or a random slope and intercept model (using the AIC criterion to compare models fitted on the same data) (ii) select the optimal fixed components (sea-ice variables) to consider in the model using the AIC criterion with the ML method (iii) present the estimated parameters and other results of the optimal model using the REML method. For mixed models, the R^2 can be divided in two components. The marginal R^2 (R^2m) describes the proportion of variance explained by the fixed factor(s) and the conditional R^2 (R^2c) the one explained by both the fixed and random factors. When data were not normally distributed (Generalized Linear Mixed Models GLMMs), we performed models using the Bobyqa optimizer. LMMs were performed using the lme function of the R package 'nlme' (Pinheiro et al., 2016) (Appendix IV).

Diving efficiency, descent rate and TCPUE were analysed in a LMM with a normal error distribution. To test for differences in the maximum depth and the post-dive duration between sea-ice conditions, a LMM with log10 transformed response values was applied. The number of wiggles was analysed in a GLMM with a Poisson error distribution.

2.4.5. Methodological comments on diving data

It is necessary to note the differences in sampling interval of the loggers used (5s in 1995 and 2007 and 1s for all other years) (Table 2). These differences introduce a bias in the analysis of the diving parameters, above all those that are using durations in their calculation. Measuring one value every 5s instead of 1s implies that the very short and very shallow dives are missed.

Because some analyses might not be reliable for these two years, we chose to adjust the protocol for each analysis. Two main options were adopted: (i) exclude 1995 and 2007 from the analyses and (ii) keep 1995 and 2007 in the dataset but only select the deep dives (>15m deep) because the diving parameters won't be too much affected by the differences in sampling interval for these dives. This 15 meters threshold was extracted from the dive depth – dive duration graph applied to all years. The cloud of points has two main portions and the technique assumes that deep dives (i.e. foraging dives) and surface dives (i.e. transit or resting dives) emerge from different processes.

This strategy to try both methods has been applied for all the diving metrics' analysis and the day/night patterns. The influence of different sampling intervals has been shown to have little, if no, influence on the DFA analysis (Macintosh et al., 2013). This is the reason why all years (9 years) have been considered in the fractal analysis (complexity of behavior). For the bout analysis, because considering deep dives only has no sense (just like for the fractals), the choice has been made to exclude 1995 and 2007 from the analysis. Options chosen for each analysis are presented in Table 3.

Table 3: Presentation of the methods chosen for each analysis.

Data	Analysis	Comments
Breeding success	**GAM**	-
Diving metrics	**PCA (variables selection)**	7 years all dives and 9 years deep dives
	Exploratory graphs	7 years all dives and 9 years deep dives
	Mean comparisons	7 years all dives and 9 years deep dives
	Mixed models	7 years all dives and 9 years deep dives
Fractals	**DFA**	9 years all dives (not biased)
Bout analysis	**Exploratory graphs**	7 years all dives
	Mean comparisons	7 years all dives
Day/night patterns	**Exploratory graphs**	7 years all dives and 9 years deep dives

3. Results

3.1. Temporal dynamics of sea ice in the Dumont D'Urville Sea

In this section, the different sea-ice conditions over the years will be examined. Sea-ice concentration changed drastically among years but also within year. A season starting with heavy ice can end up with no ice, which was for instance the case of the season 1995-1996 (Fig. 6).

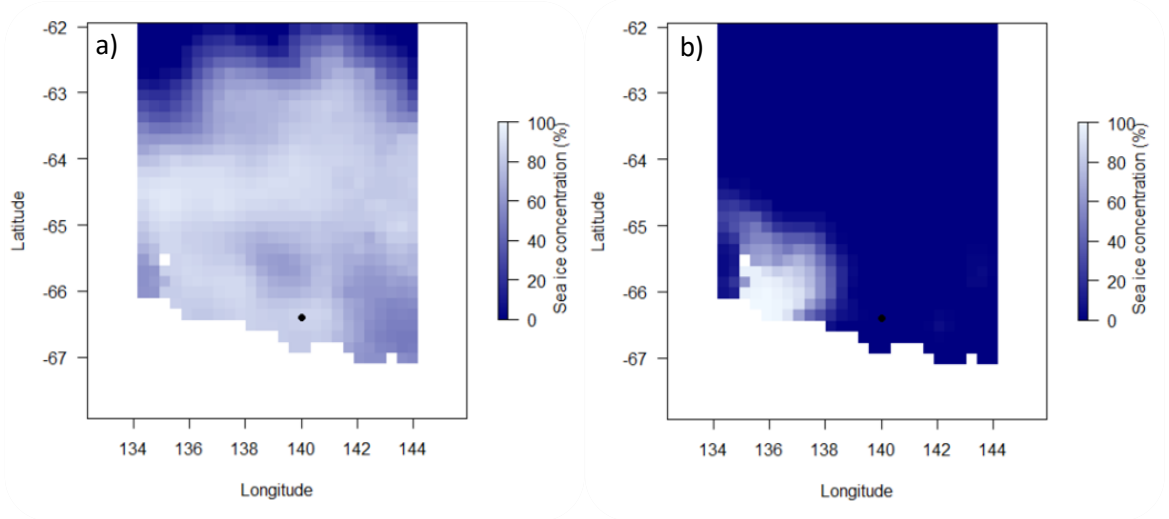


Figure 6: Maps of sea-ice concentration in the Dumont D'Urville area for two different days within the same season 1995-1996: a) 01/11/1995 and b) 31/01/1996. White represents sea ice and dark blue represents open water.

Daily sea-ice concentrations and sea-ice extents concerning the days when diving data were recorded showed very contrasted conditions among years (Fig. 7a). The evolution of the distance between the colony and the open water shows how far the ice edge was at the beginning of each season and how it decreased differently during the summer for each year (Fig. 7b).

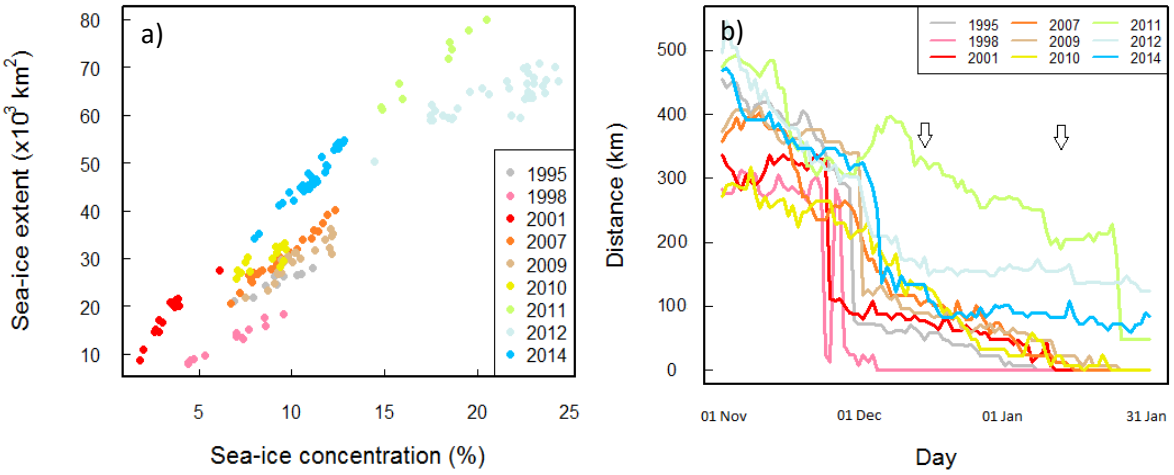


Figure 7: Sea-ice parameters over the years concerning a) the relationship between sea-ice extent (km^2) and sea-ice concentration (%) and b) the evolution of the distance colony-open water over the season (diving data concerning guard stage are available for the period between the two arrows).

The first graph permits to identify 1998 and 2001 as low sea-ice coverage years. In contrast, 2011 and 2012 were considered as years of high sea-ice coverage (Fig. 7a) with open water being far from the colony over the whole seasons (Fig. 7b). For all years, sea-ice concentration was strongly correlated with sea-ice extent (R^2 between [0.508, 0.976], p-value < 2.10^{-16}) (Table 4).

Table 4: Correlation parameters of the relationship between SIE and SIC for all years.

Year	*SIE vs SIC (SIE=a*SIC+b)*			
	B	A	R^2	p-value (t)
1995	9740.38	1660.99	0.885	< 2e-16
1998	-834.11	2038.79	0.976	< 2e-16
2001	3560.00	4322.10	0.913	< 2e-16
2007	2065.50	2989.97	0.964	< 2e-16
2009	5718.00	2336.00	0.742	< 2e-16
2010	14123.40	1840.80	0.627	< 2e-16
2011	11508.12	3353.85	0.966	< 2e-16
2012	37452.00	1262.00	0.508	< 2e-16
2014	-3571.5	4514.7	0.908	< 2e-16

This strong positive relationship was observed only for these two sea-ice parameters. When the distance between colony and open water or polynyas was involved, the relationship was not that strong. Five polynyas were identified over the years. However, the resolution did not enable us to detect smaller polynyas that could be close to the colony, which could potentially contribute to the food availability of Adélie penguins.

3.2. Inter-annual variations in breeding success in relation with sea ice

For the whole period of interest (1995-2014), breeding success values were highly contrasted, ranging from 0 in 2013 to 1.336 in 1995. However, two seasons were very specific and deserved a closer inspection. The breeding season 2014 had intermediate sea-ice

concentration values but in January/February, sea ice took a long time to retreat. The distance between the colony and the open water was still around a hundred kilometers at the end of January (Fig. 7 b). In addition, there were a lot of snow events in December and only few sunny days (Reports from the overwintering teams of the Terres Australes et Antarctiques Françaises). All this can explain the relatively low breeding success in 2014 (around 0.3). Therefore, a generalized additive model (GAM) was fitted to the time series of breeding success with and without 2014 (Fig. 8 a and b). In addition, the low sea-ice value in 2001 resulted from the unusual presence of a huge iceberg in the Ross Sea, covering 11 000 km^2, that clearly affected Adélie penguins. As such, a GAM was also performed with and without 2001 because adding or not this year clearly changed the shape of the GAM (Fig. 8 a and c). Naturally, the model excluding both years (2001 and 2014) has also been done (Fig. 8 d).

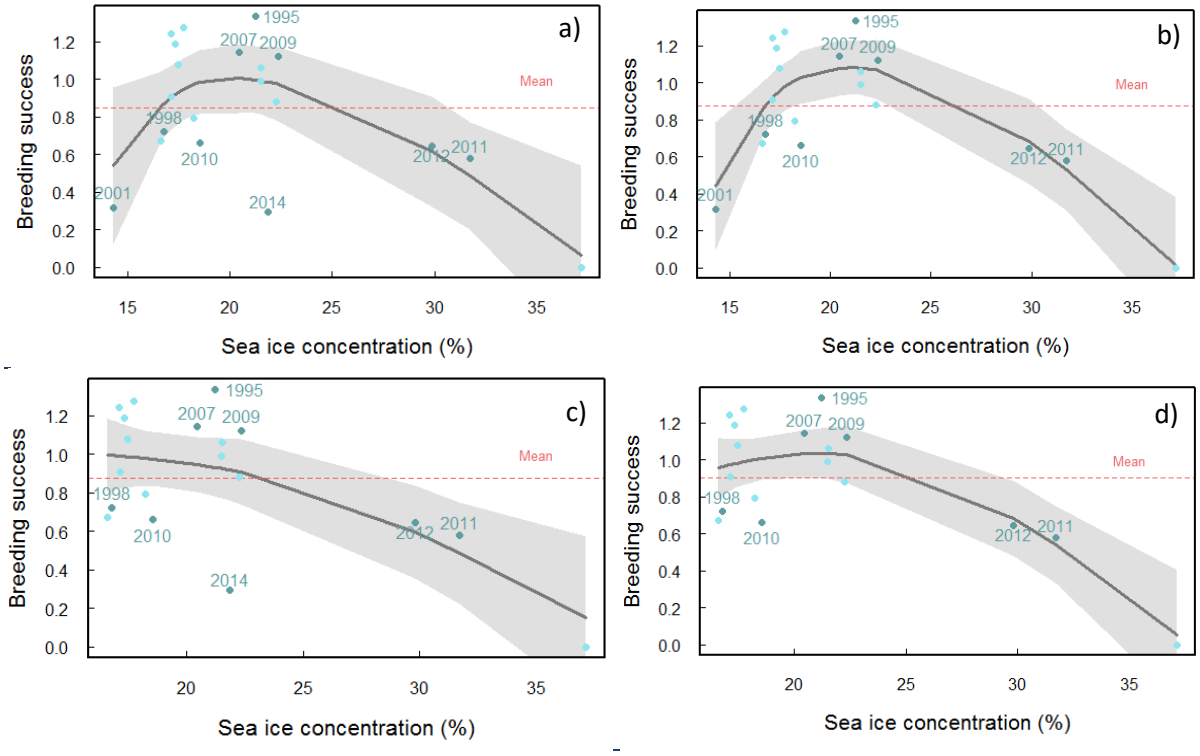


Figure 8: Fitted GAMs results concerning Adélie penguins' breeding success showing: a) the GAM fitted on all years, b) the GAM fitted on all years except 2014, c) the GAM fitted on all years except 2001 and (d) the GAM excluding both 2001 and 2014. Shades indicate 95% confidence intervals. Dark dots represent the studied years and light dots correspond to added data concerning the period of interest 1995-2014.

The effect of sea-ice concentration was significant for all models. The model excluding 2014 had the best fit (Adjusted R^2 = 0.643, p-value < 0.001) (Fig. 8 b; Table 5). In addition, the model including all years had nearly the same shape (Adjusted R^2 = 0.426 and p-value = 0.0119) (Fig. 8 a; Table 5). In contrast, the model excluding 2001 showed the lowest adjusted R^2 value (Adjusted R^2 = 0.395; p-value < 0.01) (Fig. 8 c; Table 5). The trend of this GAM suggests that the curve we observed with the two previous models is driven by a single point on the bottom-left corner, corresponding to the year 2001. Finally, the model excluding all years gives nearly the same shape (Adjusted R^2 = 0.596; p-value < 0.001) (Fig. 8 d; Table 5).

Table 5: Results of fitted GAMs on breeding success.

GAM (5 knots)	*Gam fitted on breeding success*		
	F-test	Adjusted R^2	p-value
All years	4.99	0.426	0.012
Without 2014	10.12	0.643	$4.12*10^{-4}$
Without 2001	5.71	0.395	$9.58*10^{-3}$
Without 2001 and 2014	11.48	0.596	$5.91 * 10^{-4}$

3.3. Influence of sea ice on the diving activity

3.3.1. Modifications in diving rhythm

In total, the first trip of each bird across all years amounted to 180 000 dives being analysed. Investigating the effects of sea ice on the organisation of dives appears as the first step of the diving activity analysis. It concerns here the complexity of the behavior (at the scale of the foraging trip), the bout analysis (sequences of successive dives) and the organisation of dives during the day. Birds were expected to differ in temporal organisation of foraging behavior according to changes in the environment between years (Fig. 9).

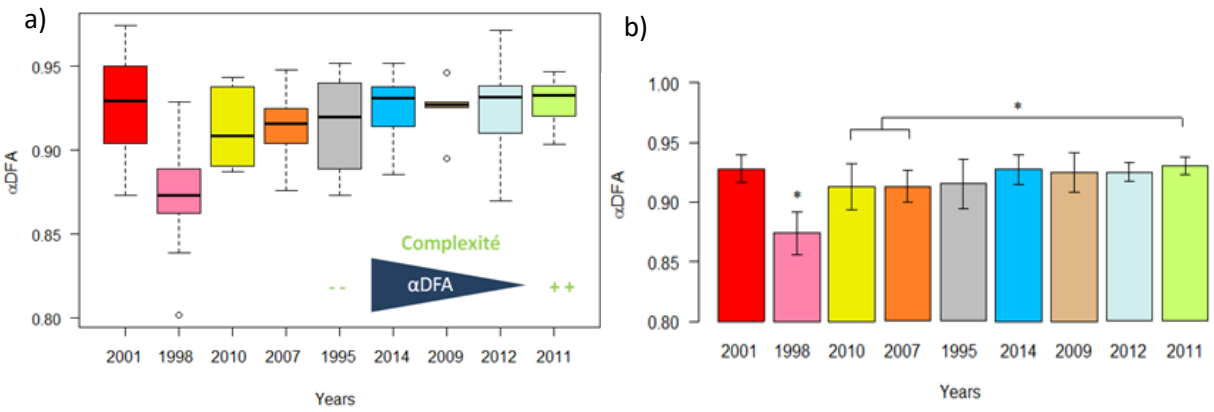


Figure 9: Results of the fractal analysis performed on all years considering all dives: a) boxplots of αDFA according to years classed by increasing sea-ice concentration and b) barplot for mean comparisons (t-test). Vertical bars height corresponds to the mean. Results are given for 9 years considering all dives.

Except for the year 2001, αDFA increases along the sea-ice concentration gradient, revealing a decrease in the complexity of the diving behavior (Fig. 9 a and b). In other words, diving sequences were characterized by higher degrees of long-range dependence when the sea-ice cover was important (i.e. dive and post-dive times of a given length are more likely to be followed by dive and post-dive times of a similar length). The highest value recorded was attributed to 2011 (0.9300 ± 0.0036) and the lowest one to 1998 (0.8739 ± 0.0090). The year 2001 presents values that significatively depart from this trend (0.9280 ± 0.0058) (t-test: p-value < 0.001) considering the low sea-ice concentration for this year. The global trend observed has been confirmed by the GAM performed on αDFA values (Fig. 10).

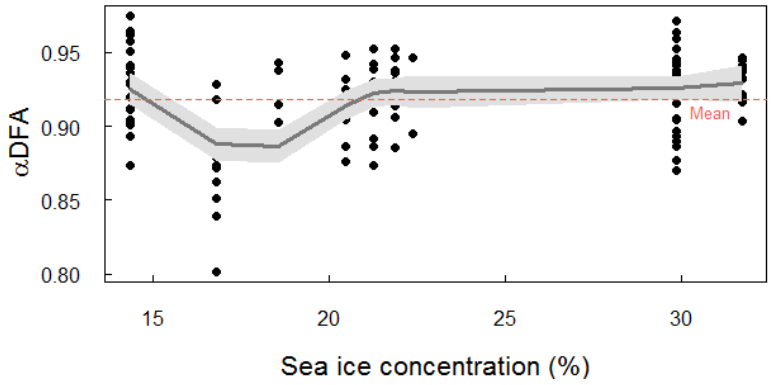


Figure 10: GAM performed on αDFA values according to sea-ice concentration concerning all years.

Results have shown that the effect of sea-ice concentration is significant (F-test=10.09, Adjusted R^2=0.322, p-value <0.001). Findings confirm the increase in αDFA from the year 1998 (around 17% of SIC) and the presence of high values for the year 2001 (around 14.30% of SIC).

Concerning the bout analysis, a total of 3310 bouts were identified over the nine years, according to the BCI values, which are ranged between 168.2s and 247.5s. Years with intermediate sea-ice concentrations, i.e. around 20%, were characterized by lower number of dives per day and lower number of bouts per day (Student test: p-value > 0.05) (Fig. 11).

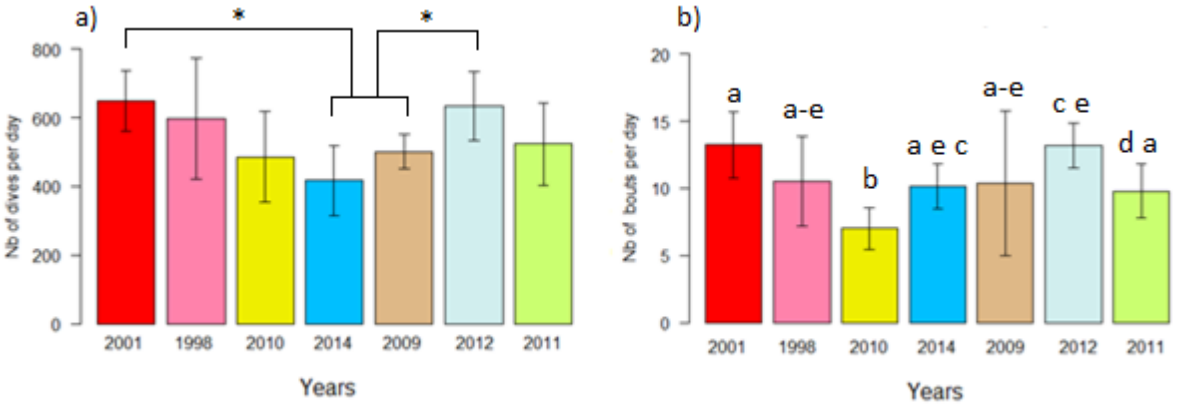


Figure 11: Barplots of a) the number of dives per day and b) the mean number of bouts per day, according to years classed by increasing sea-ice concentration. Vertical bars height corresponds to the mean. Results are given for 7 years considering all dives.

Concerning the number of dives per day, 2001 and 2012 showed the highest values (with 649.91 ± 43.93 and 633.70 ± 50.33, respectively). The lowest number of dives per day was attributed to the year 2014 (417.22 ± 50.76). For the number of bouts per day, 2001 and 2012 possessed the most elevated values (with 13.22 ± 1.23 and 13.18 ± 0.85, respectively) and the year 2014 showed the lowest value (6.99 ± 0.78). Concerning the number of dives per bout, some differences between years were significant but the trend observed is difficult to describe. However, no trend was observed for the bout duration and the bout bottom duration.

Finally, concerning the day/night analysis, during intermediate years (2007, 1995 and at a lesser extent 2014), birds performed dives at any time of the day, i.e. dives were homogeneously distributed over 24 hours (Appendix V). In addition, in 2011 and 2012 (years

of extreme sea-ice cover), birds dove deeper during night time (between 1900 and 0400 hours) but it was not statistically tested. In contrast, no daily pattern in dive depth was found for birds during years of low SIC and intermediate years. For deep dives (i.e. foraging dives), we observed that during intermediate sea-ice conditions, birds also dove at any time of the day. In contrast, for extreme sea-ice conditions, more foraging dives were performed during night time (Appendix V). However, no daily pattern was observed for maximum depth considering deep dives.

3.3.2. Variations in diving metrics

The next step consisted in analysing the diving metrics. Results of the PCAs performed on the diving metrics are given in Fig. 12.

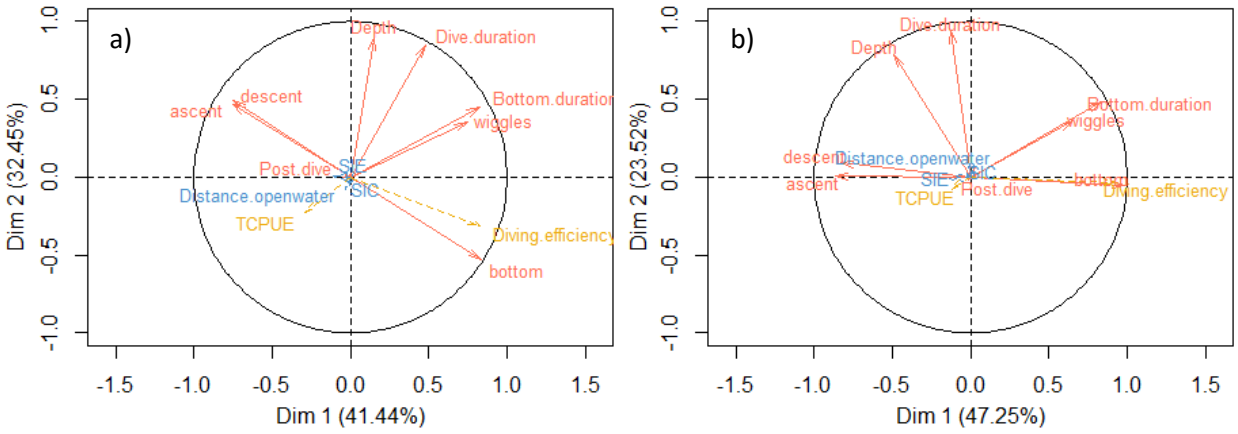


Figure 12: Variables factor maps of the PCAs performed on diving parameters for (a) 7 years all dives and (b) 9 years deep dives. Orange variables correspond to active variables; yellow variables refer to supplementary variables and the blue ones to supplementary sea-ice parameters.

Concerning the PCA performed on 7 years with all dives, the eigenvalues indicated that the first two axes accounted for 73.9% of the total variance, while the PCA performed on all years with deep dives only, the first two axes accounted for 70.77% (Fig. 12 a and b). As both PCAs gave similar results, the choice has been made to present the detailed results for the first PCA only (made on 7 years only). The bottom duration, the percentage of the bottom duration and the number of wiggles were the parameters the most involved in the construction of the first axis, with 0.83, 0.82 and 0.75 correlation coefficients respectively; accompanied by the percentages of the descent and ascent phases on the left side, presenting a correlation coefficient of 0.75 each. The parameters the most correlated to the second axis were the maximum depth and the dive duration, with a coefficient of correlation of 0.90 and 0.85, respectively. In addition, according to the length of arrows, the diving efficiency was quite well represented compared with the TCPUE (cos^2=0.688 and cos^2=0.086, respectively). The individuals showing higher diving efficiencies corresponded to birds that spent long periods at the bottom phase of dives, with a lot of wiggles, which is reflecting the way the diving efficiency is calculated (Eq. 1). On the opposite, TCPUE was associated with a lower number of wiggles and higher descent and ascent rates. Using the results of the PCAs (i.e. considering all correlation coefficients), some relevant metrics were chosen on an ecological basis to

investigate the effects of a sea ice only on these remaining variables. All further analyses were therefore conducted on the following selected variables only: maximum depth, number of wiggles, post-dive duration and descent rate, as well as diving efficiency and TCPUE. An example of a strong correlation between two variables is given for the relationship between dive depth and duration, for which a linear model was fitted for each year (p-values< 2.10^{-16}; R^2>0.685) (Appendix VI).

Then, an exploratory analysis was performed on this selection of variables in order to link the diving metrics with sea ice. The majority of dives were shallower than 5 meters and the maximum dive depth recorded was 139.7 meters. Results are indeed given for mean number of wiggles, mean of maximum depth, mean post-dive duration, percentage of descent phase duration, diving efficiency and TCPUE for both options : (i) considering 7 years with all dives (Fig. 13) and (ii) considering 9 years with deep dives only (Fig. 14).

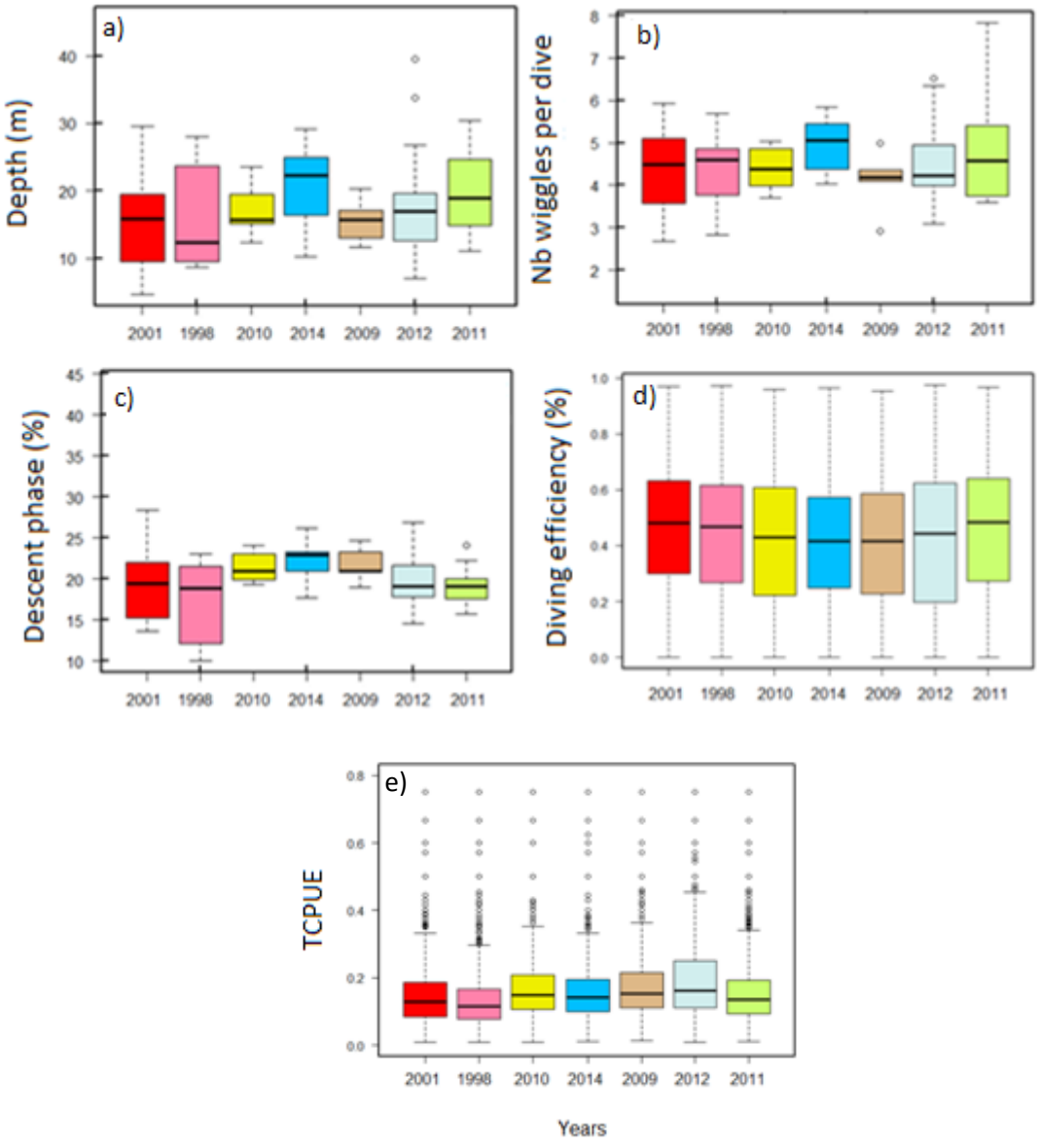


Figure 13: Boxplots of a) maximum depth, b) number of wiggles, c) descent phase, d) diving efficiency and e) TCPUE; according to years classed by increasing sea-ice concentration. These boxplots were made using 7 years and considering all dives.

For the maximum depth, the highest values have been recorded for intermediate years (2010, 2014 and 2009) with a mean of 17.26 m ± 0.32, 20.00 m ± 0.16 and 15.92 m ± 0.32, respectively (Fig 13 a). The lowest values were attributed to the years 2001 and 2012, with a mean of 13.93 m ± 0.12 and 13.83 m ± 0.08, respectively. Welch tests revealed that the trends observed on the boxplots are significant. The same conclusions could be done for the descent rate, with a mean of 0.171 % ± 0.002 in 2010, 0.203 % ± 0001 in 2014 and 0.179% ± 0.002 in 2009 (Fig. 13 b). Concerning the number of wiggles, it looks like intermediate years are different but Welch tests revealed that there is no significant trend (Fig. 13 c). The difference between 2001 and 2010 was not significant (t=-1.7908, df=8109.99, p-value=0.0734), such as the difference between 2009 and 2012 (t=-0.5818, df= 5991.92, p-value=0.5607). Considering all dives, no trend could be confirmed for this parameter. The lowest diving efficiencies have been recorded for 2010, 2014 and 2009, with a mean of 0.454 ± 0.003, 0.436 ± 0.002 and 0434 ± 0.003, respectively (Fig. 13 d). The only comparisons which were not significant concerned the years 2001 and 2011 (t=0.8933, df=48385, p-value=0.3717) and the years 2009 and 2010 (t=-1.6458, df=11002.4, p-value=0.099). Therefore, the trends observed were confirmed thanks to Welch tests. Finally, for the TCPUE, no trend could be found (Fig. 13 e).

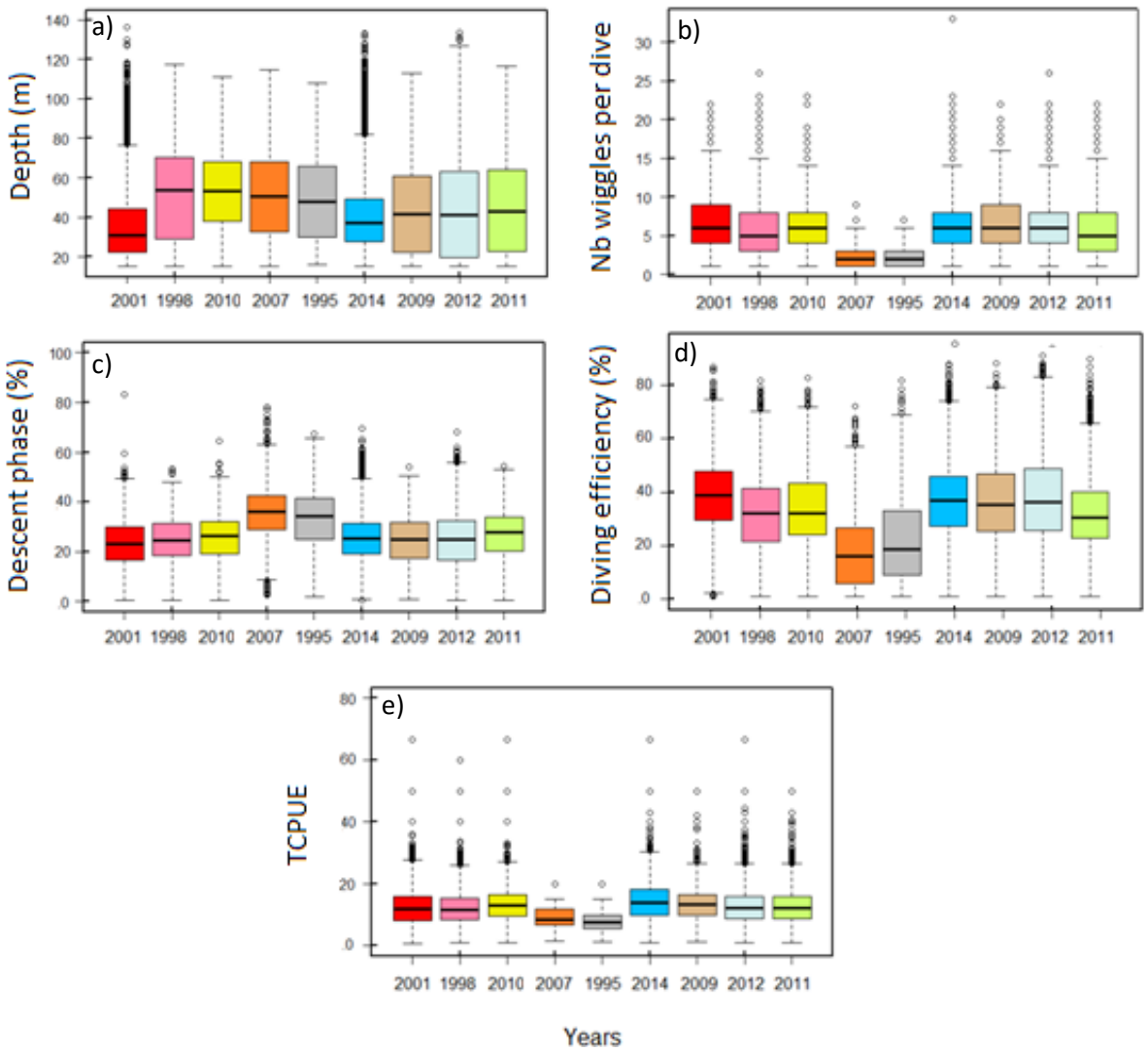


Figure 14: Boxplots of a) maximum depth, b) number of wiggles, c) descent phase, d) diving efficiency and e) TCPUE; according to years. Boxplots were made with 9 years considering deep dives only.

Considering all years with deep dives only, Welch tests showed that intermediate years (above all 1995 and 2007) were always significantly different from the others (p-values<-0.00139). This could be seen in terms of mean maximum depth (50.62 m ± 0.56 and 51.48 m ± 0.37, respectively), mean number of wiggles per dive (2.18 ± 0.03 and 2.26 ± 0.02, respectively) percentage of descent phase duration (35% ± 0.002 and 36% ± 0.002, respectively), but also diving efficiency (22% ± 0.003 and 17% ± 0.002, respectively) and TCPUE (8.65% ± 0.1 and 9.73% ± 0.1, respectively) (Fig. 11). In other words, considering deep dives only (i.e. foraging dives), intermediate years were characterized by deeper dives, greater ascent, descent and post-dive durations and lower time spent at the bottom phase of the dives, lower number of wiggles, diving efficiency and TCPUE (Fig. 14).

The last parameter, which is the post-dive duration, needed closer investigation. This diving metric has been divided in two components: the post-dive duration considering dives within bouts only (post-dive duration < BCI) and the post-dive duration considering dives between bouts only (post-dive duration > BCI) (Fig. 15 a and b).

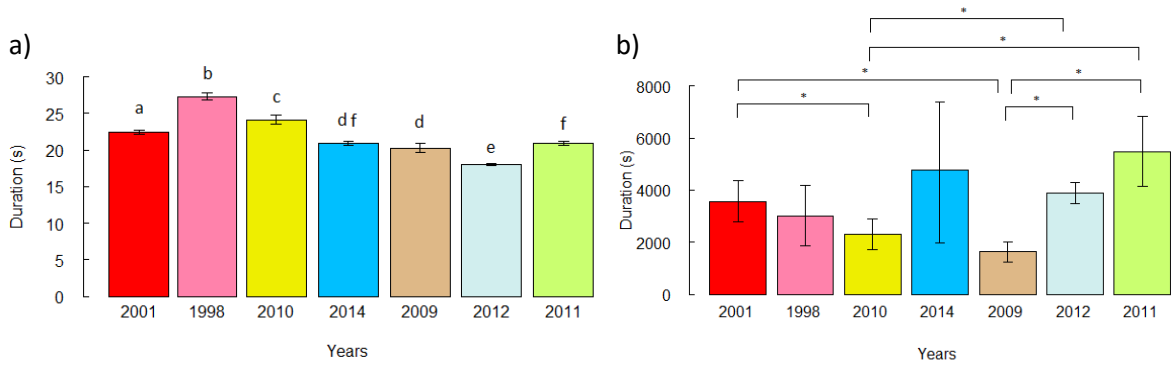


Figure 15: Barplots representing the post-dive duration across years considering a) dives within bouts only (post-dive duration <207.7 s) and b) dives between bouts only (post-dive duration > 207 s).

Concerning the post-dive duration within bouts, the trend is difficult to describe (Fig. 15 a). The year 2010, as an intermediary year, is characterized by a high post-dive value compared to extreme years, with a mean of 24.13 s ± 0.32). On the opposite, the year 2012 presents the lowest value for this parameter, with 18.07 s ± 0.07). Results are more mitigated for 2014 and 2009, with a mean of 20.92 s ± 0.15 and 20.28 ± 0.30, respectively). However, for the post-dive duration between bouts, it appeared that lower values can be attributed to intermediate sea-ice conditions (Fig. 15 b). This is especially the case of 2009 and 2010 (with a mean of 1623.31 s ± 187.30 and 2317.66 s ± 292.49, respectively). These values are significantly different from the values obtained for extreme years (Welch test: p-value < 0.00238). The year 2011 present the highest value of high coverage years, with 5470.49 s ± 670.80 and 2001 the highest value of low coverage years, with 3560.63 s ± 395.38.

All mixed models tables and residuals are presented in Appendix VII and VIII. In this section, the most relevant model for each parameter was selected (Fig. 16 and 17; Table 6). Because considering all dives for some parameters has no sense, the models selected for all parameters considered only the deep dives (i.e. foraging dives).

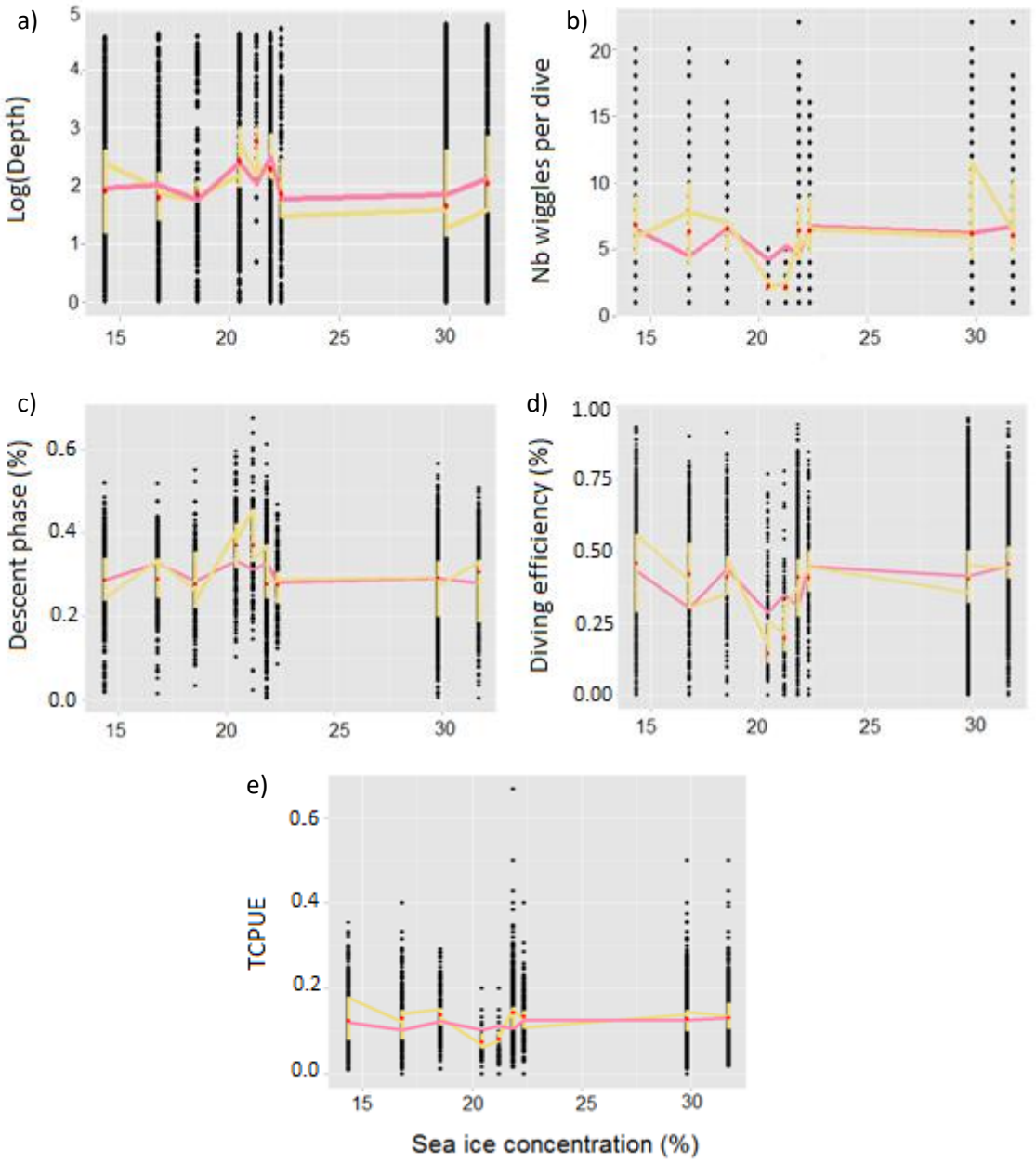


Figure 16: Results of the mixed models for each parameter according to sea-ice concentration: a) maximum depth (9 years deep dives), b) number of wiggles (9 years deep dives), c) descent rate (9 years deep dives), d) diving efficiency (9 years deep dives) and e) TCPUE (9 years deep dives). The fixed part is represented in pink and the random part in yellow.

All mixed models confirmed the findings revealed by the exploratory graphs and the mean comparisons, both with the fixed part (representing sea-ice parameters) and the random part (representing the individual variability) (Table 6).

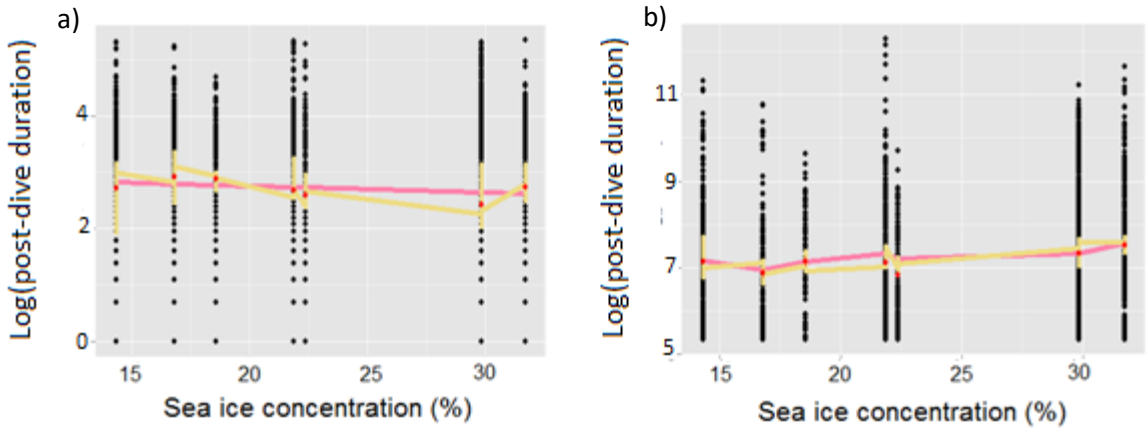


Figure 17: Results of the mixed models for the post-dive duration concerning: a) dives within bouts (post-dive duration <207.7 s), b) dives between bouts (post-dive duration >207.7 s), according to the sea-ice concentration gradient. The fixed part is represented in pink and the random part in yellow.

With the mixed model, we could not confirm the trend observed for the post-dive duration analysis which considers only the dives within bouts (Fig. 17 a). However, it looks like the trend observed for the post-dive duration considering the dives between bouts has been confirmed by the mixed model as well (Fig. 17 b).

Table 6: Results of the main mixed effects models for each metric.

Chosen models	Significant explanatory variables	R^2c	R^2m	AIC	p-values
Maximum depth					
9 years deep dives	SIC	0.417	0.0597	1442.75	0.0010
Diving efficiency					
9 years deep dives	SIC SIE	0.2780	0.0758	-8917.093	0.0094 <0.0001
Descent rate					
9 years deep dives	SIC SIE	0.2623	0.0463	-15540.09	0.0463 0.0001
TCPUE					
9 years deep dives	SIC SIE	0.1571	0.0287	-20224.61	0.0012 0.0034
Number of wiggles					
9 years deep dives	SIC SIE	0.4156	0.1133	35367.23	<0.0001 <0.0001
Post-dive duration					
7 years all dives within bout	SIC	0.101	0.006	19273.06	0.0301
7 years all dives between bouts	SIC Distance open water	0.1266	0.0091	10165.69	0.0027 0.0156

The trends observed with the boxplots and the mean comparisons were confirmed for all parameters except the post-dive duration (dives within bouts only) both with the random and the fixed part, showing different values for intermediate years. The sea-ice concentration

appears to be significant for all selected models (p-value<0.05) (Table 6). In addition, except for the post-dive duration, the fixed part largely contributed to the variability compared to the random part, which is however non-negligible.

4. Discussion

Our study showed that foraging strategies and breeding success of Adélie penguins changed according to a key environmental variable: sea ice. Guard stage is a critical breeding stage for adults because their foraging activity depends not only on their own energetic requirements (to forage, to ensure their basal metabolism and to restore their body condition from the long trips of incubation) but also on the energy demand of the chicks (Charrassin et al., 1998). Because at this stage, the extent of the foraging area is smaller (shorter trips) than during other stages, the foraging activity of Adélie penguins reflects local conditions.

4.1. An optimal range of sea-ice cover at the seasonal scale

Concerning breeding success, which is measured at the seasonal scale, our results corroborate those of Barbraud et al. (2015) and show that there is an optimal range of sea-ice concentration concerning Adélie penguins' breeding success. Ainley (2002) already suggested the idea that there could be a "perfect" sea-ice cover for Adélie penguins. On the one hand, as there is considerable evidence that krill feeds on under-ice communities (microalgae) but that its abundance is low where sea ice is at its maximal extent (Nicol, 2006), we can assume that there is an optimal density of krill in relation with sea-ice coverage (Flores et al., 2012). On the other hand, foraging costs of chick-rearing adults increase when sea-ice cover is extreme, forcing parents to walk longer distances on ice to reach the foraging areas (Davis, 1982). This may increase body mass loss for parents and as their foraging trips are longer, the frequency of meal deliveries to the chicks is reduced (Davis, 1982). In that case, the intermediate sea-ice conditions can be characterized by both prey presence and accessibility (Table 7).

Table 7: Table gathering main conclusions concerning Adélie penguins in relation with sea-ice cover.

	Low sea-ice cover	Intermediate sea-ice cover	High sea-ice cover
Prey presence	Krill not present	Krill present	Krill present
Prey accessibility	Accessible	Accessible	Not accessible (Long distances to reach the foraging areas)
Breeding success	Low (Low profitability of foraging trips and low chicks' body mass)	High	Low (Nest desertion and chicks' starvation)

Findings evidenced the importance of a synchronicity between breeding events and sea-ice retreat. However, two years deserved special inspection. Because sea ice took a long time to retreat in 2014 (the distance between the colony and the open water was still around a hundred kilometers at the end of January), the breeding success was quite low for this season. The year 2001 was also characterized by a low breeding success value. This may results from the unusual presence of a huge iceberg, which probably prevented ocean currents and winds from assisting the summer break-up of sea ice (that forms polynyas) in the Dumont D'Urville Sea (Comiso, 2010). This could affect Adélie penguins that needed to walk longer distances to reach the foraging areas in the open sea. If excluding 2001 changes the shape of the curve so dramatically, maybe the year 2001 deserves a close investigation in another study to see whether the hypothesis of higher travel times over fast is true. The breeding success for this year is not extremely low and does not correspond to an outlier either. This phenomenon is associated to a real sea-ice event. During guard stage, polynyas are indeed profitable foraging areas for two reasons: the high productivity and the reduced travel and search time required to reach them. Rain can also make the breeding success decreasing because the thermo-regulation capacities of the chicks weaken rapidly (Ropert-Coudert et al., 2015). The year 2013 (total breeding failure), with high sea-ice coverage, exemplifies this phenomenon, with chicks dying because of rain, starvation and predators.

4.2. Seabirds foraging response to changes in sea-ice distribution at finer scales

We observed an optimal range of sea-ice concentration that influenced most of the diving parameters studied. Our findings showed that differences in foraging strategies occurred at different temporal scales: foraging trip, day, bout and dive. Although inter-individual variability was strong and, consequently trends were not as visible as for breeding success, results on the foraging activity of penguins mirror those on breeding success. The link between foraging success and breeding success is due to the strong correlation between average meal size and quality delivered to a chick and its growth rate, regulated by the body condition of the parents (Lorentsen, 1996). As such the mirroring trends with sea ice could be expected and a "perfect" sea-ice cover for Adélie penguins had been suggested by Ainley (2002).

4.2.1. Adaptations in activity rhythm revealing the local conditions

At the foraging trip scale, fractal analysis has shown that an increase in behavioral complexity along the decreasing gradient of sea-ice concentration, suggesting higher degrees of long-range dependence when the sea-ice cover was important. This deterministic behavior occurring during high sea-ice coverage years could be due to the fact that birds are more constrained in their diving movements. The presence of polynyas in these conditions becomes crucial to explain the foraging activity of the birds: waters with more predictable prey fields should lead to more stereotyped foraging sequences (Meyer, 2016). In addition, following Reynolds et al. (2015), a greater determinism observed in diving sequences may result from a process that favours exploitation over exploration, which is once again more likely to occur

when the prey field is more homogeneous and confined like in polynyas. On the other side, the greater complexity in foraging behavior observed during low sea-ice coverage years could be explained by different theories. At first, several studies have already linked greater stochasticity in foraging behavior with greater heterogeneity in the vertical distribution of prey (Ropert-Coudert et al., 2009; Pelletier et al., 2012), which could be the case when birds are diving in deeper waters. In other words, according to the results of the present study, birds may target higher depths, inducing variability in dive durations and the associated post-dive durations. In addition, MacIntosh et al. (2011) suggested that individuals in more complex environments or exploiting prey that are harder to catch (i.e. mobile prey) foraged in a less deterministic way. To summarize this idea, complex behavioral sequences are more likely to occur when environments are less predictable in terms of prey type, density and distribution, probably offering mechanisms to enhance the foraging success. Other studies have highlighted that animals which favour the exploration of their environment were more likely to display complex behavior (Shimada et al., 1995; Kembro et al., 2009). The last mechanism that could be involved here concerns the fact that diving seabirds are physiologically constrained by their oxygen reserves (Wilson, 2003) during periods of heavy prey exploitation. The patterns of alternation between dive and post-dive times are thus much less periodic.

Then, concerning the daily scale, the fact that no daily pattern was observed during intermediary years concerning the frequency of dives (all dives and deep dives) could indicate that the density of krill was sufficient to satisfy the foraging activity of Adélie penguins all day long. In the same way, no daily patterns were observed for maximum depth considering deep dives and all dives for intermediary sea-ice conditions. As krill is generally more present in deep waters during the day and rises to the surface at night, in this case, diving patterns are not in relation with the known day/night vertical migration of krill (Croxall et al., 1988). These results could also indicate that the balance fish/krill in Adélie penguins has changed during these years, meaning that birds targeted different types of prey (probably more energetic prey when the cost of reaching the foraging grounds is higher). These findings corroborate the ones resulting from the fractal analysis. Furthermore, we observed that during extreme sea-ice conditions, more foraging dives were performed during night time. This can be linked to the diurnal vertical migration of krill, above all for low sea-ice coverage years, where birds forage in open water. These findings could suggest that birds adopt different foraging strategies to maximise the profitability of foraging trips by optimising the prey encounter rate and by reducing the diving effort.

In addition, the number of dives per day and the number of bouts per day were found to be negatively related to breeding success. This finding suggests that an increase in diving activity per time unit is associated with a lower abundance of prey (or non profitable distribution of prey) or a foraging behaviour applied on poor quality patches. Results concerning the post-dive duration revealed that for the dives between bouts, this parameter presents lower values for intermediate years. This suggests that birds could reach another prey patch in a shorter time (Sommerfeld et al., 2015). In other words, intermediate years are probably characterized by a higher prey encounter rate, suggesting a more favourable prey

availability. The competition between species or between conspecifics may also explain the increase in diving activity and the decrease in foraging success during extreme years because diving individuals are more constrained (Warwick-Evans et al., 2016).

4.2.2. The flexibility of foraging strategies highlighted with diving metrics

At the dive scale, our study showed that plasticity exists for most of the diving parameters in relation with changes in sea-ice distribution. At first, results revealed that birds dove deeper during intermediary years. The choice of diving deeper can be explained once again either by the quantity of prey (density and distribution) or the quality of prey (balance fish/krill) occurring in deep waters. These results confirm the findings obtained with the analyses of bouts and day/night patterns. Concerning the descent and ascent rates, it has been shown that during intermediate years presented higher values. Descent and ascent rates relate to the dive angle, a small angle suggesting a more exploratory dive. During high sea-ice coverage conditions, assuming that penguins are feeding in polynyas, dive profiles present a slow ascending phase probably because birds are looking for an access to the surface (Kato et al., 2009). Some researchers have also suggested that birds can adjust these phases according to previous dives (if successful or not) and future dives as well (Wilson, 2003; Sato et al., 2004). The high descent and ascent rates observed during intermediate years could be due to the high mean maximum depth. In other words, as birds have to go deeper, they spend more time for the ascent and decent phases, at the expense of the bottom phase duration. It seems that bottom duration is negatively correlated to foraging success. This finding suggests that Adélie penguins are able to adapt their diving activity to the prey patch encountered, tending to reduce the time spent at the bottom when successful. As wiggles occur during the bottom phase, the lower number of wiggles per dive observed during intermediate years can be explained by the low mean bottom duration associated. Indeed, the number of wiggles is also negatively correlated to foraging success. This finding is the opposite from other studies (Hanuise et al., 2010). Once again, this result suggests that for intermediate sea-ice conditions, the quantity of prey encountered for each patch was higher and that a lower number of undulations was required for each dive. This could also mean that the prey found at the bottom phase was not moving to deeper water to escape the penguins. However, successful foraging dives occurring during intermediary years are probably energetically more costly. Indeed, as birds dove deeper, longer post-dive durations (time at the surface) were observed as a behavioural response in order to maintain aerobic metabolism (to reduce the risk to have a large lack of oxygen). Post-dive duration actually contains a recovery phase, depending on the amount of oxygen used during previous dives (Wilson, 2003; Pütz and Cherel, 2005) and a preparatory phase for the next dive. Various studies have shown that birds are able to adjust their air volume for each dive depending on the target maximum dive depth in order to optimize the costs and benefits of buoyancy (Sato et al., 2002; Noda et al., 2016).

Predicting how changes in sea-ice conditions can affect this marine predator relies on our ability to assess the foraging success, which is a particularly difficult task (Viviant et al., 2014). In the present study, we have shown that only using diving patterns, we can tend to predict foraging success. The use of diving metrics permitted to highlight the adaptation of

Adélie penguins' activity patterns to the density and distribution of prey and we could show that there is flexibility in foraging strategies in relation with changes in sea-ice distribution.

4.3. Effect of foraging investment on breeding success in relation with sea ice

Our results did not show that parents with high foraging investment (high diving rhythm and bottom duration) induce higher breeding success. This can be explained by two main reasons: (i) a very low foraging success (due to a low prey availability or accessibility); (ii) a different allocation of food between parents and offspring (Takahashi et al., 2003). The second hypothesis could not be tested in the present study. The investment is expected to reflect breeding success only when they feed in good conditions. In the present study, it has been found that the diving efficiency (ratio between bottom duration and total dive cycle duration) seemed to be negatively correlated to the breeding success (Fig. 16). However, several studies have linked breeding success to foraging success (meal size provided to the chicks and their fledging mass) (Clarke et al., 2002).

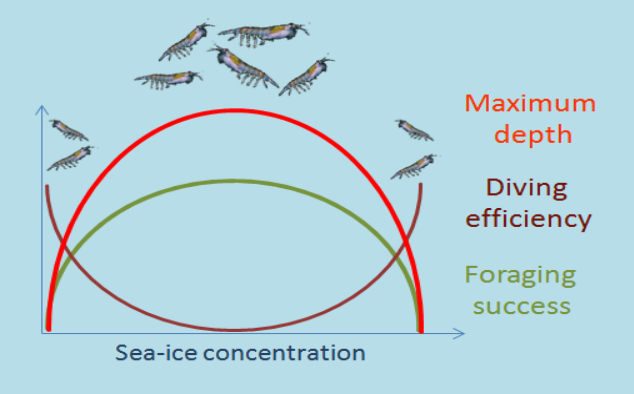


Figure 18: Schematic drawing representing the trends observed concerning breeding success, diving efficiency and foraging efficiency along the sea-ice concentration gradient.

Successful foraging is a determinant parameter involved in individual survival. But in the case of high diving efficiency values, the fact that birds spent a lot of time at the bottom phase of the dive doesn't necessarily mean they foraged successfully (Viviant et al., 2016) but they made more effort to find prey at the dive scale. Considering both the quality and the quantity of prey is necessary to understand the mechanisms involved. In the Southern Ocean, Antarctic krill (*E. superba*) density is not homogeneously distributed along the depth gradient. Indeed, krill density appears to be higher around 30-40 meters deep than around 10-20 metres (Godlewska et al., 1991). Even if little is known concerning the ice krill (*E. crystallorophias)*, as the Antarctic krill (*E. superba)* was well represented in stomach contents of Adélie penguins (Ridoux and Offredo, 1989), we could conclude that for intermediate sea-ice conditions, birds probably foraged on bigger krill patches by reaching higher depths. Moreover, the quality of krill could change with sea-ice conditions. Generally krill larvae are found just under sea ice, while juveniles and adults are a bit farther (both deeper and far from ice edge) (Nicol, 2006). When the sea-ice concentration is high, travel and access to open water is difficult, and presumably krill under the ice will be dispersed over much greater distances, making it more difficult for the penguins to find. In seasons with moderate amounts

of sea ice, travelling dives should be easy and the krill is not so dispersed, so maybe that supports the idea of an "optimum" amount of sea ice. In addition, the balance between krill and fish might be subject to change with sea-ice variations, forcing birds to adjust their diving depth (fish are more able to escape at higher depths).

The most obvious signal of optimality appears in breeding success. The optimal range of sea ice can be defined as the range of sea ice which is clearly enhancing the breeding. Meanwhile, foraging success couldn't be measured in this study but it has been shown that some foraging parameters peak for the same range of sea ice (around 20%). As such, it can be expected that these parameters are those that enhance foraging success, which is directly in relation with breeding success. However, it cannot be stated that the observed "optimal" values are the real optimal values that birds are able to perform. Penguins adjust their behavior to the different conditions in order to achieve high foraging success. This adjusted behavior is not necessarily "optimal".

4.4. Methodological concerns and perspectives

This work could be complemented with more information about the individuals to highlight the response of a seabird to year-to-year variations of sea-ice conditions but the corresponding data doesn't exist for the years used in the present study. Coupling TDR data and GPS data may enable us to have a three-dimensional vision of the birds' habitat. In that way, we could investigate which areas seem more beneficial for the birds and know if penguins dive in polynyas or in open water. In addition, having more direct proxies of ingestion (such as data from accelerometers or oesophageal temperature measurements) and diet data could also enrich the discussion because we would be able to identify successful dives (Ropert-Coudert et al., 2001).

We could also investigate the influence of other environmental parameters, such as chlorophyll a concentration, meteorological parameters or data of currents. Indeed, in these ecosystems, eddies are known to be particularly important for predators, concentrating the food (Cottin et al., 2012). The strategy is energetically efficient as the birds are following the currents, at least during the first part of the trip (when they are in their lowest body condition). Note that some of these environmental parameters can be difficult to obtain with the presence of sea ice as they are depending on the remote sensing data obtained by satellites.

Furthermore, even if we worked on mean diving parameters, the fact that different spatial resolutions were used according to the different types of data can be a problem. Indeed, sea-ice concentration data were extracted at a large scale (25 km resolution) and diving data were recorded at a fine scale. However, the main limitation in this study is the differences in sample intervals. The differences between years were a real issue for analysing diving data. The bias emerging from differences in sampling intervals among years made the results hard to interpret. With the improvements made on bio-logging, the capacities of the electronic devices are subject to change but for long-term analyses, there is a real need to homogenise the protocol.

Long-term studies could arouse the interest of international institutions such as the Ecosystem Monitoring Program (CEMP) of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) which aims to detect changes in critical components of this marine ecosystem and to distinguish them between changes due to environmental variability and other changes. Even if working with 121 birds over 9 years is already acceptable, working over a longer period could enable researchers to better characterize the optimal range of sea ice (i.e. to identify if it is narrow or not) both in terms of foraging performance and breeding success. Long-term studies on this species should be done for several colonies because the trends observed for all colonies are not the same. In the Dumont D'Urville area, the last years were characterized by high sea-ice cover. As a consequence, the trends observed for this colony might not reflect the overall trend for this species, especially in a context of global warming.

Still considering that having a larger view is necessary, different breeding stages (incubation and chick-rearing) could be compared (Widmann et al., 2015). In the same way, coupling summer and winter studies would be judicious because the responses of birds to changes in sea-ice conditions can be different among stages. Winter studies could be particularly useful to better understand a second fundamental biological trait: the adults' survival. In addition, low food availability in winter can delay the arrival of birds to the colony. Therefore, events occurring in winter can have an influence on the foraging behaviour of parents during the summer.

4.5. Relevance of this marine predator as an eco-indicating species

Through this study, the ultimate aim was to assess if this marine predator can be a relevant eco-indicating species. Seabirds are known to be good eco-indicators of the environment (Furness and Camphuysen, 1997). The first main reason for which seabirds are largely used as eco-indicators is due to the fact that the study of central-place foragers is facilitated because the access to the different colonies is quite easy. In addition, the concept of using characteristics from upper trophic levels to bring information on ecosystem structure and functioning (including lower trophic levels) is interesting.

By its abundance and its circumpolar distribution, the Adélie penguin appears as a key species of the Southern Ocean ecosystem, subject to the full range of environmental changes. Populations' trends are very different among regions. For instance, in the Antarctic Peninsula area, corresponding to the fastest-warming place on Earth (Bromwich et al., 2013), populations have been decreasing during the past decades (Fraser and Patterson, 1997), whereas those in the Ross Sea increased (Taylor et al., 1990; Wilson et al., 2001). It appears that declining populations experienced several years with high sea surface temperature compared to those that are increasing (Cimino et al., 2016). The increase in Ross Sea populations might be due to an increase in wind strength and warmer winter temperatures that have resulted in thinner sea-ice cover and a more important presence of polynyas (Lyver et al., 2014). These changes in sea ice probably enhanced the foraging efficiency of foraging trips. Thus, breeding success has increased and populations have grown. Another factor that

has facilitated the increase in Adélie Penguin colonies in this area is the extraction by whalers of the penguins' main competitor for food, the Antarctic minke whale (*Balaenoptera bonaerensis*) (Lyver et al., 2014). In addition, this increase can be explained by the arrival of a commercial fishery which targets a fish species that competes for food with the penguins: the Antarctic toothfish (*Dissostichus mawsoni*), feeding mainly on Antarctic silverfish (Lyver et al., 2014). Meteorological factors and anthropogenic pressures (fishery development) also play a major role in population trends. To summarize, various factors can affect Adélie penguins' survival and fitness, two fundamental biological traits.

Global warming appears as the main factor affecting this long-lived marine predator, in relation with sea-ice retreat that causes habitat loss. A recent study has shown that Antarctica will potentially be responsible for sea-level rise of more than one metre by 2100 and more than 15 metres by 2500 (DeConto and Pollard, 2016). Adélie penguins depend on ice for foraging, resting, avoiding predators (leopard seals *Hydruga leptonix* and killer whales *Orcinus orca*), moulting, migrating and therefore breeding. To use Adélie penguins as indicators of the environment, we must consider relevant parameters that can be easily measured, sensitive to environmental change and integrative (Iverson et al., 2007). Among these, foraging behaviour parameters appear as an obvious choice. Indeed, the present study has shown that there might be an optimal range of sea ice (around 20%) in terms of foraging efficiency and breeding success, meaning that this species represents a great indicator of rising global warming. But this is not the only factor associated with global warming that is impacting this species. Because their spatial distributions are dependent on the matching between their physiological optima and biotic and abiotic conditions, marine invertebrates and fish species are known to respond to increasing water temperatures through distribution shifts (Cheung et al., 2013). With global warming, these species are susceptible to migrate toward poles. The arrival of new species might modify the structure and the functioning of the food web in the Southern Ocean, bringing new potential prey for Adélie penguins and their competitors. Therefore, top-down and bottom-up forces might be modified and the Southern Ocean's ecosystem will therefore experience major changes.

Other disturbances are also referred for this species. Adélie penguins populations are affected by krill fisheries in the Southern Ocean (Trathan et al., 2015). Even if the CCAMLR (fisheries management authority) regulates the Antarctic krill fishery, we are in a context of increasing krill harvesting because of the increasing population trend (Cury et al., 2011). Because they need to maintain their plumage in a good condition (Trathan et al., 2015), Adélie penguins can also be affected by another non-negligible anthropogenic factor: water pollution (García-Borboroglu et al., 2008).

It can be highlighted that the Adélie penguin is a species that can give an exhaustive picture of what is happening in term of sea-ice variability. Other species present in Adélie Land with a circumpolar distribution is also of particular interest to many researchers. This is the case of the South Polar skua (*Catharacta maccormicki*), the Emperor penguin (*Aptenodytes forsteri*), the Weddell seal (*Leptonychotes weddellii*), the Snow petrel (*Pagodroma nivea*) or other petrels. Being a diving marine predator (such as the Emperor penguin and the Weddell seal) and not a flying bird, Adélie penguins are more constrained

and dependent on sea-ice. As they breed in winter (Wilson, 1907), emperor penguins are really hard to work on (researchers need to work in extreme cold, wind and dark). In addition, it is difficult to follow the same individuals because they don't make any nest. Furthermore, the Emperor penguin is a protected species (BirdLife International, 2012b), making it difficult to get a permit to work on them. Finally, unlike the Weddell seal, which is a coastal species, Adélie penguins can give relevant information concerning the "entire" ecosystem.

5. Conclusion

The Adélie penguin is one of the species monitored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). It takes part of its CCAMLR Ecosystem Monitoring Program (CEMP) to detect anthropogenic impacts on Antarctic marine ecosystems.

Thanks to a multi-scale approach confronting breeding success and diving data concerning Adélie penguins with sea-ice data, this work allowed us to provide evidence that birds can adjust their foraging strategies according to sea-ice variations, suggesting that there could be an optimal range of sea-ice concentration for this species (around 20%). Therefore, we gave new clues for taking into account Antarctic marine predators when investigating the effects of global warming on the Southern Ocean's ecosystem. However, the work has to be complemented with long-term studies conducted on more individuals that could highlight the responses of this marine predator to year-to-year variations of environmental variables and thus contribute to refine the predictions made on this species in relation with global warming.

The Adélie penguin is a long-lived species whose breeding success depends on several environmental and anthropogenic pressures. In a context of predicted alteration of sea-ice cover, it is timely to better investigate the optimal range of sea ice in relation to behavioral flexibility.

References

Aguilar-Islas AM, Rember RD, Mordy CW, Wu J (2008) Sea ice-derived dissolved iron and its potential influence on the spring algal bloom in the Bering Sea. Geophys Res Lett 35:10–14. doi: 10.1029/2008GL035736

Ainley DG (2002) The Adélie Penguin: Bellwether of climate change. Columbia University Press, New York, 310p.

Alados C, Huffman M (2000) Fractal long-range correlations in behavioural sequences of wild chimpanzees: a non-invasive analytical tool for the evaluation of health. Ethology 106:105–116.

Asher L, Collins LM, Ortiz-Pelaez A, et al (2009) Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. J R Soc Interface 6:1103–1119. doi: 10.1098/rsif.2009.0221

Barbraud C, Delord K, Weimerskirch H (2015) Extreme ecological response of a seabird community to unprecedented sea ice cover. R Soc Open Sci. 2:140456. doi: 10.1098/rsos.140456

Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. Proc R Soc B Biol Sci 270:2111–2116.

BirdLife International (2012a) Pygoscelis adeliae. The IUCN Red List of Threatened Species 2012: e.T22697758A40175259.

BirdLife International (2012b) Aptenodytes forsteri. The IUCN Red List of Threatened Species 2012: e.T22697752A40172193.

Bonferroni C (1935) Il calcolo delle assicurazioni su gruppi di teste. In: Studi in Onore del Professore Salvatore Ortu Carboni. Rome: Italy, pp 13–60

Bost CA, Cotté C, Bailleul F, et al (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376. doi: 10.1016/j.jmarsys.2008.11.022

Bost C-A, Handrich Y, Butler P, et al (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. Deep Sea Res Part II Top Stud Oceanogr 54:248–255.

Boyd IL (1996) Temporal scales of foraging in a marine predator. Ecology 77:426–434.

Boyd IL, Murray AWA (2001) Monitoring a marine ecosystem using upper trophic level predators. J Anim Ecol 70:747–760. doi: 10.1046/j.0021-8790.2001.00534.x

Bradbury R, Reichelt R (1983) Fractal dimension of a coral reef at ecological scales. Mar Ecol Prog Ser 10:169–171.

Brierley A, Fernandes P, Brandon M, et al (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. Science 295:1890–1892.

Bromwich DH, Nicolas JP, Monaghan AJ, et al (2013) Central West Antarctica among the most rapidly warming regions on Earth. Nat Geosci 6:139–145. doi: 10.1038/ngeo1671

Brooke MDL (2004) The food consumption of the world's seabirds. Proc Biol Sci 271 Suppl:S246–S248. doi: 10.1098/rsbl.2003.0153

Buckley R, Trodahl H (1987) Scattering and absorption of visible light by sea ice. Nature 326:867–869.

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271. doi: 10.1080/01965581.1987.10749517

Charrassin JB, Bost CA, Pütz K, et al (1998) Foraging strategies of incubating and brooding king penguins Aptenodytes patagonicus. Oecologia 114:194–201. doi: 10.1007/s004420050436

Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. Mar Biol 154:813–821. doi: 10.1007/s00227-008-0974-3
Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. Nature 497:365–369. doi: 10.1038/nature12156
Cimino MA, Lynch HJ, Saba VS, Oliver MJ (2016) Projected asymmetric response of Adélie penguins to Antarctic climate change. Sci. Rep. 6:28785. doi: 10.1038/srep28785
Clarke A, Harris CM (2003) Polar marine ecosystems: major threats and future change. Environ Conserv 30:1–25.
Clarke J, Knowles K, Irvine L, Phillips B (2002) Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. Polar Biol 25:21–30.
Comiso J (2010) Polar Oceans from Space. Atmospheric and Oceanographic Sciences Library, 41, Springer Science & Business Media, New-York
Constable AJ, Melbourne-Thomas J, Corney S, et al. (2014) Change in Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. Glob Chang Biol 20:3004–3025.
Constantine W, Percival D (2011) Fractal: fractal time series modeling and analysis. R package v. 1.1-1.
Cottin M, Raymond B, Kato A, et al (2012) Foraging strategies of male Adélie penguins during their first incubation trip in relation to environmental conditions. Mar Biol 159:1843–1852. doi: 10.1007/s00227-012-1974-x
Cribb N, Seuront L (2016) Changes in the behavioural complexity of bottlenose dolphins along a gradient of anthropogenically-impacted environments in South Australian coastal waters : Implications for conservation and management strategies. J Exp Mar Bio Ecol 482:118–127. doi: 10.1016/j.jembe.2016.03.020
Croxall J, Lishman GS (1987) The food and feeding ecology of penguins. In: Croxall J (ed) Seabirds: Feeding ecology and role in marine ecosystems. Cambridge University Press, pp 101–133
Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. Science 297:1510–1514. doi: 10.1126/science.1071987
Cury P, Boyd lan L, Bonhommeau S, et al (2011) Global seabird response to forage fish depletion - one third for the birds. Science 334:1703–1706.
Davis L (1982) Timing of nest relief and its effect on breeding success in Adélie penguins (Pygoscelis adeliae). Condor 84:178–183.
DeConto R, Pollard D (2016) Contribution of Antarctica to past and future sea-level rise. Nature 531:591–597.
Durant JM, Hjermann DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283.
Flores H, van Franeker JA, Siegel V, et al (2012) The association of Antarctic krill Euphausia superba with the under-ice habitat. PLoS One 7:1–11. doi: 10.1371/journal.pone.0031775
Fraser W, Patterson D (1997) Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. In: Battaglia B, Valencia J WD (ed) Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, pp 445–452
Fraser W, Trivelpiece W, Ainley DG, Trivelpiece S (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biol 11:525–531.

Frederiksen M, Mavor RA, Wanless S (2007) Seabirds as environmental indicators: The advantages of combining data sets. Mar Ecol Prog Ser 352:205–211. doi: 10.3354/meps07071
Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. ICES J Mar Sci 54:726–737. doi: 10.1006/jmsc.1997.0243
García-Borboroglu P, Boersma D, Reyes LM, Skewgar E (2008) Petroleum pollution and penguins: Marine conservation tools to reduce the problem. In: Hofer T (ed) Marine Pollution: New Research. Nova Science Publishers Inc, New York, USA, pp 339–356
Gaston AJ, Gilchrist HG, Hipfner JM (2005) Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (Uria lomvia L.). J Anim Ecol 74:832–841. doi: 10.1111/j.1365-2656.2005.00982.x
Godlewska M, Klusek Z, Kamionka L (1991) Distribution and abundance of krill -Euphausia superba Dana - at the ice edge zone between Elephant Island and the South Orkney Islands in the season 1988/89. Polish Polar Res 12:593–603.
Halsey LG, Handrich Y, Fahlman A, et al (2007) Fine-scale analyses of diving energetics in king penguins Aptenodytes patagonicus: How behaviour affects costs of a foraging dive. Mar Ecol Prog Ser 344:299–309. doi: 10.3354/meps06896
Hanuise N, Bost C-A, Huin W, et al (2010) Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. J Exp Biol 213:3874–80. doi: 10.1242/jeb.044057
Hardy A, Gunther E (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. Discov Rep 11:1–456.
Heck A, Perdang J (1991) Applying fractals in astronomy.
Hickmott LS (2005) Diving Behaviour and Foraging Ecology of Blainville's and Cuvier's Beaked Whales in the Northern Bahamas. Masters Thesis, University of St. Andrews, Scotland, UK, 107p.
Hijmans R, van Etten J, Cheng J, et al (2016) Package " raster ". CRAN -R.2.5-8.
Hindell M, Bradshaw C, Harcourt R, Guinet C (2003) Ecosystem monitoring: Are seals a potential tool for monitoring change in marine systems? In: Gales NJ, Hindell MA KR (ed) Marine Mammals. Fisheries, Tourism and Management Issues. CSIRO Publishing, Melbourne, pp 330–343
Hooker SK, Baird RW (2001) Diving and ranging behaviour of odontocetes: a methological review and critique. Mamm Rev 31:81–105. doi: 10.1046/j.1365-2907.2001.00080.x
Husson F, Lê S, Pagès J (2009) Analyse de données avec R. Presses Universitaires de Rennes
Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability : qualitative and quantitative diet analyses using fatty acids. Mar Ecol Prog Ser 352:235–244. doi: 10.3354/meps07073
Jenouvrier S, Barbraud C, Weimerskirch H (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. Polar Biol 29:413–423.
Jiang J (2007) Linear and Generalized Linear Mixed Models and Their Applications. Springer Science + Business Media, 271p.
Kalinowski J, Witek Z (1980) Diurnal vertical distribution of krill aggregations in the West Antarctic. Polish Polar Res 1:127–146.
Kato A, Ropert-Coudert Y, Naito Y (2002) Changes in Adelie penguin breeding populations in Lutzow-Holm Bay, Antarctica, in relation to sea-ice conditions. Polar Biol 25:934–938. doi: 10.1007/s00300-002-0434-3
Kato A, Yoshioka A, Sato K (2009) Foraging behavior of Adélie penguins during incubation period in Lützow-Holm Bay. Polar Biol 32:181–186. doi: 10.1007/s00300-008-0518-9
Kembro J, Perillo M, Pury P, et al (2009) Fractal analysis of the ambulation pattern of Japanese quail. Br Poult Sci 50:161–170.

Kirkwood R, Robertson G (1997) The foraging ecology of female emperor penguins in winter. Ecol Monogr 67:155–176.
Knox GA (2006) Biology of the Southern Ocean. Second Edition. CRC Press, 640p.
Le Boeuf BJ, Laws RM (1994) Elephant seals: Population ecology, Behavior and Physiology. University of California Press.
Libertelli MM, Coria N, Marateo G (2003) Diet of the Adelie penguin during three consecutive chick rearing periods at Laurie Island. Polish Polar Res 24:133–142.
Lorentsen S (1996) Regulation of food provisioning in the Antarctic petrel Thalassoica antarctica. J Anim Ecol 65:381–388.
Lovejoy S (1985) Fractals properties of rain, and a fractal model. Tellus 37:209–232.
Luque SP (2007) Diving behaviour Analysis in R. An Introduction to the diveMove Package.
Luque SP, Fried R (2011) Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. PLoS One 6:1–9. doi: 10.1371/journal.pone.0015850
Lynch AH, Larue M (2014) First global census of the Adélie Penguin. Auk 131:457–466. doi: 10.1642/AUK-14-31.1
Lyver PO, Barron M, Barton KJ, et al (2014) Trends in the breeding population of Adélie penguins in the Ross Sea, 1981-2012: a coincidence of climate and resource extraction effects. PLoS One 9:e91188. doi: 10.1371/journal.pone.0091188
MacIntosh AJ, Alados C, Huffman M (2011) Fractal analysis of behaviour in a wild primate: behavioural complexity in health and disease. J R Soc Interface 8:1497–509.
MacIntosh AJJ (2014) The Fractal Primate : Interdisciplinary Science and the Math behind the Monkey. Primate Res 30:95–119.
Macintosh AJJ, Pelletier L, Chiaradia A, et al (2013) Temporal fractals in seabird foraging behaviour: diving through the scales of time. Sci Rep 3:1884. doi: 10.1038/srep01884
Mandelbrot B (1977) Fractals: form, chance and dimension. W.H. Freeman and Company, San Francisco.
Martin J, Gordon R, Fitzwater S (1990) Iron in Antarctic waters. Nat Geosci 345:156–158.
Martin P, Bateson P (1993) Measuring Behaviour: An Introductory Guide. Cambridge University Press
Meier WN, Fetterer F, Stewart JS, Helfrich S (2015) How do sea-ice concentrations from operational data compare with passive microwave estimates? Implications for improved model evaluations and forecasting. Ann Glaciol 56:332–340. doi: 10.3189/2015AoG69A694
Meier WN, Gallaher D, Campbell GG (2013) New estimates of Arctic and Antarctic sea ice extent during September 1964 from recovered Nimbus I satellite imagery. Cryosph 7:699–705. doi: 10.5194/tc-7-699-2013
Meyer X (2016) Does complexity in behavioral organization allow seabirds to adapt to changes in their environment? phD Thesis, Université de Strasbourg.
Muggeo VMR (2015) Regression Models with Breakpoints/Changepoints Estimation. CRAN version 0.5-14.
Nicol S (2006) Krill, Currents, and Sea Ice: Euphausia superba and Its Changing Environment. Bioscience 56:111. doi: 10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2
Noda T, Kikuchi DM, Takahashi A, et al (2016) Pitching stability of diving seabirds during underwater locomotion: a comparison among alcids and a penguin. Anim Biotelemetry 4:1–15. doi: 10.1186/s40317-016-0102-y
NSDIC National Snow and Ice Data Center [Accessed 1 March 2016] "All About Sea Ice." https://nsidc.org/cryosphere/seaice/data/terminology.html

Orians G, Pearson N (1979) On the theory of central place foraging. In: Horn D, Mitchell R, Stairs G (eds) Analysis of Ecological Systems. The Ohio State University Press, Columbus, pp 154–177
Pelletier L, Kato A, Chiaradia A, Ropert-Coudert Y (2012) Can thermoclines be a cue to prey distribution for marine top predators? a case study with little penguins. PLoS One 7:4–8.
Peng C, Buldyrev S, Goldberger A, et al (1992) Long-range correlations in nucleotide sequences. Nature 356:168–170.
Peng C, Havlin S (1995) Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. Chaos 5:82–87.
Peng C, Mietus J, Hausdorff J, et al (1993) Long-range anticorrelations and non-Gaussian behavior of the heartbeat. Phys Rev Lett 70:1343.
Piatt JF, Sydeman WJ, Wiese F (2007) Introduction: A modern role for seabirds as indicators. Mar Ecol Prog Ser 352:199–204. doi: 10.3354/meps07070
Pinheiro J, Bates D, DebRoy S, et al (2016) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128.
Pütz K, Cherel Y (2005) The diving behaviour of brooding king penguins (Aptenodytes patagonicus) from the Falkland Islands: Variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies. Mar Biol 147:281–290. doi: 10.1007/s00227-005-1577-x
Quetin L, Ross R (2001) Environmental variability and its impact on the reproductive success of Antarctic krill. Am Zool 41:74–89.
Redfern J V, Ferguson MC, Becker EA, et al (2006) Techniques for cetacean - habitat modeling. Mar Ecol Prog Ser 310:271–295. doi: 10.3354/meps310271
Reynolds A, Ropert-Coudert Y, Kato A, et al (2015) A priority-based queuing process explanation for scale-free foraging behaviours. Anim Behav 108:67–71.
Richardson A, Polocsanska E (2008) Under-Resourced, Under Threat. Science 320:1294–1295.
Ridoux V, Offredo C (1989) The diets of five summer breeding seabirds in Adélie Land, Antarctica. Polar Biol 9:137–145. doi: 10.1007/BF00297168
Riley M, Turvey M (2002) Variability and determinism in motor behavior. J Mot Behav 34:99–125.
Ropert-Coudert Y, Kato A, Baudat J, et al (2001) Feeding strategies of free-ranging Adélie penguins Pygoscelis adeliae analysed by multiple data recording. Polar Biol 24:460–466. doi: 10.1007/s003000100234
Ropert-Coudert Y, Kato A, Chiaradia A (2009) Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. Proc Biol Sci 276:4105–9. doi: 10.1098/rspb.2009.1399
Ropert-Coudert Y, Kato A, Gremillet D, Grenner F (2012) Bio-logging: recording the ecophysiology and behaviour of animals moving freely in their environment. In: Le Galliard J-F, Guarini J-M, Gaill F (eds) Sensors for ecology: towards an integrated knowledge of ecosystems. pp 17–41
Ropert-Coudert Y, Kato A, Meyer X, et al (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. Ecography 8:111–113. doi: 10.1111/ecog.01182
Ropert-Coudert Y, Kato A, Sato K, et al (2002) Swim speed of free - ranging Adélie penguins Pygoscelis adeliae and its relation to the maximum depth of dives. J Avian Biol 33:94–99.
Ropert-Coudert Y, Kato A, Wilson RP, Cannell B (2006) Foraging strategies and prey encounter rate of free-ranging Little Penguins. 149:139–148. doi: 10.1007/s00227-005-0188-x

Ropert-Coudert Y, Sato K, Kato A, et al (2000) Preliminary investigations of prey pursuit and capture by king penguins at sea. Polar Biosci 13:101–112.
Ropert-Coudert Y, Wilson R (2005) Trends and perspectives in animal- attached remote sensing. Front Ecol Env 3:437–444. doi: 10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2
Sakamoto KQ (2012) Ethographer - WaterSurface ver.2.1. https://sites.google.com/site/ethographer/add-in/watersurface. Accessed 1 Jan 2016
Sakamoto KQ, Sato K, Ishisuka M, et al (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS One 4:e5379.
Sato K, Charrassin J, Bost C-A, Naito Y (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? J Exp Biol 207:4057–4065.
Sato K, Naito Y, Kato A, et al (2002) Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? J Exp Biol 205:1189–1197.
Schaefer M (1954) Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bull Inter-American Trop tuna Comm 1:25–56.
Schwartz M, Boness D, Schaeff C, et al (1999) Female-solicited extrapair matings in Humboldt penguins fail to produce extrapair fertilizations. Behav Ecol 10:242–250. doi: 10.1093/beheco/10.3.242
Sedwick PN, DiTullio GR (1997) Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. Geophys Res Lett 24:2515–2518.
Shimada I, Minesaki Y, Hara H (1995) Temporal fractal in the feeding behavior of Drosophila melanogaster. J Ethol 13:153–158.
Shlesinger M, West B (1991) Complex fractal dimension of the bronchial tree. Phys Rev Lett 67:2106–2108.
Sinervo B (1997) Optimal Foraging Theory: Constraints and Cognitive Processes. Behav Ecol 105–130.
Smith A (1984) Plants, fractals, and formal languages. Comput Graph (ACM) 18:1–10.
Smith RC, Ainley D, Baker K, et al (1999) Marine Ecosystem Sensitivity to Climate Change. Bioscience 49:393–404. doi: 10.2307/1313632
Smith W, Nelson D (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: Spatial coherence with the density field. Science 227:163–166.
Sommerfeld J, Kato A, Ropert-Coudert Y, et al (2015) Flexible foraging behaviour in a marine predator, the Masked booby (Sula dactylatra), according to foraging locations and environmental conditions. J Exp Mar Bio Ecol 463:79–86. doi: 10.1016/j.jembe.2014.11.005
Southwell C, Mckinlay J, Emmerson L, et al (2010) Improving estimates of Adélie penguin breeding population size : developing factors to adjust one-off population counts for availability bias. CCAMLR Sci 17:229–241.
Stretch JJ, Hamner PP, Hamner WM, et al (1988) Foraging behavior of Antarctic krill Euphausia superba on sea ice microalgae. Mar Ecol Prog Ser 44:131–139.
Takahashi A, Watanuki Y, Sato K, et al (2003) Parental foraging effort and offspring growth rate in Adélie penguins: does working hard improve reproductive success? Funct Ecol 17:590–597.
Taqqu M, Teverovsky V, Willinger W (1995) Estimatos for long-range dependence: an empirical study. Fractals 3:785–788.
Tarboton D, Bras R, Rodriguez-Iturbe I (1988) The fractal nature of river networks. Water Resour Res 24:1317–1322.

Taylor R, Wilson P, Thomas B (1990) Status and trends of Adélie penguin populations in the Ross Sea region. Polar Rec (Gr Brit) 26:293–304.
Thiebot J, Ito K, Raclot T, et al (2016) On the significance of Antarctic jellyfish as food for Adélie penguins, as revealed by video loggers. Mar. Biol. 163:108.
Trathan PN, Agnew D (2010) Climate change and the Antarctic marine ecosystem: an essay on management implications. Antarct Sci 22:387–398. doi: 10.1017/S0954102010000222
Trathan PN, Garcia-Borboroglu P, Boersma D, et al (2015) Pollution, habitat loss, fishing, and climate change as critical threats to penguins. Conserv Biol 29:31–41. doi: 10.1111/cobi.12349
Viviant M, Jeanniard-du-Dot T, Monestiez P, et al (2016) Bottom time does not always predict prey encounter rate in Antarctic fur seals.
Viviant M, Monestiez P, Guinet C (2014) Can we predict foraging success in a marine predator from dive patterns only? Validation with prey capture attempt data. PLoS ONE 9,e88503.
Volkman NJ, Presler P, Trivelpiece WZ (1980) Diets of pygoscelid penguins at King George Island, Antarctica. Condor 82:373–378. doi: 10.2307/1367558
Wang S, Bailey D, Lindsay K, et al (2014) Impact of sea ice on the marine iron cycle and phytoplankton productivity. Biogeosciences 11:4713–4731. doi: 10.5194/bg-11-4713-2014
Warwick-Evans V, Atkinson P, Arnould J, et al (2016) Changes in behaviour drive inter-annual variability in the at-sea distribution of nrthern gannets. Mar Biol 163:1–15. doi: 10.1007/s00227-016-2922-y
WaveMetrics I (2015) Igor Pro Manual, Version 6.37.
Weeks W, Ackley S (1982) The growth, structure, and properties of sea ice. CCREL Monograph 82-1, United States Army Cold Regions Research and Engineering Laboratory, Hanover, NH
Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness : factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622.
Widmann M, Kato A, Raymond B, et al (2015) Habitat use and sex-specific foraging behaviour of Adélie penguins throughout the breeding season in Adélie Land, East Antarctica. Mov Ecol 3:30. doi: 10.1186/s40462-015-0052-7
Wilson E (1907) Aves. In: British National Antarctic Expedition, 1901-1904. Vol 2. Zoology. British Museum Natural History, London, pp 1–31
Wilson P, Ainley DG, Nur N, et al (2001) Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Mar Ecol Prog Ser 213:301–309.
Wilson R (1995) Foraging ecology. In: Williams T (ed) The Penguins. Oxford University Press, Oxford, pp 81–106
Wilson R, Wilson M-P (1989) Tape: a package attachment technique for penguins. Wildl Soc Bull 17:77–79.
Wilson RP (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? Mar Ecol Prog Ser 94:101–104.
Wilson RP (2003) Penguins predict their performance. Mar Ecol Prog Ser 249:305–310.
Woehler E (1995) Consumption of Southern Ocean resources by penguins. In: Dann P, Norman I, Reilly P (eds) The penguins: ecology and management. Surrey Beatty & Sons, Chipping Norton, pp 267–291
Woehler E, Johnstone G (1991) Status and Conservation of the Seabirds of the Australian Antarctic Territory. In: Croxall JP (ed) Seabird Status and Conservation : A Supplement. ICBP Technical Publication No. 11. pp 279–308

Womble JN, Horning M, Lea MA, Rehberg MJ (2013) Diving into the analysis of time-depth recorder and behavioural data records: A workshop summary. Deep Res Part II Top Stud Oceanogr 88-89:61–64. doi: 10.1016/j.dsr2.2012.07.017

Wood S (2006) Generalized additive models: an introduction with R. J Stat Softw. doi: 10.1111/j.1541-0420.2006.00574.x

Ydenberg R, Clark C (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. J Theor Biol 139:437–449.

Zimmer I, Ropert-Coudert Y, Poulin A, et al (2011) Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: a case study on female little penguins. Mar Biol 158:715–722.

Zuur A, Ieno E, Smith G (2007) Analysing Ecological Data. Springer Science + Business Media, New-York

Appendices

Appendix I: Simplified R-Script: The extraction and calculation of sea-ice parameters for one year.

```
#### Camille Le Guen - February 2016 - PCA on diving data Adélie penguins DDU


### Data and packages
library(raster)
library(devtools)
library(rgdal)
ice1995 <- brick("seaicedaily_NDJ_1995.grd")
# The .grd file contains 92 layers: one layer for each day of the season (from 01-nov to 31-jan).

### Plot a map of sea-ice concentration for each day

mapLL <- projectRaster(ice1995, crs =  "+proj=longlat +ellps=WGS84")

# Plot for the first day (01-nov)
# The navyblue colour corresponds to open water and aliceblue to sea ice.
plot(mapLL[[1]], xlim=c(134,144), ylim=c(-68,-62), col=colorRampPalette(c("navyblue", "aliceblue"))(100), zlim = c(0, 100) , xlab="Longitude", ylab="Latitude", main= "Sea ice concentration")

# Plot for the last day (31-jan)
plot(mapLL[[92]],xlim=c(134,144), ylim=c(-68,-62), col=colorRampPalette(c("navyblue", "aliceblue"))(100),zlim = c(0, 100) , xlab="Longitude", ylab="Latitude", main= "Sea ice concentration")

mapLL<-trim(mapLL) # isolates the map from the background of the plot
text(locator(1),"Sea ice concentration (%)", cex=1, srt=90, xpd=T)
points(140.01,-66.40,col="black",lwd=1,pch=16) # indicates the location of the colony on the map


### Calculation of mean sea-ice concentration for each day

daymean1995<-data.frame(date=getZ(ice1995),meanice=cellStats(ice1995, mean,na.rm=T))
# Calculates a single mean value of SIC for each day
write.csv2(daymean1995$meanice, file='daymean1995.csv')
# Creates a file gathering the 92 values of SIC (one value for a day)

### Calculation of sea-ice extent (area covered by sea ice)

# Define our region of interest
mapLL <- projectRaster(ice1995, crs =  "+proj=longlat +ellps=WGS84")
roi=raster(xmn=134,xmx=144,ymn=-68,ymx=-62) # Define our region of interest in long/lat
lonlatproj="+proj=longlat +ellps=WGS84" # Define the projection
projection(roi)=lonlatproj
```

```
 # Check that everything has worked as expected doing daily plots (not presented here)
# Extract the sea ice in our region of interest

for (x in 1:92) {
ice_roi=intersect(mapLL[[x]],roi) # Select the cells of the region of interest
icegrid_cellarea=area(ice_roi) # Calculate the area of every grid cell in the region of interest
# !!!!! All the cells don't have the same area!!!!!!!!
 area<-sum(values(icegrid_cellarea),na.rm=T) # Calculate the total area of the region of interest

# We need to select the cells which are covered by sea ice. Usually a concentration of 15% is used as the cutoff to define open water

ice_mask=ice_roi>=15 # This will have values of 1 where ice was >=15%, and 0 otherwise

# Now mask out the area information with the sea ice information
temp=ice_mask*icegrid_cellarea # values will be 0 for open-water cells and 1 when sea ice covered
ice_area=sum(values(temp),na.rm=TRUE) ## total area of ice-covered grid cells in region of interest

# or, to calculate total sea ice area
a<-sum(values(ice_roi*icegrid_cellarea/100),na.rm=TRUE)
print(a)
}

### Distance colony - open water

map<-crop(mapLL[[1]], extent(134,144,-67,-62))
plot(map,xlim=c(134,144), ylim=c(-68,-62),col=rainbow(20),zlim = c(0,100) , xlab="Longitude", ylab="Latitude", main= "Sea ice concentration")
points(140.01,-66.40,col="black",lwd=1,pch=16) # indicates the location of the colony
a<-click(map,n=1, id=FALSE, xy=TRUE) # Select the closest cell of open water with the computer mouse. A contains two values: a$x and a$y, its two coordinates.
pointDistance(c(140.01,-66.40),c(a$x,a$y),lonlat=TRUE) # use its coordinates to calculate the distance between the colony and this point (in meters)

### Distance colony - polynya
```

The same process was applied for polynyas, meaning that we use the coordinates of the closest point with 15% of SIC or less to calculate the distance between the colony and the first polynya.

Appendix II: Simplified R-Script: GAM performed on Adélie penguins' breeding success.

```
#### Camille Le Guen - April 2016 - Breeding success Adélie Penguins


## Data and packages
repro.all<-read.table("breeding success all years.csv", sep=";", header=TRUE)
head(repro.all)
library(mgcv)

## Choice to consider all years or not
repro.all<-subset(repro.all, subset=c(repro.all$Year!=2014))
repro.all<-subset(repro.all, subset=c(repro.all$Year!=2001))

## Flexible way of specifying the colouring
tracking_years <- c(1995,1998,2001,2007,2009,2010,2011,2012,2014) # 9 years for tracking data
plot_colour <- rep("cadetblue2",nrow(repro.all)) # colour by default
plot_colour[repro.all$Year %in% tracking_years] <- "cadetblue" # colour for tracking data

# Visualisation of data
plot(repro.all$SIC.global, repro.all$Breeding.success, tck=0.02, cex.lab=1.3, pch=16, las=1,
xlab="Global sea ice concentration (%)", cex.axis=1,ylab="Breeding success", col=plot_colour,
main="Breeding success of Adélie penguins")
box(lwd=2)
legend("topright", cex=0.7, legend=c("Data - study period","Data - added"),
col=c("cadetblue","cadetblue2"), pch=16)

###Modelling part

# One issue in using the cubic regression spline basis for the smooth term (bs="cr") is that the results
can be sensitive to where the knots are placed (and how many knots), and choosing these values is not
always obvious. By default, k=10 knots and they are placed evenly throughout the values of
SIC.global. In this case, we have a small data set (20 rows = 20 years) and the SIC.global values are
not evenly spaced (there are a lot of values around 17-22%). So by default, bs="cr" will tend to place
multiple knots around 17 and 22. This will tend to overfit in these regions, which explains why the
curve using 10 knots looks too wiggly.

# Deal with overfitting

# Test 1: amount of smoothing not fixed with cubic regression spline
model.test<-gam(Breeding.success ~ s(SIC.global, fx=F, k=-1, bs="cr"), data=repro.all)
plot(model.test)
place.knots(repro.all$SIC.global,10) ## to see where R will place the knots with
# It gives  [1] 14.33 16.79 17.14 17.46 18.22 20.46 21.49 22.26 29.84 37.15 so, yes, it is putting
multiple knots around 17 and 22. One way to avoid this is to reduce the number of knots (e.g. k=5) as
Zuur et al. (2009) suggested it, but in doing this the result might still be sensitive where those knots
are placed.
model.test2<-gam(Breeding.success ~ s(SIC.global,k=5, bs="cr"), data=repro.all)
If you look at gam.check(model.test2) below it is suggesting that k=5 may not be enough knots.
Another way to get around the overfitting seen in model.test is to use the default 10 knots but place
them evenly between the minimum and maximum values of SIC.global.
kn <-list(SIC.global=seq(from=min(repro.all$SIC.global),to=max(repro.all$SIC.global),
length.out=10))
```

```
fit10 <- gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)),data=repro.all,knots=kn)
# However, this looks pretty similar to model.test2. If we reduce the number of knots (but still keeping them evenly spaced) we get largely the same result
kn <- list(SIC.global=seq(from=min(repro.all$SIC.global),to=max(repro.all$SIC.global), length.out=8))
fit8 <- gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)), data=repro.all,knots=kn)
# AIC-based model selection says they are equally good
AIC(fit8,fit10)
# However, evenly-spaced knots is perhaps not a great idea, because it places knots at values where there are no data points. It might be better to put the knots near data points, but just make sure that we don't put multiple knots close to each other. What if we choose knots at unique values of SIC after first rounding the SIC values to the nearest multiple of 2
kn <- list(SIC.global=sort(unique(round(repro.all$SIC.global/2)*2)))
fit <- gam(Breeding.success~s(SIC.global,bs="cr",k=length(kn$SIC.global)),data=repro.all,knots=kn)
# another way to avoid the overfitting is to use the default thin-plate spline basis for the smooth. This doesn't require knot placement (it places one knot at each data point) and the smoothness penalty works differently (and seems to be more reliable in this case). This gives the same smooth fit as we are seeing previously. But tp splines are harder to explain than cubic regressions, so if you want to stay with bs="cr" I would use evenly-placed knots. We are getting basically the same curves for all of these options, so we can be fairly confident that these are reasonable fits.


# Should the year 2001 be included in the analysis or not?

# If we look at the plot of breeding success against SIC, the far-left point has very low breeding success as well as very low sea ice. This was year 2001, which was a very unusual year for sea ice (Iceberg B15). We could try to perform the GAM with and without 2001 to see if this point is having a large effect on the fit.This is what we get with 2001:
repro.all<-read.table("breeding success all years.csv", sep=";", header=TRUE)
fit_tp <- gam(Breeding.success ~ s(SIC.global),data=repro.all)
plot(fit_tp)
# In this plot (and all the previous smooth fits) the breeding success starts low for SIC around 15%, then peaks at SIC around 22%, then drops again. Here is what we get without 2001:
fit_tp2 <- gam(Breeding.success ~ s(SIC.global),data=subset(repro.all,Year!=2001))
plot(fit_tp2)
# Now, breeding success does not drop for low SIC. That trend is being driven by the 2001 season.


# Example of graph of a chosen model

model<-model.test2

fit <- predict(model ,se = TRUE)$fit
se <- predict(model ,se = TRUE)$se.fit
lcl <- fit - 1.96 * se
ucl <- fit + 1.96 * se
plot(repro.all$SIC.global, repro.all$Breeding.success, tck=0.02, cex.axis=1, cex.lab=1.3, pch=16, las=1, xlab="Sea ice concentration (%)", ylab="Breeding success", col=c("cadetblue","cadetblue2","cadetblue2","cadetblue","cadetblue2","cadetblue2","cadetblue","cadetblue2","cadetblue2","cadetblue2","cadetblue2","cadetblue2","cadetblue","cadetblue2","cadetblue","cadetblue","cadetblue","cadetblue2","cadetblue"),main="Breeding success of Adélie penguins all years - 5 knots")
```

```
i.for <- order(repro.all$SIC.global )
i.back <- order(repro.all$SIC.global , decreasing = TRUE )
x.polygon <- c(repro.all$SIC.global[i.for] , repro.all$SIC.global[i.back] )
y.polygon <- c( ucl[i.for] , lcl[i.back] )

polygon( x.polygon , y.polygon , col = "gray88" , border = NA )
lines(repro.all$SIC.global[i.for] , fit[i.for], col = "gray48" , lwd = 3 )

abline(h=mean(repro.all$Breeding.success) , lty = 2, col="indianred2" )
text(35, 0.93,labels="Mean", cex=0.8, col="indianred2")
axis(side=2,lwd=2,lwd.ticks = 2,labels=F,tck=0.02)
axis(side=1,lwd=2,lwd.ticks = 2,labels=F,tck=0.02)
box(which="plot",lty="solid",lwd=2)
legend("topright", cex=0.8, legend=c("Data - study period", "Data - added"),
col=c("cadetblue","cadetblue2"), pch=16)
```

Appendix III: Presentation of two correlation structure applicable to the mixed models: the compound symmetry and the first order autoregressive structure.

$$\sigma^2 \begin{pmatrix} 1 & \rho & \rho \\ \rho & 1 & \rho \\ \rho & \rho & 1 \end{pmatrix} \qquad \sigma^2 \begin{pmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{pmatrix}$$

Compound symmetry AR1

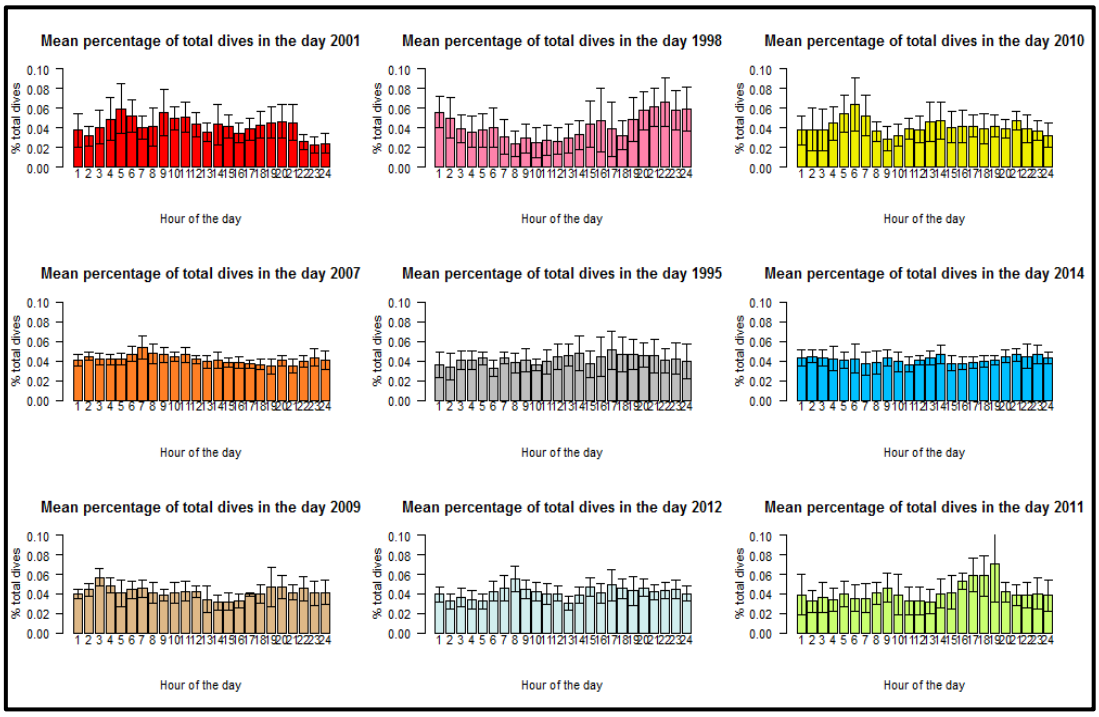
Appendix IV: Simplified R-Script: mixed model applied on diving efficiency for all years including all dives at the seasonal scale.

```
#### Camille Le Guen - May 2016 - Script mixed models - Adélie P data DDU 1995-2014

### Data and packages
library(nlme) ; library(lme4) ; library(lattice) ; library(MASS) ; library(MuMIn) ; library(mgcv) ; library(ggplot2) ; library(car) ; library(MASS) ;library(plyr)
test3<-read.table("Multiyear diving data first trip.csv",header=T,sep=";")
test3$Year<-as.factor(test3$Year)
head(test3)
str(test3)

### Subset required (because of R memory issues)
test3 <- test3[sample(1:nrow(test3),7000),]

### Fraction of zero
temp<-ddply(test3,.(Year), function (z)data.frame(fraction_with_zero=sum(z$Bottom.duration<1e-06)/nrow(z)))
ggplot(temp,aes(Year,fraction_with_zero))+
  geom_bar(stat="identity")+
  labs(y="Fraction of dives with a bottom duration of zero")
# There are a lot of zero in the dataset. That is why we tried delta modelling (script not presented here). We need to find a probability distribution that can handle this.

### Rescaling variables for convergence purposes

test3$SIC.global.demeaned<-test3$SIC.global-mean(test3$SIC.global)
test3$SIC.global.rescaled<-test3$SIC.global.demeaned/sd(test3$SIC.global)
test3$SIE.global.demeaned<-test3$SIE.global-mean(test3$SIE.global)
test3$SIE.global.rescaled<-test3$SIE.global.demeaned/sd(test3$SIE.global)
test3$dOW.global.demeaned<-test3$dOW.global-mean(test3$dOW.global)
test3$dOW.global.rescaled<-test3$dOW.global.demeaned/sd(test3$dOW.global)

### Modelling part

## Random intercept model (RI) or random slope and intercept model (RS)? Comparison using the ML method.

  m2.ri.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled +  dOW.global.rescaled + SIC.global.rescaled:SIE.global.rescaled, control=list(niterEM=100000), random=~1|Bird.ID, method="ML",data=test3)
  m2.rs.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled + dOW.global.rescaled + SIC.global.rescaled:SIE.global.rescaled, control=list(niterEM=100000), random=~SIC.global.rescaled|Bird.ID, method="ML",data=test3)

AIC(m2.ri.ML,m2.rs.ML)
model<-m2.rs.ML
summary(model)
anova(model)
## In favour of the random intercept and slope model (RS)

## Selection of variables
```

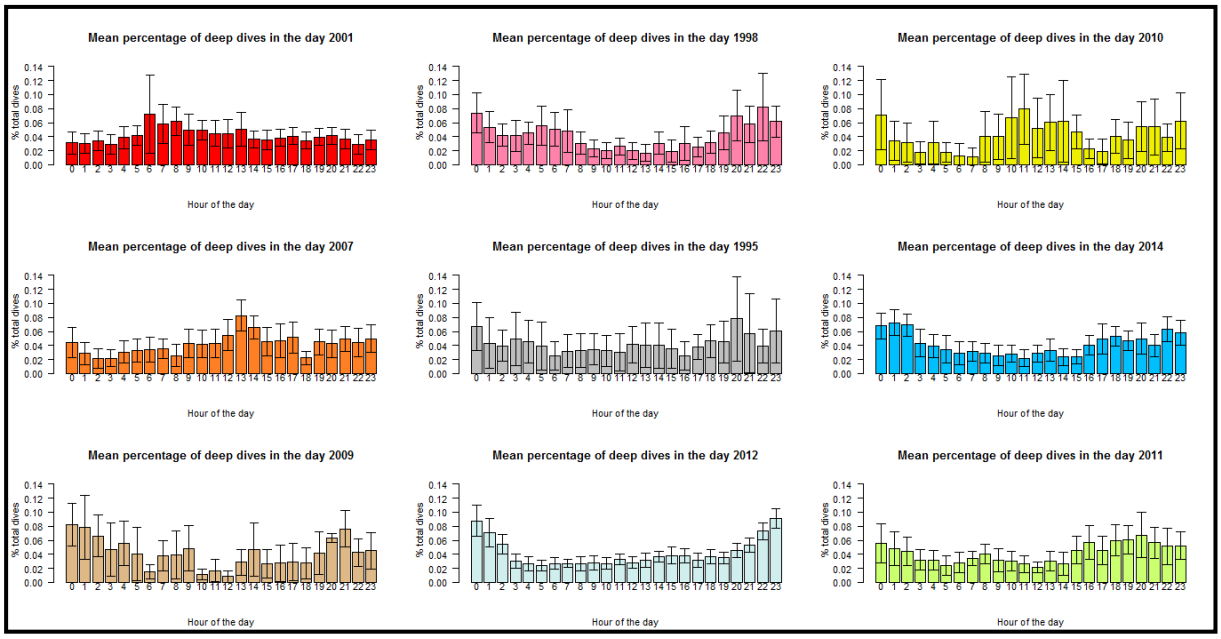
```
m3.rs.a.ML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled,
          control=list(niterEM=100000),
          random=~SIC.global.rescaled|Bird.ID, method="ML",data=test3)

AIC(m2.rs.ML,m3.rs.a.ML)
#better AIC for m3.rs.a.ML

## Estimation of the different parameters using the REML method.

  m3.rs.a.REML<-lme(Dive.intensity ~ SIC.global.rescaled + SIE.global.rescaled,
          control=list(niterEM=100000),
          random=~SIC.global.rescaled|Bird.ID, method="REML",data=test3)

r.squaredGLMM(m3.rs.a.REML)
summary(m3.rs.a)
anova(m3.rs.a)
AIC(m2.rs,m3.rs.a)
#both parameters are significant

## Hypothesis testing for the chosen model

model<-m3.rs.a.REML
plot(resid(model))
hist(resid(model))
qqnorm(resid(model))
qqline(resid(model), col="red")

## Making graphs

new.dat<-data.frame(Dive.intensity=test3$Dive.intensity, Year=test3$Year,
                SIC.global=test3$SIC.global,SIC.global.rescaled=test3$SIC.global.rescaled,
                SIE.global=test3$SIE.global, SIE.global.rescaled=test3$SIE.global.rescaled,
                dOW.global=test3$dOW.global, dOW.global.rescaled=test3$dOW.global.rescaled,
                Bird.ID=test3$Bird.ID)
ggplot(data=new.dat, aes(x=SIC.global, y=Dive.intensity))+
  geom_point(size=2)+
  geom_line(aes(y=predict(model), group=Bird.ID),colour="orange")+
  geom_line(data=new.dat,aes(y=predict(model,level=0,newdata=new.dat)),colour="palevioletred1",
lwd=2)+

geom_line(data=new.dat,aes(y=predict(model,level=1,newdata=new.dat)),colour="lightgoldenrod2",l
wd=2)+
  stat_summary(data=new.dat, fun.data=mean_se, geom="pointrange", color="red")
  geom_smooth(color="skyblue3", lwd=2, se=T, method=loess)
```

Appendix V: Day/night analysis performed on a) the frequency of dives considering all dives, b) the frequency of dives considering deep dives only, c) the mean maximum depth considering all dives and d) the mean maximum depth considering deep dives only. Plots are organised according to an increasing gradient of sea-ice concentration. Values for each year are grand mean of all birds + SE.

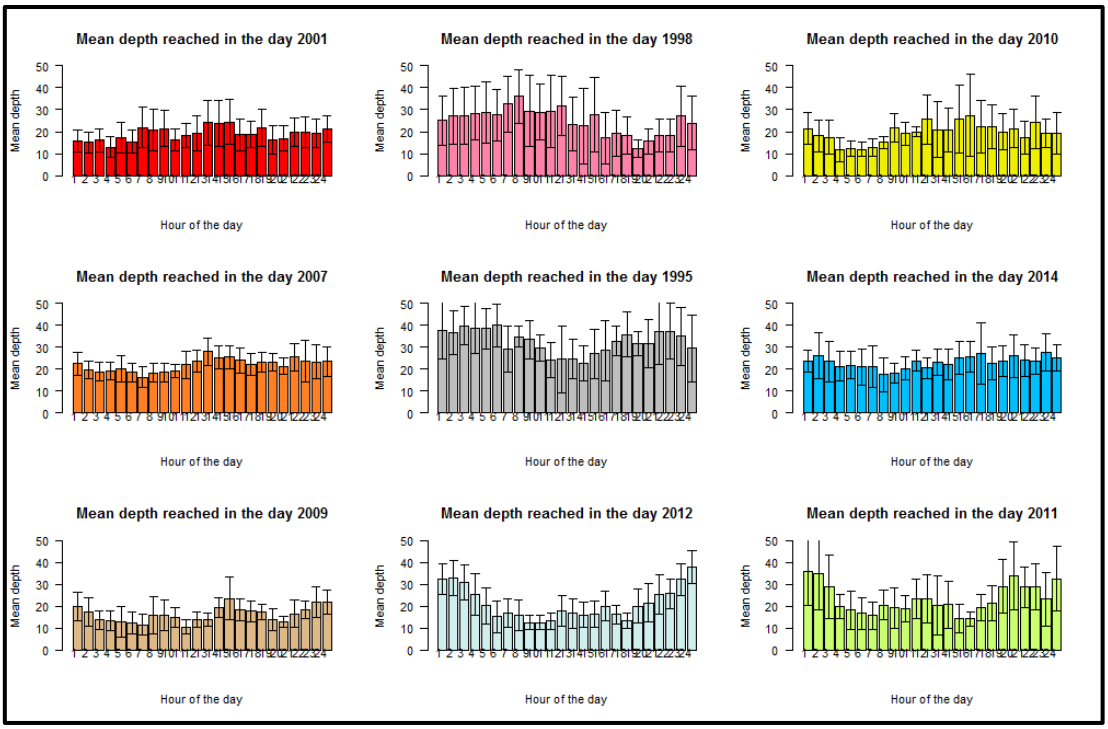
a)



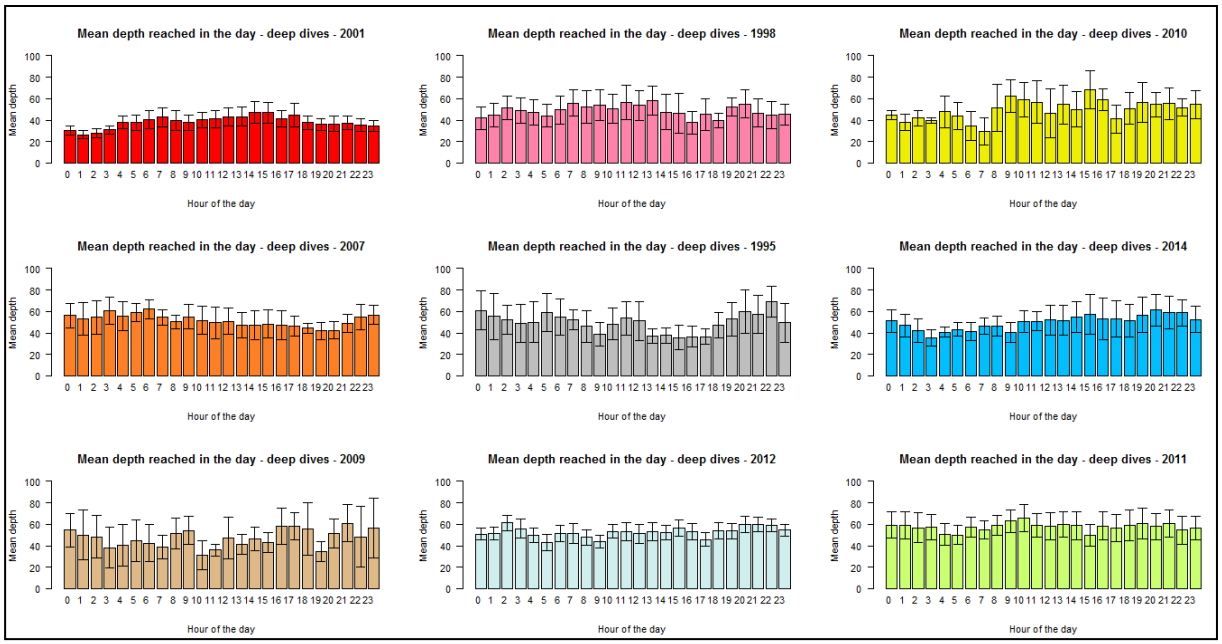
b)



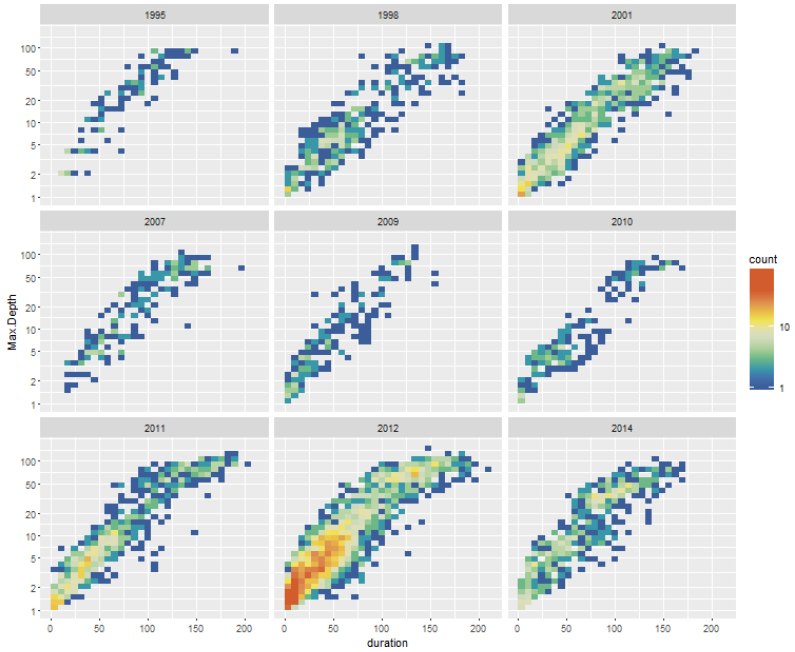
c)


Mean depth reached in the day 2001
Mean depth reached in the day 1998
Mean depth reached in the day 2010
Mean depth reached in the day 2007
Mean depth reached in the day 1995
Mean depth reached in the day 2014
Mean depth reached in the day 2009
Mean depth reached in the day 2012
Mean depth reached in the day 2011
Mean depth
Hour of the day

d)


Mean depth reached in the day - deep dives - 2001
Mean depth reached in the day - deep dives - 1998
Mean depth reached in the day - deep dives - 2010
Mean depth reached in the day - deep dives - 2007
Mean depth reached in the day - deep dives - 1995
Mean depth reached in the day - deep dives - 2014
Mean depth reached in the day - deep dives - 2009
Mean depth reached in the day - deep dives - 2012
Mean depth reached in the day - deep dives - 2011
Mean depth
Hour of the day

Appendix VI: Study of the relationship between dive depth and dive duration for all years.



Density plot representing the relationship between dive duration and maximum depth for each year

Results of correlation parameters concerning the relationship between depth and duration for each year.

Year	*Depth vs Duration (Depth=a*Duration+b)*			
	B	a	r^2	p-value (t)
1995	-7.60	0.569	0.795	***
1998	-9.10	0.417	0.685	***
2001	-5.66	0.332	0.691	***
2007	-10.59	0.500	0.785	***
2009	-5.73	0.464	0.769	***
2010	-6.59	0.441	0.741	***
2011	-10.55	0.502	0.788	***
2012	-6.20	0.448	0.748	***
2014	-7.22	0.436	0.740	***

*** <2e-16

Appendix VII: Results of mixed models for each diving parameter.

Maximum depth	Significant explanatory variables	R^2c	R^2m	AIC	p-values
7 years all dives					
By season	SIE. Distance open water	0.1376	0.0212	16639.27	0.0010 0.0002
By day	Polynya	0.1255	0.0295	16807.88	<0.0001
9 years deep dives only					
By season	SIC	0.417	0.0597	1442.75	0.0010
By day	Polynya	0.499	0.01	1292.87	0.0053

Post-dive	Significant explanatory variables	R^2c	R^2m	AIC	p-values
7 years all dives (dives within bouts)					
By season	SIC	0.101	0.006	19273.06	0.0301
By day	SIC SIE	0.0859	0.0141	18977.17	0.0150 0.0199
7 years all dives (dives between bouts)					
By season	SIC Distance open water	0.1266	0.0091	10165.69	0.0027 0.0156
By day	SIC	0.1391	0.0170	11526.54	0.0021

Diving efficiency	Significant explanatory variables	R^2c	R^2m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.2780	0.0758	-8917.093	0.0094 <0.0001
By day	SIE	0.3237	0.0293	-8695.841	0.0032

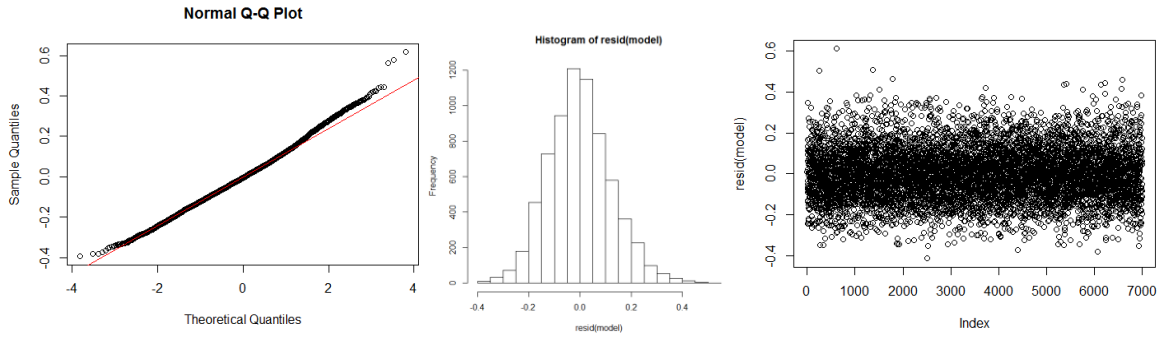
Descent rate	Significant explanatory variables	R^2c	R^2m	AIC	p-values
7 years all dives					
By season	SIC SIE	0.1590	0.0391	-5769.58	0.0076 <0.0001
By day	SIE Distance.open water Polynya	0.1295	0.0194	-5637.723	0.0062 0.0103 0.0031
9 years deep dives only					
By season	SIC SIE	0.2623	0.0463	-15540.09	0.0463 0.0001
By day	SIE	0.2799	0.0231	-15309.61	9.10^{-4}

TCPUE	Significant explanatory variables	R^2c	R^2m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.1571	0.0287	-20224.61	0.0012 0.0034
By day	SIC	0.1881	0.0231	-20342.81	2.10^{-4}

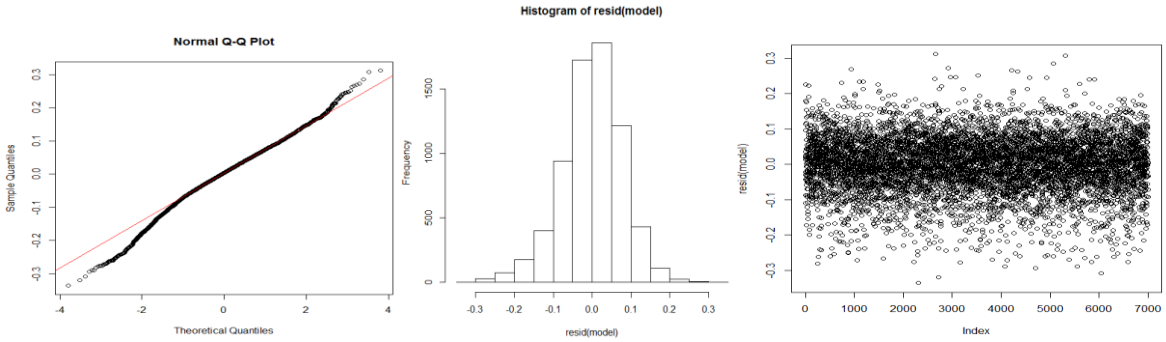
Nb wiggles	Significant explanatory variables	R^2c	R^2m	AIC	p-values
9 years deep dives only					
By season	SIC SIE	0.4156	0.1133	35367.23	<0.0001 <0.0001
By day	SIE	-	0.0744	33258.95	$5.06*10^{-6}$

Appendix VIII: Residuals of the chosen mixed model of each diving parameter.

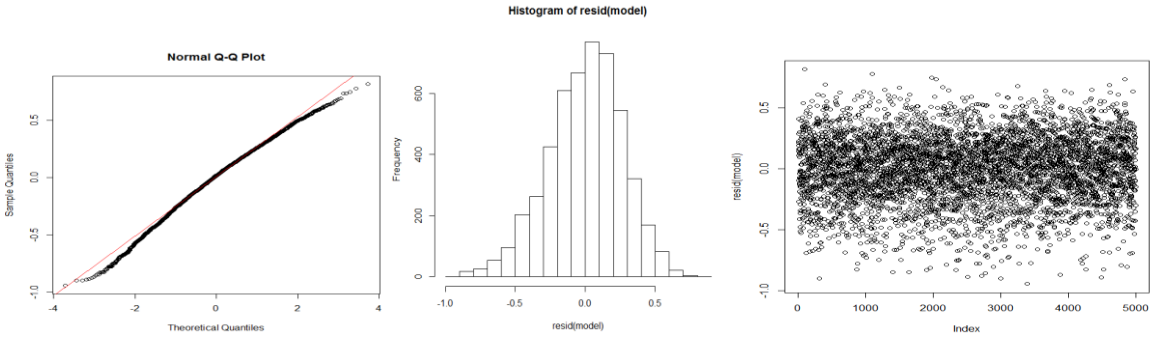
a) Diving efficiency



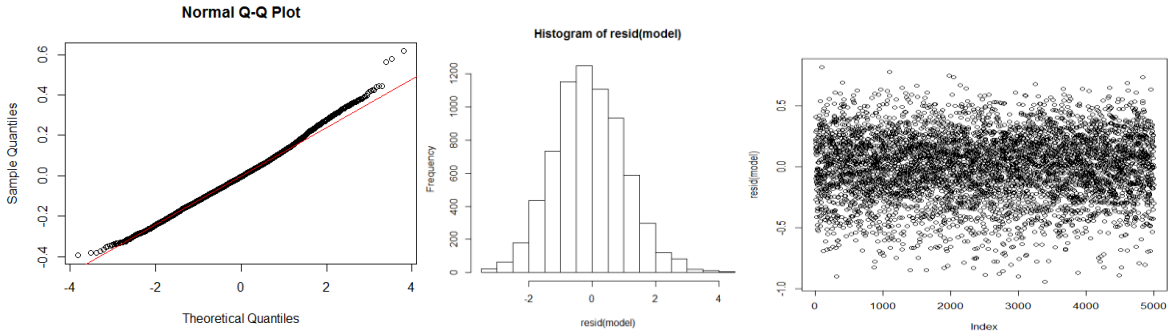
b) Descent rate



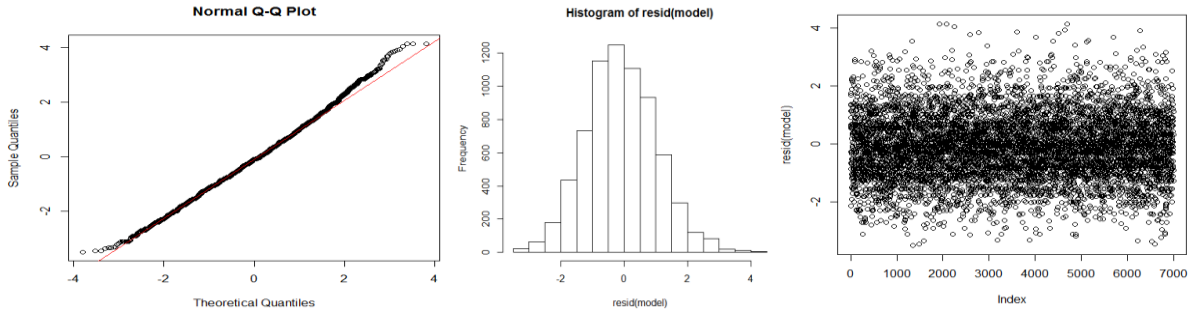
c) Maximum depth



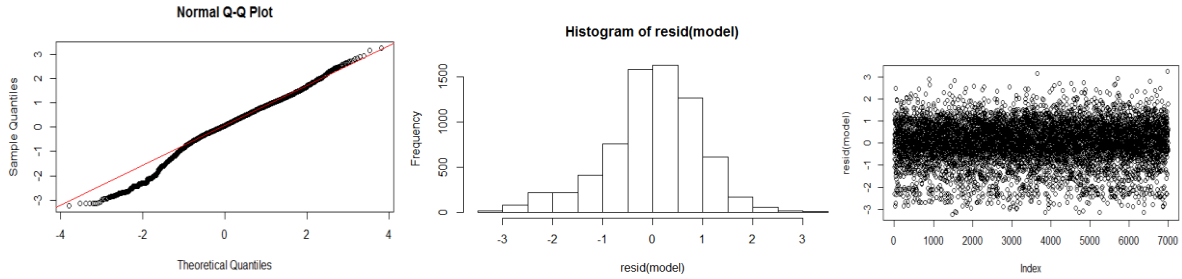
d) TCPUE



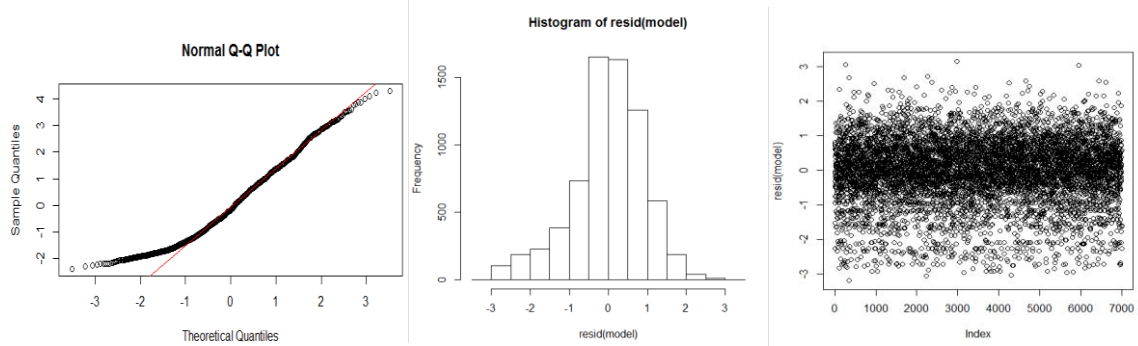
e) Number of wiggles



f) Post-dive duration (dives within bouts)



g) Post-dive duration (dives between bouts)



	Diplôme : Ingénieur Agronome Spécialité : Halieutique Spécialisation / option : Ressources et Ecosystèmes Aquatiques Enseignant référent : **Elodie Réveillac**

Auteur : **Camille Le Guen** Date de naissance* : 31/12/1992	Organisme d'accueil : **Centre d'Etudes Biologiques de Chizé** CNRS UMR 7372 79360 Villiers-en-Bois Maître de stage : **Yan Ropert-Coudert**
Nb pages : 59 Annexe(s) : 8	
Année de soutenance : 2016	

Titre français : Influence des conditions de glace de mer sur l'activité de plongée d'un prédateur marin: le manchot Adélie (*Pygoscelis adeliae*)
Titre anglais : Influence of sea ice conditions on the diving activity of a marine predator: the Adélie Penguin (*Pygoscelis adeliae*)

Résumé :
L'océan Austral fait l'objet de changements environnementaux majeurs, notamment concernant la glace de mer, connue pour influencer la structure et le fonctionnement de l'écosystème et pour affecter la survie et la reproduction des oiseaux marins en conditionnant la disponibilité et l'accès à la ressource. Le succès reproducteur du Manchot Adélie varie selon la couverture de glace, présentant un pic dans la gamme intermédiaire. Pour comprendre cette relation entre la glace de mer et le succès reproducteur, l'activité de plongée a également été étudiée. Cette étude a été menée sur 9 années contrastées en terme de glace à différentes échelles temporelles (saison, voyage alimentaire, journée et plongée). L'étude de l'organisation des plongées (analyses des fractales, des séquences de plongées et du rythme jour/nuit) a révélé que pour une gamme de glace moyenne, les oiseaux sont contraints dans leur comportement, avec une activité plus régulière et moins intense. L'analyse des paramètres de plongée a montré que lors des années intermédiaires, les individus ajustent leurs stratégies alimentaires pour maximiser la profitabilité des voyages alimentaires. Ils ciblent des zones plus profondes et ajustent leur effort de plongée pour rencontrer des proies de meilleure qualité ou en plus grande quantité. Ceci suggère l'existence d'une gamme optimale de glace chez ce prédateur marin longévif (autour de 20%). Le manchot Adélie étant considéré comme un bon eco-indicateur de l'Océan Austral, une étude à plus long terme est nécessaire pour mieux caractériser cette gamme optimale.

Abstract :
The Southern Ocean experiences major environmental variations, including changes in sea-ice cover, which is known to influence the ecosystem structure and functioning and to affect the survival and the reproduction of seabirds by limiting the availability and the access to food resources. Adélie penguins' breeding success varies according to sea ice with a peak at intermediate sea-ice coverage. To better understand this relationship, their diving activity was also investigated. This study was conducted over 9 contrasted years in term of sea ice using a multi-scale approach (season, foraging trip, day and dive). The analysis of the temporal organisation of dives (fractal analysis, bout analysis and day/night patterns) revealed that for intermediary sea-ice conditions, birds are less constrained in their behavior, having a more regular and less intense activity. The analysis of the diving metrics has shown that during intermediary years, individuals adjust their foraging strategies to maximize the profitability of foraging trips. They target higher depths and adjust their diving effort to encounter different prey of higher quality or quantity. However, during extreme years, the availability or the accessibility of prey can be limited. This suggests the existence of an optimal range of sea ice for this long-lived marine predator (around 20%). As the Adélie penguin can be considered as good eco-indicator of the Southern Ocean, working on a longer time-series is required to better characterize this optimal range.

Mots-clés : Océan Austral, glace de mer, succès reproducteur, activité de plongée, efficacité alimentaire, stratégie alimentaire, optimum écologique, manchot Adélie.
Key Words: Southern Ocean, sea ice, breeding success, diving activity, foraging efficiency, foraging strategies, ecological optimum, Adélie penguin.

VIII. Résumé de la these

Le développement et la miniaturisation croissante des appareils d'enregistrements embarquées (bio-logging) sur animaux a permis à l'étude du mouvement animal de rentrer dans son âge d'or et les principales priorités du domaine ont été récemment identifiées (Hays *et al.*, 2016). A ce titre, les auteurs soulignent la nécessité de comprendre comment l'environnement influence les mouvements mais également comment des règles a priori simples peuvent produire des motifs de mouvements complexes, tout ceci dans le contexte des changements globaux actuellement en cours. Ainsi, la compréhension des mécanismes à l'origine des mouvements animaux et de sa flexibilité peut ainsi apporter un nouveau regard sur les possibles adaptations comportementales que les animaux peuvent exhiber en réponse à des changements dans l'environnement, tout particulièrement ceux affectant les écosystèmes marins. Ces derniers comptent parmi les écosystèmes les moins étudiés en raison de leur étendue, du coût et de la difficulté de suivi. Afin de contourner ces difficultés, il a été montré que les changements affectant le bas de chaîne trophique étaient amplifiés chez les espèces au sommet de la chaîne trophique et que par conséquent, les réponses comportementales des prédateurs supérieurs peuvent être utilisées comme éco-indicateurs de l'écosystème. Les oiseaux marins, tels les manchots, sont des candidats parfaits au titre d'éco-indicateur. De plus, grâce au développement du bio-logging, nous pouvons suivre en détails sur de longues périodes leur comportement de recherche alimentaire.

Différentes méthodes ont été développées afin de déterminer comment les oiseaux marins ajustent leur comportement de recherche alimentaire aux changements environnementaux mais jusqu'à présent, la majorité des études ont uniquement utilisées des paramètres descriptifs. Dans certains cas, l'utilisation d'un trop grand nombre de ces paramètres descriptifs peut compliquer l'interprétation des changements observés dans les

paramètres de plongée (Zimmer *et al.*, 2011). Récemment, de nombreuses études ont montré que les analyses fractales pouvaient apporter une solution adéquate à l'étude des mécanismes à l'origine de la flexibilité du comportement de recherche alimentaire (MacIntosh, 2014).

Ma thèse s'inscrit donc dans ce cadre et a pour objectif d'étudier la flexibilité du comportement de recherche alimentaire chez deux espèces de manchots, le manchot pygmée (*Eudyptula minor*) et le manchot Adélie (*Pygoscelis adeliae*), sous le prisme des fractals. Ces deux espèces sont considérées comme des espèces indicatrices des changements environnementaux dans leurs milieux marins respectifs, à savoir l'Australie et la Nouvelle-Zélande pour le manchot pygmée et l'Antarctique pour le manchot Adélie. Le comportement de recherche alimentaire en mer de ces deux espèces a été suivi durant plusieurs années et sur plusieurs colonies (pour le manchot pygmée), et j'ai participé au total à deux campagnes de terrain durant l'été austral 2013-2014, l'une sur le manchot pygmée (2 mois à Phillip Island, Australie) et l'autre sur le manchot Adélie (3 mois à Dumont d'Urville, Antarctique). A partir des données de plongées obtenues, j'ai utilisé une Detrented Fluctuation Analysis (DFA) pour étudier la distribution séquentielle des périodes de plongée et des périodes de récupération en surface au cours du temps et mesurer la dépendance à long-terme dans les séquences de comportement. Les études dans ce domaine ont adopté le terme « complexité » afin de décrire la structure corrélative de la série temporelle utilisée (Bradbury & Verhencamp, 2014).

Afin de comprendre comment cet indice de complexité comportementale change en réponse à différentes variables écophysiologiques, j'ai dans un premier temps utilisé une situation dans laquelle l'oiseau était handicapé par un stress hydrodynamique (par exemple,

un enregistreur de profondeur ou une bague alaire) **(Article A)**. Les facteurs de stress en général sont connus pour induire des changements dans ces motifs comportementaux mais tant la direction que l'interprétation de ces changements n'est pas toujours claire. Cette première étude a ainsi montré que les séquences de recherche alimentaire produites par les manchots pygmées portant des enregistreurs de profondeur plus large sont plus complexes, c'est-à-dire tendant vers une plus grande stochasticité, que ceux portant des enregistreurs de profondeur plus petits. Au contraire, il apparaît que la taille des enregistreurs de profondeurs n'affecte pas la complexité des séquences de recherche alimentaire chez le manchot Adélie et que la position de l'enregistreur de profondeur sur le dos du manchot pygmée est seulement associée faiblement avec une complexité comportementale altérée. Ainsi, les individus portant l'enregistreur de profondeur au milieu du dos montrent que leur comportement de plongée est légèrement plus complexe que ceux le portant au bas du dos. Enfin, bien qu'on leur connaisse un effet délétère sur le succès reproducteur des manchots, les bagues alaires n'ont montré ici aucun effet sur la complexité des séquences de plongée chez le manchot pygmée. Malgré le fait que ces enregistreurs de profondeur et bagues alaires peuvent modifier certains paramètres comportementaux des oiseaux plongeurs, nous avons ici trouvé seulement des preuves contradictoires envers l'hypothèse que ces appareils peuvent significativement modifier l'organisation temporelle des séquences de recherche alimentaire chez les deux espèces de manchots ici étudiées. Cependant, des espèces de petite taille portant des enregistreurs de profondeurs plus large, et peut-être aussi positionné plus haut sur le dos, peuvent exhiber des séquences comportementales comportant un bruit supplémentaire dans leurs séquences comportementales, indiquant alors une déviation du comportement de recherche alimentaire observé sous des conditions « normales ». Cette première étude a ainsi permis d'étudier l'utilité de mon index fractal en

tant qu'indicateur de changements comportementaux et, se basant sur ces premiers résultats, la deuxième partie de cette thèse **(Article B et C)** s'est attelée à étudier les effets d'un ensemble de paramètres environnementaux, comme par exemple l'environnement physique ou la distribution des proies, sur la complexité du comportement de recherche alimentaire. La seconde étude **(Article B)** composant ce travail s'est donc tout d'abord intéressé à l'effet de différentes caractéristiques de l'environnement physique, comme la bathymétrie, entre quatre différentes colonies de manchots pygmées. Ces derniers ont l'une des plus large distribution parmi les espèces de manchots, cela les exposant ainsi à différentes contraintes écologiques au sein de leur aire de distribution. En réaction à ces contraintes écologiques différentes, les animaux vont théoriquement présenter des variations dans leur comportement de recherche alimentaire, leur permettant de s'adapter aux conditions environnementales locales. De plus, la complexité du comportement de recherche alimentaire au niveau spatial et temporel a été théoriquement liée à l'efficacité de recherche alimentaire dans des environnements hétérogènes. J'ai donc examiné comment la complexité de l'organisation temporelle des séquences de recherche alimentaire correspond aux caractéristiques de la zone de recherche alimentaire au sein de ces quatre différentes colonies. Utilisant des méthodes d'analyses des séries temporelles fractales (Detentred Fluctuation Analysis), cette étude a montré que la complexité de la recherche alimentaire sur un gradient de stochasticité-déterminisme était associée avec la bathymétrie dans les zones de recherche alimentaire ; les manchots pygmées plongeant en eaux plus profondes présentent des séquences de recherche alimentaire plus stochastique/moins déterministique que les individus plongeant en eaux moins profondes. Les données de succès d'envol correspondantes suggèrent également que les manchots recherchant leur nourriture en eaux plus profondes ont un succès reproducteur réduit. Une analyse par

composante principale a montré que l'index de complexité du comportement de recherche alimentaire se lie positivement avec l'efficacité de recherche alimentaire alors que l'effort de recherche alimentaire s'y lie négativement. Les modèles statistiques corroborent ces deux relations. Ainsi, la production de séquence de recherche alimentaire complexe avec un haut degré de stochasticité semble donc avoir un coût énergétique, bien que je n'ai pas pu déterminer ici quelle stratégie maximisera le succès de recherche alimentaire, une variable que je n'ai pas pu mesurer, sous les conditions observées. Cette étude propose que l'augmentation des éléments stochastiques dans le comportement de recherche alimentaire est nécessaire en cas de conditions environnementales difficiles mais peut-être pas suffisant pour atteindre les gains de fitness réalisés sous des conditions plus favorables.

A la suite de cette seconde étude, j'ai alors cherché à comprendre comment la complexité de l'organisation temporelle des séquences de recherche alimentaire des manchots pygmées est affectée par d'autres variables environnementales comme la température de surface de l'océan, la concentration en chlorophylle-a, la force et la direction du vent dans le détroit de Bass entre 2001 et 2012 **(Article C)**. J'ai ici trouvé que la complexité de recherche alimentaire sur un gradient de stochasticité-déterminisme était associée avec la température de la surface de l'eau mais pas avec la vitesse du vent, la direction du vent et la concentration en chlorophylle-a. Les manchots pygmées cherchant leur nourriture dans des eaux plus chaudes ont des séquences de recherche alimentaire plus déterministique et montrent une efficacité de recherche alimentaire supérieure et un effort de recherche alimentaire inférieure que ceux recherchant leur nourriture en eaux plus froides. Comme prédit, les animaux cherchant leur nourriture dans des conditions environnementales plus difficiles, comme par exemple des eaux plus froides qui sont réputées pour être associées à des patchs de proies moins prédictibles, vont présenter une plus grande stochasticité dans

leur séquence de plongée. Enfin, cette dernière étude a également confirmé le lien observé dans l'article B entre complexité du comportement de recherche alimentaire, efficacité de recherche alimentaire et effort de recherche alimentaire sur cette même période.

Ces différents résultats et la littérature existante sur le sujet (Seuront & Cribb, 2011 ; MacIntosh, 2014) suggèrent que cet index de complexité du comportement de recherche alimentaire pourrait être utilisé comme un indicateur des changements environnementaux. Il serait ainsi plus sensible pour mettre en lumière des changements dans les séquences comportementales que les mesures comportementales plus classiques utilisées dans l'étude des caractéristiques de la plongée. Il pourrait donc fournir un cadre d'analyse objectif et quantitatif à l'étude de ces changements. Cependant, l'utilisation des analyses fractales ne remplacera pas les approches plus traditionnelles et ces deux types d'approches ont donc vocation à être utilisé en tandem.

Je soulève également dans cette thèse la difficulté d'interpréter les mécanismes conduisant aux variations observées dans la complexité du comportement de recherche alimentaire, mais également la difficulté de déterminer si la complexité du comportement de recherche alimentaire est une conséquence de l'environnement ou une adaptation à ce dernier. Des études complémentaires devront être conduites afin de comprendre plus amplement la mécanistique de ce processus et l'aspect adaptif de ce processus à l'origine de la complexité du comportement de recherche alimentaire. Enfin, bien que l'utilisation des fractales en écologie est actuellement débattue tant l'outil analytique que l'interprétation des causes sous-jacentes à ces motifs (Mercik *et al.*, 2003 ; Benhamou, 2004, 2007 ; Edwards *et al.*, 2007 ; Turchin, 2007 ; James et al., 2011 ; Bryce & Sprague, 2012 ; Benhamou & Collet, 2015 ; Pyke, 2015), nombreuses de ces critiques concernant l'outil analytique employé dans

cette thèse ont été corrigé (Seuront *et al.*, 2004 ; Seuront, 2010, 2015). Je souligne également l'importance de suivre une série d'étapes dans l'application d'outil analytique afin d'éviter tous biais dans les résultats.

En conclusion, ma thèse a révélé l'influence de certains challenges, tant d'origine artificielle qu'environnementale, sur la complexité du comportement de recherche alimentaire de deux espèces d'oiseaux marins, le manchot pygmée et le manchot Adélie. Une plus grande complexité comportementale pourrait donc être une solution pour amortir les effets des changements environnementaux. De plus, j'ai également souligné l'opportunité d'utiliser les analyses fractales dans l'étude du comportement de prédateurs supérieurs et leur utilisation en tant qu'éco-indicateur des changements environnementaux. Enfin, en plus de cette application directe, ma thèse a ouvert de nouvelles pistes dans l'étude de la flexibilité du comportement de recherche alimentaire et la valeur adaptative associée à ce dernier. Malheureusement, je n'ai pas pu étudier dans le cadre de ma thèse les coûts énergétiques liés à la flexibilité du comportement de recherche alimentaire. Les futures études devront se concentrer plus particulièrement sur les liens entre signatures complexes, succès de recherche alimentaire, dépense énergétique et fitness.

UNIVERSITÉ DE STRASBOURG

Xavier MEYER

École Doctorale des Sciences de la Vie et de la Santé STRASBOURG

Does complexity in behavioral organization allow seabirds to adapt to changes in their environment?

Résumé

En raison des changements climatiques actuels, il est primordial de comprendre comment les écosystèmes vont réagir et tout particulièrement comment les chaînes trophiques vont être impactées. Pour cela, le comportement des oiseaux marins peut être utilisé comme des indicateurs des changements se déroulant au sein de l'écosystème. Cependant, un des défis actuels dans l'étude du comportement animal est d'identifier comment la structure temporelle du comportement est dépendante des conditions intrinsèques et extrinsèques et comment la complexité de cette organisation comportementale évolue sur un gradient allant de la stochasticité au déterminisme en fonction des changements environnementaux. Ma thèse a donc pour objectif d'étudier si un comportement complexe est adapté pour faire face à une perturbation du système chez les oiseaux marins et plus particulièrement chez deux espèces de manchots étant exposées à des changements environnementaux.

Mots-clés: Analyse fractale, complexité comportementale, changements environnementaux, oiseaux marins, recherche alimentaire, comportement de plongée

Résumé en anglais

Due to ongoing climate change, it is necessary to understand how ecosystems will react and more particularly, how species may cope with the challenges of living in unstable systems. Seabirds' behavior provides a way to monitor changes occurring in the marine environment, but identifying how the temporal structure and complexity of behavior depend on intrinsic and extrinsic parameters are underexplored topics in the field of animal behavior. My thesis aims to investigate if behavioral organization, through a gradient of stochasticity-determinism complexity, allows little and adélie penguins to buffer changes in the environment under a fractal analysis approach.

Mots-clés: Fractal analysis, behavioral complexity, environmental changes, seabirds, foraging behavior, diving behavior.