



Stratégies de recherche alimentaire d'un prédateur plongeur en période de reproduction : le Gorfou Macaroni des îles Crozet et Kerguelen

Cécile Bon

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ÉCOLE DOCTORALE
Spécialité Biologie de l'Environnement, des Populations, Ecologie

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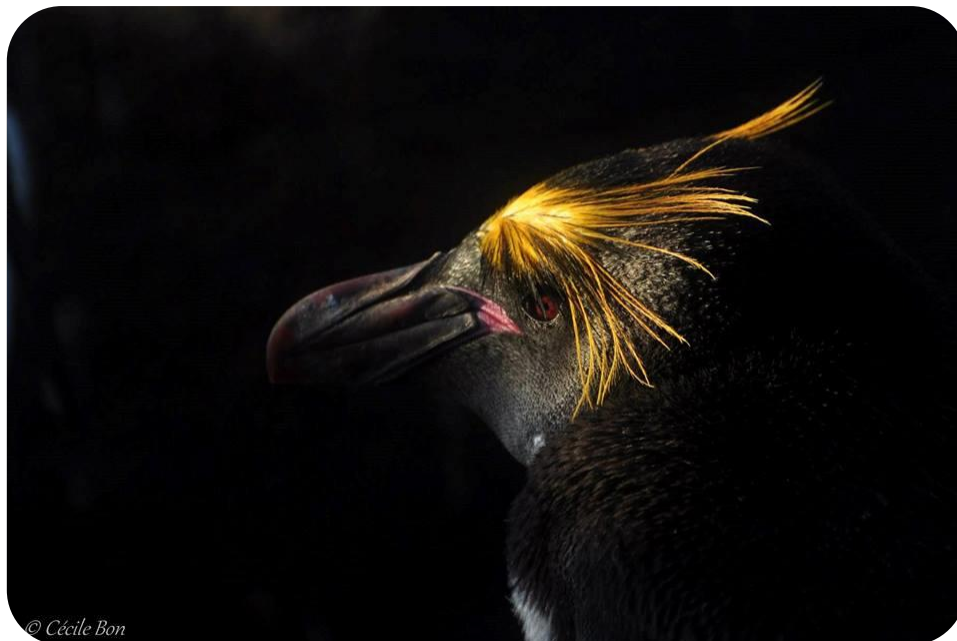
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Cécile BON

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STRATEGIES DE RECHERCHE ALIMENTAIRE D'UN PREDATEUR PLONGEUR EN PERIODE DE REPRODUCTION : LE GORFOU MACARONI DES ILES CROZET ET KERGUELEN



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« Au plus fort de l'orage, il y a toujours un oiseau pour nous rassurer »

René Char

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IV	2	Bon C , Scheffer A, Loisel A, Cherel Y, Powolny T, Arnould J, Jenouvrier S, Bost CA. Foraging strategies of Macaroni penguins at Crozet islands during the breeding season. <i>Marine Ecology Progress Series</i>	to be submitted
V	3	Bon C , Scheffer A, Cherel Y, Powolny T, Arnaud, Jenouvrier S, Bost CA. Foraging strategies of Macaroni penguins during the breeding season at Kerguelen islands. <i>Marine Ecology Progress</i>	in preparation
no presented in this thesis		Bon C , Viviant, Sato K, Handrich Y, Bost CA. Can we Predict foraging success along the track in a marine predator using predictive models based on diving behaviour and prey ingestion data. <i>Marine Biology</i>	to be submitted

Collaboration on the following studies

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International Conferences

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5th International Bio-Logging Science Symposium (BL5), 22-26th September 2014, IPHC - Université de Strasbourg, Strasbourg, France - **Poster presentation**

Other communications and scientific popularization

Scientific conferences, animations and data transmission in the framework of an educational project: **ARGONAUTICA-- ArgoNimaux** (CNES, Centre National d'Etudes Spatiales).
<https://enseignants-mediateurs.cnes.fr>

Public conferences at the **Festival International du Film Ornithologique de Ménagoute (FIFO)**, Ménagoute, France. October 2012-2013-2014

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TABLE OF CONTENTS

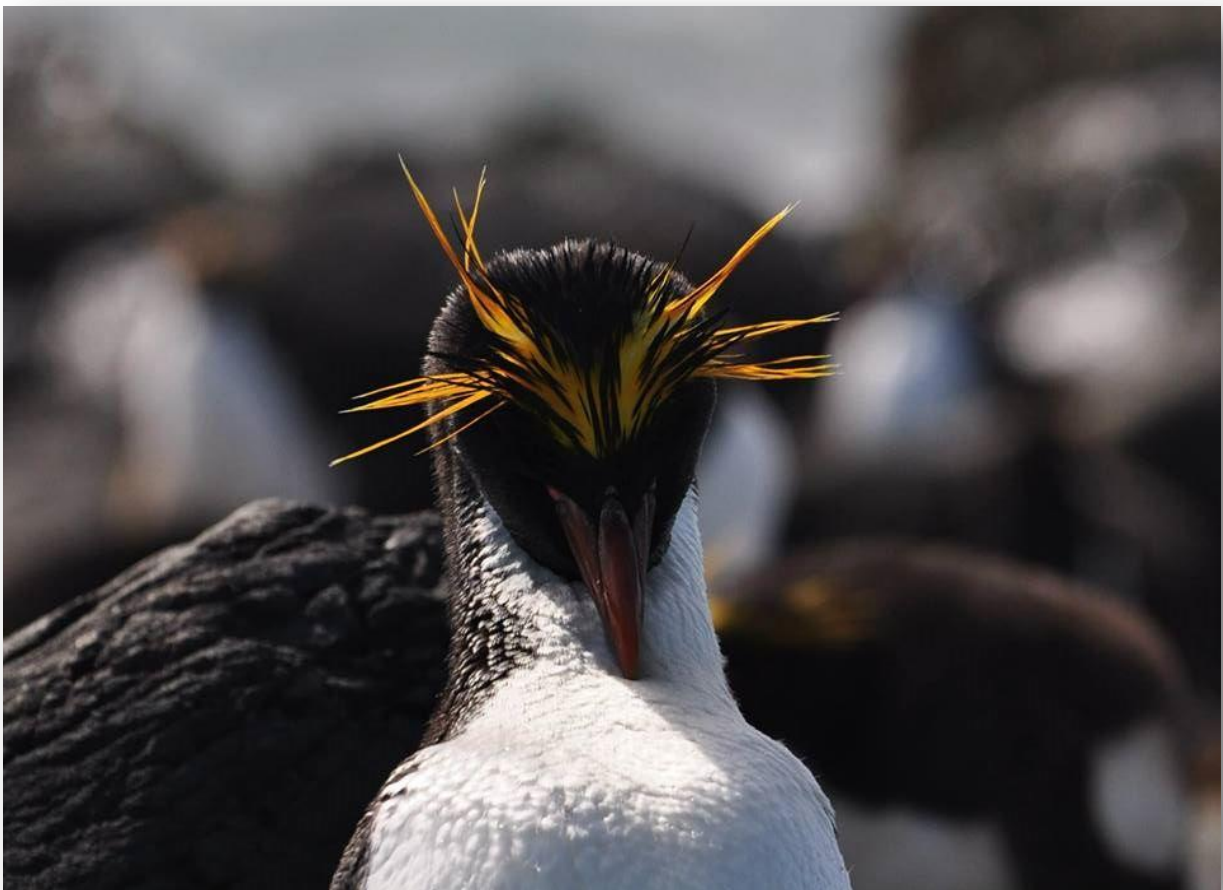
CHAPITRE I: INTRODUCTION	2
I.1. Cadre général de la thèse	2
I.2. Cadre théorique du comportement de recherche alimentaire	2
2.1. Aptitude phénotypique et traits biologiques	2
2.2. La gestion du temps et de l'énergie	3
2.3. La recherche alimentaire en écologie	4
2.3.1. Stratégies alimentaires : aspect temporel	5
2.3.2. Stratégies alimentaires : aspects spatiaux	5
2.3.3. Les différents mécanismes de déplacement	6
2.3.4. Le cas du prédateur à site central	7
I.3. Les stratégies de recherche alimentaire en milieu océanique	8
3.1. La recherche alimentaire des prédateurs marins	8
3.1.1. Traits d'histoire de vie liés à la reproduction	8
3.1.2. Le Cas de l'Océan austral : des oasis de vie dans des déserts océaniques	10
3.1.3. Structuration spatiale des ressources	12
3.1.4. Des échelles de recherche alimentaire hiérarchisées	14
3.1.5. La 3 ^{ème} dimension chez les manchots	16
3.1.6. Des stratégies de couple	19
I.4. Problématique et structure de la thèse	21
CHAPITRE II: MATERIEL AND METHODS	26
II.1. Site d'étude	26
1.1. L'Océan Austral	26
1.2. Les Archipels des îles Crozet et Kerguelen	27
1.2.1. L'archipel des îles Crozet	28
1.2.2. L'archipel des Kerguelen	28
II.2. Modèle biologique : le gorfou macaroni	29
2.1. Taxonomie et Distribution	29
2.2. Cycle reproducteur du gorfou macaroni	33
2.3. Régime alimentaire	37
II.3. Récolte des données biologiques	38
3.1. Pose et récupération des appareils	39
3.2. Suivi des gorfous macaroni par la technologie ARGOS	40
3.3. Le système GPS	41

3.4. Les capteurs de pression	42
3.5. Importance des lots témoins	43
II.4. Les méthodes d'analyses	45
4.1. Analyses spatiales	46
4.1.1. Mise en forme des données	47
4.1.2. Estimation du temps passé par secteur	47
4.2. Identification et analyse des plongées	50
II.5. Obtenir les données océanographiques	52
5.1. Le principe de l'altimétrie	52
5.2. Variables océanographiques utilisées.....	54
II.6. Analyses statistiques	56
6.1. Principaux tests réalisés	56
6.2. Construction d'un modèle statistique explicatif	57
6.2.1. Choisir un modèle candidat	57
6.2.2. Sélection de modèle : 'Meilleur modèle' versus 'Model averaging'	58
6.2.3. Estimer la qualité du modèle	59
 CHAPITRE III: INFLUENCE OF OCEANOGRAPHIC FEATURES ON FORAGING STRATEGIES	 62
III.1. Context and objectives	62
III.2. Methods	62
III.3. Results	63
III.4. Discussion	65
 CHAPITRE IV: FORAGING STRATEGIES OF MACARONI PENGUINS AT CROZET ISLANDS.....	 70
IV.1. Context and objectives	70
IV.2. Methods.....	71
IV.3. Results	71
IV.4. Discussion	78
 CHAPITRE V: FORAGING STRATEGIES OF MACARONI PENGUINS IN CONTRASTED ENVIRONMENTS.....	 84
V.1. Context	84
V.2. Methods	85
V.3. Results	85

3.1. Foraging strategies of Kerguelen Islands	85
3.2. Comparisons with the Crozet population	91
V.4. Discussion	96
 CHAPITRE VI: GENERAL DISCUSSION AND FUTURE RESEARCH.....	102
VI.1. Stratégies de recherche alimentaire des gorfous macaroni dans l'Océan Austral	102
1.1. Synthèse des résultats obtenus à Crozet et Kerguelen	102
1.1.1. <i>Caractéristiques des traits d'histoire de vie intrinsèques à l'espèce</i>	103
1.1.2. <i>Variations dans l'effort d'approvisionnement entre les sites</i>	104
1.1.3. <i>Le paradoxe de Crozet</i>	107
1.2. Paramètres océanographiques « clés » des habitats alimentaires utilisés au cours de la reproduction : comparaison des stratégies alimentaires à l'échelle de l'aire de répartition	109
1.2.1. <i>Utilisation des structures frontales et abords de plateau</i>	112
1.2.2. <i>Influence des courants et de la couche de mélange</i>	113
1.2.3. <i>Liens avec la productivité primaire</i>	114
1.2.4. <i>Compétition potentielle à l'échelle interspécifique</i>	117
1.2.5. <i>Effet « Ahsmole » à proximité des colonies</i>	119
VI.2. Rôle du sexe dans les stratégies de recherche alimentaire	121
2.1. Différence sexuelle dans l'effort d'approvisionnement au cours du cycle	123
2.2. Variation interindividuelle chez les mâles	126
VI.3. Plasticité phénotypique chez le gorfou macaroni	128
3.1. Degré de plasticité des gorfous macaroni dans l'Océan Austral	128
3.2. Quelles réponses face aux changements globaux ?	130
VI.4. Conclusions et perspectives	134
4.1. Apport de l'étude	134
4.2. Limites de l'étude	135
4.3. Perspectives d'études	137
 LIST OF FIGURES.....	140
BIBLIOGRAPHY	144
ANNEXES	174
SUMMARY	259

CHAPITRE I

INTRODUCTION



Preening behaviour in Macaroni penguin © Cécile Bon

I.1. Cadre général de la thèse

Tout organisme a besoin au cours de sa vie à accéder à certaines ressources et sites pour s'alimenter et se reproduire. Les **déplacements dans l'environnement** sont donc les premiers paramètres permettant d'identifier **les conditions environnementales vitales d'une espèce**. Lors de ces déplacements, les organismes peuvent faire face à une hétérogénéité d'environnements qui peuvent ou non leur convenir. La gamme de facteurs environnementaux qu'une espèce utilise pour sa survie et sa reproduction est regroupée sous le terme '**habitat**' (Block & Brennan 1993). **L'utilisation de l'habitat** fait référence aux **moyens** par lesquels un individu bénéficie d'un site donné pour accomplir les activités de son cycle biologique (Block & Brennan 1993). Ce champ d'étude consiste à **décrire la distribution contemporaine d'individus à travers différents types d'habitats** et le type de relations qui existe avec les différentes propriétés environnementales (Hutto 1985).

I.2. Cadre théorique du comportement de recherche alimentaire

Les stratégies de recherche alimentaire ont été au centre des concepts développés par l'écologie comportementale au cours des 40 dernières années. Celle-ci constitue l'étude des relations entre le comportement et l'environnement d'un point de vue évolutif. Le comportement est défini ici comme *"l'ensemble des processus de décision par lesquels les individus ajustent leur état et leur situation par rapport aux variations biotiques et abiotiques du milieu"*. L'étude du comportement s'effectue en trois étapes: 1- l'élaboration de questions pertinentes par rapport aux connaissances scientifiques, 2- l'émission d'hypothèses cohérentes avec les théories du champ du domaine scientifique concerné et 3- la mise en place de stratégies de recherche expérimentales et/ou analytiques permettant de mesurer la prédictibilité et la vraisemblance des hypothèses (Danchin et al. 2005).

2.1. Aptitude phénotypique et traits biologiques

Les caractéristiques d'un organisme sont regroupées sous le terme "**phénotype**", c'est à dire la résultante de l'interaction entre l'expression du génome de l'organisme et l'environnement dans lequel il s'est développé. Ainsi, les comportements **alimentaires, reproducteurs**, etc.. adoptés par un organisme constituent une mesure (non exhaustive) de son phénotype. La recherche en écologie comportementale va consister à mesurer l'impact du comportement sur **l'aptitude phénotypique** des individus, c'est à dire *"la capacité du phénotype qui exprime le comportement en question à produire des descendants mâtures relativement aux autres phénotypes de la même population au même moment"* (Danchin et al. 2005).

Comparer l'aptitude phénotypique d'individus appartenant à une même population permet de mesurer indirectement la **valeur sélective** de l'individu. *Stricto sensu*, la valeur sélective se mesure sur le

succès relatif d'un allèle ou d'une combinaison d'allèles entre deux générations. N'ayant pas accès au génome des individus étudiés, les écologistes étudient les « **traits d'histoire de vie** » (ou **trait biologique** *Life history parameters*) des organismes. Ceux-ci se caractérisent par un ensemble de descripteurs biologiques et comportementaux mesurables et observables par le biais du phénotype. Il existe par définition une relation entre les traits biologiques et l'aptitude phénotypique. Ces traits varient entre les organismes, sont héréditaires, ne sont pas neutres et subissent des pressions de sélection (Stearns 1992)

La **théorie des traits d'histoire de vie** prédit qu'au cours de leur vie, les organismes tendent à optimiser leur valeur sélective, c'est-à-dire maximiser leur contribution génétique aux générations futures (Stearns 1992). Cette contribution sera maximale pour les individus produisant le plus grand nombre de descendants qui survivent et se reproduisent (Hirshfield & Tinkle 1975, Newton 2010). Les traits sont mesurables à l'échelle individuelle, mais également à celle de l'espèce. Par exemple, les principaux traits concernant la reproduction sont l'âge et taille à la maturité, le nombre, la taille, la sex-ratio de la descendance et l'investissement reproducteur. Ceux concernant la survie et la croissance peuvent être la masse et la condition corporelle des individus au cours de leur vie, mais également le degré de plasticité phénotypique (Stearns 1992, McNamara & Houston 1996).

Au cours de leur vie, les individus sont cependant confrontés à un ensemble de contraintes qui peuvent avoir des conséquences sur leur survie ou leur reproduction, et auxquelles les animaux doivent s'ajuster (McNamara & Houston 1996, Weimerskirch et al. 2012). Sous le processus de la sélection naturelle, des traits comportementaux et physiologiques ont été sélectionnés et aboutissent à un ensemble de **stratégies comportementales**, observables à différentes échelles temporelles et spatiales (*e.g* recherche alimentaire à l'échelle d'une journée, d'une saison entière) et dans tous les domaines d'activités de vie d'un organisme (parade, reproduction, recherche alimentaire, migration, dispersion etc...).

Cependant, les mécanismes physiologiques sous-jacent à ces activités nécessitent de l'énergie, et ainsi, **chaque trait biologique est associé à un « coût » énergétique et physiologique pour l'organisme.**

2.2. La gestion du temps et de l'énergie

Les principales contraintes économiques affectant le comportement animal sont **le temps et l'énergie** (Cuthill & Houston 1997). Ainsi, l'acquisition des ressources via une stratégie adéquate est une activité centrale tout au long de la vie des organismes, qui détermine leur croissance, leur condition corporelle, leur survie et leur succès reproducteur. Cependant, l'énergie disponible dans l'environnement est limitée et ainsi, un individu ne peut pas acquérir de l'énergie *ad libitum*. Par

conséquence, les organismes doivent répartir le budget énergétique entre la reproduction courante, leur survie et la possibilité de mener à bien de futures reproductions (valeur reproductive résiduelle, Williams 1966). D'autre part, le temps alloué à ces activités peut être également limité. Par exemple, pour les organismes nocturnes, l'alternance jour-nuit va déterminer le temps disponible pour s'alimenter.

Ces limites de temps et d'énergie provoquent l'émergence de « conflits » pour l'organisme au niveau des différentes activités à mener. Ces conflits renvoient à un concept clé en écologie : les organismes sont amenés à effectuer des **compromis** dans l'allocation d'énergie et de temps entre les différentes activités. Les traits d'histoire de vie sont ainsi connectés entre eux par de nombreux compromis, tels que le succès reproducteur versus la future reproduction ou bien la condition corporelle des parents versus la taille de la progéniture. **Ainsi, un compromis est défini comme un ensemble de décisions prises par l'organisme tout au long de sa vie pour allouer l'énergie ou le temps entre le maintien de sa balance énergétique pour sa survie, la reproduction, et la croissance** (Lack 1968, Smith et al. 1989, Stearns 1989, Cuthill & Houston 1997) . Il est clair que tous les organismes ne sont pas toujours conscients de ces compromis et de leurs conséquences.

2.3. La recherche alimentaire en écologie

L'acquisition des ressources est une activité centrale tout au long de la vie des organismes qui est le point crucial de la réussite de la reproduction. Par conséquent, les comportements associés à la recherche et à la prise alimentaire sont fortement soumis aux mécanismes de la sélection naturelle et possèdent une forte valeur sélective (Bell 1980). **Le comportement d'approvisionnement** ("*foraging*" en anglais) d'un organisme est défini comme l'ensemble des activités de **recherche**, de **capture** et d'**ingestion** de proies. Cet approvisionnement dépend de deux types majeurs de ressources : 1- les **proies**, ou l'ensemble des éléments dont l'animal pourra extraire l'énergie nécessaire à leurs activités, et 2- les **espaces** qui leur sont nécessaires pour effectuer leur cycle annuel (Begon et al. 2006). Il est généralement considéré que la distribution des proies est parcellaire, c'est à dire en agrégats de densité variable (« *patches* ») séparés par des espaces où les ressources sont moins concentrées.

La notion de '**stratégie de recherche alimentaire**' correspond à un **faisceau d'adaptations comportementales, écophysiologiques et morphométriques ayant conféré à l'organisme un avantage adaptatif lui permettant de s'alimenter de manière optimale en fonction des contraintes temporelles et énergétiques auquel il est soumis** (Stephens & Krebs 1986). De ce constat est né le théorème de l'approvisionnement optimal (Emlen 1966, MacArthur & Pianka 1966, Schoener 1971). Ce dernier postule que les **stratégies alimentaires permettent de maximiser le**

rapport bénéfice/coût des comportements d'alimentation et au final la valeur sélective des organismes (Mcarthur & Pianka, 1966).

Cette théorie se découpe en deux volets. Le premier aspect concerne l'étude du régime alimentaire ou sélection des proies. Un postulat est que les organismes devraient sélectionner les items menant au plus haut taux d'acquisition énergétique (MacArthur & Pianka 1966, Pyke 1984). Le second aspect concerne **la recherche spatio-temporelle des ressources**.

2.3.1. Stratégies alimentaires : aspect temporel

L'aspect temporel de la recherche alimentaire a été particulièrement étudié depuis l'énonciation du théorème de la valeur marginale (Charnov 1976) puis amélioré par la prise en compte de la nature stochastique ou non de la rencontre des proies (Oaten 1977, McNamara 1982). En effet, une des questions fondamentales pour un organisme est quand et combien de temps mener ou arrêter une activité d'alimentation. Dans ce cadre, ces théorèmes permettent d'estimer le **temps optimal de résidence** dans une zone qu'un organisme exploite au sein d'un milieu hétérogène où la ressource est distribuée en agrégats. **Le temps de résidence optimal dans une parcelle serait atteint lorsque le taux d'énergie net obtenu devient inférieur ou égal à celui espéré en quittant la zone**. La majorité de ces modèles ont été testés sur des oiseaux (Cowie 1977, Kacelnik 1984), mammifères (Grether et al. 1992, Kotler et al. 1994) ou insectes (Roitberg 1990, Roitberg et al. 1992). Bien que ces modèles permettent de décrire de manière assez réaliste les comportements optimaux des individus (Valone 1991), la qualité des prédictions dépend fortement du type d'environnement et des capacités d'acquisition de l'information propres à chaque espèce (Kohlmann & Risenhoover 1998).

2.3.2. Stratégies alimentaires : aspects spatiaux

L'aspect spatial de la recherche alimentaire constitue l'étude des mouvements (changement de direction) des organismes (Turchin 1997, Jonsen et al. 2003). Un animal en mouvement dans un milieu a avantage à ajuster son chemin selon son expérience récente (Hassell & May 1973, Kareiva & Odell 1987, Walsh 1996, Fauchald 1999). Par exemple, les consommateurs peuvent augmenter leur sinuosité et réduire leur vitesse en réponse à une augmentation de leur taux de capture. Dans un milieu de type parcellaire, il est attendu que les prédateurs adoptent un **comportement de recherche en zone restreinte** (*'Area Restricted Search'*, Kareiva et Odell 1987) afin de concentrer leur activité de recherche dans une zone à forte densité de proies (Cezilly & Benhamou 1996). Ce comportement a été

observé chez de nombreux taxons, notamment chez les oiseaux marins (Haskell 1997, Pinaud 2008, Le Corre et al. 2008, Bailey 2009, Hamer et al. 2009).

De ces études, les concepts majeurs sont : i- le consommateur n'est pas omniscient de la distribution de la ressource, ii- les proies sont distribuées sous forme parcellaire, et iii- les organismes tendent à maximiser le temps passé dans une zone profitable.

2.3.3. Les différents mécanismes de déplacement

La recherche alimentaire et les déplacements associés peuvent être effectués selon trois mécanismes majeurs : **non-orientés, orientés et issus de la mémoire individuelle** (Mueller et Fagan 2008).

- **Les mécanismes non orientés** impliquent des déplacements simples dirigés aléatoirement dans l'espace mathématiquement associés à des marches aléatoires corrélées. Les modifications des paramètres de ces déplacements (vitesse, angles) sont issues de stimuli sensoriels (conditions environnementales). Ces mécanismes non orientés ont été intensément étudiés pour expliquer notamment la dispersion des insectes (Turchin 1998).

- **Les mécanismes orientés** sont reliés à la perception de signaux qui guident l'animal et induisent un changement de direction dans une **direction prédictible**. Les mécanismes orientés utilisent des signaux sensoriels (visuels, olfactifs, acoustiques) et se basent sur la perception active de ressources. Ces mécanismes ont été étudiés sur des organismes de différents taxons, comme les insectes, les petits mammifères ou les oiseaux (Zollner & Lima 1999, Schooley & Wiens 2003, Biro et al. 2004). Cependant bien qu'il existerait une certaine corrélation positive avec la taille des organismes (Mech & Zollner 2002), il reste encore difficile d'estimer si les perceptions individuelles s'opèrent à la même échelle spatio-temporelle que les échelles de variations de disponibilité des ressources.

- **Les déplacements effectués par mécanismes issus de la mémoire** sont liés à l'expérience personnelle de l'animal qu'il utilise pour se diriger dans l'environnement et cibler des zones d'alimentation. Ces informations peuvent provenir de l'accumulation d'une expérience personnelle individuelle impliquant la mémorisation des zones d'alimentation (grands herbivores, Bailey et al. 1996), de la communication entre congénères (abeilles, Von Frisch 1974) ou d'une mémoire génétique (papillons, Brower 1996). Ce domaine d'étude est en plein expansion. Il est suggéré que les individus qui utilisent de tels mécanismes pour s'orienter pourraient utiliser deux techniques : la **mémorisation active des trajectoires** ou **l'utilisation d'une carte cognitive**. Les **oiseaux** utiliseraient par exemple un combiné de plusieurs signaux : olfactifs, célestes, basé sur le champ magnétique, des coordonnées

géomagnétique et sur la mémorisation du paysage (Alerstam 2006, Wiltschko & Wiltschko 2006, Akesson & Hedenström 2007).

2.3.4. Le cas du prédateur à site central

Le concept du consommateur à place centrale est un cas particulier du théorème de la valeur marginale. Il consiste à s'alimenter dans des zones dissociées d'un **site central** auquel les organismes sont contraints de revenir régulièrement pour assurer des activités de reproduction ou de mue (Orians et Pearson, 1966). Le lien d'un organisme avec le site central peut être permanent (tout au long de sa vie) mais aussi saisonnier : par exemple, chez les mammifères et les oiseaux, la succession des périodes de reproduction et de migration induisent de fortes variations sur la contrainte de retour au point central (colonie de reproduction). En reproduction, les animaux auront des **contraintes d'éloignement** à la colonie fortes en raison de la nécessité de l'approvisionnement régulier du juvénile. En période de migration (hors période de reproduction), la dispersion pourra être considérablement plus grande (Thiebot et al. 2011).

En milieu naturel, on s'attend à ce que des animaux qui subissent de telles contraintes temporelles et spatiales aient acquis des stratégies d'approvisionnement leur permettant de maximiser leur succès alimentaire (Davies et al. 2012). Chez les oiseaux et les grands mammifères, les déplacements seraient probablement donc issus de **mécanismes orientés et/ou issus d'une mémoire individuelle leur permettant de limiter les coûts d'une recherche aléatoire et de cibler efficacement des zones productives** (Bradshaw et al. 2004, Weimerskirch 2007).

Au cours de cette partie, nous avons vu que **l'étude des stratégies de recherche alimentaire peut être abordée sous de multiples points de vue : descriptif, mécanistique, historique, adaptatif etc.** C'est le couplage de l'ensemble de ces approches qui permet d'améliorer la compréhension de la diversité des stratégies alimentaires existant en milieu naturel. Par ailleurs, dans un environnement soumis à des fluctuations régulières (Stenseth et al. 2002), le lien entre l'écologie trophique et l'environnement est un pilier pour comprendre la dynamique des populations d'animaux sauvages (Boggs 1992).

I.3. Les stratégies de recherche alimentaire en milieu océanique

3.1. La recherche alimentaire des prédateurs marins

Dans l'étude des stratégies de recherche alimentaire, les **oiseaux marins** constituent des modèles biologiques d'un grand intérêt. Prédateurs endothermes, ils doivent faire face à des contraintes énergétiques très fortes, particulièrement dans les zones des hautes latitudes (Costa 1991).

Se nourrissant en mer mais se reproduisant à terre, leurs activités de reproduction et de recherche alimentaire sont nettement séparées dans le temps et l'espace. La distance maximale séparant le lieu de reproduction et les ressources marines est une contrainte majeure pour l'acquisition de leur source d'énergie alimentaire. Ceci favorise l'existence d'un gradient de stratégies alimentaires, reproductives et démographique en fonction des distances à parcourir (Weimerskirch 2007). Ils sont contraints de rester à proximité des colonies pour assurer les soins parentaux et se comportent ainsi comme des **prédateurs à site central**.

Chez les oiseaux marins, la **distribution spatio-temporelle des ressources, la qualité des patches riches en proies, leur distance à la colonie et les capacités de déplacements** des espèces va considérablement moduler les stratégies de recherche alimentaire. Ces prédateurs exploitent un environnement où les **proies sont réparties de manière très hétérogène** dans l'espace et le temps, mais dont la distribution peut être prévisible à l'échelle saisonnière (Hunt et al. 1999).

De plus, au cours du cycle reproducteur, ils sont soumis à des contraintes énergétiques et temporelles très **spécifiques** du stade de la reproduction (Ricklefs 1983). Ces différentes contraintes (incubation, élevage du poussin) ont favorisé la mise en place de stratégies de recherche alimentaires différentes dans l'espace et le temps, permettant d'aborder l'éventail de ces stratégies pour une espèce donnée.

Chez les manchots qui s'alimentent en plongée et en apnée, l'accès à la ressource est soumis à des contraintes supplémentaires, liées à la profondeur de la ressource, la durée de la plongée et l'immersion complète dans l'eau (Costa 1991).

3.1.1. Traits d'histoire de vie liés à la reproduction

Les oiseaux marins partagent des traits d'histoire de vie communs. Leur cycle de vie est partagé entre trois grandes activités : **la reproduction, la mue et la survie inter-nuptiale** (impliquant ou non une migration). Chez ces espèces, les individus ont une stratégie démographique lente (K), c'est à dire que la survie à long terme est maximisée plutôt que l'investissement reproducteur sur une saison donnée. Ils sont ainsi **longévifs, généralement monogames, itéropares** (plusieurs épisodes

reproductifs au cours de leur vie), ont une **faible fécondité** par épisode reproductif, dispensent des **soins parentaux** et ont une **maturité sexuelle tardive**. D'un point de vue évolutif, la valeur sélective des adultes est généralement plus forte que celle de leur descendance favorisant l'existence d'un important **compromis entre la reproduction et leur propre survie** (Lack 1968, Goodman 1975, Stearns 1992).

La saisonnalité de l'océan implique des périodes de durée variable propice à la reproduction des oiseaux, en raison de la **productivité biologique saisonnière**. La nature très hétérogène et variable de l'environnement prospecté limite la quantité d'énergie disponible pour la reproduction. Selon l'hypothèse proposée par Lack (**'Energy limitation hypothesis'**, Lack 1968) cette limitation d'énergie et de temps favoriserait ainsi la stratégie démographique lente des oiseaux marins, une taille de ponte réduite et un temps de croissance long, permettant de maximiser la probabilité de succès à l'envol du jeune pour chaque œuf pondu.

La **période de reproduction** s'étend ainsi sur une période plus ou moins courte pendant l'été où l'abondance des ressources est maximale et les températures plus clémentes (à quelques exceptions, comme le manchot empereur qui se reproduit l'hiver mais dont le poussin part en mer en été). La reproduction des oiseaux marins s'effectue à terre au sein de grandes colonies. Ces colonies sont situées sur de nombreuses îles et côtes continentales de l'Océan austral, composées de quelques dizaines d'individus (manchot papou) à plusieurs centaines de milliers (Manchot royal, Guinet et al. 1996, Delord et al. 2008).

Les oiseaux marins se comportent comme des **"income breeder"**. A l'inverse des phocidés par exemple qui vont rester à terre, jeûner et puiser dans leurs réserves corporelles jusqu'à ce que la progéniture devienne autonome (**"capital breeder"**), les oiseaux marins vont plutôt **alterner** la garde et l'élevage de la progéniture par des **voyages réguliers** en mer pour s'alimenter. La **période inter-nuptiale** correspond à plusieurs mois où certaines espèces migrent sur des milliers de kilomètres (*e.g.* gorfou macaroni), tandis que certaines restent sédentaires (*e.g.* manchot papou, Tanton et al. 2004, Thiebot, Cherel, et al. 2011). Au cours de cette période intervient la **mue**, phase où les oiseaux renouvellent une partie ou l'intégralité de leur plumage. Cette activité est essentielle au maintien d'une bonne isolation thermique et d'un bon profilage hydro- ou aérodynamique. La conductivité thermique de l'eau est 30 fois supérieure à celle de l'air. Le renouvellement régulier du plumage se fait donc sous des contraintes fortes, surtout pour les manchots. Ainsi la mue des manchots **s'effectue à terre pendant 3 à 4 semaines** après l'acquisition de réserves corporelles importantes (Williams 1995). Les oiseaux volants sont capables de muer en mer pendant la période de non reproduction de façon beaucoup plus étalée (Warham 1996).

3.1.2. Le Cas de l'Océan austral : des oasis de vie dans des déserts océaniques

L'**Océan Austral** abrite une communauté riche en **oiseaux marins** avec plus de 360 millions d'individus reproducteurs (Van Franeker et al. 1997). Les quatre principaux ordres taxonomiques observés dans l'Océan Austral sont les Procellariiformes (albatros, pétrels), les Charadriiformes (labbes, goélands, sternes), les Pélécaniformes (cormorans) et une spécificité : les **Sphénisciformes** (manchots). Ce dernier ordre contient au total 18 espèces vivant exclusivement dans l'hémisphère sud.

Plus vaste océan du globe, l'océan austral englobe la partie sud des océans atlantique, indien et pacifique, ceinturant le continent antarctique.

La ressource ciblée par les oiseaux marins de l'Austral appartient à des chaînes alimentaires complexes composées de multiples interactions. Ces chaînes alimentaires peuvent être cependant décomposées en 3 grands groupes : les oiseaux marins (et autres prédateurs supérieurs situés au sommet des chaînes alimentaires : pinnipèdes, cétacés, grands poissons), le niveau secondaire composé d'herbivores ou de carnivores, et le niveau primaire composé d'organismes autotrophes, défini comme la base de la chaîne alimentaire.

Le phytoplancton - biologie et distribution

Le phytoplancton désigne l'ensemble des **organismes autotrophes végétaux vivant en suspension dans l'eau**. Les cellules phytoplanctoniques sont très diversifiées (~ 20 000 espèces) et appartiennent à différentes groupes taxonomiques (*e.g.* diatomées, cyanobactéries etc.). Le phytoplancton est le premier maillon des éléments organiques dans la chaîne alimentaire et serait responsable de 75% de la **productivité primaire océanique** (Falkowski & Raven 2013, Figure 1.1). Il vit principalement dans la **zone euphotique, située dans la couche de mélange**, lui permettant d'accéder à des niveaux suffisant de lumière pour effectuer la **photosynthèse** (Figure 1.2). La couche de mélange est bordée en profondeur par la **thermocline**. Cette structure, peu turbulente, est définie par une diminution rapide de la température, associée à une augmentation de salinité et de densité (Park et al. 1998). En dessous se situent des **eaux profondes** plus froides et plus salées. La thermocline peut jouer un véritable rôle de **barrière hydrologique** pour la migration verticale des organismes marins (Angel 1968) surtout si elle est associée à une baisse d'oxygène importante.

La **saisonnalité** présente aux moyennes et hautes latitudes induit des variations de profondeur des différentes couches d'eaux de l'océan. En automne et en hiver lorsque la température baisse, la remontée des eaux profondes concentrées en éléments minéraux permet d'enrichir les eaux des surface en nutriments vitaux au développement du **phytoplancton** (nitrates, silicate etc.). Au printemps lorsque la lumière s'intensifie dans la zone euphotique riche en nutriments, des blooms phytoplanctoniques se développent de manière hétérogène dans l'Océan Austral (Moore & Abbott 2002, Figure 3.1).

L'Océan Austral est la région du globe typiquement caractérisée par des **eaux riches en nutriments et pauvres en chlorophylle (HNLC, High Nutrient Low Chlorophyll, Martin 1990)** en milieu pélagique. **Bien qu'il existe d'importantes différences entre localités, les eaux côtières de l'Austral sont généralement plus riches en éléments nutritifs (azote, fer, ...) et plus productives que les eaux pélagiques** (El-Sayed 1988, Tréguer & Jacques 1993). **Les eaux pélagiques peuvent ainsi être considérées comme de vastes « déserts » océaniques, caractérisés par une faible productivité primaire (phytoplancton) et secondaire (zooplancton, necton. Elle va dépendre notamment des processus physiques et biologiques responsables de leur formation.**

Bien que d'importantes concentrations de sels minéraux soient disponibles en milieu océanique, la faible concentration de fer est un facteur limitant au développement des cellules végétales (Martin et al. 1990, de Baar et al. 1995). La principale fertilisation en fer des eaux serait d'origine terrestre, et donc accentuée aux abords des côtes (continents, îles) en raison d'un relargage des sédiments vers la mer (pluie, vent, fleuves). Ce processus est nommé appelé "*island-mass effect*". En conséquence, **des blooms phytoplanctoniques sont régulièrement observés aux abords des îles de l'Océan Austral** comme Kerguelen (Blain et al. 2001, Venables et al. 2007, Borriane & Schlitzer 2013).

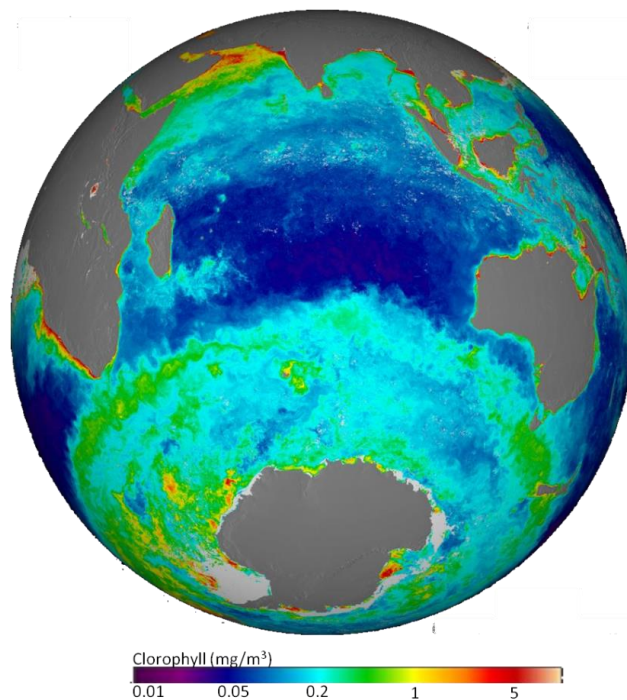


Figure 1.1: Ocean Chlorophyll Concentrations (Southern Hemisphere) during the southern summer 2011/2012. The image shows season-long composites of ocean chlorophyll concentrations derived from visible radiometric measurements. Credit: NASA/Suomi NPP/Norman Kuring.

Apparté:

La chlorophylle *a* est le pigment photosynthétique le plus commun du règne végétal. Sa gamme d'absorption spectrale est nulle entre 470 à 610 nm associée aux nuances de la couleur verte, donnant ainsi cette couleur aux végétaux possédant ce pigment. La méthode commune pour mesurer la **concentration phytoplanctonique de surface** en milieu aquatique s'effectue grâce à **la couleur de l'eau** (Figure 2). La couleur est mesurée par satellite dans le cadre des missions SeaWiFS organisées par la NASA (*Sea-viewing Wide Field-of-view Sensors Project*).

Réseau trophique associé

Les **chaines trophiques** sont composées de nombreuses espèces dont la biologie de certaines est encore très mal connue. Les premiers échelons sont constitués de **micro-zooplancton** (*e.g.* **ciliés, dinoflagellés hétérotrophes**) et **macro-zooplancton** qui peuvent être brouteurs mais également carnivores de zooplancton (*e.g.* **crustacés** : euphausiacés, amphipodes, décapodes). Le macro-zooplancton constitue une des ressources majeures des oiseaux marins, notamment les manchots. Les **poissons sont composés d'une grande variété d'espèces** (*e.g.* myctophidés pélagiques *Krefftichthys sp*, *Electrona sp*, poissons nérétiques *Squalus asper*, abyssaux *Muraenolepis sp*, des glaces *Champscephalus gunnari*). Certaines espèces, comme les myctophidés, sont essentielles à l'alimentation des prédateurs marins comme les otaries, les manchots royaux ou les éléphants de mer. **On trouve également des céphalopodes, proies ciblées par les albatros** (*e.g.* famille des Brachioteuthidae). Enfin le dernier niveau de la chaîne alimentaire est composé de nombreuses populations de **prédateurs marins supérieurs** qui dépendent de cet assemblage trophique (**oiseaux, mammifères marins** et grands poissons (*e.g.* Froneman & Perissinotto 1996, Bocher et al. 2001, Cherel et al. 2007, Delord et al. 2013, Duhamel 1997, Laws 1984).

3.1.3. Structuration spatiale des ressources

On distingue dans l'Océan Austral l'existence de processus physiques observables sur trois **niveaux d'échelle spatiale**, ayant chacun un rôle dans la distribution et l'écoulement des ressources marines primaires (Moore & Abbott 2002, Lévy et al. 2012) et attractives pour les oiseaux marins (Bost et al. 2009). Le premier niveau concerne les **grands fronts océanographiques**.

Ainsi l'Océan Austral se caractérise par la présence de grandes masses d'eau aux propriétés physico-chimiques différentes (température, salinité, densité etc.). Les zones de rencontre entre ces masses d'eaux, appelées **fronts**, sont associées à des discontinuités des gradients physiques et permettent de caractériser différentes régions dans l'Océan Austral (Orsi et al. 1995, Thomas & Lee 2005) observables sur des milliers de kilomètres.

Les deux autres niveaux font référence aux structures **méso-** (10-300km) et **sub-mésoéchelle** (0.3 - 10km). Les changements et les instabilités dans le régime des vents et des pressions atmosphériques sont à l'origine de variations locales des hauteurs de la surface de l'eau (**anomalie de hauteur d'eau**). Ces anomalies, représentables comme des creux et des bosses à la surface de la mer, engendrent des changements dans le champ de vitesse de l'écoulement de l'eau, qui, associés à la force de Coriolis, peuvent provoquer la formation de vortex circulaires : les **tourbillons**.

Ces **structures mésoéchelle** sont observables de plusieurs dizaines à plusieurs centaines de kilomètres. Sous certaines conditions, les tourbillons favorisent la rétention circulaire de parcelles d'eaux et leur contenu biotique ou abiotique, de quelques jours à plusieurs mois, voire plus longtemps (Bracco et al. 2000, Perruche et al. 2011, d'Ovidio et al. 2013). Dans l'hémisphère sud, les tourbillons anticycloniques (sens antihoraire) sont caractérisés par un centre relativement chaud et épais (dépression des isopycnes, *i.e.* les lignes de densité égales) lié à un enfoncement des eaux de surface vers les profondeurs (Figure 1.2). A l'inverse, les tourbillons cycloniques (sens horaire) sont généralement constitués d'un dôme central associé à une couche de mélange peu épaisse, processus lié à une remontée d'eaux profondes riches en nutriments pouvant être favorables à la productivité biologique (Figure 1.2).

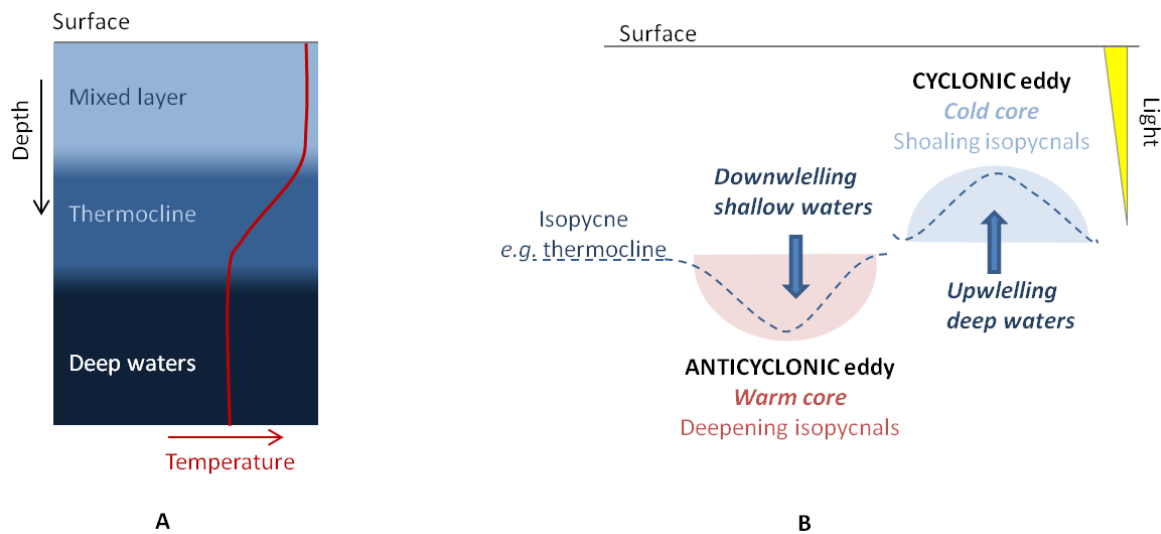


Figure 1.2: Vertical characteristics of the water column. A: Three main layers of the water column. The red line indicates a line of equal temperature. B: Process of vertical movements of waters masses in case of anticyclonic or cyclonic eddy. Cyclonic eddies are associated with a higher primary productivity from the upwelling of rich nutrients waters in the euphotic layer. Adapted from McGillicuddy et al. 1998.

L'interaction des tourbillons favorise également le brassage vertical (Taupier-Letage et al. 2003, Lévy 2003) et la création de structures **sub-mésoéchelles**. Les **filaments**, veines de courants issues de

l'étirement des masses d'eaux, sont des structures de moins de 10km qui possèdent des propriétés physiques différentes de leur environnement. Ainsi, selon leur intensité, elles peuvent être considérées comme de véritables routes de **transport de la production biologique** autant sur le plan spatial que vertical (d'Ovidio et al. 2010, Lévy et al. 2012). On observe par exemple que la distribution du phytoplancton est étroitement liée aux structures filamenteuses (Figure 1.3). A l'échelle d'un tourbillon, les **vitesse verticales** sont plus importantes en bordure périphérique des tourbillons et au sein des filaments, de même que la dynamique d'échange des sels minéraux (Lévy et al. 2001). La stabilité de ces structures est également **variable dans le temps**, pouvant évoluer et changer de place d'une journée sur l'autre.

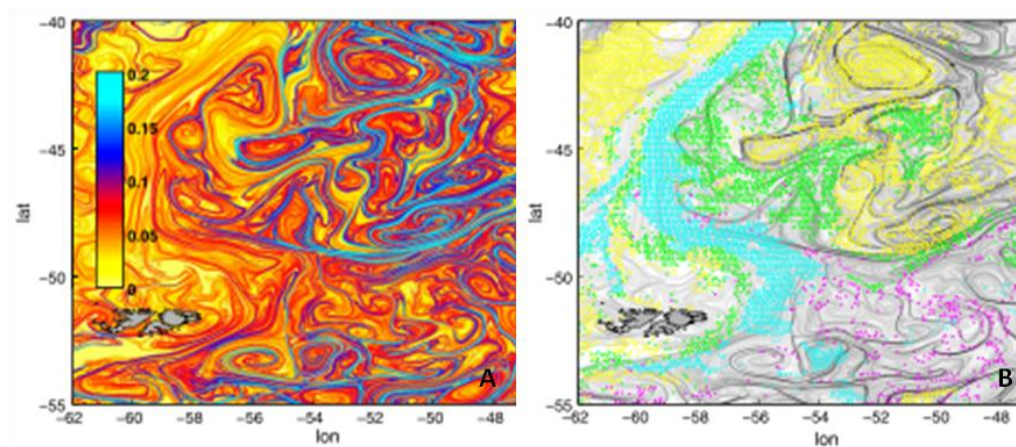


Figure 1.3: Maps of filamentary structures (A) and phytoplankton distribution (B) at the confluence of the Brazil and Malvinas currents (from d'Ovidio et al. 2010). There is strong similarities between the two distributions. A: Stirring rates of waters parcels allow to identify filaments. B : Observed dominant phytoplankton types indicated by different colors, see details in d'Ovidio et al. 2010.

3.1.4. Des échelles de recherche alimentaire hiérarchisées

Apports du *bio-logging*.

Depuis les années 1990, la **télémétrie** et le **bio-logging** ou suivi des individus dans leur milieu naturel s'est développé de façon exponentielle grâce aux progrès de la microélectronique permettant la mise au point d'émetteurs ou appareils enregistreurs de données miniaturisés très performants. Les balises Argos, les GPS (*Global Positioning System*) ou GLS (*Global Location Sensing*) permettent de suivre les déplacements horizontaux des animaux tandis que les déplacements verticaux sont mesurés par des capteurs de pression (*Time Depth Recorder*, Kooyman 2004). En couplant ces capteurs, il est possible de reconstituer le comportement d'exploration de l'environnement des animaux dans les 3 dimensions de l'espace marin (Ropert-Coudert & Wilson 2005). Depuis, un nombre considérable d'études ont permis de mettre à jour les zones de prospection

d'oiseaux marins, volants et plongeurs. Ces études de déplacement couplées aux caractéristiques environnementales mesurées par satellite ont permis de caractériser les **structures hydrologiques ciblées** en rapport aux besoins vitaux au cours de la reproduction.

Il a été mis en évidence que les échelles de la recherche alimentaire étaient **hiérarchisées** dans l'espace, en réponse à l'utilisation des structures hydrologiques multi-échelles (Fauchald 2009). Les oiseaux de mer utilisent les **fronts océanographiques** dont la variabilité est relativement faible d'une année sur l'autre (Schneider 1991), les **tourbillons** (d'une durée de vie de plusieurs semaines à plusieurs mois), les **zones filamentaires** (de quelques jours à une semaine) mais également les **abords de plateau** souvent associés à des remontées d'eaux froides riches en nutriments (*e.g.* Weimerskirch et al. 1993, Tremblay & Cherel 2000, Charrassin & Bost 2001, Barlow & Croxall 2002, Cotté et al. 2007, Kai et al. 2009, Bost et al. 2009). L'utilisation de structures **prédictibles** permet ainsi aux prédateurs de maximiser leur probabilité de trouver des ressources en quantité favorable pour répondre à leurs exigences énergétiques. Le mot "**prédictible**" utilisé dans cette thèse définit **l'ensemble des structures prévisibles, favorisant la productivité primaire et/ou secondaire**. En raison de leur récurrence, ces structures peuvent ainsi être attractives pour les prédateurs supérieurs (Weimerskirch 2007).

Les structures méso et sub-mésoéchelle peuvent être profitables pour les oiseaux marins si elles sont associées à une importante **agrégation par advection des ressources ciblées**. La structure devra être stable suffisamment longtemps pour permettre le développement et l'attraction des différents maillons de la chaîne alimentaire pour être favorable aux niveaux les plus élevés (Jacquet et al. 1997, Durant et al. 2005). Les études à très fines échelles nécessitent l'utilisation de technologies embarquées (caméras, accéléromètres) sophistiquées mais peuvent permettre de montrer des ajustements jusqu'à l'échelle du banc de proie (Watanabe et al. 2014).

Ainsi, il a été montré que les prédateurs marins ont une capacité à **répondre aux variations d'agrégation** des ressources sur de multiples **échelles spatiales mais également temporelles** (Hunt et al. 1999, Fritz et al. 2003). A l'échelle de la journée, les prédateurs peuvent répondre aux mouvements de leurs proies (*e.g.* migration nyctémérale des myctophidés, Bost et al. 2002). Aux échelles saisonnières et interannuelles, les grandes variations climatiques peuvent considérablement moduler la distribution spatiale des larges fronts océaniques. Les prédateurs marins sont capables de palier à ces variations, jusqu'à certaines limites au-delà desquelles les paramètres démographiques des populations (succès reproducteur, croissance, survie) peuvent être affectées (Le Bohec et al. 2008, Lea et al. 2009, Ropert-Coudert et al. 2015, Bost et al. 2015).

3.1.5. La 3^{ème} dimension chez les manchots

Les prédateurs plongeurs pulmonés à place centrale (oiseaux, phoques) sont des **modèles de choix** pour l'étude des stratégies d'alimentation en milieu marin. En effet, ces prédateurs qui accèdent à leurs proies en profondeur (Houston & Carbone, 1992) présentent des contraintes temporelles très fortes liées à leur respiration aérienne. Celle-ci les oblige à revenir régulièrement à la surface pour respirer. La gestion des **stocks d'oxygène** est donc une contrainte majeure pour les oiseaux plongeurs puisqu'elle **limite le temps qu'ils peuvent passer dans les zones d'alimentation**, et donc par conséquent le gain énergétique par unité de temps. De plus, l'eau est un milieu 800 fois plus dense et 60 fois plus visqueux que l'air (Dejours 1987) tandis que la conductivité thermique est 20 fois supérieure au milieu aérien. Par conséquent, les activités telles que la localisation, la poursuite et la capture des proies, mais aussi leur absorption et leur digestion, peuvent représenter un coût énergétique significatif pour ces animaux (Green et al. 2005).

Au niveau théorique, le modèle de la valeur marginale a été transposée sur le comportement de plongée, la ressource à maximiser n'étant plus le temps mais d'abord le **taux de restauration des stocks d'oxygène** (Kramer 1988) puis **la proportion du temps passé à la profondeur de chasse la plus favorable : « bottom », et le gain énergétique** (Houston & Carbone 1992, Carbone & Houston 1996). D'un point de vue conceptuel, les manchots sont des prédateurs à place centrale doublement contraints, dépendant de deux sites centraux: la **colonie** et la **surface**. Leur approvisionnement nécessite en effet des phases de transit horizontales mais également verticales pour accéder aux ressources (Figure 1.4) Ils sont donc des **modèles d'études de choix dans l'approche des stratégies optimales de recherche alimentaire en milieu marin**.

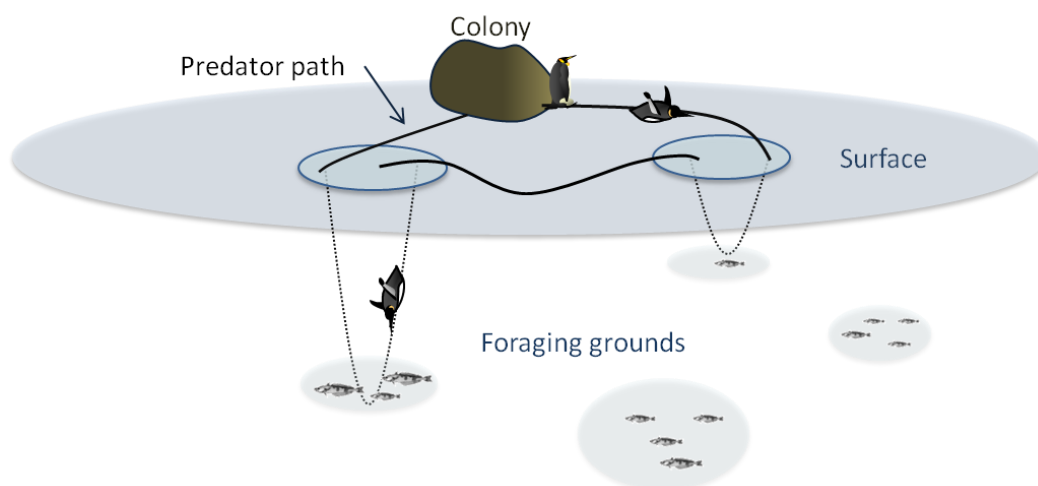


Figure 1.4: Shema of central place foraging behaviour in diving predators. During the breeding season, individuals are dependant of two central places: the colony for breeding duties and the surface for air-breathing.

La famille des **manchots (sphensicidés)** regroupe 18 espèces réparties en 6 genres : *Aptenodytes* (royal et empereur), *Eudyptula* (manchot pygmée, à ailerons blancs), *Megadyptes* (manchot antipode), *Pygoscelis* (manchot papou, Adélie, à jugulaire), *Spheniscus* (manchot du Cap, de Magellan, Humboldt, des Galápagos) et *Eudyptes* (gorfous de Fiorland, Snares, de Moseley, huppé, sauteur, macaroni).

Les manchots présentent des relations allométriques marquées entre leur taille et leur capacité de plongée (Mori 2002). La plus petite espèce (pesant 1kg en moyenne) n'atteindra pas les **70m** (manchot pygmée *Eudyptes minor*, record : 67m, Ropert-Coudert, Chiaradia, et al. 2006) tandis que la plus grande (pesant entre 25 et 45 kg) dépassera **500m** de profondeur (manchot empereur *Aptenodytes forsteri*, record : 534m, Kooyman & Kooyman 1995). La plupart des **plongées** se découpent en **quatre phases** : la phase de descente, la phase de fond (*bottom phase*), la phase de remontée et le temps de récupération post-plongée. A plus large échelle, la majorité des plongées profondes des oiseaux plongeurs et mammifères marins se déroule en successions rapides, appelées **séquences de plongées** ('bouts') séparées par des intervalles de surface (Boyd 1997).

Pour gérer efficacement la ressource en oxygène, les oiseaux plongeurs comme les manchots ont des **adaptations physiologiques** spectaculaires :

1) L'efficacité avec laquelle le sang peut stocker et transporter l'oxygène varie en fonction de la **concentration d'hémoglobine** au sein des globules rouges. Chez les manchots, cette concentration est haute comparée à celle des oiseaux non plongeurs. De plus, l'hémoglobine présente une **affinité relativement faible avec l'oxygène**, ce qui induit une libération rapide des molécules d'oxygène dans les tissus.

2) Le stockage d'oxygène est augmenté dans les tissus internes, notamment dans les muscles locomoteurs au niveau de la **myoglobine** (protéines) qui présentent une affinité forte à l'oxygène liée à leur structure hémique. Les muscles natatoires du manchot empereur peuvent ainsi contenir 19% plus d'oxygène que la totalité de leur volume sanguin entier (Kooyman & Ponganis 1998, Ponganis & Kooyman 2000). La mise en hypothermie de certains organes internes serait également une stratégie physiologique qui permettrait de réduire les coûts énergétiques liés au maintien de la chaleur corporelle en eaux froides (Handrich et al. 1997)

3) Enfin, ils utiliseraient une stratégie métabolique mixte basée sur la **respiration aérobie et anaérobie**. La plongée aérobie se termine lorsque la concentration d'acide lactique croît subitement au dessus des niveaux de repos, nécessitant une augmentation marquée du temps de récupération en surface pour métaboliser le lactate (Kooyman et al. 1983, Ponganis et al. 1997). Cette respiration peut être optimale dans les cas d'une importante profitabilité de la parcelle exploitée (taux de rencontre élevé avec les proies). Dans les autres cas, les manchots seraient plus avantagés à remonter à la surface

avant un épuisement complet de leurs réserves d'oxygène (Mori 1998, Thompson & Fedak 2001, Thompson et al. 1993).

En réponse à l'importante densité de l'eau, la morphologie des manchots est fuselée et hydrodynamique tandis que le volume d'air dans le plumage est réduit, limitant ainsi au maximum les frottements. Les membres antérieurs (ailerons) servent de palettes natatoires très efficaces leur permettant de se propulser au moindre coût (Sato et al. 2002, Sato 2004, Hanuise et al. 2013). Grâce à ces adaptations, les manchots sont d'**excellents nageurs et plongeurs**.

Le **pouvoir bio-indicateur du temps passé au fond** et du nombre d'ondulations associés (*wiggles*), **relatif au succès de chasse a depuis été validé** par des études effectuées en captivité et en milieu naturel couplant des mesures de tentatives de captures de proies (par accélérométrie), ingestions œsophagiennes ou stomacales et analyses comportementales des profils de plongée (Wilson et al. 1992, 2002, Charrassin et al. 2001, Ropert-Coudert, Kato, et al. 2006, Bost et al. 2007, Viviant et al. 2009, 2014, Hanuise et al. 2010, Kokubun et al. 2011, Carroll et al. 2014). **L'optimisation du temps passé au fond** semble être une stratégie adoptée au cours des plongées, dépendante en revanche de la qualité de la parcelle prospectée (Mori & Boyd 2004a, b, Mori et al. 2007, Hanuise et al. 2013, Watanabe et al. 2014, Carroll et al. 2014).

Chez les manchots, la caractérisation des **stratégies de recherche alimentaire** passe par la prise en compte des **déplacements dans la dimension à la fois horizontale et verticale**.

En revanche, obtenir une vision précise de l'ajustement des comportements face aux différentes conditions environnementales rencontrées dans les deux dimensions nécessite un travail et des connaissances spécifiques à chaque aspect. Dans cette thèse, **l'aspect horizontal de l'utilisation de l'habitat sera privilégié** mais l'analyse des comportements de plongées sera aussi présentée.

3.1.6. Des stratégies de couple

Les différentes demandes énergétiques liées à la recherche alimentaire indiquées jusqu'à présent soulignent **l'importance de la condition corporelle** des animaux pour mener à bien la reproduction (Weimerskirch 1998). L'énergie dans l'environnement étant limitée, des stratégies d'anticipations sont observées pour palier aux événements et la **masse** est un indicateur majeur de cette anticipation. En effet, plusieurs études montrent qu'une **bonne condition corporelle** en début de saison de reproduction favorise la progéniture (survie et croissance, Chastel et al. 1995, Tveraa et al. 1997, Robinson et al. 2005). Par exemple, les manchots Adélie femelles qui se reproduisent ont un poids supérieur de 12% à celles qui ne se reproduisent pas (Vleck & Vleck 2002). De plus, **au cours de la reproduction**, la capacité des adultes à maintenir leur condition corporelle à des niveaux corrects est positivement reliée au gain de masse des poussins (Weimerskirch et al. 2001, Crawford et al. 2003, 2006, Gaston & Hipfner 2006).

Chez les oiseaux marins, **l'incubation et l'élevage du poussin est partagé à part égale entre les deux conjoints**. Monogame, les deux sexes s'investissent dans la reproduction par l'alternance de **tâches parentales** à terre (apport de chaleur, gardiennage) et en mer (recherche de nourriture pour le poussin). Cependant, cette nécessité de partage des tâches ne signifie pas une parfaite équité entre les deux partenaires.

Ces différences peuvent se traduire par différents facteurs :

La **capacité des deux partenaires à acquérir de l'énergie** peut varier en raison de facteurs intrinsèques au sexe (Clarke et al. 1998a, Peck & Congdon 2006). L'existence d'un **dimorphisme sexuel** peut en effet engendrer des capacités de déplacements différentes amenant à des ségrégations spatiales d'habitat et un succès de chasse différent (*e.g.* Weimerskirch et al. 2014, Green et al. 2007). La **durée de vie** peut également varier entre les deux sexes. Un sexe qui vit moins longtemps aura tout intérêt à être plus efficace dans la recherche alimentaire, minimiser les coûts d'un épisode reproducteur pour maximiser potentiel nombre total d'épisodes reproducteurs (*e.g.* Dugger et al. 2006). L'âge des deux partenaire, indicateur de **l'expérience individuelle**, peut engendrer un écart d'approvisionnement (Angelier et al. 2007, Limmer & Becker 2009, Weimerskirch et al. 2014).

Jusqu'à présent, le raisonnement sur la recherche alimentaire était individu-centré. Cependant, **chez des espèces nidicoles où les deux sexes effectuent des soins parentaux, les stratégies de recherche alimentaire optimales peuvent être étudiées à l'échelle des deux partenaires** (Shoji, Aris-Brosou, Fayet, et al. 2015). La probabilité du succès reproducteur, étroitement relié à la valeur sélective individuelle, va en effet dépendre de l'investissement des **deux** parents.

Chez les manchots, les adultes se relaient pour la garde de l'œuf pendant l'incubation. Pendant qu'un des parents est parti en mer s'alimenter, l'autre incube (Williams 1995). Le non-retour de l'adulte parti en mer, ou une mauvaise couvaison de celui resté à terre entraîne forcément à un échec reproducteur (Ancel et al. 1998). Cet exemple extrême peut se refléter dans une moindre mesure sur des écarts de condition corporelle (ou **qualité individuelle**) entre les deux partenaires. Cependant, il est possible d'observer un **ajustement** des comportements de recherche alimentaire à l'échelle du couple. Par exemple, lorsqu'un partenaire d'un couple de pétrel antarctiques *Thalassoica antarctica* présente une condition corporelle plus basse que la moyenne, l'autre parent est capable d'ajuster sa durée de jeûne pour lui laisser le temps de s'approvisionner (Tveraa et al. 1997).

Selon la variation de la qualité individuelle, la théorie présume que les soins biparentaux constituent une **stratégie évolutivement stable** (SES, Houston & Davies 1985) lorsque chaque parent compense **partiellement** la baisse d'investissement de l'autre parent. Cependant, cette compensation peut s'avérer être **complète**, **absente** (pas de modification) ou encore **négative** (diminution de l'investissement parental). Ces différents cas de figure sont reliés à un coût pour la survie et/ou le succès reproducteur total de l'individu qui compense, et l'abandon peut survenir au delà d'un certain seuil de contrainte individuelle trop importante (Houston & Davies 1985, Jones et al. 2002). Chez les espèces longévives à stratégies lentes, si les risques énergétiques sont trop importants, on s'attend à ce que les individus privilégient leur propre survie au détriment de l'épisode reproducteur. Ces animaux ont en effet la possibilité de recommencer une reproduction plus tard, avec un nouveau partenaire (*e.g.* manchot papou, Bost & Jouventin 1991).

Les stratégies de recherche alimentaires ont été sélectionnées pour permettre aux partenaires de maximiser le succès reproducteur. Au niveau des soins parentaux, ceci peut être observé à travers un compromis dans les tâches parentales permettant à chaque partenaire de maximiser sa propre transmission génétique. Chez les oiseaux marins, le **degré de contraintes de la reproduction imposées sur chaque sexe peut être ainsi variable** selon leurs capacités à y répondre. Si l'on veut correctement comprendre les comportements alimentaires à l'échelle du cycle reproducteur, **la prise en compte du sexe doit être impérative.**

I.4. Problématique et structure de la thèse

L'objectif de cette thèse a été d'étudier les stratégies de recherche alimentaire d'un prédateur plongeur épipélagique majeur de l'océan austral, le gorfou macaroni *Eudyptes chrysolophus*, pendant l'intégralité de son cycle de reproduction.

La population mondiale de cette espèce de manchot est considérée comme la biomasse aviaire la plus importante de l'océan austral. Le gorfou macaroni est aussi le plus grand consommateur mondial des ressources secondaires, parmi tous les oiseaux marins (13.2% , Brooke 2004). Cependant, depuis les 30 dernières années, les effectifs de gorfous macaroni sont en diminution drastique (30% en Géorgie du Sud et sur l'île Marion, (Crawford et al. 2003, 2009, Crossin et al. 2013). L'espèce est à présent considérée comme « vulnérable » (BirdLife International 2016).

Les populations de **Crozet** et **Kerguelen** situées dans les **Terres Australes et Antarctiques Françaises** abritaient des colonies parmi **les plus grandes populations à l'échelle mondiale** selon les comptages disponibles, soit **55%** et **29 % des effectifs totaux** respectivement (2.2 et 1.8 millions de couples à Crozet et Kerguelen respectivement en 1985). Récemment, les comportements de recherche alimentaire en période hivernale de ces deux populations ont été bien étudiés dans le cadre d'un doctorat (Thiebot 2011). En revanche, les **connaissances disponibles** sur leurs stratégies de recherche alimentaire **au cours de la reproduction** étaient encore très **limitées**. Le cycle reproducteur, leur phénologie et leur régime alimentaire ont fait l'objet de plus d'études (Camprasse et al. *in prep*, Mougin 1984, Stahl et al. 1985, Ridoux 1994, Cherel & Hobson 2007, Cherel et al. 2007).

Au cours de cette thèse, nous avons voulu pallier à ce manque de connaissances et étudier en détail les comportements de recherche alimentaire sur la totalité du cycle de reproduction.

Nous avons essayé de répondre aux questions suivantes :

- **Quelle est la distribution en mer des gorfous Macaroni à Crozet et Kerguelen ?** Quelles sont les zones géographiques ciblées par les individus au cours du cycle ? Quel effort de prospection alimentaire effectuent-ils? Comment sont organisés spatialement leurs déplacements ?
- **Quels sont les habitats utilisés par les gorfous macaroni au cours des phases de leur cycle ?** Quelles structures hydrologiques et/ou conditions océanographiques sont ciblées ? Comment les gorfous macaroni les utilisent-ils ? Existe-il des variations entre les différentes phases du cycles ? entre les sexes?

- **Comment les gorfous ajustent-ils leurs comportement de recherche alimentaire en fonction des contraintes énergétiques de leur cycle reproducteur ?** Ciblent-ils les mêmes proies ? Quelles sont les stratégies entre les mâles et les femelles ?
- Enfin, **existe-il des différences populationnelles entre les îles Crozet et Kerguelen ?** Quel est le degré d'influence du site géographique sur les stratégies de recherche alimentaire ? **Est ce qu'une localité est plus favorable pour l'approvisionnement ?**

Le couplage de données **téléométriques** (suivi par balise Argos, Gps et/ou capteur de pression), de l'étude du **régime alimentaire** (analyse de régurgitats, isotopiques), de **variations de masses** à des données **environnementales pertinentes** (localisation des fronts, tourbillons, estimation de la productivité primaire, des courants etc.) a été utilisé afin de répondre à ces questions. **Au final, une approche comparative avec les autres localités de l'Océan Austral sera également effectuée afin d'aborder le degré de plasticité phénotypique de l'espèce.**

Aspect appliqué de la thèse

Le XX^e siècle a été caractérisé par une **exploitation humaine intensive** des ressources naturelles de l'Océan Austral, notamment sur les **stocks de baleines, de pinnipèdes et de poissons** (Pauly et al. 1998, Myers & Worm 2003, Ainley & Blight 2009, Ainley et al. 2010). Des pêcheries intensives ont eu lieu dans l'Océan Austral depuis les années 1970 et ont été associées à une surexploitation des stocks de poissons des glaces (*Notothenia rossi*, *Champsocephalus gunnari*, (Croxall & Nicol 2004). Les diminutions drastiques des effectifs de consommateurs de krill antarctiques et leur remontée progressive suite à l'arrêt du commerce de l'huile a eu et a encore des conséquences sur les relations trophiques des écosystèmes (Barlow et al. 2002, Trathan et al. 2012, Watanabe et al. 2014, Horswill et al. 2014).

Concernant les **manchots**, la perspective de nouvelles pêcheries visant le krill Antarctique ou les myctophidés (poissons lanternes) pourraient considérablement menacer leurs populations qui sont extrêmement dépendantes de ces ressources (Cresswell et al. 2008). Les manchots sont également sensibles aux modifications environnementales liées aux changements climatiques et des mouvements dans leur aire de répartition sont à envisager (Barbraud & Weimerskirch 2001, Ainley 2002, Barlow et al. 2002, Bohec et al. 2008, Lynch et al. 2012, Péron et al. 2012, Bost et al. 2015). Actuellement, 10 espèces ont vu leurs effectifs diminuer et ont un statut considéré comme "préoccupant" (statut IUCN : 5 "Vulnerable", 5 "Endangered", 5 "Near Threatened" et 3 "Least Concerned", BirdLife 2016).

Définir les **zones prioritaires à protéger** est un objectif majeur des dernières années pour la CCAMLR (*Convention on the Conservation of Antarctic Marine Living Resources*). Tous les ans, elle a pour objectif de mesurer l'état de santé des ressources marines. Elle s'est également définie l'objectif

de préconiser la mise en place d'**Aires Marine Protégées** (AMP) dans l'Océan Austral et Antarctique afin de protéger la biodiversité qui s'y trouve.

Dans ce contexte, l'utilisation de **prédateurs marins supérieurs** est particulièrement utile car leur position aux sommets des chaînes trophiques leur confère un rôle **bio-indicateur de l'état de santé des écosystèmes**. Ce concept d'espèce « parapluie » est lié à l'hypothèse que la présence d'une espèce implique et/ou nécessite la présence d'autres espèces, proies ou autres prédateurs dépendant du même type de ressources (Zacharias & Roff 2001). Protéger cette espèce revient donc à protéger une biodiversité importante.

Délimiter les zones de conservation nécessite une étude approfondie de **l'aire de distribution et des habitats utilisés** de l'espèce considérée, ceci en prenant compte des **différentes phases de son cycle de vie**. BirdLife International est une organisation internationale (119 partenaires dans 117 pays) qui a, entre autres, vocation à définir les **Zones Importantes pour la conservation des Oiseaux** (*Important Bird Areas, IbAs*). Dans ce cadre et en partenariat avec cette organisation, **cette thèse a pour vocation d'apporter des connaissances cruciales sur la distribution d'une espèce majeure de l'Océan Austral, le gorfou macaroni *Eudyptes chrysolophus*.**

Cette étude a été complémentaire au projet EU-BEST ("*Identifying important marine areas for macaroni penguins (*Eudyptes chrysolophus*) in the UK and French Overseas Territories*"). Ce programme coordonné par Norman Ratcliffe du BAS (*British Antarctic Survey*) en partenariat avec le CEBC (CA Bost) et BirdLife (Ben Lascelle) a eu pour vocation de modéliser les habitats des gorfous macaroni à l'échelle de l'Océan Austral. Ainsi, notre étude a permis d'apporter des données indispensables au projet sur l'utilisation de l'habitat des populations des TAAF.

CHAPITRE II

MATERIEL AND METHODS



Preening behavior before going at sea © Cécile Bon

II.1. Site d'étude

1.1. L'Océan Austral

L'**Océan Austral** est situé dans l'hémisphère sud et représente 20% de l'océan mondial. Sa particularité est d'être parcouru par le **Courant Circumpolaire Antarctique** (ACC, *Antarctic Circumpolar Current*). Sans barrière continentale, l'ACC s'écoule d'ouest en est sans déviation majeure, à l'exception de quelques plateaux sous-marins et au niveau du passage de Drake qui constitue un entonnoir situé entre l'Amérique du Sud et la Péninsule Antarctique (Orsi et al. 1995).

En l'absence de barrière, le régime des vents est particulièrement important, tandis que le débit estimé du courant est plus d'une centaine de fois supérieur à tous les fleuves du monde.

L'action du vent provoque un déplacement horizontal des couches d'eaux superficielles de l'océan appelé le **transport d'Ekman**. Associé à la force de Coriolis, ces deux facteurs entraînent une remontée d'eau profonde (*upwelling*, pompage d'Ekman) ou un enfoncement des eaux de surface (*downwelling*, ventilation) qui vont influencer la distribution et l'abondance des ressources primaires (Yoder et al. 1993, Thomas & Lee 2005).

L'Océan Austral se caractérise par la présence de grandes masses d'eau aux propriétés physico-chimiques différentes (température, salinité, densité..). Les zones de rencontre entre ces masses d'eaux, appelées **fronts océanographiques**, sont associées à des discontinuités des gradients physiques et permettent de caractériser différentes régions dans l'Océan Austral (Figure 2.1, Orsi et al. 1995, Thomas & Lee 2005).

La bordure nord de l'ACC est définie par le **front subtropical** (STF, *SubTropical Front*) qui sépare les eaux tièdes et salées subtropicales des **eaux subantarctiques** plus fraîches. Le STF constitue la limite nord de l'Océan Austral. Au Sud se trouve le **front subantarctique** (SAF, *SubAntarctic Front*) caractérisé par une température de surface comprise entre 8 et 9°C (Park et al. 1993, Orsi et al. 1995). Ce front marque la limite nord des eaux de la **zone polaire frontale** (PFZ, *Polar Frontal Zone*) bordées au sud par le **front polaire** (PF, *Polar Front*). Le front polaire se caractérise par un isotherme de 2°C à 200m de profondeur, soit une signature thermique de surface située entre 4 et 5°C pendant l'été (Park et al. 1998). Au sud du front polaire sont situées les eaux Antarctiques, bordées par la **limite sud de l'ACC** (SACCF, *Southern Antarctic Circumpolar Front*) qui marque la remontée d'eaux abyssales (Figure 2.1). Ces fronts océanographiques constituent de véritables zones de brassages de nutriments mais forment également des frontières écologiques à la distribution horizontale des ressources marines.

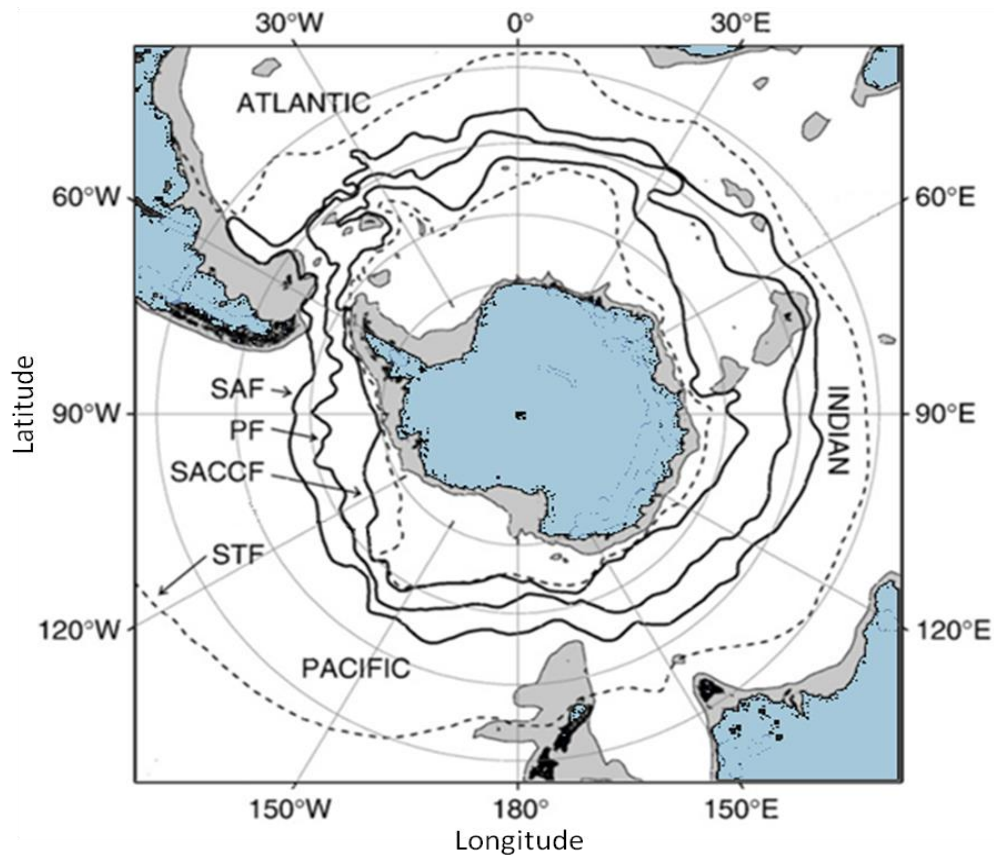


Figure 2.1: Circumpolar distribution of the Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF), Southern ACC Front (SACCF). Figure adapted from Roquet et al. 2009.

1.2. Les Archipels des îles Crozet et Kerguelen

Les **Terres Australes et Antarctiques Françaises (TAAF)** sont depuis 1995 un territoire d'outre-mer doté de l'autonomie financière et administrative. Les TAAF sont formées par **l'archipel des îles Crozet, l'archipel des Kerguelen, les îles Saint Paul et Amsterdam, la Terre Adélie et les îles Eparses**. Cet ensemble procure à la France la **plus grande emprise maritime** au monde après les Etats-Unis car elle possède une Zone Economique Exclusive de plus de 2.300.000km². En 2006, les TAAF ont créé **la plus grande réserve naturelle** de France, soit 700.000 hectares dans les îles subantarctiques. Chaque année, des campagnes scientifiques se déroulent dans les TAAF et un personnel important (scientifiques, agents de la réserve, agents de l'IPEV, personnel de maintenance : militaires, informaticiens, plombiers, électriciens, mécaniciens, médecins, cuisiniers etc.) est envoyé dans les districts grâce à 4 rotations annuelles du Marion Dufresne (départ de la Réunion) dans les îles subantarctiques et l'Astrolabe pour la Terre Adélie (départ de Hobart, Tasmanie).

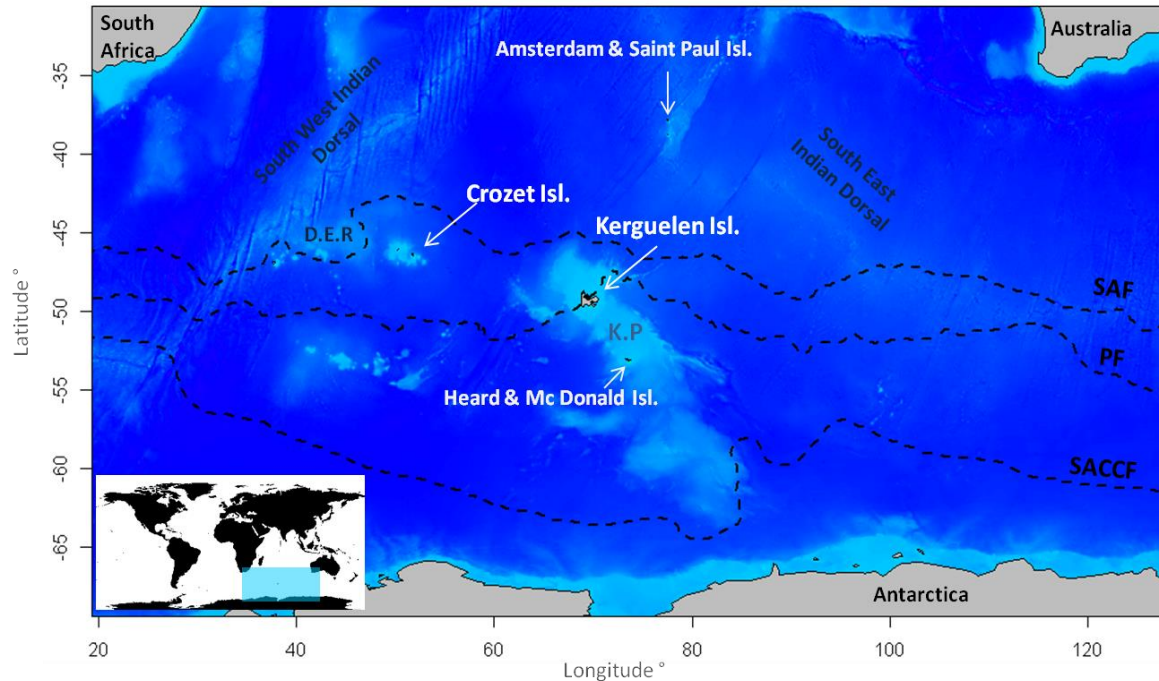


Figure 2.2: Localisation of Crozet and Kerguelen islands in the Indian Basin. Dashed lines indicate three main oceanographic fronts constrained by the bathymetry of Del Caño Rise (D.E.R) and/or the Kerguelen Plateau (K.P). SAF: SubAntarctic Front. PF: Polar Front. SACCF: Southern ACC Front. Adapted from J.B Thiebot (2011).

1.2.1. L'archipel des îles Crozet

Les **îles Crozet** (340km²) sont composées de **5 îles d'origine volcanique** situées entre 45° 95' et 46° 50' Sud et 50° 33' et 52° 58' Est (Figure 2.2). Ces îles sont les restes de sommets de volcans situées sur un vaste plateau sous-marin et seraient âgées au maximum de 8 millions d'années. Le climat est caractéristique de la zone subantarctique, venteux et pluvieux, où la température moyenne de l'air est de 5°C. Les vents de secteur ouest dominant soufflent avec des rafales de plus de 100km/h à raison de 120 jours par an, justifiant l'appellation donnée à ces latitudes : les « 40^{èmes} rugissants ». Il pleut beaucoup (2500mm/an) et la neige peut survenir à n'importe quelle période de l'année. Les îles Crozet abritent une faune exceptionnelle composée de 4 espèces de manchots (gorfous sauteurs, gorfous macaroni, manchots papous et royaux) des albatros (hurleurs, à tête grise, à sourcils noirs, à bec jaune, fuligineux) des pétrels (géants, à mentons blancs, prions), des goélands dominicains, skuas et des mammifères marins (otaries à fourrure antarctique, éléphants de mer, orques)¹.

1.2.2. L'archipel des Kerguelen

L'archipel des Kerguelen est localisé entre 48°35' et 49°54' Sud et entre 68°43' et 70°35 Est à une distance de 3400km de la Réunion et environ 1500km de Crozet. Cet archipel d'environ 7.215km² est constitué d'une île principale, la Grande Terre, d'une superficie égale aux 3/4 de la Corse, entourée

¹ www.taaf.fr

de plus de 300 îles. Le Mont Ross et sa calotte glaciaire culmine à 1850m qui est le point le plus haut de l'archipel. Les îles Kerguelen, âgées de 40 millions d'années, sont la partie immergée d'un immense plateau volcanique sous-marin nommé Plateau de Kerguelen qui descend au-delà de 60°S (Figure 2.2). Ce plateau de plus de 2 millions de km² constitue une barrière physique à l'ACC. Le climat rencontré sur ces îles est océanique, froid et très venteux. La température annuelle est en moyenne de 4.5°C avec une amplitude faible d'environ 6°C. Les précipitations sont fréquentes sur la partie Est (820mm/an) mais seraient 3 fois plus importantes sur la partie Ouest, non protégée par les montagnes du centre de l'archipel¹. Le vent souffle quasi-continuellement à une moyenne de 35km/h et les vents de 150km/h sont monnaie courante sous ces latitudes justement nommées les « 50^{èmes} hurlants ».

Ces îles hébergent, tout comme Crozet, une biodiversité incroyable. Les îles Crozet et Kerguelen abritent les communautés d'oiseaux marins les plus riches au monde, avec 36 espèces nicheuses recensées pour Crozet et 35 pour Kerguelen. On estime que 20 millions de couples d'oiseaux marins viendraient se reproduire chaque année à Crozet et probablement au moins autant à Kerguelen (Jouventin et al. 1984).

II.2. Modèle biologique : le gorfou macaroni

2.1. Taxonomie et Distribution

Le **gorfou macaroni** *Eudyptes chrysolophus* (J.F. von Brandt, 1837) a divergé des autres gorfous à crêtes, notamment des gorfous snares (*E.robustus*) et des gorfous du Fiorland (*E.pachyrhynchus*) au début des glaciations du Pléistocène, il y a 2 millions d'années (Baker et al. 2006). Le gorfou de Schegel (*E.schegeli*) qui vit sur les îles Macquarie et Bishop a longtemps été considéré comme une sous-espèce du gorfou macaroni. Cependant, l'isolement reproducteur des gorfous de Schegel sur Macquarie associé à des différences morphologiques précises, suggèrent qu'une divergence entre les deux espèces aurait déjà eu lieu (Parkes 1992). Cette hypothèse rejoint des observations effectuées sur les flux de gènes entre populations. Chez les oiseaux marins, ce flux est considérablement réduit dans 85% des populations étudiées, qui se reproduisent dans des régimes océanographiques différents (Friesen 2015).

Le gorfou macaroni a le dos, la tête et la queue noire qui contrastent avec le blanc de son ventre. Caractéristique du genre *Eudyptes*, il possède sur la tête une paire d'aigrettes de longueur moyenne, jaunes orangées situées au dessus de la tête (Figure 2.3). Ses pattes palmées sont dotées de puissantes griffes lui permettant de grimper sur les parois rocheuses où il peut parfois se reproduire. Son bec rose très dur est un excellent outil de défense du nid contre les indésirables (congénères, prédateurs).

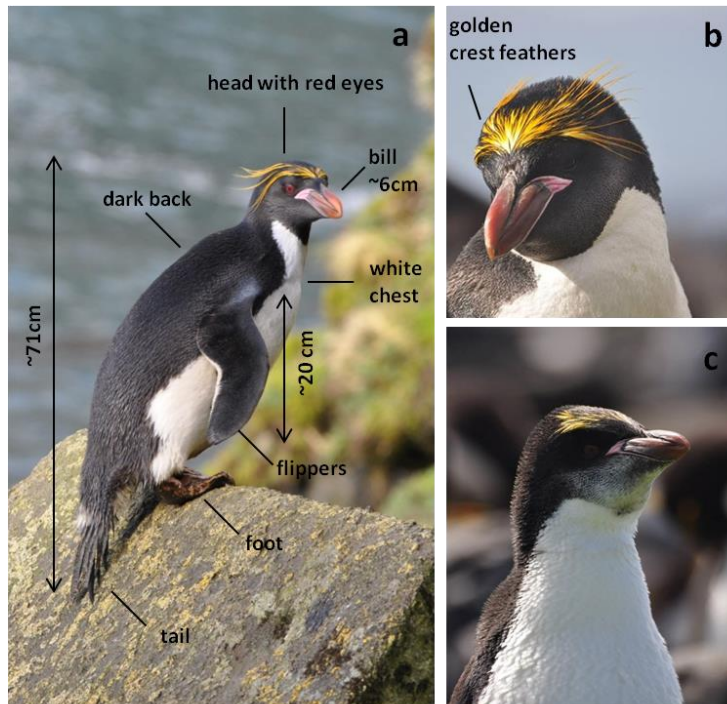


Figure 2.3: Macaroni penguins. a. An adult on a rock. b. Adult are recognizable by their golden-yellow crest feathers. c. immature fledglings and one-years-olds macaroni do not have as well developed crest feathers as adults. © Cécile Bon

Les gorfous présentent d'importantes variations de masse au cours de leur cycle annuel. Sur l'ensemble de l'année, les extrêmes sont observés avant et après la mue, soit 6.1kg (pré) et 3.1kg (post-mue) et pour les mâles, et 6.3kg (pré) et 2.8kg (post) pour les femelles (individus de Géorgie du Sud, Crossin et al. 2013).

L'aspect des deux sexes est similaire mais un dimorphisme morphologique existe en faveur des mâles, qui sont 15 à 20% plus gros que les femelles. Les gorfous présentent d'importantes variations de masse au cours de leur cycle annuel. Sur l'ensemble de l'année, les extrêmes sont observés avant et après la mue, soit 6.1kg (pré) et 3.1kg (post-mue) et pour les mâles, et 6.3kg (pré) et 2.8kg (post) pour les femelles (individus de Géorgie du Sud, Crossin et al. 2013). La variabilité temporelle des masses pouvant prêter à confusion pour la reconnaissance des deux sexes, nous utilisons la mesure du bec qui est plus importante chez le mâles (~ 60mm) que chez les femelles (~53mm, Williams 1995).

La **distribution** des gorfous macaroni est **circumpolaire** (Figure 2.4). Environ 258 colonies sont situées sur 55 sites de reproduction localisés entre 46°S (île Marion) et 65°S (Péninsule Antarctique). Durant l'hiver, les gorfous sont capables de se déplacer dans l'Océan Indien sur plus de 3 millions de kilomètres carrés depuis les îles Kerguelen et Crozet (Bost et al. 2009). Les estimations des populations présentées sont incomplètes en raison de données manquantes sur certaines îles, notamment l'archipel des îles Crozet, mais la population mondiale d'individus reproducteurs serait en 2013 de l'ordre de **6.300.800 couples reproducteurs**. Actuellement, les populations les plus **importantes** sont situées aux **îles Crozet** (2.172.000 couples, 1985), à **Kerguelen** (1.812.000 couples, 1985), en **Géorgie du Sud** (>1.000.000 de couples, 2002), sur **l'île Heard** (<1.000.000 de couples, 2003/2004) et les îles **Princes Edward** (303.900 couples, 2008/2009, Crossin et al. 2013).



Figure 2. 4 :
Distribution and abundance of Macaroni penguins populations. Counts are based on pairs. From Crossin et al. 2013

Depuis 1993, on estime que la population mondiale a subi une diminution de 30% de ses effectifs. Cette baisse d'effectifs est observée depuis environ 50 ans, mais surtout expliquée par une diminution rapide depuis les années 1980 en Géorgie du Sud qui comptabilisait la moitié de la population (5 millions en 1980, 2.7 millions à la moitié des années 1990 et moins de 1 millions de couples en 2002). Sur l'île Marion, la population totale a chuté de 30% en 15 ans (400.000 à 290.000 couples entre 1994 et 2009). La population des îles Crozet n'a pas été comptabilisée depuis les années 1985 mais une diminution est suspectée car des petites colonies ont été désertées (Figure 2.5, Bost, *pers. com*). En revanche, à Kerguelen, il semble que la population ait augmenté depuis les années 1960 (Barbraud, *pers. com*). Cette baisse des effectifs a placé cette espèce sous le statut d'espèce "vulnérable" auprès de l'IUCN (30% de baisse d'effectifs sur 10 ans ou 3 générations et persistance de stress anthropogénique).

Un premier site d'étude se situe sur l'île de La Possession. La colonie d'étude (Colonie Wilson) est localisée dans le Jardin Japonais au nord-est de Pointe Basse (Figure 2.5). Dans cette étude, le terme "gorfous macaroni de Crozet" signifie les gorfous macaroni de la colonie Wilson située sur l'île de la Possession.

Un deuxième site d'étude est situé à Cap Cotter au nord de la Péninsule Courbet située sur la partie est de la Grande -Terre de Kerguelen (Figure 2.6). De même que précédemment, le terme "gorfous macaroni de Kerguelen" signifie gorfous macaroni provenant de la colonie d'étude de Cap Cotter.

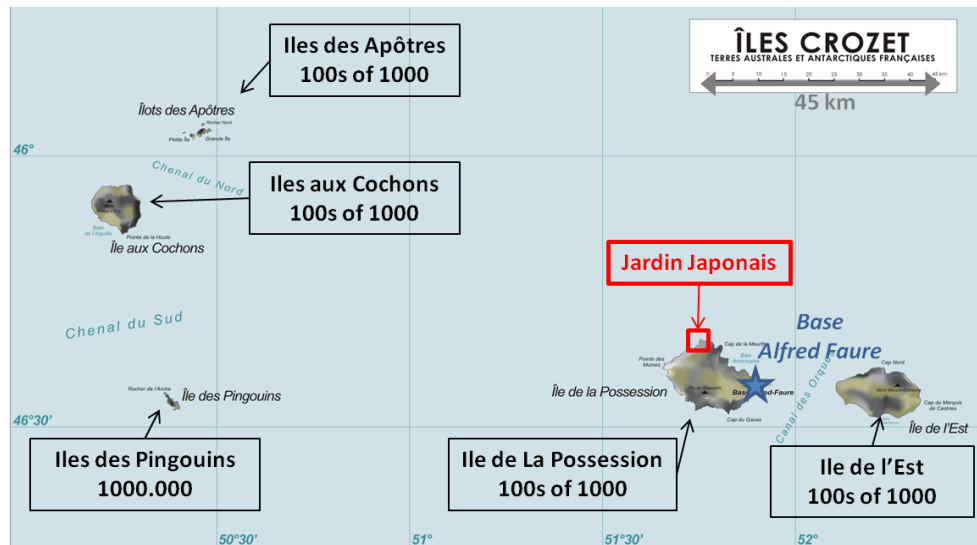


Figure 2.5: Estimated size of Macaroni penguins population from Crozet islands (number of pairs). Total number: ~2.2 millions of pairs. Red box indicates the location of the studied colony. Blue star: central logistic base (Jouventin et al. 1984).

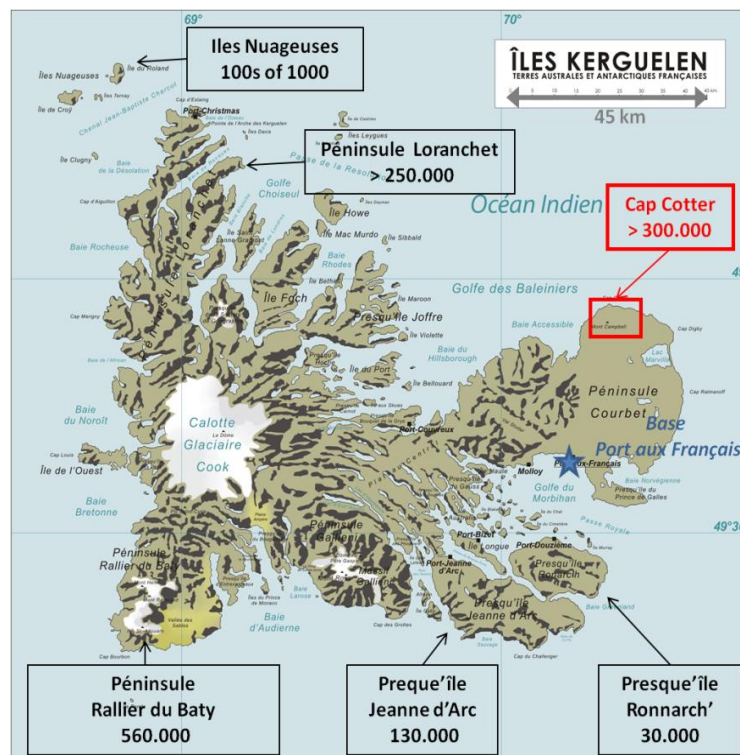


Figure 2.6: Estimated size of Macaroni penguins population from Kerguelen islands (number of pairs). Total number: ~1.8 millions of pairs. Red box indicates the location of the studied colony. Blue star : central logistic base (Weimerskirch et al. 1989).

2.2. Cycle reproducteur du gorfou macaroni

Les gorfous macaroni se reproduisent sur des **parties rocheuses très proches de l'océan**, pentues ou non, avec peu de végétation. Ils se regroupent en **colonies** de quelques centaines à plusieurs centaines de milliers d'individus (une colonie située à Cap Cotter est composée de plus de 100.000 individus, Figure 2.7). Les nids sont peu structurés, composés de cailloux, os et petits bouts de bois que les mâles rapportent sur le nid.

Le cycle reproducteur est synthétisé dans la figure 2.8. Les mâles arrivent sur la colonie début octobre, une semaine avant les femelles et occupent le nid jusqu'à l'arrivée de ces dernières. Les gorfous macaroni sont monogames, philopatriques et particulièrement fidèles au nid et à leur partenaire (71-79% de fidélité au partenaire sur 2 ans, plus de 50% sur 3 années). Le genre *Eudyptes* se caractérise par sa capacité unique à effectuer une **ponte asynchrone inversée**, c'est à dire la ponte décalée de deux œufs dimorphiques où le 1^{er} (œuf A) est plus petit que le 2^{ème} (œuf B).



Figure 2.7: Studied colony of Macaroni penguins at Cap Cotter, Kerguelen Archipelago. Some colony size can reach hundreds of thousand pairs.

Chez les gorfous macaroni, l'œuf A est environ 61 à 64% plus petit que le B. Ce ratio peut atteindre les 85% chez le gorfou de Sclater (*E.sclateri*). Cette stratégie est en rapport avec une réduction de la taille de ponte, qui se traduit par l'élimination systématique du 1^{er} œuf pondu. Les gorfous macaroni sont parmi les oiseaux marins les plus synchrones puisqu'une dizaine de jours tout au plus va séparer la 1^{ère} et la dernière ponte à l'échelle d'une colonie (Stahl et al. 1985, Williams 1995).

L'incubation commence réellement à partir du 2^{ème} œuf pondu et dure 35 jours. Les 12 premiers jours, les deux adultes alternent la garde de l'œuf en restant sur le nid. Autour du 22 novembre après plus de 30 jours de jeûne, les mâles partent en mer pendant environ 12 à 18 jours. Lors de leur retour, les femelles partent en mer à leur tour pendant environ 11 jours.

Elles reviennent à terre entre le 15 et le 21 décembre. Environ **85% des femelles** reviennent avant **l'éclosion** qui a lieu vers le **17 décembre** (succès à l'éclosion : entre 65 et 83%). Cette période marque le début de la période d'**élevage** individuel (*brood*) qui durera 25 jours. Pendant cette période, les **mâles vont jeûner** et prendre soin du nid et du poussin (maintien sous les plumes pour le garder au chaud, défense du nid contre les prédateurs). Lors de l'éclosion, le poussin pèse environ 116g et nécessite un nourrissage fréquent exclusivement dispensé par la femelle. Celle-ci va alterner par la suite les voyages alimentaires en mer et les courts séjours à terre. Les poussins sont nourris par régurgitation de la part de leur mère et ont besoin d'un apport journalier de 100 à 400g entre le début et la fin de l'élevage (Green et al. 2007). L'intervalle entre les nourrissages est situé entre 12h et 36h (78%) pour des poussins de moins de 5 jours. Cet intervalle augmente pour atteindre les 36h, 60h puis plus de 80h vers le début de la crèche. A 16 jours, un poussin est capable de jeûner 132h (5.5 jours).

Lorsque le poussin est **autonome thermiquement**, le mâle le laisse seul et part à son tour en mer pour restaurer ses réserves corporelles après un jeûne alimentaire de 36 jours. Cette étape marque la **formation de petits groupes de poussins** âgés d'environ 25 jours que l'on appelle des **crèches**. Leur regroupement leur permet de se protéger contre les intempéries et contre les prédateurs. C'est une période critique pour les poussins car sans les adultes pour les défendre, ils subissent une importante pression de prédation de la part des pétrels géants et des skuas subantarctiques notamment (Hunter 1983, Horswill et al. 2014). Pendant la période de la crèche, les adultes continuent à nourrir fréquemment le poussin. Au début, le nourrissage incombe aux femelles, puis les mâles participent à leur tour lorsqu'ils reviennent d'un voyage leur ayant permis de reconstituer leurs réserves adipeuses. Au cours de la reproduction, les gorfous macaroni sont cantonnés à un rayon de prospection inférieur à 400 km pendant les phases où le temps disponible en mer est le plus important (incubation, crèche) mais les femelles ne s'éloignent pas à plus de 80 km pendant la période d'élevage.

Leur croissance achevée à l'âge de 70 jours, les poussins quittent la colonie entre fin février et fin mars. Le succès reproducteur varie entre les localités et les années (de 48 à 92% des poussins survivent jusqu'au départ en mer). La masse et le taux de croissance des poussins dépendent essentiellement des stratégies d'approvisionnement des parents (Barlow & Croxall 2002b, Green et al. 2007). Les poussins seront matures sexuellement à l'âge de 5 ans pour les femelles, 6 pour les mâles. Les adultes quant à eux partent en mer fin février pour s'alimenter de manière intensive pendant des voyages de durée variable (15, 50 et 40 jours en moyenne en Géorgie du Sud, Crozet et Kerguelen

respectivement). Ces voyages d'hyperphagie où les oiseaux peuvent gagner jusqu'à 70% de leur masse corporelle ont pour but de préparer la **période de la mue** qui démarre fin mars et début avril respectivement à Crozet et Kerguelen. La désertion totale des colonies s'effectue fin avril, une fois que les oiseaux ont totalement renouvelé leur plumage.

Les oiseaux des îles Crozet et Kerguelen entament alors une **migration hivernale** vers des zones d'alimentation situées à plus de 3000km des colonies (Thiebot et al. 2011b, 2014).

La phénologie du cycle reproducteur est décalée entre les différentes zones géographiques de l'Océan Austral. Une corrélation positive est observée entre le début du cycle et la latitude à laquelle se situent les populations. Ainsi, la population de l'île Marion est la première à se reproduire (ponte: 1-5 novembre) suivi de Crozet (6-10 novembre), Kerguelen (8- 14 novembre, Camprasse et al. *in prep*) puis les populations situées dans des latitudes plus hautes, telle que la Géorgie du Sud (10-30 novembre) (Camprasse et al. *in prep*, Williams 1995, Crawford et al. 2003, Crossin et al. 2013).

Cette adaptation de la phénologie de la ponte à la latitude est observée chez d'autres espèces demanchots (Bost et Jouventin 1991) et des oiseaux marins de l'Austral (Croxall 1984).

II. MATERIEL AND METHODS : MACARONI PENGUIN AND STUDIED SITES

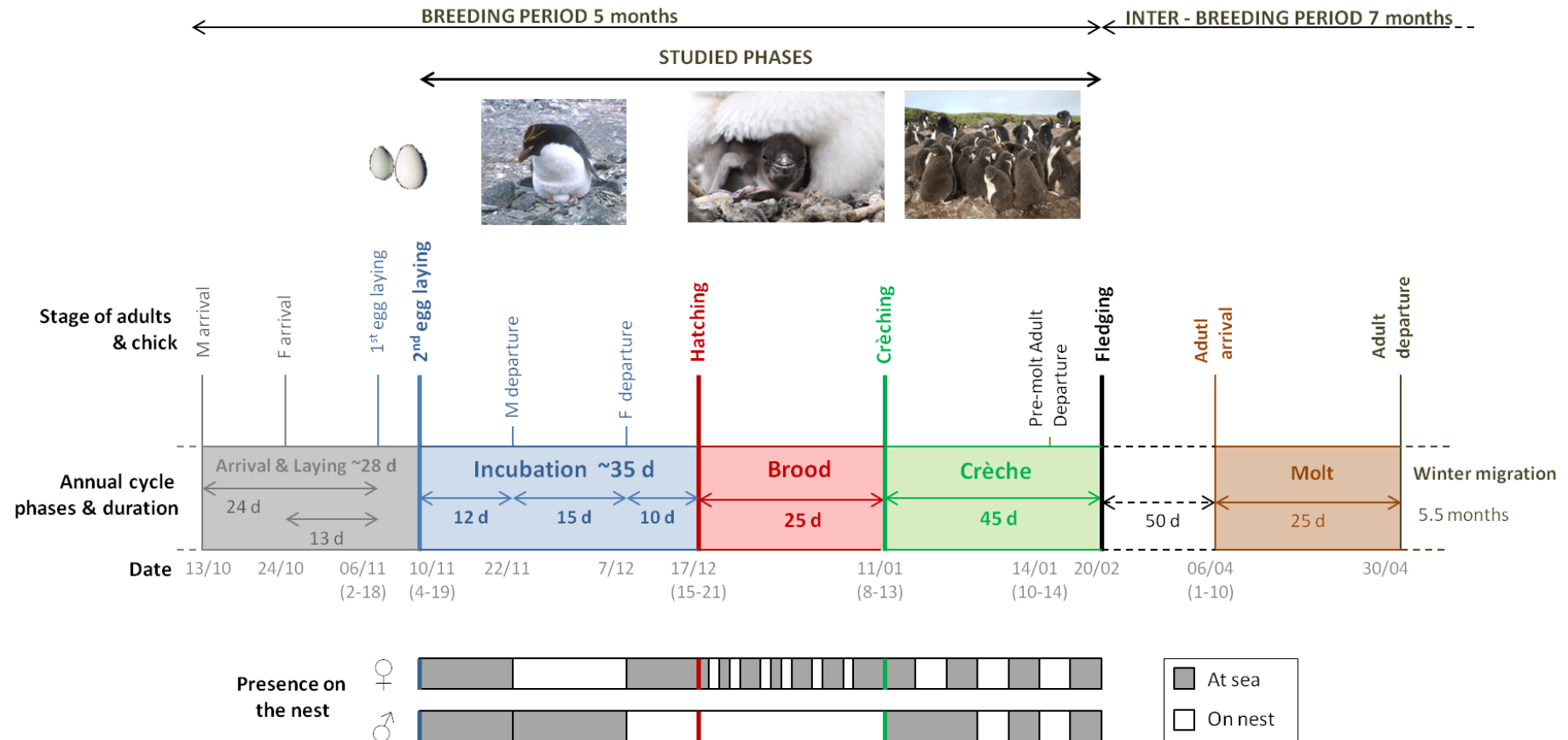


Figure 2.8: Annual cycle of Macaroni penguins from Crozet Islands. Mean durations are given in day (d). Calendar was built from Thiebot et al. 2014, Thiebot et al. 2011, Stahl et al. 1985, Williams 1995.

2.3. Régime alimentaire

Les gorfous macaroni s'alimentent de plusieurs types de proies selon la localité où ils se trouvent. Le Krill antarctique (*Euphausia superba*) domine le régime alimentaire des gorfous macaroni de la partie sud-ouest de l'Océan Austral mais le régime alimentaire des dernières années semble être devenu plus mixte (Croxall et al. 1997, Waluda et al. 2012). Dans la partie indienne, les gorfous macaroni s'alimentent majoritairement de Krill subantarctique (Euphausiacées : *E.vallentini*, *Thysanoessa gregaria*, Amphipodes : *Themisto gaudichaudii*) et de poissons myctophidés (*Krefftichthys anderssoni* et *Protomyctophum* sp) (Klages et al. 1989, Ridoux 1994, Deagle et al. 2007, 2008, Figure 2.9). Les myctophidés sont des poissons lanternes célèbres pour leur capacité à émettre de la bioluminescence de même que certaines espèces de crustacés.

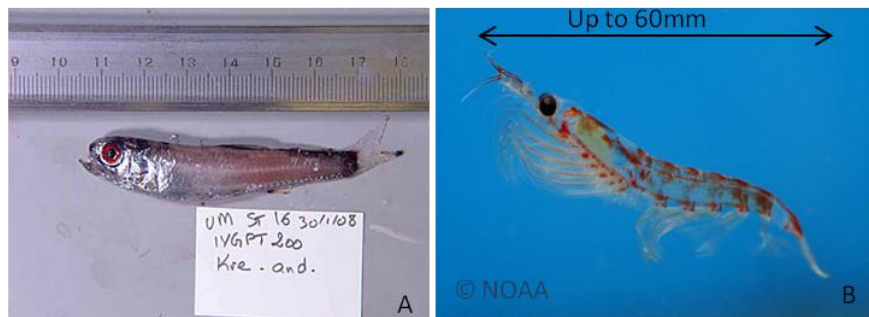


Figure 2.9: Two main preys of Macaroni penguin. A. myctophid *K.anderssoni*. B. Antarctic krill *E.superba*.

Ces différentes proies effectuent des migrations nycthémerales, c'est à dire qu'elles effectuent des déplacements liés aux variations journalières de la luminosité transmise dans la colonne d'eau. A l'aurore, elles se déplacent vers des eaux profondes (e.g. myctophidés > 75m au minimum, jusqu'à plus de 600m). Elles y restent durant la journée puis migrent à nouveau vers des eaux moins profondes à la tombée de la nuit. Les gammes de profondeurs varient entre les espèces, les myctophidés étant localisés à des profondeurs plus importantes que les crustacés (Reins & Adelung 1993, Demer & Hewitt 1995, Duhamel et al. 2000, Bost et al. 2002, Gurney et al. 2002). Le comportement des plongées de gorfous macaroni suit le même patron de migration journalière. Ainsi, les gorfous plongent en moyenne entre 15 et 60m pendant la journée et dans des profondeurs inférieures à 10m pendant la nuit. Ils plongent fréquemment à plus de 100m en journée. Le record de profondeur a été mesuré à 154m (Green et al. 1998).

II.3. Récolte des données biologiques

La révolution technologique des deux dernières décennies a permis le développement et la miniaturisation considérable d'appareils performants dans **le suivi des animaux en milieu naturel** (*bio-logging* et télémétrie). Ces appareils appartiennent à des classes différentes selon leur rôle et leurs caractéristiques, notamment leurs propriétés d'émission et/ou d'enregistrement. On distingue les appareils dont les données récoltées sont récupérées par la **voie télémétrique** (envoi des données à distance) et les appareils **enregistreurs** (*data loggers*) dont les données nécessitent d'être récupérées directement sur l'appareil. La résolution, la précision et la quantité de données varient entre les deux types d'appareils, étant généralement plus importants sur les appareils de la 2^{ème} catégorie. Cependant, le couplage des deux types de technologies est de plus en plus performant. Ces développements technologiques ont permis d'augmenter considérablement la connaissance sur les déplacements en milieu naturel des vertébrés sauvages, notamment les oiseaux marins (Ropert-Coudert & Wilson 2005).

Au cours de notre étude, nous avons utilisé différents types d'appareils appartenant aux deux types de technologie : des **balises Argos** (estimation de la localisation, collecte des données par voie satellitaire), des **GPS Fastloc 2** (estimation de la localisation, *Global Positionning System*) et des **enregistreurs de pression et de température** (*Temperature Depth Recorder*, TDR Lotek Lat 1800 et MK9, estimation de la profondeur). Les animaux ont été équipés de l'un ou l'autre type d'appareil. Un seul individu a été équipé avec un GPS et un TDR.

Dans cette thèse, plusieurs sessions de terrain ont été réalisées au cours de **plusieurs périodes de reproduction, entre mi-octobre et fin février sur les deux sites d'études : les colonies 10 et 11 à Cap Cotter (situées au nord de la Péninsule Courbet de l'île principale de Kerguelen) et la colonie Wilson du Jardin Japonais (située au nord de l'île de La Possession à Crozet) (Figure 2.5 et 2.6)**. La synthèse totale des équipements réalisés est présentée dans le tableau 2.1. Le travail sur le terrain a été réalisé par des équipes mixtes, composées de chercheurs, de doctorants, de vétérinaires et des Volontaires au Service Civique (VSC), agents de l'Institut Polaire Paul Emile Victor (IPEV) travaillant pour les programmes (n° 109 et n° 394) menés dans les TAAF par l'équipe Prédateurs Marins du Centre d'Etudes Biologiques de Chizé.

Table 2.1: Number of instrumented Macaroni penguins studied in this PhD.

Sexe	Stage	Logger type		
		ARGOS	GPS	TDR
♂	Incubation	4	9	-
	Brood	-	-	-
	Crèche	13	6	-
♀	Incubation	3	12	8
	Brood	7	10	30
	Crèche	10	6	2
Total		37	43	40

3.1. Pose et récupération des appareils

L'équipement des appareils ne s'effectue pas au hasard. Une première phase consiste à repérer les individus que l'on désire équiper. L'approche à la colonie se fait toujours de manière calme et la plus silencieuse possible pour éviter d'effrayer les animaux. Il est important de bien déterminer si les animaux que l'on choisit sont des animaux en reproduction. Un individu reproducteur sera sur son nid (en train de couvrir ou garder son poussin) ou collé à son partenaire qui effectue les mêmes tâches.

Les équipements s'effectuent toujours lorsque l'individu s'apprête à repartir en mer, une fois la relève avec le partenaire effectuée. Enfin les individus sélectionnés se reproduisent toujours dans les 2 à 5 premiers rangs de la colonie, ceci pour éviter un maximum de dérangement des autres couples lors de notre avancée dans la colonie.

Lors de la capture, un masque est mis sur la tête des gorfous pour les mettre dans le noir et diminuer le stress. Des mesures biométriques sont effectuées : la **mesure du bec** (longueur, hauteur), la **longueur de l'aileron**, le **tour de poitrine** et la **masse**. Les prises de masse à l'équipement et au déséquipement renseignent sur le gain de masse et donc la **qualité du succès d'approvisionnement** lors d'un voyage alimentaire. Des **prises de sang** sont également effectuées au retour de l'oiseau à terre pour obtenir des indices de régime alimentaire à partir d'analyses isotopiques. L'ensemble de ces données sont référencées dans un tableau dit de "métadonnées". Le sexe, le stade reproducteur, l'identifiant de l'individu, la date de pose, la durée de l'équipement, les numéros des appareils déployés, le niveau de stress comportemental de l'animal, évalué par le comportement d'halètement et de défense, sont également ajoutés.

La **pose de l'appareil** nécessite un **plumage sec** (l'équipement ne se faisant jamais sous la pluie). Des **points de colle** spécifique (loctite 401), des **bandes de scotch** (Tesa) et des serreflex sont utilisés pour fixer l'appareil au dos de l'animal (Figure 2.10). Des bandes de scotch colorées sont fixées

à la base des ailerons, de manière assez lâche pour ne pas gêner le manchot lors de ses mouvements et pouvoir repérer l'individu lors de son retour. **Une marque d'identification** (lettre/numéro) est également peinte sur le haut du corps de l'animal avec du colorant spécifique (coloration capillaire non permanente) qui peut tenir plusieurs mois (Figure 2.10). Le départ en mer est surveillé et le couple étudié régulièrement, observé pour s'assurer que la reproduction n'est pas impactée par la manipulation.

Lors du retour suspecté de l'animal, une surveillance accrue est effectuée aux points de passage principaux qui amènent à la colonie (couloir de passage). Le guet permet de repérer l'animal et de le capturer avant qu'il ne vienne relayer son partenaire. Le **déséquipement** est rapide, la loctite une fois sèche forme une bande dure qui se décolle des plumes sans difficulté lorsqu'on passe une lame ronde dessous. L'animal est de nouveau pesé puis relâché. L'équipement et le déséquipement durent chacun moins de 20 minutes.



Figure 2.10: Some aspects of field work. A. Equipment of a Macaroni penguin with an Argos tag. B. Equipped individual are marked with hair color which remain temporarily on the feathers (~3weeks). C. Tesa scotch tape is placed at the base of the flipper to better see the individual in the colony. D. One equipped individual with a GPS logger. GPS are put on the mid of the back, Argos tag at the base of the back.

3.2. Suivi des gorfous macaroni par la technologie ARGOS

Argos est un système performant de localisation et de collecte de données géo-positionnées par satellite, à vocation environnementale. Ce programme a été créé par trois organismes, l'agence américaine d'océanographie et d'étude de l'atmosphère (NOAA, *National Oceanic and Atmospheric Administration*), l'administration nationale de l'aéronautique et de l'espace (NASA, *National Aeronautics and Space Administration*) et un organisme français, le CNES (Centre National d'Etudes Spatiales).

Le principe est basé sur **l'émission par une balise compatible** (appelée *Platform Transmitters Terminals*, PTT) **de messages en direction des satellites situés en orbite basse**. Les messages contiennent notamment les numéros d'identification de la balise. Grâce à l'effet Doppler, la balise peut être localisée et ces informations transmises à 2 centres de traitement de données assurant le traitement 24/24h. L'effet Doppler se caractérise et se calcule par un décalage de fréquence d'une onde entre

l'émission et la réception de celle-ci, processus issu d'une variation de distance entre l'émetteur (la balise) et le récepteur (le satellite). La précision des localisations varie en fonction du nombre de messages reçus par le satellite (tableau 2.2).

Table 2.2 : Locations class from Argos system.

Location class	Messages number	Spatial accuracy of the location
3	≥ 4	<150
2		[150 - 350]
1		[350 - 1000]
0		>1000
A	3	No estimation
B	2	No estimation
Z	invalid	No estimation

Les balises Argos utilisées dans cette thèse sont des balises **Kiwisat** fabriquées par le constructeur Sirtrack (Figure 2.11). L'avantage des balises Argos est qu'elles transmettent des données quasiment en temps réel, ce qui n'implique pas de récupérer les appareils pour obtenir les données. Leur durée de vie est d'environ 6 mois. Elles sont peu encombrantes (~20-30g) mais relativement chères (~1500euros + 9 euros/jour pour la réception des données). L'antenne peut représenter une gêne tel que l'hydrodynamisme des manchots. Le placement de la balise sur le bas du dos permet de limiter cet effet et de maximiser la probabilité d'émission des messages par rapport à l'angle d'inclinaison du gorfou lorsqu'il est à la surface de l'océan.



Figure 2.11: PTT Kiwisat used in this PhD (Sirtrack).

3.3. Le système GPS

Le système GPS utilise également la voie satellitaire, mais au contraire d'Argos, les balises GPS **n'émettent pas** mais **enregistrent** leur localisation dans leur mémoire interne (Figure 2.12). C'est un système de géolocalisation qui repose sur l'exploitation de signaux radios émis par 24 satellites dévoués à cette activité. Les satellites émettent en permanence sur deux fréquences des messages contenant notamment les éphémérides et la date précise. La capacité à capter les satellites est

variable (de moins d'1s à 12s). L'antenne doit être située sur une partie bien émergée du corps de l'animal (le milieu du dos chez les gorfous macaroni). L'altitude du satellite est calculée à partir du modèle géodésique WGS84 (*World Geodetic System 1984*), estimation mathématique de la surface de la terre. Par triangulation, le GPS peut ainsi calculer sa position à une précision spatiale très importante. La réception de message de 6 satellites permet une estimation comprise entre 20 et 75m.

Les balises utilisées au cours de cette thèse sont des **GPS Fastloc 2**, également construites par Sirtrack. Le grand avantage de ces appareils réside dans la précision et la fréquence d'échantillonnage disponibles (période de 15 minutes en moyenne dans cette thèse). La précision obtenue sur les localisations est un atout de taille lorsqu'on cherche à étudier les mouvements à fine échelle des prédateurs.

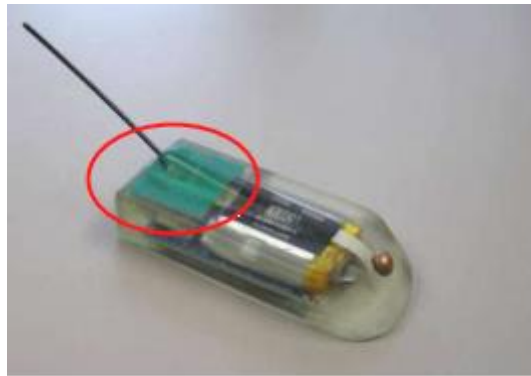


Figure 2.12: GPS Fastloc 2 used in this PhD. Red circle shows the antenna (green part).

Cependant, cette technologie dépend de la bonne récupération des appareils et nécessite une surveillance accrue de la colonie d'étude pour maximiser la probabilité de retrouver l'animal équipé. Si l'animal ne revient pas au même endroit, aucun moyen ne sera possible pour localiser l'appareil. Son prix est élevé (environ 2100euros) et nécessite une utilisation parcimonieuse. De plus la batterie est un facteur limitant et environ 15 jours d'enregistrement sont possibles pour les gorfous macaroni équipés dans cette thèse. La charge des Fastloc 2 est longue (plusieurs heures) et nécessite une interface particulière (souvent 2 à disposition en session de terrain) qui limite la quantité d'appareils disponibles que l'on peut préparer lors d'une période de déséquipement des anciens animaux et pose sur des nouveaux. Le relais des partenaires sur le nid peut être rapide, de quelques heures à un ou 2 jours.

3.4. Les capteurs de pression

Les capteurs de pression sont également des systèmes embarqués équipés de deux sondes qui vont mesurer la pression et la température. Obtenir la profondeur atteinte par unité de temps d'un prédateur plongeur nous permet de reconstruire efficacement le comportement de plongées en 2 dimensions lors de ses séjours en mer. L'utilisation de ces appareils ne renseigne pas sur les

déplacements géographiques mais uniquement dans la colonne d'eau. Ces appareils nous apportent des informations précieuses sur le comportement d'approvisionnement des gorfous (à quelle profondeur s'alimentent-ils ?) et nous permettent d'obtenir des **indices fiables** sur **l'effort de prospection et le succès de chasse** de ces prédateurs plongeurs.

Les deux types d'appareils utilisés dans cette thèse sont des **Lat Lotek 1800** (*Lotek Wireless*) et des **MK9** (*Wildlife Computer*, Figure 2.13). Le Lotek est la nouvelle génération des TDR (plus petit et hydrodynamique). Cependant le nombre d'oiseaux plongeurs (manchots royaux, papous, gorfous macaroni, sauteurs, cormorans de Kerguelen) équipés au sein du programme 394 pendant une campagne d'été peut être considérable. Le remplacement de l'ensemble des MK9 implique un coût et bien qu'ils soient plus gros, leur utilisation a été nécessaire lors de certaines campagnes par manque de Loteks. Les Loteks et les MK9 ne sont pas rechargeables, même chez le constructeur, (2 ans d'enregistrement maximum) mais la plus grosse pile des MK9 leur accorde une plus grande durée de vie.

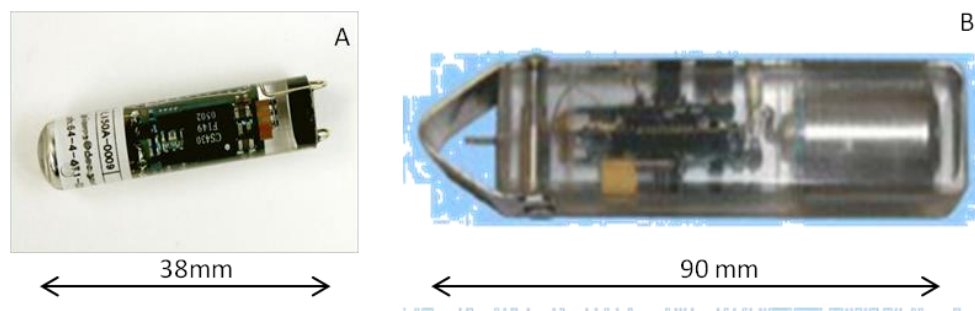


Figure 2.13: Temperature depth recorder (TDR) devices with external fast-responding temperature sensor, used in this PhD. A: Lat 1800 (Lotek Wireless) B: MK9 (WildLife Computer)

Leur utilisation est relativement simple. La fréquence d'échantillonnage est élevée (période 1s soit 1 Hz) de même que la précision ($\pm 1\%$, soit 0.2m à 2bars = 20m) et la résolution (0.05%). Le critère le plus important est de régler et de garder en note **la base de l'horloge interne de l'appareil**. Les GPS et Argos obtiennent des données basées sur l'heure civile internationale UTC. Les TDR peuvent être réglés sur l'heure locale ou UTC, il convient aux expérimentateurs de bien noter la référence pour éviter de faire des erreurs d'interprétation liées à un décalage temporel et non à une réalité biologique (Heure locale de Kerguelen : UTC + 5h en été austral, +4h en hiver austral).

3.5. Importance des lots témoins

En plus des sessions d'équipements réalisées, des mesures sur des **groupes témoins** ont été effectuées. Ceci consiste à choisir un groupe d'oiseaux suffisamment éloignés pour ne pas être dérangés par les sessions d'équipement mais suffisamment proches pour appartenir au même ensemble. En effet, un décalage phénologique d'une semaine peut être observé entre des colonies

proches de plusieurs centaines de mètres. Des transects de masse (par exemple prise de masse sur une ligne de 20 couples d'un lot témoin) et un suivi temporel d'animaux marqués ont été réalisés pour obtenir des informations sur le gain de masse et la durée des voyages d'animaux non équipés.

Cette procédure a permis de mettre en évidence qu'un lot équipé a eu des comportements biaisés par le port de l'équipement (Figure 2.14). Pour cette session, les oiseaux ont été équipés de deux appareils : un accéléromètre (GCDC) et un Lat 1800 (lot non étudié dans cette thèse). Cet équipement a probablement gêné l'hydrodynamisme des oiseaux par un effet de traîne important. Ainsi, le temps passé en mer des oiseaux équipés a été significativement supérieur chez le groupe d'oiseaux équipés par rapport au groupe contrôle (test non paramétrique Mann Whitney $W = 2422.5$, $p\text{-value} = 0.001$).

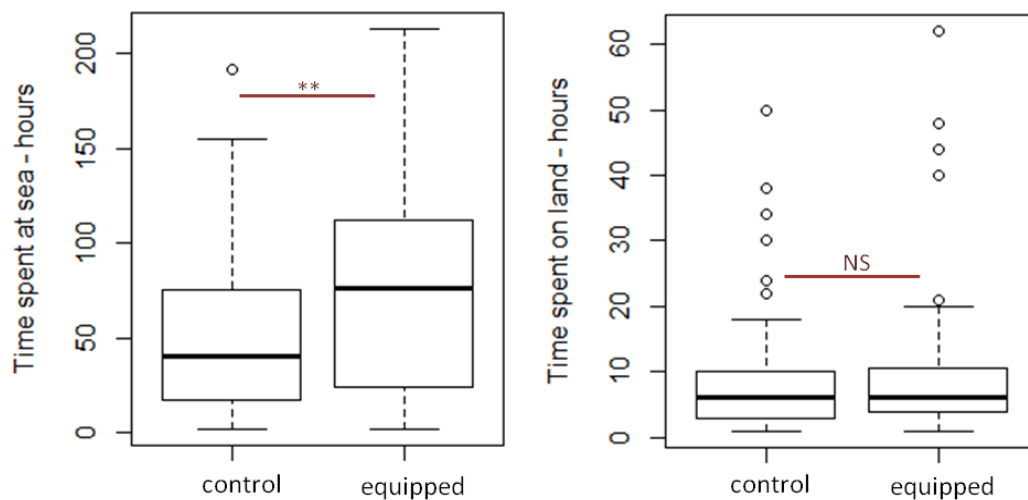


Figure 2.14: Effect of equipment on at-sea trips duration and time spent on land in brooding Macaroni penguins, Kerguelen Island. Equipment was composed of accelerometer (GCDC) and lotek Lat 1800. Time spent at sea was almost twice longer than the control group.

Enfin la comparaison de deux groupes permet de mettre en évidence des **effets d'habitation** aux appareils et aux expérimentateurs (Figure 2.15). Lors de cette session, les oiseaux étaient pesés à chaque retour au nid. Nous avons pu observer que le temps passé en mer diminuait significativement de manière plus importante après chaque manipulation que dans le groupe témoin où le temps passé en mer est moins élevé et reste relativement constant.

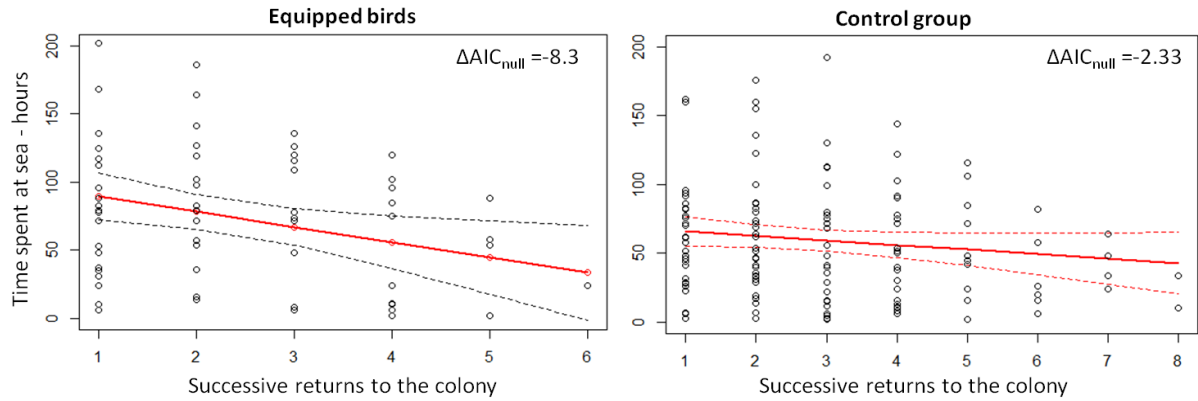


Figure 2.15: Time spent at sea after the different returns to the colony where birds were weighed in comparison with a control group. In the 1st group, time spent at sea was higher than for the control group. This suggests that there was a phenomena of habituation to handling or equipment. Mixed model was used to modelize the time spent at sea with the number of times that birds have returned to the colony (and handled). Individual was put as random effect. ΔAIC_{null} is the difference of the AIC with the null model.

II.4. Les méthodes d'analyses

Une fois les données récoltées, les données brutes vont être extraites des différents appareils (en utilisant un logiciel fourni propre à l'instrument utilisé) et transformées dans un format facilement manipulable (csv). S'ensuit une longue partie analytique qui a pris l'essentiel du temps de cette thèse. Un court résumé sera présenté ici et expliqué de nouveau dans les articles scientifiques.

L'intégralité du traitement des données (mise en forme et calcul de variables), analyses statistiques et graphiques a été réalisé sur le logiciel R, libre de droit sous la licence "GNU". Ce logiciel donne une grande liberté d'action sur la manipulation et l'analyse des données. Son fonctionnement communautaire est un atout puisqu'il permet d'accroître en permanence la base des fonctions existantes par l'ajout de packages. Son code de programmation (similaire à C++ et Matlab) est relativement simple une fois que l'on a compris le langage. Cet outil offre une grande liberté d'action sur la **mise en forme, le traitement des données, la conception graphique, le calcul et les analyses statistiques**. Au cours de cette thèse, les **scripts ont été entièrement construits par rapport à nos jeux de données sans utilisation de scripts déjà pré écrits** (à l'exception du script de First Passage Time écrit par D. Pinaud et disponible dans l'équipe). Nous avons également utilisé les fonctions de nombreux packages relatifs aux analyses spatiales et de la modélisation statistique. Plusieurs versions ont été utilisées pour répondre aux besoins des différents packages, notamment R 2.15 et R 3.2 ("The R Foundation for Statistical Computing 2013").

4.1. Analyses spatiales

Les analyses spatiales regroupent deux champs d'études à distinguer qui ne font pas appel aux mêmes compétences : l'analyse du mouvement et l'analyse de la distribution. Au cours de cette thèse, les deux types d'analyse ont été utilisés.

4.1.1. Mise en forme des données

Filtration. De mauvaises estimations de localisation peuvent induire l'ajout de données aberrantes au jeu de données. Un moyen usuel pour éliminer ces localisations non désirables est d'utiliser un filtre de vitesses itératif. La méthode repose sur l'algorithme de Mc Connel et al. (1992). Les points associés à des segments possédant une moyenne quadratique (racine carré de la moyenne du carré des valeurs) supérieure à la vitesse seuil fixée (ici 8km.h^{-1}) sont supprimés. Les trajets ont été filtrés en utilisant la fonction *speedfilter* du package "trip".

Interpolation. Comme énoncé précédemment, la fréquence d'échantillonnage obtenue à partir des données GPS et Argos n'est pas similaire. Cette différence d'échantillonnage peut induire des biais dans l'estimation des paramètres comportementaux (vitesses, changements d'angles, distance parcourue). Pour une même unité de temps (*e.g.* 1 heure), si le nombre de localisations enregistré est plus important, la vitesse et la distance parcourue seront implicitement augmentés (Figure 2.16). Le biais obtenu par l'utilisation de ces données est bien connu (Kuhn et al. 2009).

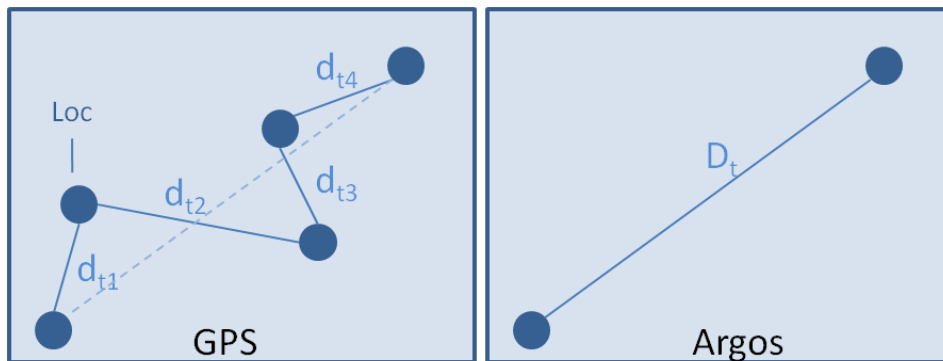


Figure 2.16: Schematic path recorded by GPS and Argos devices. For a same duration, total distance ($d_{t1} + d_{t2} + d_{t3} + d_{t4}$), and so travel speed are higher than D_t .

Afin d'enlever le biais lié aux données, nous avons dégradé le signal obtenu par GPS pour le mettre à la même fréquence d'échantillonnage que les balises Argos, soit 100min (80% des localisation Argos sont espacées d'une durée de 100minutes, Figure 2.17). La dégradation a été effectuée en utilisant la fonction *redisltraj* du package *adehabitatLT* (Calenge 2011).

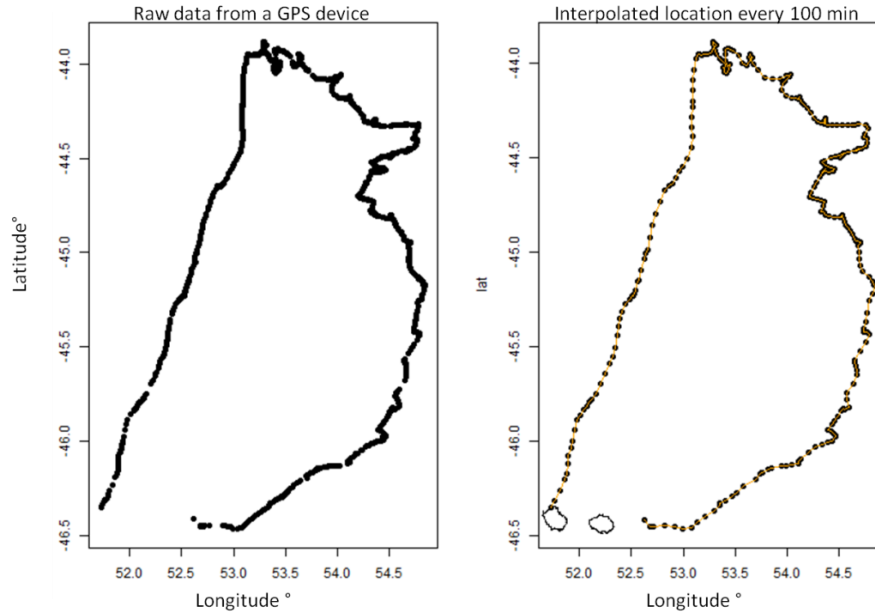


Figure 2.17: Interpolation of GPS track to the sampling rate of Argos tags.

Estimation des paramètres principaux. Les trajets ont été fermés lorsque les dernières localisations possibles n'étaient pas trop éloignées de la colonie par interpolation linéaire simple, basée sur la vitesse moyenne du trajet. Les paramètres suivants ont été calculés : distance maximale à la colonie, distance totale parcourue, vitesse de déplacement (distance/unité de temps) entre chaque localisation puis moyennée à l'échelle du trajet, direction du trajet, forme du trajet (directionnel vs circulaire).

Ces calculs ont été effectués en prenant compte de la courbure de la terre et en utilisant un système de projection géodésique (WGS84). Les distances orthodromiques (*Great Circle Distance*) ont été calculées en utilisant notamment la fonction `trackDistance` (package "trip"). Les angles et directions ont été mesurés puis analysés grâce à des fonctions dites circulaires (*e.g.* package "circular").

4.1.2. Estimation du temps passé par secteur

Le temps passé par secteur est une méthode permettant d'estimer la distribution spatiale d'un animal. Il repose sur l'hypothèse suivante : tout organisme tend à maximiser le temps passé dans une zone favorable. Au niveau spatial, ceci se traduit par adopter un comportement en recherche restreinte (*Area Restricted Search*, ARS Kareiva & Odell 1987) identifiable par la méthode du *First-Passage Time* (FPT, Fauchald & Tveraa 2003). Ces comportements ont été identifiés comme des stratégies de recherche alimentaire adoptées par les oiseaux volants, et plus récemment chez les éléphants de mer (Suryan et al. 2006, Pinaud & Weimerskirch 2007, Weimerskirch et al. 2007, Bailleul et al. 2007, Bailleul, Lesage, et al. 2010, Pinaud 2008). Chez les manchots, la recherche alimentaire serait adaptée à des patches organisés de manière hiérarchique (Watanabe et al. 2014). Cependant, à l'inverse des oiseaux volants qui peuvent parcourir des distances considérables à des coûts énergétiques moindres

(Weimerskirch et al. 2000), les manchots sont beaucoup plus contraints dans leurs déplacements (Costa 1991). La recherche alimentaire est **dirigée** vers des structures prédictibles et est moins exploratoire que celle observée chez les oiseaux volants. Dans cette thèse, des analyses de *First Passage Time* ont été réalisées. Nous avons trouvé des zones où les gorfous macaroni adoptaient un comportement de recherche alimentaire en aire restreinte, mais elles représentaient une faible portion du trajet (moins de 20%). Ces zones étaient généralement situées pendant la phase centrale des trajets, là où ils amorcent le retour vers la colonie (Figure 2.18).

Cependant, les gorfous macaroni plongent tous les jours au cours d'un voyage alimentaire, et donc présentent un effort d'approvisionnement en dehors de ces périodes d'ARS. La **méthode des ARS semble sous-estimer le nombre de zones favorables à l'approvisionnement des gorfous macaroni**. En conséquence, nous avons choisi d'utiliser un autre indice pour identifier les zones d'approvisionnement : les variations de temps passé au cours du temps dans des zones de dimension fixe (*i.e.* 0.2°), représentatives de plusieurs parcelles exploitables au cours d'une journée.

En effet, il est établi que dans des zones favorables, les prédateurs plongeurs vont réduire leur vitesse horizontale au profit d'une augmentation de l'effort de plongée et du temps passé à s'alimenter (Boyd 1996, Bost et al. 1997, Viviant et al. 2014).

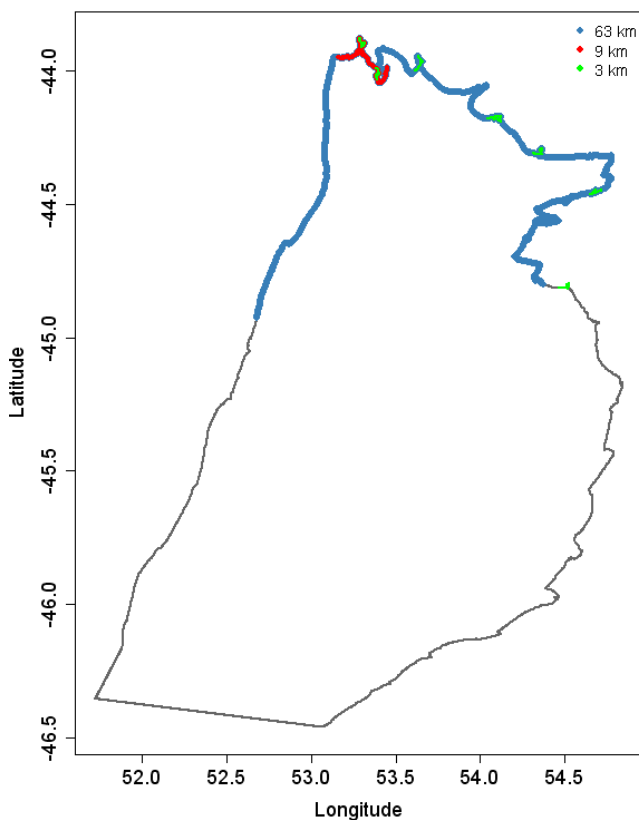


Figure 2.18: ARS behaviours found on a track of male Macaroni penguin at the incubation stage from Crozet islands, following the FPT analysis (Fauchald & Tveraa, 2003). Colours indicate the different temporal scales (see legend). ARS method is not the best tool to identify foraging areas in penguins.

Nous avons donc utilisé la méthode du **temps passé par secteur** (TPPS) pour identifier les zones d'alimentation des gorfous macaroni. Cette méthode maille les déplacements des animaux sur une grille composée de cellules d'une taille de 0.2° (dimensions à Crozet : 22.2km sur l'axe des latitudes, 15.4 km sur l'axe des longitudes). En se basant sur la date de la localisation et une interpolation linéaire entre les positions, cette technique permet de mesurer **le temps passé dans chaque cellule**. Une résolution temporelle de 100min équivaut à une distance parcourue maximale de 5km (en se basant sur une vitesse moyenne de déplacement de 3km/h). Les vitesses maximales de 8km/h permettront de laisser au moins une localisation par cellule (13.3km parcourus en 100min).

Ces valeurs de TPPS n'ont pas été utilisées de manière absolue mais de manière **relative pour chaque trajet** (sommées puis divisées par la durée totale du trajet, Figure 2.19). A l'échelle du trajet, il était important de définir dans quelles zones géographiques un individu allait passer le plus de temps, relativement à sa propre vitesse de déplacement afin de prendre en compte la variabilité interindividuelle. La standardisation de ces valeurs confère également l'avantage de pouvoir ensuite effectuer des **analyses comparatives**, entre les différents trajets, individus, sexes, stades etc. A l'échelle du cycle reproducteur, cette technique permet de mesurer très facilement les zones géographiques ciblées entre les différentes phases du cycle. L'intérêt porté de cette méthode est qu'elle permet de regrouper de manière simple au sein d'une même valeur plusieurs indices comportementaux d'une recherche alimentaire (sinuosité, ralentissement). Son utilisation peut être appliquée dans le domaine de la conservation pour la détermination des *hotspots* de biodiversité (Delord et al. 2014). Le temps passé par secteur a été calculé à l'aide de la fonction *tripGrid* du package "trip".

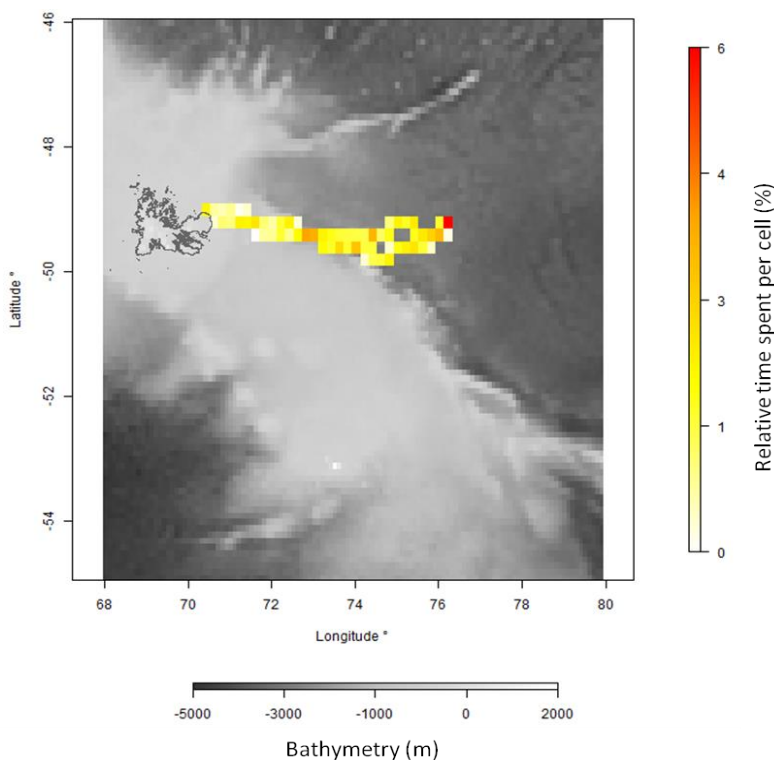


Figure 2.19: Relative time spent per cell for a Macaroni penguin from Kerguelen Islands (crèche stage).

4.2. Identification et analyse des plongées

Le logiciel Multi Trace- Dive (Jensen Software Systems, Laboe, Allemagne) permet de visualiser les données brutes de profondeur et de température en fonction d'une période de temps modulable (totalité du jeu de données, quelques jours, une journée ou sur une plongée). Ce logiciel est également très pratique pour remettre à zéro la ligne de surface lorsqu'une dérive intervient au cours du temps, cette étape s'appelle la **correction de la ligne de surface** (*Zero Offset correction*). L'autre avantage est qu'il suffit de rentrer des critères de définition d'une plongée pour que le logiciel les identifie automatiquement, bien qu'une vérification visuelle et une correction en directe soient également possibles. Nous avons opté pour cette dernière option car nous avons observé quelques artéfacts dans les données. L'identification de l'ensemble des plongées, plusieurs dizaines de milliers (*e.g.* 127626 plongées pour 11 individus étudiés à Crozet) a donc été vérifiée par visualisation directe. Ce travail a été effectué en collaboration avec Ayala Loisel lors de son stage de master 2.

Afin de supprimer les perturbations de signal dues à l'effet des vagues, nous avons considéré qu'un **événement de plongée débutait** lorsque la profondeur dépassait les **3 mètres**. **Les plongées ont été découpées en 4 phases : la phase de descente, de fond, de remontée puis l'intervalle post-plongée** passé en surface qui précède la plongée suivante (Figure 2.20).

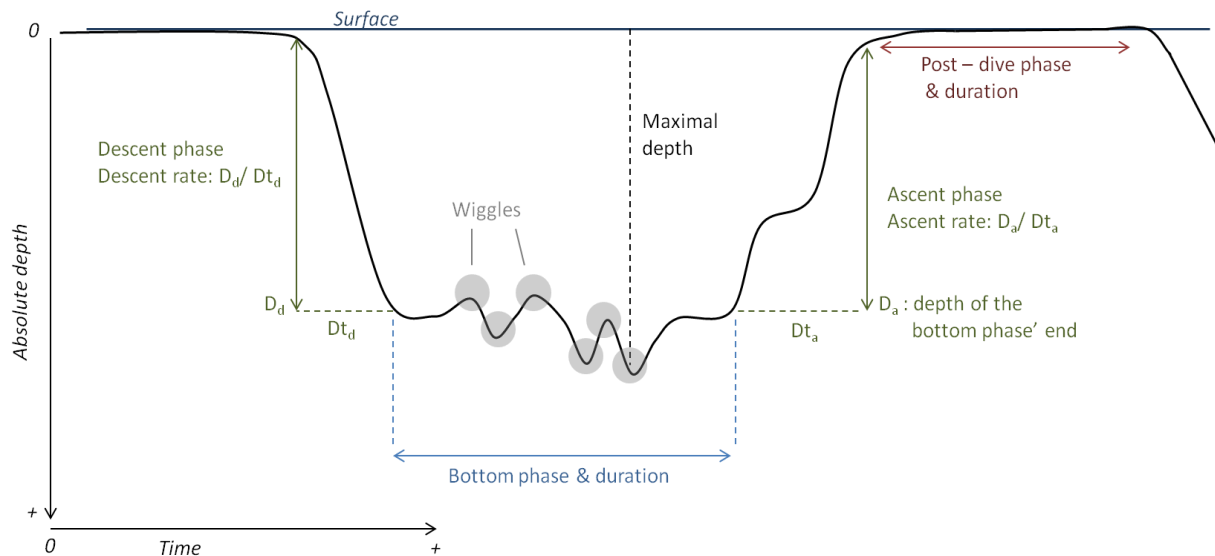


Figure 2.20: Schema of dive cycle structure composed of four main phases : descent, bottom, ascent and post-dive phases. Wiggles are indicative of events of prey capture attempts. Diving efficiency (DE) is computed by bottom duration / (dive duration + post - dive duration).

La **phase de fond** a été définie comme le temps passé entre 75 et 100% de la profondeur maximale, et doit durer au minimum 15% de la durée totale de la plongée. Ce critère n'a pas été choisi arbitrairement. La sélection de plusieurs critères a été effectuée et nous avons conservé celui qui permettait de mieux détecter les phases de *bottom* que l'on observait. Les **ondulations** correspondent

à des déviations de la profondeur en 3 points sur lesquels la vitesse verticale passe en dessous de 0m/s (Tremblay & Cherel 2000, Halsey et al. 2007).

La profondeur maximale des plongées est généralement bimodale et permet de différencier des plongées profondes des plongées de surface. Ces dernières sont généralement associées à des comportements de déplacement, tandis que les plongées profondes sont dévouées à l'approvisionnement. La bimodalité n'a pas été observée dans notre jeu de données (Figure 2.21).

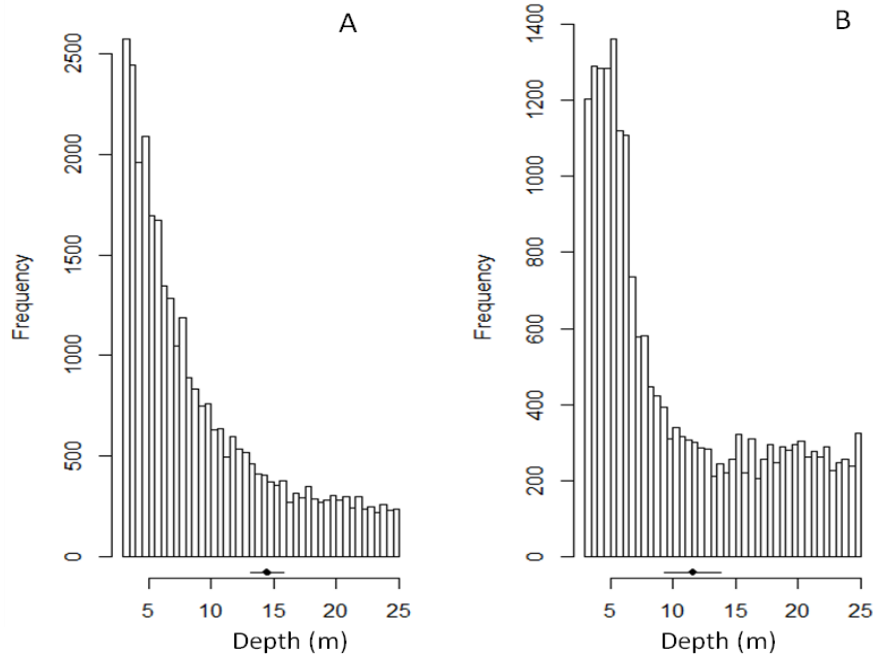


Figure 2.21: Zoom of the distribution of maximal dive for individuals from A. Kerguelen and B. Crozet. "Broken-stick model" was used to estimate a break point (small line under the graphics). We see that there is no evident bimodality in this distribution. The increase of depth dives and dives rate per hour at the beginning of the day (dawn) were better cues to define a foraging dive.

De plus, les gorfous macaroni effectuent des migrations nycthémérales et commencent à intensifier leur effort de recherche alimentaire dès l'aube, à de faibles profondeurs (10 - 15m) avant d'accroître cette profondeur au cours de la journée, comme la plupart des autres manchots. En observant l'effort de prospection par unité de temps (nombre de plongées effectuées par heure), nous avons pu estimer à quel moment de la journée les gorfous intensifiaient leur effort de plongées. La mise en relation de cet indice avec l'augmentation de la profondeur a permis de définir un critère de profondeur à partir duquel les plongées étaient considérées comme "profondes - d'approvisionnement" ou "de surface". La profondeur de plongée, la durée du temps passé au fond, le nombre d'ondulations et l'efficacité de plongée sont des indicateurs fiables de l'effort et du succès d'approvisionnement. L'efficacité de plongée est définie comme le ratio entre la durée de la phase de fond et la durée du cycle de plongée (durée de la plongée + durée de l'intervalle de surface post-plongée) selon l'équation de Ydenberg et Clark (1989).

L'aspect **séquentiel des plongées profondes** a été étudié selon l'hypothèse que les plongées sont regroupées en **successions rapides séparées par des intervalles de surface longs** (*bouts*, Gentry & Kooyman 1986). Ces comportements sont supposés être de bons indicateurs de la qualité de l'approvisionnement (Boyd 1996, Mori & Boyd 2004) et le temps de surface entre ces séquences peut être considéré comme des déplacements entre zones alimentaires. Il a été montré que les ajustements comportementaux peuvent s'effectuer à l'échelle de la plongée, mais également à l'échelle des séquences de plongées (Viviant et al. 2014). Le critère pour définir les séquences de plongées (BEC, *Bout Ending Criterion*) peut s'effectuer en regardant la différence absolue des temps de surface entre plongées profondes (Luque & Guinet 2007). Une séquence est validée lorsqu'elle contient au minimum 3 plongées profondes.

II.5. Obtenir les données océanographiques

Une partie importante de cette thèse a cherché à comprendre comment les gorfous macaroni utilisaient leur habitat. La caractérisation des conditions environnementales rencontrées était donc primordiale. **Plusieurs variables ont été extraites à partir de données satellitaires**, notamment sur le site AVISO/CNES. Ces variables ont été mises ensuite en relation avec les grilles de temps passé par secteur pour caractériser l'environnement favorable à l'approvisionnement des gorfous macaroni. **Nous listons ci-dessous les variables océanographiques utilisées et leur signification.**

5.1. Le principe de l'altimétrie

L'altimétrie est une méthode d'estimation de l'altitude. En océanographie, elle permet de mesurer plusieurs variables. La première est la **hauteur de la mer** (utilisée dans cette thèse, ***Sea Surface Heigh, SSH***) qui correspond au niveau des océans à un instant donné par rapport à une ellipsoïde de référence qui correspond à la forme élémentaire de la Terre, une 'sphère' aplatie aux deux pôles. Cette mesure est obtenue facilement par simple différence entre l'orbite d'un satellite et la distance altimétrique (Figure 2.22).

La hauteur de la mer peut être décomposée selon plusieurs états :

- la surface de la mer qu'elle aurait en absence totale de perturbation (courants, vents, marées). Cette surface correspond au **géoïde** qui va « mouler » la forme de la planète selon les effets de l'attraction terrestre et du fond sous-marin. Un pic sous-marin aura pour effet de remonter le niveau basal de la mer et donc de créer une bosse sur le géoïde.

- la **topographie dynamique** (ADT) qui correspond à la circulation océanique issue des deux processus : la topographie moyenne (circulation permanente liée aux vents permanents, à la force de Coriolis etc.) et un processus beaucoup plus variable lié à des phénomènes méso-échelles non constants dans le temps : l'anomalie de hauteur d'eau (utilisée dans cette thèse, *Sea Level Anomaly*, SLA, Figure 2.23).

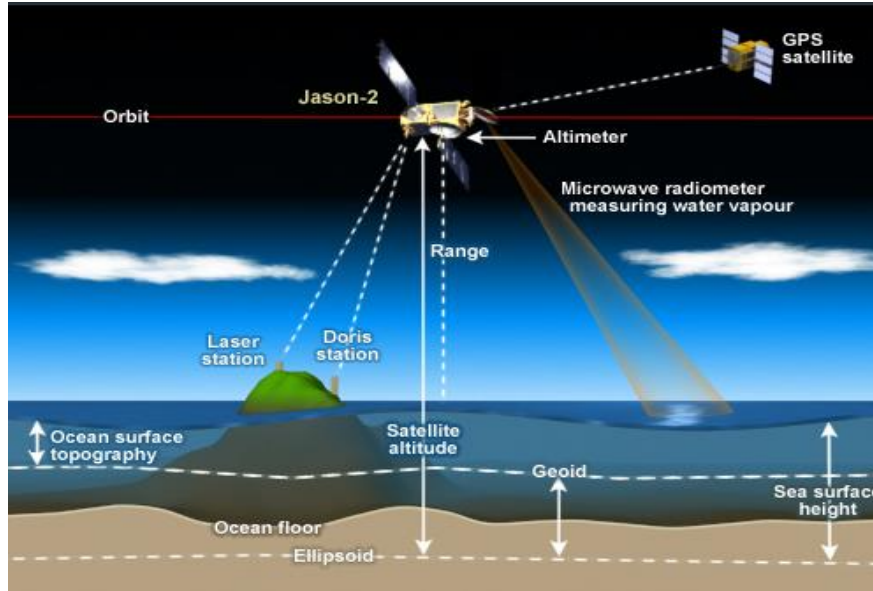


Figure 2.22: Altimetry method components ©The Comet Program

En pratique, il suffit de soustraire la hauteur du géoïde à la hauteur du niveau de la mer (SSH) pour obtenir des valeurs de circulation océanique. Cependant, la précision du géoïde reste encore assez faible et par conséquent, c'est la topographie moyenne qui est soustraite à la hauteur d'eau pour obtenir les anomalies de hauteur d'eau: $SLA = SSH - \text{géoïde} - \text{Topographie Moyenne}$.

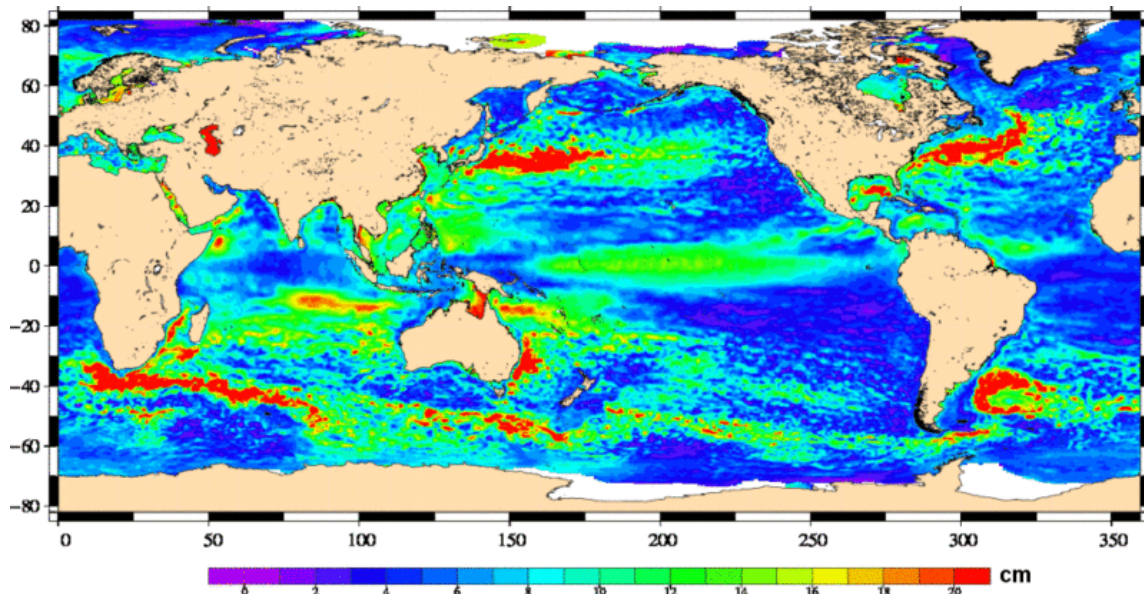


Figure 2.23: Root mean square of the Sea level Anomalies (SLA) over the whole Jan 1993-March 2010 period. Red areas are the one where the sea surface heights change the most ©Cnes/CLS

5.2. Variables océanographiques utilisées

De nombreuses variables physiques, dynamiques et biologiques peuvent caractériser les environnements et les structures hydrologiques rencontrés par les oiseaux marins (Tremblay et al. 2009). Le choix de ces variables dépend du modèle d'étude. La liste des variables océanographiques sélectionnées dans cette thèse est résumée dans le tableau 2.3.

Table 2.3: Biological and physical meanings of oceanographic variables used in habitat use investigation.

Variables used	Units	Relative oceanographic process
Fixe		
Bathymetry (m)	m	Neritic, oceanic areas
Gradient of Bathymetry	%	Edge of plateau, submarine peak
Distance to the colony	km	Constraints of the central - place foraging behaviour
Dynamic		
Geostrophic currents	m/s	Currents and turbulence of waters at large scale
Gradient of sea Surface Height	cm	Frontal structures
Sea Level Anomaly	cm	Meso-scale activity: eddies
Eddy Kinetic Energy	cm ² /m ²	Currents and turbulence associated with eddies
Net primary Production	mg C/m ² /day	Abundance of phytoplankton
Gradient of NPP	%	Aggregation of resources
Finite Size Exponent Lyapunov	1/day	Sub-mesoscale activity: filamentary structures

La résolution spatiale de chaque variable était de 0.2° pour les chapitres III.2 et III.3, 0.33° pour le chapitre III.1. **Les valeurs ont été extraites pour chaque trajet et moyennées sur la période du trajet.** Les données des vitesses de courants et de hauteur d'eau ont été téléchargées sur le site Aviso¹ (CNES/AVISO). Les données de production primaire ont été obtenues à partir du site Ocean Productivity². Les localisations des structures frontales issues des isothermes de surface ont été obtenues à partir du portail Bloom Watch³. **Ces données ont été obtenues grâce à une collaboration importante avec Annette Scheffer (post - doctorante au British Antarctic Survey, BAS).**

Les données altimétriques permettent de calculer d'autres variables en plus de la SLA et de la SSH, tels les **courants géostrophiques**. Ce sont des courants de vitesse constante considérés comme non altérés par les frottements qui résultent de l'équilibre entre le gradient de pression et de la force de Coriolis. En prenant en compte uniquement l'équilibre entre les deux forces, il est possible d'obtenir les composantes $(\bar{u}, \bar{v})$ des courants géostrophiques.

$$\bar{u} = - \frac{g}{f} \frac{\partial(ADT)}{\partial y} ; \quad \bar{v} = - \frac{g}{f} \frac{\partial(ADT)}{\partial x} \quad \text{où } g \text{ correspond à la l'accélération engendrée par la gravité (9.81m.s}^{-2}\text{), } f \text{ est la force de}$$

¹ www.aviso.altimetry.fr

² www.science.oregonstate.edu/ocean.productivity/standard.product.php

³ <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp>

Coriolis, et ∂y , ∂x sont les distances sur l'axe nord-sud et est-ouest.

- **La vitesse des courants de surface régionaux**, a été calculée à partir des courants géostrophiques corrigés par le transport d'Ekman à 15m (pression du vent sur la surface de l'eau) (cf Della Penna et al. 2015).

- **La bathymétrie** permet d'indiquer si l'animal est situé en eaux néritiques ou océaniques et peut renseigner sur la proportion de plongées benthiques qu'un oiseau plongeur peut effectuer (Tremblay & Cherel 2000).

- **L'énergie cinétique des tourbillons** (*Eddy Kinetic Energy*, EKE) provient de la somme vectorielle des composants des courants géostrophiques $EKE = \frac{1}{2} \times (\bar{u}^2 + \bar{v}^2)$ avec u^2 et v^2 les carrés des composantes $\bar{u}$ et $\bar{v}$ des courants géostrophiques. Cette variable permet de caractériser **la variabilité méso-échelle relative aux tourbillons**.

- un **indice de la productivité primaire** (*Net Primary Productivity*, NPP) est calculé à partir du modèle standard VGPM (*Vertically Generalized Production Model*). L'équation standard du modèle est :

$$NPP = chl \times pb_opt \times day_length \times f(par) \times z_eu$$

ou **chl** est la concentration de chlorophyll *a*, **pb_opt** l'efficacité photosynthétique maximale dépendante de la température de surface, **day_length** la longueur du jour, **f(par)** est un terme relié à la quantité de lumière disponible et **z_eu** correspond à la profondeur de la zone euphotique. La productivité primaire s'exprime en mg Chl *a*/m²/jour. NPP s'exprime en milligrammes de carbone fixés par jour par unité de volume. **Puisque la température est utilisée dans le produit de productivité primaire, nous n'avons pas utilisé cette variable dans nos modèles.**

- Nous avons également calculé des **gradients** de bathymétrie à partir de l'utilisation d'une fenêtre glissante de 5×5 pixels appliquée sur les grilles de bathymétrie permettant de calculer la pente (%).

$$gradient = \sqrt{\left(\frac{\delta Bathy}{\delta x}\right)^2 + \left(\frac{\delta Bathy}{\delta y}\right)^2} \times 100$$

Un filtre passe-bas Gaussien a ensuite été appliqué sur ces valeurs pour retirer les bruits et obtenir un produit plus lissé. Les gradients productivité primaire et de SSH ont été calculés de la même manière.

- Les grilles des **exposants de Lyapunov** ont été calculées et fournies par Alice DellaPenna (Doctorante à LOCEAN). Les exposants de Lyapunov indiquent la présence de **structures sub-mésoéchelle** dans l'environnement marin. A la différence des données précédentes qui

¹ www.aviso.altimetry.fr

² www.science.oregonstate.edu/ocean/productivity/standard.product.php

³ <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp>

se basent sur des méthodes Eulériennes (instantanés de champ de courants), ces valeurs sont issues de **méthodes Lagrangiennes**, c'est à dire qu'elles suivent l'écoulement des particules dans le temps. Parmi elles, la méthode des **exposants de Lyapunov en taille finie** (*Finite Size Exponent Lyapunov, FLSE*) se réfère au **taux exponentiel de divergence**, moyenné sur un temps infini, de points initiaux infinitésimalement proches.

Elle peut se définir ainsi : deux points (ou traceurs) x_0 et x_1 séparés initialement par une distance δ_0 infinitésimalement proche se déplacent en fonction du temps. Le temps τ est le temps nécessaire pour que la distance de séparation de x_0 et x_1 devienne supérieure à la distance δ_f . La valeur λ (ou valeur du paramètre FSLE) correspond ainsi au taux de divergence de ces deux traceurs. Ils expriment l'échelle de temps inverse nécessaire à l'étirement de particules aggrégées au départ, comme par exemple à proximité d'un front (d'Ovidio et al. 2004). Les FSLE se calculent par l'équation suivante:

$$\lambda(x, t, \delta_0, \delta_f) = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0}$$

où δ_0 correspond à la séparation initiale des deux parcelles d'eau, τ le temps mis pour obtenir une séparation temporelle égale à δ_f . Pour cette étude, les paramètres utilisés sont $\delta_f = 0.6^\circ$, $\delta_0 = 0.01^\circ$ et τ a une durée limitée à 100 jours.

Les FSLE utilisés dans cette thèse ont été calculés par une méthode dite "de retour en arrière" (backward-in-time). Les valeurs les plus hautes de FSLE représentent de cette manière les zones de convergence maximale, alors que l'intégration en avant attribuait des FSLE plus importants dans les zones de divergence importante. **Cette méthode permet d'identifier les zones de transport sub-mésoéchelle des particules en suspension, comme le phytoplancton** (Lévy et al. 2012)

II.6. Analyses statistiques

6.1. Principaux tests réalisés

Au cours de cette thèse, des tests statistiques paramétriques (où l'on considère que les variables suivent une loi de distribution normale) et non paramétriques ont été effectués.

La normalité des données a été examinée par le test de Shapiro-Wilk et l'homogénéité des variances par le test de Bartlett. Les tests de **comparaison de moyennes** (test t, test de comparaisons multiples

Kruskal Wallis, test de rang de Wilcoxon) ou **d'analyses de variances** (ANOVA) ont été réalisés dans le but de comparer des grandeurs (durée des voyages, distances maximales, masses) en fonction des localités, des individus, du stade reproducteur *etc.* Des **tests circulaires** (*e.g.* Watson) ont également été réalisés pour tester des différences de directions entre des groupes de trajets. Le rejet de l'hypothèse nulle a été effectué lorsque la statistique du test dépassait le seuil α égal à 0.05%.

Le lien entre les variables environnementales et le comportement d'approvisionnement des gorfous macaroni a été étudié et validé à l'aide de la modélisation statistique. Cette méthode consiste à mettre en relation une **variable réponse** avec plusieurs **variables explicatives** (quantitatives ou factorielles) par le biais de régressions linéaires (LMM, GLMM) ou non linéaires (GAMM). Elle permet d'estimer la part de variance de la variable réponse expliquée par les variations des variables explicatives. De cette manière, il est possible de **mesurer le poids de chaque variable** explicative dans le comportement observé. L'ensemble des variables explicatives a été **standardisé** (centré réduit) dans le cas de régressions multiples afin de faciliter les convergences des modèles et pouvoir comparer le poids des différentes variables entre-elles (Zuur et al. 2009).

Les modèles utilisés ont été principalement des **modèles mixtes** pour prendre en compte **l'effet de l'individu** dans les processus de variation de la variable réponse (*e.g.* vitesse de déplacement). Des transformations logarithmiques ou racine carré ont été réalisées pour transformer la variable réponse en loi normale. Lorsque ce n'était pas possible, des modèles mixtes généralisés ont été construits où une famille de distribution était attribuée à la variable réponse (Poisson, binomiale négative, binomiale *etc.*). Des termes d'auto corrélation ont été ajoutés lorsque les observations de la variable réponse n'étaient pas indépendantes entre elles (*e.g.* profondeur maximale de plongées successives).

6.2. Construction d'un modèle statistique explicatif

La construction d'un modèle explicatif s'effectue en trois étapes 1-établir un modèle global, 2- effectuer une sélection de variables, 3- estimer la qualité du modèle.

6.2.1. Choisir un modèle candidat

Déterminer un lot de modèles candidats est une tâche subjective, essentiellement basée sur la littérature et une analyse exploratoire profonde du jeu de données (Tukey 1980). Le modèle global comprend toutes les variables possibles que l'on estime avoir une influence sur la variable réponse et doit permettre un ajustement correct aux données (Burnham & Anderson 2002). En effet, si ce modèle explique correctement les données, alors un modèle dérivant de ce dernier après une sélection de variables va également bien s'ajuster aux données. Toutefois, un nombre de variables trop élevé et un effectif trop petit peut mener à des corrélations fausses (Anderson et al. 2001) et ce

nombre doit être jugé avec pertinence. De plus, lorsque deux variables sont très corrélées ($R^2 > 0.8$), l'une des deux variables doit être supprimée afin d'éviter une mauvaise estimation des coefficients.

6.2.2. Sélection de modèle : 'Meilleur modèle' versus 'Model averaging'

La sélection de variables est un aspect critique des analyses de données qui mène à la validation ou à la réfutation des prédictions de départ. La plupart du temps, des procédures séquentielles sont employées qui consistent à ajouter ou supprimer des variables à chaque étape et effectuer des tests successifs entre les modèles emboîtés. Le problème principal de cette méthodologie vient du fait que le modèle final choisi dépend du 'chemin pris', c'est-à-dire le choix de l'expérimentateur dans la sélection ou la suppression des variables (Burnham & Anderson, 2002).

Une autre approche plus correcte consiste à effectuer **l'ensemble des combinaisons possibles** des variables présentes dans le modèle global puis de quantifier précisément la probabilité de chaque modèle d'être sélectionné comme meilleur modèle.

La sélection de modèle se base sur le principe de parcimonie menant au modèle avec le nombre de paramètres (complexité) le plus petit possible pour une représentation adéquate (ajustement) des données. C'est à dire faire un compromis entre le biais (écart entre les données simulées par le modèle et la réalité) et la variance (dispersion des données simulées autour de la réalité) du modèle.

L'utilisation du **critère d'Akaike** (Akaike 1981) apporte une manière simple, efficace et objective de **comparer la qualité de chaque modèle testé**. Akaike formula un critère permettant d'estimer la distance attendue entre les données estimées par le modèle et le processus réel inconnu qui génère les données observées : $AIC = -2\log(L(\theta|y)) + 2K$ avec $L(\theta|y)$ le maximum de vraisemblance du modèle et K le nombre de paramètres du modèle. Notons qu'une valeur d'AIC absolue n'apporte pas d'information. Ce sont les **différences entre les AIC** des modèles qui sont importantes.

-Meilleur modèle. Deux modèles sont considérés comme différents lorsque la variation d'AIC est supérieure à 2. En pratique, un AIC est calculé pour chaque modèle et **le meilleur modèle sera celui possédant le plus petit AIC**. En effet, ce modèle sera considéré comme le plus proche du processus générant les données observées, parmi l'ensemble des modèles candidats. Cependant, la sélection d'un unique meilleur modèle soulève souvent le **problème de 'l'incertitude du modèle'**. Cette incertitude peut se résumer par la question suivante : si d'autres jeux de données sont disponibles, est-ce que le modèle sélectionné sera le même ? (Posada & Buckley 2004).

Cette question renvoie au problème du sur-ajustement du modèle aux données, c'est-à-dire que le modèle s'ajuste très bien aux données observées mais présente une capacité de généralisation très faible. **Dans le cas de l'élaboration de modèles visant à comprendre l'utilisation de l'habitat, l'objectif est de mesurer le poids de chaque variable dans les décisions comportementales qu'effectue l'individu.** Il est courant de n'avoir aucun modèle clairement supérieur aux autres ($\Delta_{AIC} < 2$). Si les valeurs ajustées diffèrent clairement entre les modèles, il devient risqué de baser sa prédiction sur un modèle unique.

- **Model averaging.** Une des solutions pour palier ces problèmes est d'effectuer des inférences robustes sur l'ensemble des modèles candidats. Cette procédure s'appelle la **'multi-model inference' ou 'model averaging'** qui provient de l'approche Bayésienne (Hoeting et al. 1999, Burnham & Anderson 2004). Celle-ci considère l'ensemble des modèles en calculant la **moyenne des coefficients de tous les modèles candidats pondérée par leurs poids w , c'est-à-dire leur probabilité d'être sélectionnés comme le meilleur modèle.** Le poids w du modèle peut être considéré comme un rapport de vraisemblances relatives des modèles avec $L(g_i|x)$, (probabilité d'un modèle g_i d'exister selon les données x) qui est proportionnelle à la différence d'AIC entre le modèle g_i et le meilleur modèle : $L(g_i|x) \sim \exp(-0.5\Delta_{AIC})$

$$.W_i = \exp(-0.5\Delta_{AICi}) / \sum (\exp(-0.5\Delta_{AICi}))$$

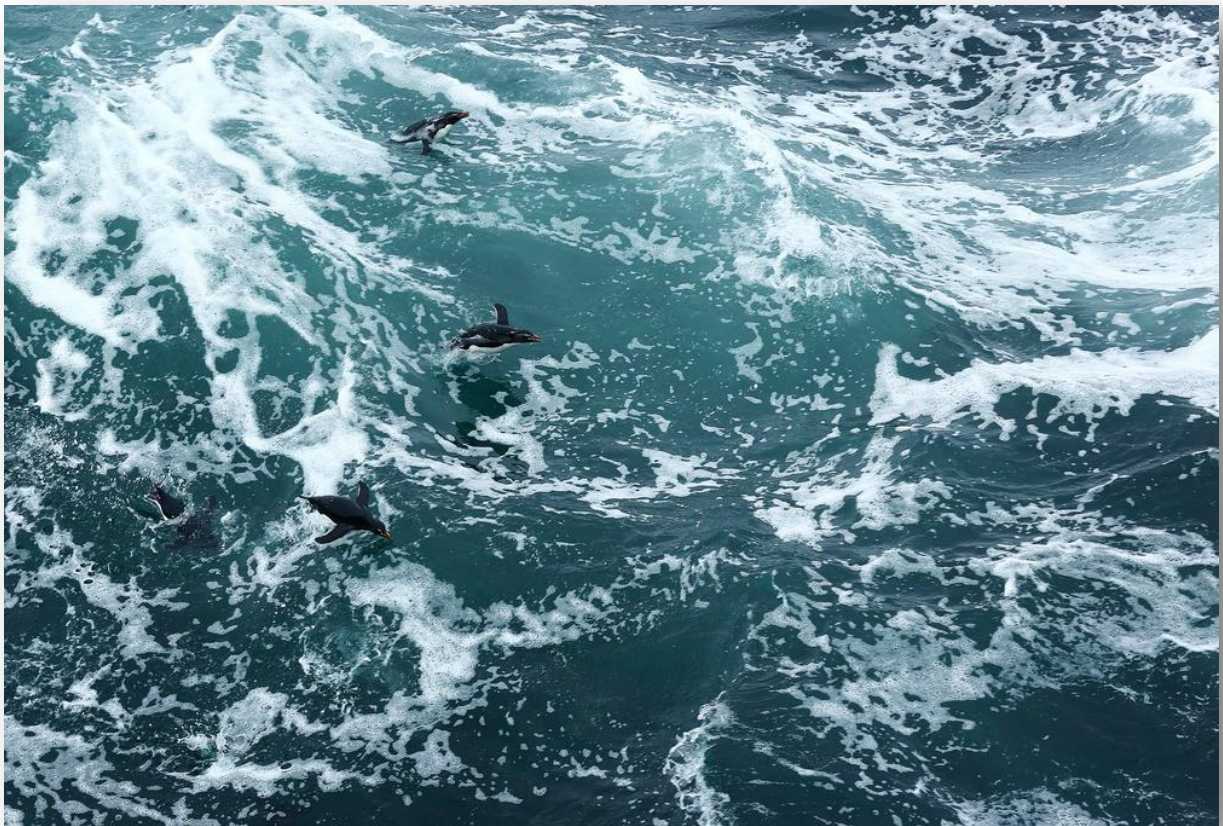
De manière simple, plus la différence d'AIC entre un modèle i et le modèle au plus faible AIC est élevée, plus le poids du modèle est petit (voir Burnham et Anderson, 2002, p75 pour plus de détails). L'approche usuelle est d'effectuer **une procédure de 'model averaging' sur les n premiers modèles dont la somme cumulée de w atteint 0.95**, considéré comme **l'intervalle de confiance du meilleur modèle** (Burnham et Anderson, 2002, p169).

6.2.3. Estimer la qualité du modèle

Une fois le modèle final sélectionné, différentes méthodes permettent de mesurer son adéquation aux données observées. Les tests les plus courants sont les tests de la déviance normalisée ou le test du χ^2 de Pearson dont la statistique mesure l'écart relatif entre les données prédites et les données observées (McCullagh & Nelder 1989). Une autre technique consiste à examiner les résidus, c'est-à-dire les différences entre les données observées et prédites. On s'intéresse principalement aux **résidus normalisés** qui doivent suivre une loi normale et être dans l'intervalle $[-2 ; 2]$ si le modèle est bon (McCullagh & Nelder, 1989). L'analyse des résidus s'effectue ensuite la plupart du temps de manière graphique par leur mise en relation avec chaque variable explicative.

CHAPITRE III

INFLUENCE OF OCEANOGRAPHIC FEATURES ON FORAGING STRATEGIES



At-sea diving Macaroni penguins © Stanley Leroux

Paper 1: Bon C, Della Penna A, d'Ovidio F, Arnould J, Poupart T, Bost CA (2015). **Influence of oceanographic structures on foraging strategies: macaroni penguins at Crozet Islands.** *Mov Ecol*, 3:32–42

Diving predators can respond and adjust their foraging behaviors to the hierarchic distribution of marine resources. The aim of this study is to investigate how and which oceanographic structures macaroni penguins used in the open ocean. This study concerns Macaroni penguins from Crozet islands which have never been studied yet. This chapter summarizes the paper 1 (Annexe 1).

III.1. Context and objectives

In the open ocean, the distribution and the abundance of marine resources are related to physical structures observable at different spatial and temporal scales (Fauchald 2009). We distinguish **large scale** structures (as oceanographic front, ~1000km) and **mesoscale** structures (as eddies, 10-100km) which have particular physico-chemical properties leading to the **aggregation of primary production** (Laubscher et al. 1993, Froneman et al. 1995, McGillicuddy et al. 2007, Godø et al. 2012, d'Ovidio et al. 2013). By attracting upper trophic levels and by cascading effects in the food webs, **strong relationships** were found between the foraging movements of top marine predators and the localization of such structures (*e.g.* Cotte et al. 2007, Bost et al. 2009, Bailleul et al. 2010). Recently, the development of Lagrangian diagnostics (monitoring of flowing water particles) has allowed to identify and localize **sub-mesoscale features** (<10km, *e.g.* filamentary structures) in the ocean (d'Ovidio et al. 2004, 2009). These structures are known to affect the distribution and growth of phytoplankton because of their vertical and lateral transport properties (Lévy et al. 2012). It has been shown that some top marine predators, as frigatebirds or elephant seals, use these structures to forage (Kai et al. 2009, Lowther et al. 2014, Cotté et al. 2015, Della Penna et al. 2015).

Macaroni penguins have a strong impact on the food webs of the Southern ocean since they are considered as the most abundant biomass consumer among seabird. However, **a few studies have investigated how their foraging behavior could be influenced by the occurrence of spatial oceanographic structures.** In this paper, our aim was to know if and how Macaroni penguins use the oceanographic environment to forage, from large-scale (front) to meso (eddies) and sub-mesoscale filament structures. The highlighting of such relationships is important to better understand their environmental needs relative to their foraging strategies in the open ocean.

III.2. Methods

The study was carried on **Macaroni penguins from Crozet islands** during the incubation stage in December 2012. Seven males were equipped with GPS logger (Fastloc 2, Sirtrack Ltd) before their at-sea departure. Once recovered, tracks were filtered to delete aberrant localizations (>10km.h⁻¹) and only 4 localizations per day were kept in order to be consistent with the temporal resolution of

oceanographic data. It has been shown that penguins decreased their horizontal movements, and so their travel speed, when increasing their foraging activity (Bost et al. 1997, Pütz et al. 1999). In this study, slowdown periods were thus used as an indicator of foraging activity.

Altimetry maps were obtained from the CNES/CLS AVISO website (0.33°, 1 week). There were used to compute the velocity of geostrophic currents and identify meso and sub-mesoscale structures. **Heading velocity** ($HV = TV - CV$) was computed in order to compare the travelling velocity (TV) of penguins with the currents velocity (CV). Mesoscale structures (eddies) were identified using the **Okubo-Weiss parameter** which compute the difference between the strain components and the vorticity of the flow. Sub-mesoscale structures were localized by the **Finite Size Lyapunov Exponents** (FSLE) method which allows measuring the particle transport properties of water parcels. **Frontal structures** (SAF) were identified using sea surface isotherm. **Chlorophyll concentration** data were obtained from GlobColour¹.

III.3. Results

Large scales structures. Males performed long **clockwise looping** trips off their colony (18 ± 2 days) heading north towards the Sub-Antarctic Front (SAF), up to 388km. Trips have been separated in 3 parts relative to the variation of their travel speed, outward, central and inward phase. Birds significantly **slowed within the central part of their trip** (1.9 ± 1.0 km/h) which was also the longest (9.6 ± 1.35 days ; 435 ± 69.9 km, Figure 3.1). In the central part, birds have reached the **south border of the SAF** characterized by the limit of the 8°C sea surface isotherm. At this time, their heading directions were highly correlated with the currents directions of the SAF (circular Pearson test: 5.78, $R^2 = 0.40$, $p < 0.001$) headed southeast ($118 \pm 37^\circ$). Moreover, in addition to a lower traveling speed, 25.3% of their heading velocity was below 1 km/h. This indicates a traveling speed close those of the currents.

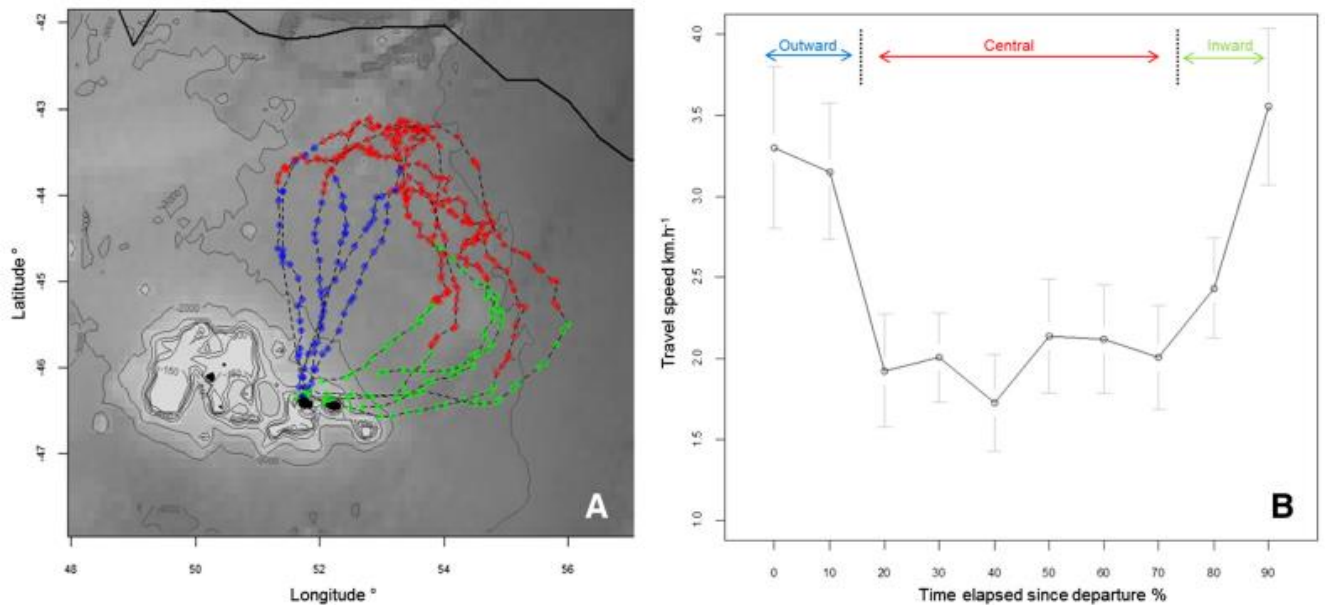


Figure 3.1: Trips and travel speed of six incubating macaroni penguins presented on a bathymetry map around the Crozet islands. **A:** The three phases defined by the variation in heading velocity are represented in distinct colours: Outward: blue, Central: red, Inward: green. Black line: sub Antarctic Front. **B:** The travel speed was averaged for each 10 % of time elapsed since the departure of travel. Arrows indicate the separation of the trip in three phases

Mesoscale structures. During their trips, birds have foraged in the **edge of two large eddies** located to the south of a large eddy field not used by the birds (Figure 3.2). The main eddy activity was observed within the central phase of the trips where the penguins have reduced their traveling speed. Eddies observed in the central phase were relatively **young** ($9.7 \pm 15d$) since 80% of waters parcels had been recirculating within the eddy for less than 8 days. In comparison, eddies in the transit phases had a longer retention time ($16 \pm 15d$, Mann-Whitney test $U = 658$, $p = 0.013$). Birds spent more time in eddies within the central phase ($43 \pm 25h$) than in the transit phases ($25 \pm 10h$). We also have found that birds have significantly slowed down within eddies during the inward phase.

Sub-mesoscale structures. Filamentary structures observed by FSLE method were present over the **whole area** prospected by the penguins (Figure 3.2). A **strong inter-variability in the level of association between these structures and birds** locations was observed since the degree of association varied between 5.6% and 35.9% according to the individuals. The main interactions with these structures were observed within the central phase of trips (66.7% of all associations). No decrease of travel speed was found when birds were within filaments. However, once birds were within these structures, the more the transport properties of the filaments were high, the more the penguins have slowed.

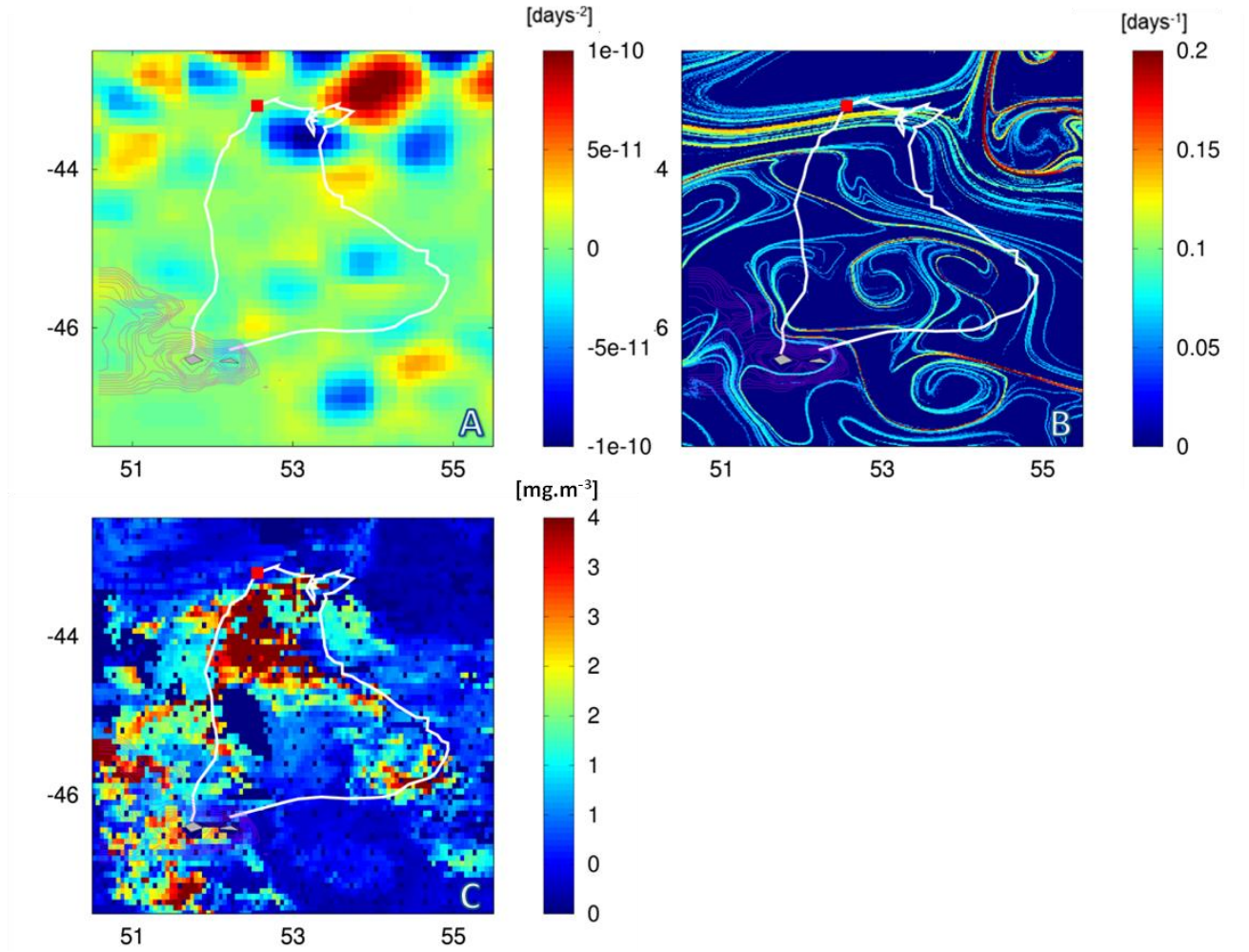


Figure 3.2: The positions of one Macaroni penguin overlaid on oceanographic features. **A:** Okubo–Weiss parameter: eddy cores are characterized by negative values. **B:** Finite-size Lyapunov exponents ($\delta_0 = 0.01^\circ$, $\delta_f = 0.6^\circ$): larger values identify stronger transport barriers. **C:** Map of chlorophyll *a* concentration.

III.4. Discussion

In this study, we have demonstrated that Macaroni penguins target and intensively foraged within a predictable large scale frontal structure, the SAF. The similarity between their directions and the strong slow-down of all birds suggest a common use of this oceanographic feature. Birds have exhibited a heading velocity of less than 1km/h in this area, close to the current velocities. It strongly suggests that birds have adopted a **drifting undirected behaviour** which could be explained by a more vertical diving activity. The strong overlap between the tracks and the Chlorophyll-*a* plume (Figure 3.2) suggests they foraged in a high productive area. A predictable phytoplankton bloom grows each year north of Crozet islands (Pollard et al. 2007, Sanial et al. 2014) which appears to be used by Macaroni penguins. The SAF is characterized by a strong mixing activity associated with an important eddy field (Kostianoy et al. 2003, Glorioso et al. 2005). In this area, no difference in the

III. INFLUENCE OF OCEANOGRAPHIC FEATURES ON FORAGING STRATEGIES

heading velocity of penguins was found within and outside of eddies in the central phase, on the contrary to the inward phase.

These results suggest also two main finding:

i) Numerous studies have shown that a high concentration of chlorophyll-a and macro-zooplankton have been found within the SAF whereas several trophic levels of organism can aggregate within eddies (Abrams 1985, Pakhomov & Froneman 1999, Bost et al. 2009, Bailleul, Cotté, et al. 2010, Godø et al. 2012). As no difference of heading velocity was found within and out of eddies, we suggest that **the prey field was extended at the spatial scale of the branch of the SAF**, and that **birds have responded to this large spatial scale** due to a relative homogeneous distribution of preys.

ii) Secondly, as suggested by Cotté et al. (2010), **all available eddies in the predator' ranges are not used** and it depend of their life time and history. Eddies encountered in the **inward phase were older** than those in the central phase suggesting that they may **retain more nutrients and enhance biological productivity** and prey aggregation. Birds have responded to the occurrence of eddies although they were out off the frontal structures, where the availability of preys may be more patchily distributed. It suggests that **Macaroni penguins may respond differently to the encountered oceanographic structures**, depending to the characteristics of the local area prospected.

We found that the Macaroni penguins traveling speeds became lower when the FSLE values have increased. Filamentary structures result of eddy-eddy interaction and higher values of FSLE are associated with an increase of horizontal stirring. These structures are associated with trapping characteristics of chlorophyll and in consequence, may have a important attracting power of the upper trophic levels. The locations of the filaments with the highest FSLE values were within the central phase. Thus, **the lack of variation of travel speed within and out off** the filamentary structures could be due to two main factors. First, the crustaceans and fishes are **mobile** in comparison to the phytoplankton which is transported by currents. It could induce a **dispersed spatial distribution** around the filamentary structure, leading to a mismatch between movements of penguins and filaments. Moreover, the **weak stirring properties** of filaments within the **transit** phases, in comparison to the central phase, could be related with weaker aggregation properties of phytoplankton leading to a less attractive power for grazers. Second, the mismatch between the temporal resolution of altimetry data (1 week) and GPS locations (6h intervals) in this study had probably biased the characteristic of the relationships.

At this period, males have to restore of a first long fasting period (arrival at the colony until their departure after their long incubation period, (~35 days) and prepare one other (brooding period, ~35 days (Stahl et al. 1984, Williams 1995). Thus, male are highly energetically constrained as they have to restore their body condition and build up reserves for the next one. Consequently, individuals

III. INFLUENCE OF OCEANOGRAPHIC FEATURES ON FORAGING STRATEGIES

would have advantage to target and adjust their foraging behavior in productive oceanographic structures. In conclusion, this work confirms the high dependence of pelagic penguins such as Macaroni penguins on large scale frontal zones such as the SAF in the Crozet area. This study highlighted the role of currents and eddy dynamic in foraging strategies of the species and its spatial adjustment to different oceanographic structures.

CHAPITRE IV

FORAGING STRATEGIES OF MACARONI PENGUINS AT CROZET ISLANDS



Sleeping Macaroni penguin © Cécile Bon

Paper 2: Bon C, Scheffer A, Loisel A, Cherel Y, Powolny T, Arnould J, Jenouvrier S, Bost CA. **Foraging strategies of Macaroni penguins at Crozet islands during the breeding season.** *To be submitted to Marine Ecology Progress Series (MEPS).*

The foraging strategy of Macaroni penguin during the whole breeding season on Crozet Islands has never been documented yet. In this chapter, we provide new information on the spatial and vertical at-sea distributions of the species, according to each breeding stage and sex. The characteristics of the marine habitat from environmental data are presented. The foraging behavior is then faced to the energetic constraints imposed by each breeding stage, leading to put in an evolutionary perspective the foraging strategies of the species on Crozet islands. This chapter summarizes the paper 2 (Annexe 2), and also brings new unpublished results.

IV.1. Context and objectives

Seabirds are central place foragers and the separation of their foraging at-sea zones and breeding colonies is one of their fundamental life-history constraints (Pennycuik et al. 1984, Weimerskirch et al. 2007).

This especially concerns non-flying diving predators such penguins which are highly constrained because of their limited foraging range (Costa 1991). During their annual cycle, the breeding season is a period with especially high energetic requirements (Ricklefs 1983, Green et al. 2009a) while the available time to forage is obligatory limited. Despite of their major role in the food webs of the Southern ocean, a limited number of studies have concerned penguins foraging strategies over the whole breeding cycle (*e.g.* (Kirkwood & Robertson 1997, Clarke et al. 1998, Charrassin & Bost 2001, Barlow & Croxall 2002b, Zimmer et al. 2008). Concerning Macaroni penguins, several studies have shown they strongly adjust their foraging behaviour in response to the breeding constraints (Barlow & Croxall 2002a, Green 2005). However, a few studies have been able to describe the detailed aspects of the foraging movements, diving activity, trophic level of the both sexes over the whole breeding cycle. The Crozet archipelago is the northernmost breeding locality of the Macaroni penguin. It is also a stronghold breeding locality as it has been evaluated that 35% of the world population could breed here (Crossin et al. 2013).

In this work, we have tried to answer the following question: **how do foraging Macaroni penguins respond to the breeding constraints of incubation, brood and crèche stages at the Crozet islands**, the northernmost breeding locality?

First, we characterized their at-sea distribution and foraging movements according to the sex and the breeding stage. Second, we investigated which oceanographic areas are targeted by the birds in order to understand how their foraging strategies are adjusted to the marine environmental features, which play a role in marine productivity, at several temporal and spatial scales. Third, we put in relation

these results to the body-mass variation and their diet to better understand how Macaroni penguins adjust their foraging behaviour to the energy requirement imposed by the breeding cycle.

We predicted that i) Macaroni penguins will adjust their foraging movements in relation to the available foraging time (distant and long trips in incubation and crèche, short range trips during the brooding phase as observed in other localities), ii) Macaroni penguins will target predictable areas of different profitability as shelf break, large eddies or frontal zones according to breeding time and their own energetic needs, *i.e.* deal with the balance between the body condition and the chick provisioning, iii) finally, we predict a temporal adjustment between the at-sea movements of penguins and the phytoplankton bloom from year to year.

IV.2. Methods

This study was realised using biological data obtained on foraging penguins during 3 breeding seasons, 2009/2010, 2012/2013 and 2013/2014 on Possession island, Crozet Archipelago.

A total of 45 birds, males and females, were instrumented either with a GPS or with a PTT to get trajectory movements. Data were speed filtered and re-sample to the more coarse temporal resolution. 11 females were equipped with time depth-recorder. Another control group was used to get information on body mass. Detailed information on equipped birds is summarized in the paper 2 (Table 1).

Trips characteristics were analyzed and maps of time spent per cell (0.2°) were realized. These maps were put in relation with oceanographic data to get information on encountered oceanographic environments. We tested the influence of 7 oceanographic parameters which could have a role on the biological production: Bathymetry (neritic or oceanic waters), Net primary productivity (NPP, phytoplankton grounds), Sea surface Height (SSH, frontal structures), geostrophic currents (degree of turbulence of waters), gradients of bathymetry (edge of plateau, submarine peaks) and NPP (aggregation of primary productivity), respectively.

IV.3. Results

At-sea distribution.

Important variations in spatial distributions were observed between the three breeding stage, for both sexes.

During the incubation stage, males performed **long, remote and looping trips** headed to the north (~360km, 18 days). Their shape was highly similar between birds. After relieved by their mates, the females have made trips headed in the **same direction** than males, but more **directly** with a shorter foraging range (~275km, 12 days). The total travelled distance was also shorter (by about 300km, Figure 4.1).

During the brood stage, females realized successive **short trips** distant on average of 32 km from the colony. A **quadratic relationship** was found with time, with an increasing remoteness between the 15th and the 26th December, and then a decreasing up to the 5th January. This relation was however overlapped by year effect (Figure 4.2) mostly due to of the timing of equipment, occurring on 3 successive weeks on the 3 studied years, respectively.

During the crèche stage, females increased their foraging range and reached areas distant from the colony of about 80km. Males, which are stopping their long fasting period, exhibited very **different trips** according to the individuals. Thus, three patterns could be pointed out: i) short trips headed north (mean range: 53km), ii) northern headed long and circular trips (mean range: 234 km) and iii) southern headed long and very directional trips (mean range: 251 km).

Relation between penguins distribution and oceanographic features.

During the incubation stage, time spent per cell by the **males** while foraging was mainly positively influenced by the **net primary production** and **geostrophic currents**. This indicates an increase of foraging time spent in the frontal structures located north of the colony. Foraging **females** which leaved the colony about 20 days later in the season (end of November) travelled less far. They were also the most influenced by **sea surface height** and **gradient of NPP** at this time of the year. It can be also pointed out a **southward displacement** of the phytoplanktonic **bloom** associated with an increase of NPP values. Interestingly, the match between the phytoplankton southward migration highly coincided with the females trips ranges (Figure 4.3).

During the brood stage, **bathymetry** and **gradient of bathymetry** were most important factors influencing the foraging time of females. Birds mainly foraged in deep waters located between 420 and 1200m (73% of cells). At this time, **NPP** was **homogeneously** distributed on the area prospected by penguins.

When females foraged during the crèche stage, only **bathymetry, correlated with distance from colony**, had an effect on the time spent per cell. Concerning males, the relations differed regarding to their trips patterns. Males performing short trips positively responded mainly to the bathymetry and NPP gradients. For the birds foraging toward the north, the bathymetry was the main common factor influencing the time spent per cell. However the random effect was high (33%) indicating that relationship between the response variable and predictors was strongly influenced by the individual. All the birds foraging toward the south increased their foraging time in the most distant part of their trips. So their foraging time were negatively linked with the NPP, SSH and bathymetry which exhibited higher values close to the colony.

IV. FORAGING STRATEGIES AT CROZET ISLANDS

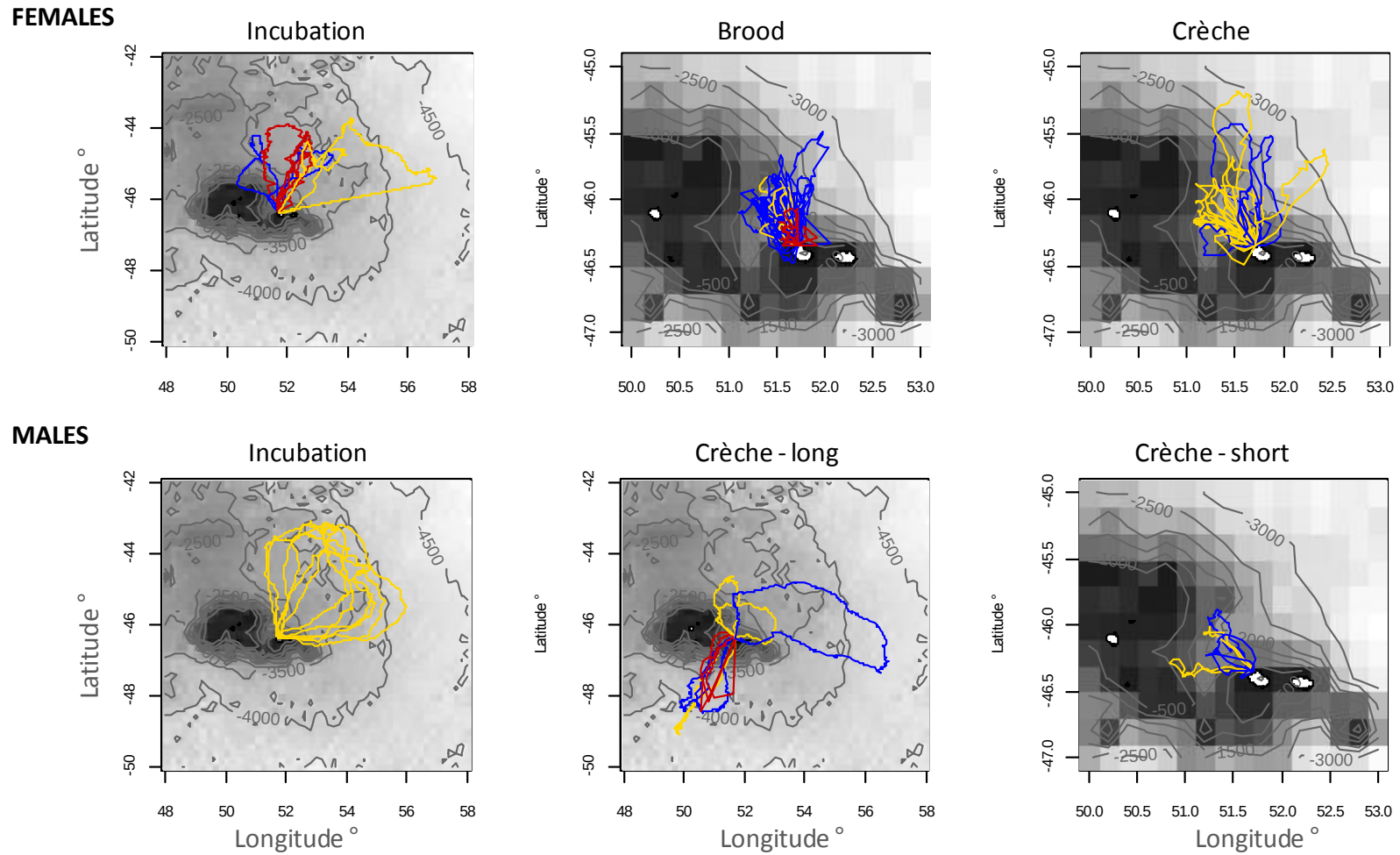


Figure 4.1: Tracks of females and males during the breeding season at Crozet islands. Trips are overlaid on bathymetry maps. red: season 09 ; gold: season 12 ; blue: season 13.

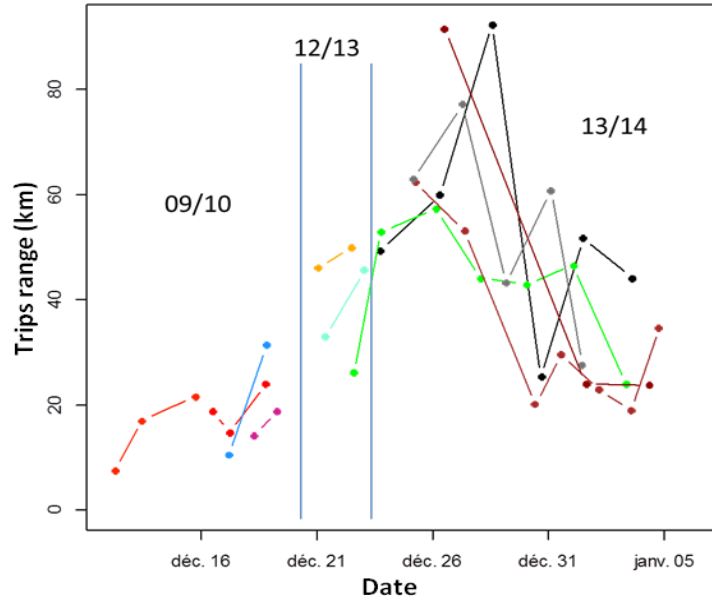


Figure 4.2: Range of successive trips in brooding females from Crozet Islands

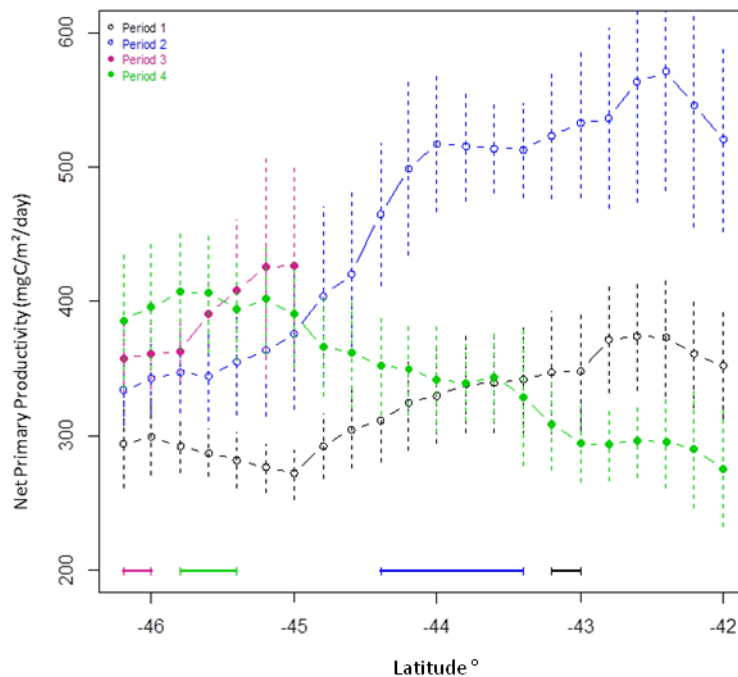


Figure 4.3: Evolution of net primary production north of Crozet Islands during the breeding season. Mean NPP values were computed every 0.2° of latitude (46.3 and 42°S) between 50 and 54° East (. Dashed lines indicate standard deviations. Horizontal lines above the horizontal axis indicate the mean maximal range of Macaroni penguins during each period. **Period 1:** 20th November - 12th December 2012 (at-sea incubating males) ; **Period 2:** 7th - 20th December 2012 (at sea incubating females) ; **Period 3:** 20th December - 3th January 2013 (brood) ; **Period 4:** 4th January - 15th January 2013 (beginning of crèche).

Diving activity.

The diving activity exhibited a strongly diel pattern during both stages. Foraging females performed mostly **shallow dives** (mean: 27m) at **night** and **deeper dives** (mean: 46m) during **daylight** whereas high foraging dives rate was the most frequently observed during dusk and dawn (Figure 4.4) indicating a strong effort during these hours.

The **rate of foraging dives** performed at the **daily, daylight and hour scales**, respectively tended to **decrease** with the breeding cycle, but the relationship was not significant. However the number of foraging dives was significantly higher during night in brood and crèche whereas the birds **dived deeper** (>10m), **longer** and performed **longer bouts** (Figure 4.5). Moreover, the time spent at the surface per hour (sum of inter-dive duration, Figure 4.5) was smaller in brood. These results suggest a **stronger diving effort** during the brood and crèches stages.

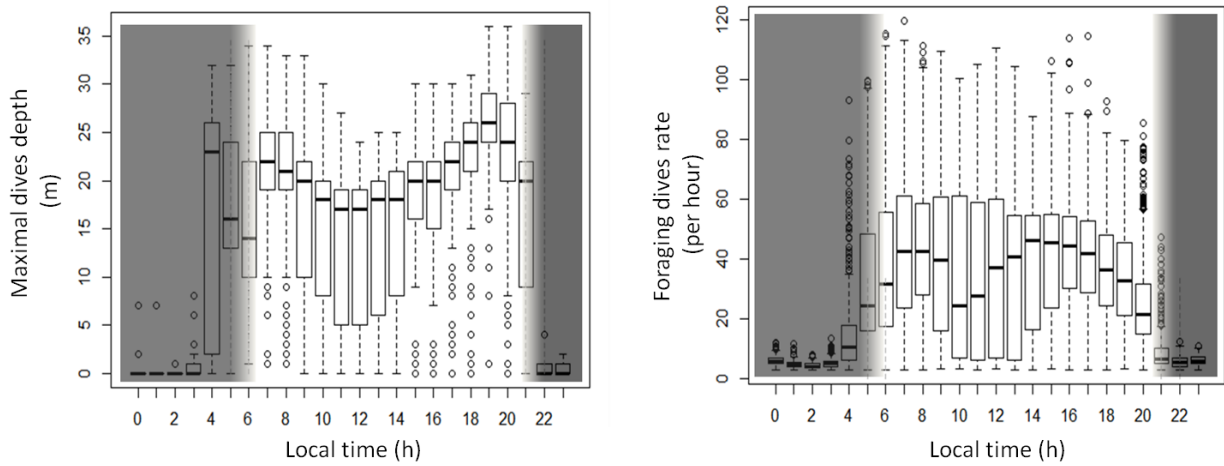


Figure 4.4: Relation of maximal diving depth and dive rate with day time. Shadow areas indicate night period

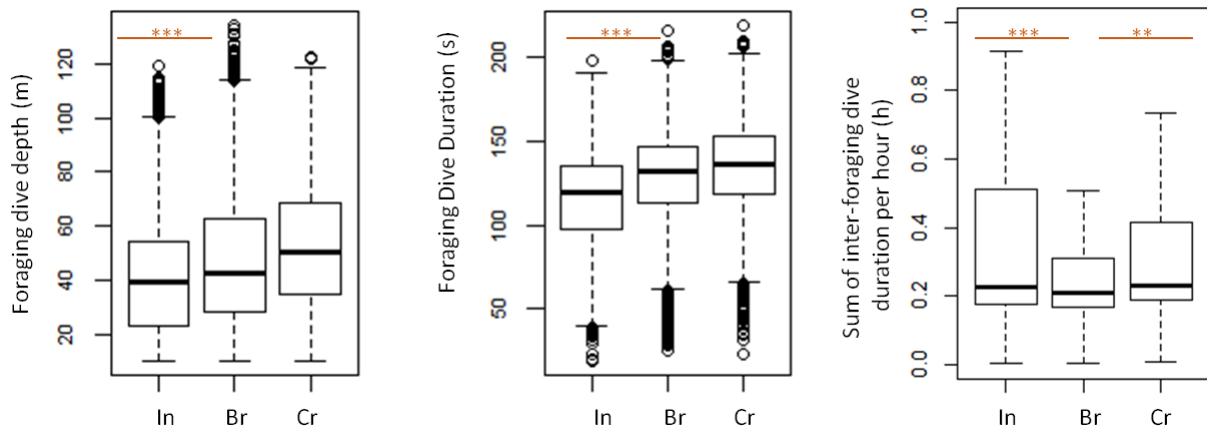


Figure 4.5: Variation of foraging dive depth, duration and inter-foraging dives durations over the breeding season. In: incubation ; Br: Brood ; Cr: Crèche.

Body Mass and Diet.

Body mass (BM) changes of males and females showed a **similar trend to the changes reported in other localities. During the incubation stage** relieved males weighted ~3240g and ~3470g at the beginning of brooding. Relieved females gained 35% of their initial BM (2780g) after their first foraging trip.

At the beginning of the brood stage, females significantly increased their BM during the first 6 days of the brooding period. Thereafter their body mass decreased up to the 8th January (data from the 3 pooled years, Figure 4.6, Table 4.1). Looking at the relation within each season, the quadratic relationship was only significant for the 2009/2010 season. None relationship with date was found for the two other seasons. **Females lose on average only 5.5% of their weight during the brood stage.**

Foraging females had a higher BM than brooding males and this relationship reversed in crèche. **Males** started the **crèche** with a BM of 3350g and **increased it considerably** during crèche (33%) (Figure 4.6).

Trophic level in relation to breeding stages.

Isotopic data indicated that **nitrogen signatures of males** were **higher** at crèche than in incubation, suggesting a **shift of diet to upper trophic levels**. No significant trend was found for females which had the same nitrogen signature, more relevant of myctophids diet, whatever the breeding stage.

Table 4.1: Results of models of the body mass of brooding females in relation with date.

Model	LME		LM	
Response variable:	BM - 3 years		BM - 2009/2010	
Predictors:	Coeff + SE	ΔAIC_{2nd}	Coeff + SE	ΔAIC_{2nd}
Intercept	3616 $\pm$ 148	-4.59	3683 $\pm$ 179	-2.1
Date	54 $\pm$ 29	Year effect	115 $\pm$ 59	<i>n</i>
Date²	-2.7 $\pm$ 1.3	22%	-6.1 $\pm$ 3.1	30

LME :linear mixed model ; LM: linear model. Year was the random effect

IV. FORAGING STRATEGIES AT CROZET ISLANDS

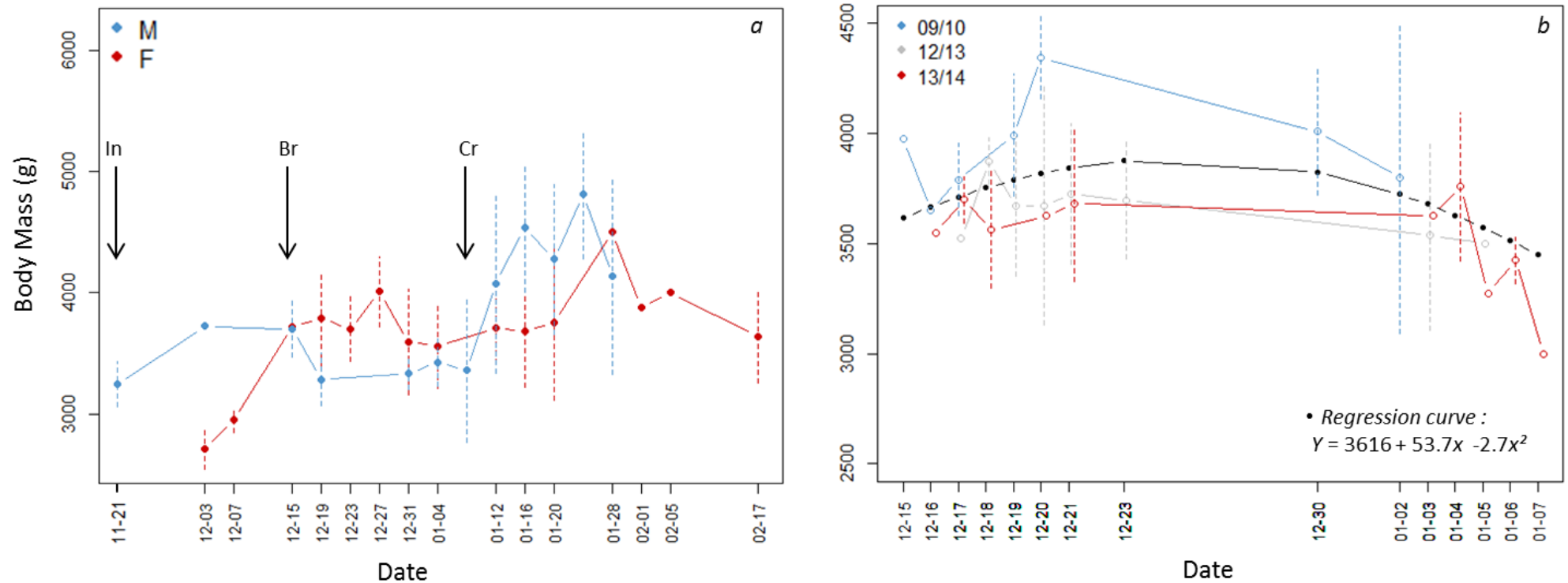


Figure 4.6: Variation of body mass during the breeding season of Macaroni penguins at Crozet islands. *a*: mean of BM of males and females averaged on successive 4 days. *b*: Variation of BM of brooding females with date according year. Black line represent the results of a significant mixed model of the BM in relation with date. In: incubation; Br: Brood; Cr: Crèche.

IV.4. Discussion

This study allowed us to characterize for the first time the at-sea distribution and the oceanographic environment used by Macaroni penguins of Crozet islands during a complete breeding season. Coupled with diet and body mass data, it led to better understand their foraging strategies regarding the energetic requirements and breeding constraints imposed by each breeding stage. The salient features of the foraging studies can be summarized as follows.

Incubation.

Firstly males and females exhibited very different foraging behavior during the breeding season, especially in brood and crèche. During the incubation stage, **males strongly targeted the Sub Antarctic front** and move in the same direction than its currents when foraging (Paper 1). In contrast, **females** which performed shorter and more directional trips seem to strongly respond to the **southward migration of the phyto-planktonic bloom**. No precise data were unfortunately available on gained mass during the trips of males for logistic reasons. However, in comparison with South Georgia, mass of males at the beginning of brood stage was much lower on Crozet island (of about 1 kg, Figure 4.7). In comparison, females from the two populations exhibited a similar gain of mass. This difference at the same breeding stage indicates that males of the Crozet Is. have gained less mass during their incubation trips while their trip was longer of about 8 days. These results support the **idea that males are more constrained** to find food around Crozet islands during the incubating stage, whereas **females seem to take advantage** of the **development** and the **southward migration** of the **annual phytoplankton bloom**.

Brood.

During the brooding stage, females performed multiple short trips highly directional associated with a **diving effort more important** than in incubation. It is known that brood stage constitute one of the highest daily energy expenditure period associated with an important body mass loss (Green et al. 2009). However, females from Crozet islands **lose less weight** (5.5%) in comparison to South Georgia (16%, Croxall 1984). In parallel, the phytoplankton concentrations close to the colony are the highest on the whole breeding cycle (Figure 4.3). These results suggest that females are prospecting in a **highly profitable area** where important stocks of resources are available.

The **phenology** of Macaroni penguins is **highly synchronous** since all birds lay within 9 days-window (Stahl et al. 1985, Williams 1995). The strong relationship found between one of the highest energetic period for females (rearing period, Green et al. 2009) and the peak food availability suggests that phenology of Macaroni penguins from Crozet islands has been adapted to the regional productivity. During the inter-breeding period, females less behave as central place forager and can forage in wider areas (Thiebot et al. 2011a, 2014). In these periods, birds could be able to cope with lower profitable

areas by adopting an highest foraging effort or moving to search other foraging places. In contrast, during the brooding season, females are **strongly time-limited** by the chicks needs and have to forage in very profitable areas. Birds which start to breed in the period which allows getting the chick (hatching) when the food availability is the highest may have a better breeding success. Thus they might be favored by natural selection process. In this study, we observed a case of matching between predators needs and resources availability. This observation supports the **Cushing hypothesis** (Cushing 1969, 1990) which assumes that recruitment in a population (*i.e.* of predator) will be high if the most energetically part of the breeding season occurs at the same time as the peak availability of the lower trophic level (*i.e.* preys).

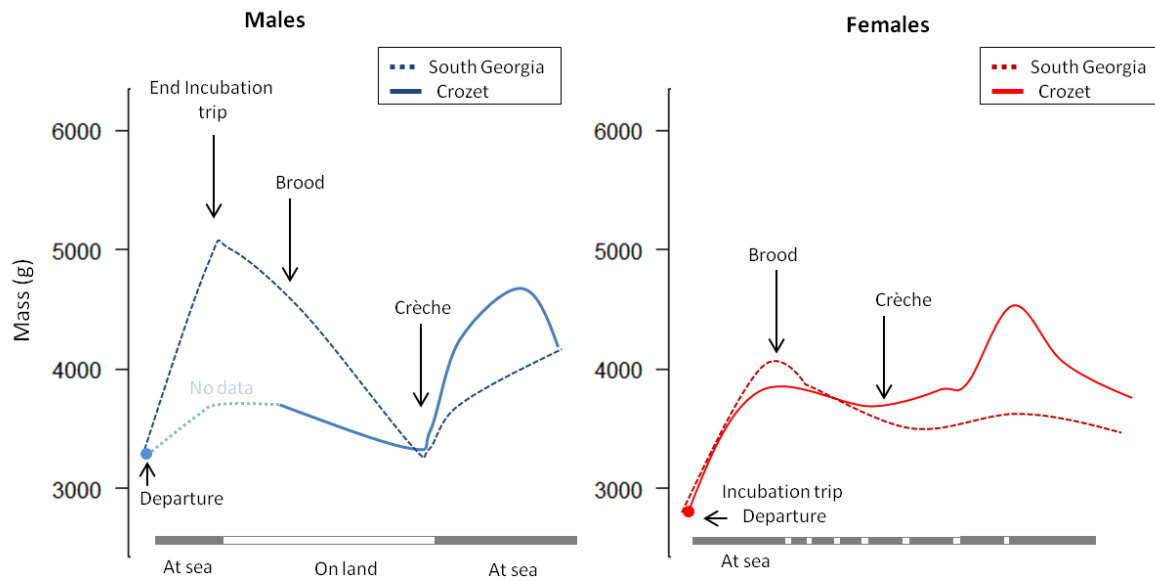


Figure 4.7: Smoothed variation of body mass of Macaroni penguins during the breeding season in Crozet islands (our data) and in South Georgia (from Green et al. 2009).

The advection of **NPP close to colony** (<100km) (Figure 4.3) is mainly due to an anti-cyclonic flow around Crozet plateau (Venables et al. 2007, Pollard et al. 2007b). The bloom movements and spreading close to the islands could advect **important stocks of resources** close to the island shelf. At Marion-Prince Edward islands, it has been hypothesized that strong wind action on Ekman layer could rapidly advect surface water on shelf, bringing with it the pelagic fish and crustaceans which were located near the surface at night. As wind is relatively strong on Crozet islands (Weimerskirch et al. 2012), we hypothesize that similar process appear near the Crozet shelf.

Interestingly, we observed a **significant quadratic relationship** between the mass of females and the advancement of the brooding stage during the year **with the highest productivity** of the three studied years (2009/2010, Figure 4.6). Likewise, a quadratic relation was also found with the range of

trips (Figure 4.2, overlapped with year effect, discussed in paper 2 - method part). We can assume that the progressive remoteness of the females foraging range associated with an increase of their weight may correspond to the searching of profitable patches. About 10 days after the beginning of the brooding period, females started to decrease their foraging range. If there was a movement of prey patches close to the colony, their body mass should still increase (or stay identical). In contrast, their body mass decreased. This strongly suggests that **prey availability** in the prospected area was either, **relatively similar**, or **lower due to a strong harvesting pressure**. In this stage, females could forage further to find more favorable areas (Barlow & Croxall 2002b, Deagle et al. 2008) but they do not. During the brooding stage, females intensively supply meals to the chick whose energetic requirements rapidly increase (100 to 350 g/day, Green et al. 2007). This shift of range could thus be linked with a response of females to the energetic constraints imposed by the chicks. They invest in breeding needs in detriment of their own body condition. This strategy was observed in other localities (Croxall 1984, Barlow & Croxall 2002a) and support the hypothesis that this **loss of mass is adaptative** (Cresswell et al. 2007). Indeed, to maximize current and future reproductive success, parents have to make decisions based on their own body conditions and the needs of their offspring (Williams 1966). In Macaroni penguin, this loss of weight is surely part of parental care strategy and should not incur to great cost to the fitness of parent (Clutton-Brock 1991).

Crèche.

When crèche begins, females forage more and more far away and dive deeper. The strong harvest pressure close to the colony during the brooding period could have lead to a **local depletion** of prey. This phenomena is commonly observed in colonial central-place foragers where large number of predators forage in relative small areas. As Macaroni penguins are highly synchronous, the intra-specific competition may be high and increase the "**Ashmole halo**" in the first 40km of the colony (Ashmole 1963).

The **increase of maximal dives** depth during the breeding cycle could be explained by a **shift in diet composition**. Indeed, it has been observed that proportions of crustaceans (mainly *E.vallentini* and *T.gaudichaudii*) decreased during the breeding season whereas proportions of myctophids fish increased in the bulk (8.5% to 17.5%, Ridoux 1995). Myctophids are found further from the islands (Perissinotto & McQuaid 1992, Bedford et al. 2015) and have more nutritive values than subantarctic krill (Cherel & Ridoux 1992). This adjustment may both ensure the energy requirement of the chick and maintain a body condition on a basal level.

We observed that females have increased their body mass just at the beginning of crèche whereas their loss of body mass during the brood stage was very low (5%). These observations contrast with the weight variation observed in South Georgia, where females considerably lose weight during brood and the beginning of crèche (Green et al. 2009, Croxall 1984). This indicates that the

stocks of **resources close to Crozet islands** at this period **are probably very important and highly profitable for females**.

In crèche, the foraging behaviour of males is highly variable since **three contrasted patterns** of distribution were observed according to the individuals. Individuals exhibited long looping north trips to the SAF, long directed trips to the Polar Front or short trips headed north-east close to the colony. These strategies seem to be very efficient since the increase of BM at Crozet island is very important (33% in 20 days). **Concerning the trips headed north**, the response to oceanographic variables was highly variable between the 3 birds suggesting that each birds have adjusted its behaviour to the local encountered environment. However, targeted areas exhibited relative important values of geotropic currents indicating they both target meanders of the SAF.

In contrast, the **birds** which traveled **toward the south** presented very similar trips all directed toward the **Polar Front**. The Polar Frontal Zone and PF provide **high concentrations of myctophids** where they are at lower depth than near the SAF (Hulley 1981, Pakhomov et al. 1994). Antarctic fur seals and King penguins which are **myctophids specialist** eater also target the PF during their breeding seasons (Bost et al. 1997, Guinet et al. 2001, Cherel et al. 2007). Otherwise, Macaroni penguins from Marion Isl. and Crozet Isl. both go to the south of Polar Front during the pre-moult foraging trips (Thiebot et al. 2014, Whitehead et al. 2016). The need to find very good foraging grounds during these period is crucial since birds have to prepare the high energy-costly molt period (Green et al. 2009). Again, this supports the hypothesis that targeting foraging grounds in the south of Crozet islands must be **highly profitable** for Macaroni penguins in crèche. Males surely adopt such behaviour to respond to **their need to recover their body condition** after the long fast period.

Otherwise, this strong inter-individual strategy (north and south) could be the part of mechanisms involved in the **inter-individual competition avoidance**. It would be very interesting to know if the diet (*i.e.* myctophids versus crustaceans eater), gain of mass and breeding success differ between these two main strategies. These investigations could lead to better understand if these strategies have an adaptative role (*i.e.* impact on the fitness).

Five trips were performed very close to the colony, similar to those exhibited by females at this stage. These short trips show that resources are still available near the colony, but probably in **preys with lower nutritive values than myctophids, as crustaceans**, since fishes are mostly found over deeper waters, further from the islands (Perissinotto & McQuaid 1992). Thus, long foraging trips might involved in **reserves recovery**, with a foraging behaviour concentrated on nutritive preys located in meso-pelagic waters. The short trips could be related to **provisioning the chick**.

Conclusion.

This study gives a good overview of the **foraging strategies of Macaroni penguins from Crozet islands over the breeding season**. It also appear that Crozet locality seems to be an environment particularly favorable for Macaroni penguins during the breeding season, due to two main factors: the **annual phytoplanktonic bloom** occuring each year north of Crozet at a very favorable timing, i.e. at the end of the incubation period, and the presence of **two major frontal zones**, the PF and the SAF, which are known to be very productive. Crozet islands are located **equidistant** from the SAF and the PF and the foraging behavior of Macaroni penguins may be advantageous since they have access to high profitable areas to forage. These characteristic could be a factor playing in the important number of breeding pairs observed on these islands.

CHAPITRE V

FORAGING STRATEGIES OF MACARONI PENGUINS IN CONTRASTED ENVIRONMENTS



Reflection @ Cécile Bon

Paper 3: Bon C, Scheffer A, Cherel Y, Powolny T, Arnaud, Jenouvrier S, Bost CA. **Foraging strategies of Macaroni penguins during the breeding season at Kerguelen islands.** *In preparation for Marine Ecology Progress (MEPS).*

V.1. Context

In the open marine environment, physical process aggregate prey at different spatial scales, from fine to mesoscales, making it available for seabirds. The respective influence of environmental features on seabird foraging movements is better known since the last decade thanks to multi-years at-sea tracking of predators and habitat modelling (Péron et al. 2012, Louzao et al. 2013).

Regional environmental conditions can shape the seabird foraging movements and feeding strategies at the population level. For example, strong differences in foraging range, bearings and degree of inter-individual variability between two contrasted sites have been observed in different seabird species including penguins (*e.g.* adélie penguins: Watanuki et al. 1997, Gentoo penguin: Lescroël & Bost 2005, crested penguins: Tremblay & Cherel 2000, Thiebot et al. 2012, 2013). Primary ecological drivers to such differences seem to be the availability and distribution of distinct prey in each site (Paiva et al. 2010). At the species level, individuals can adapt their behavioral responses, via different foraging modes, to changes in prey availability (Boyd et al. 1994). The response of populations will differ according to several parameters like prey availability and abiotic conditions (Salamolard & Weimerskirch 1993, Charrassin & Bost 2001) (Salamolard & Weimerskirch 1993, Charrassin & Bost 2001). Hence, the effects of biotic and abiotic factors on foraging strategies are difficult to discriminate. One way to cope with this challenge is to adopt a comparative approach on a regional spatial scale.

In this work, we compare the foraging strategies of Macaroni penguins facing two distinct oceanographic conditions at a regional scale, the South Indian Ocean, Kerguelen and Crozet sectors. Firstly we investigated the foraging strategies of macaroni penguins of Kerguelen islands during an entire breeding season, which was poorly known. Secondly, we compared our results with the strategy pointed out during the breeding season at the Crozet islands, one another stronghold locality also localized in the South Indian ocean. Crozet lies between the Sub-Antarctic Front and the Polar Front, supporting by a limited shelf. The proximity of several major frontal zones and its isolation has favoured the implementation of large seabird populations (Jouventin et al. 1984, Guinet et al. 1996). This archipelago hosts the northern population of the macaroni penguin and is a stronghold breeding locality (Crossin et al. 2013) but the population trend over the long-term is unknown. Kerguelen archipelago lies close to the Polar Front, and supports one of the largest shelf systems in the southern ocean. Due to the high level of marine productivity in the surrounding waters and its isolation, the Kerguelen plateau provides resources for considerable marine predators including sea mammals

and macaroni penguins (Jouventin et al. 1984, Weimerskirch et al. 1989, Guinet et al. 1996). The long-term population monitoring indicates a slight, positive increase (C. Barbraud, *pers. com.*).

V.2. Methods

The study was carried out at Cap Cotter, Péninsule Courbet, Kerguelen Archipelago, hereafter referred to as Kerguelen. In order to get information on the at-sea distribution, 45 birds were instrumented with either GPS, or Argos loggers over two breeding seasons, 2011/2012 and 2014/2015. Another group of birds (n=224 females, 5 in incubation, 19 in brood) was equipped with a time-depth recorder to get information on their diving behaviour. Ninety body masses were obtained between the beginning of November and January over the two seasons. Dietary of birds were investigated by analyzing stomach contents get from 23 birds in incubation and brooding period.

Interpolated tracks on the same lag-time (100min) were gridded on maps (cell of 0.2°) in order to get estimation of the distribution of their foraging time. Investigation of habitat use was investigated using mixed models of time spent per cell in relation of several oceanographic variables. Oceanographic parameters used were: bathymetry (shelf, slope and underwaters peaks), NPP (net primary productivion), SSH (frontal structures), SLA (mesoscale structures as eddies), EKE (turbulence of eddy fied), gradient of bathymetry (slope) and NPP (aggregation of primary production).

No oceanographic data were available for the crèche when analyzing the data.

V.3. Results

3.1. Foraging strategies of Kerguelen islands

Trips characteristics.

At the incubation stage, males performed long eastward trips remote of more than 500km from the colony (Figure 5.1). Their directions were not uniform with an important bearing variation ($>30^\circ$). Only one female trip could be used. During the brood stage, females foraged have been in areas located north - north east at about on average 80km from the colony. An important variation of range was observed in relation to the timing of the brood stage from about 30km to more than 100km between the 18th and 27th December (Figure 5.2). Concerning the crèche stage, all females still increased their foraging range, reaching areas at about 170km off their colony. They also shifted to foraging locations most oriented eastward than during the brood stage. At the crèche stage, males travelled further than females, *i.e.* about 320km from the colony. An important inter-annual variation in foraging location was observed since the maximal foraging range of males equipped in 2011/2012 was ~20% more southward than in the other studied season (2014/2015, Figure 3.1). However, the ranges were more variable within the seasons than between it. The inter-individual variation was also important since individual ranges varied between 50 and 640km at the crèche stage.

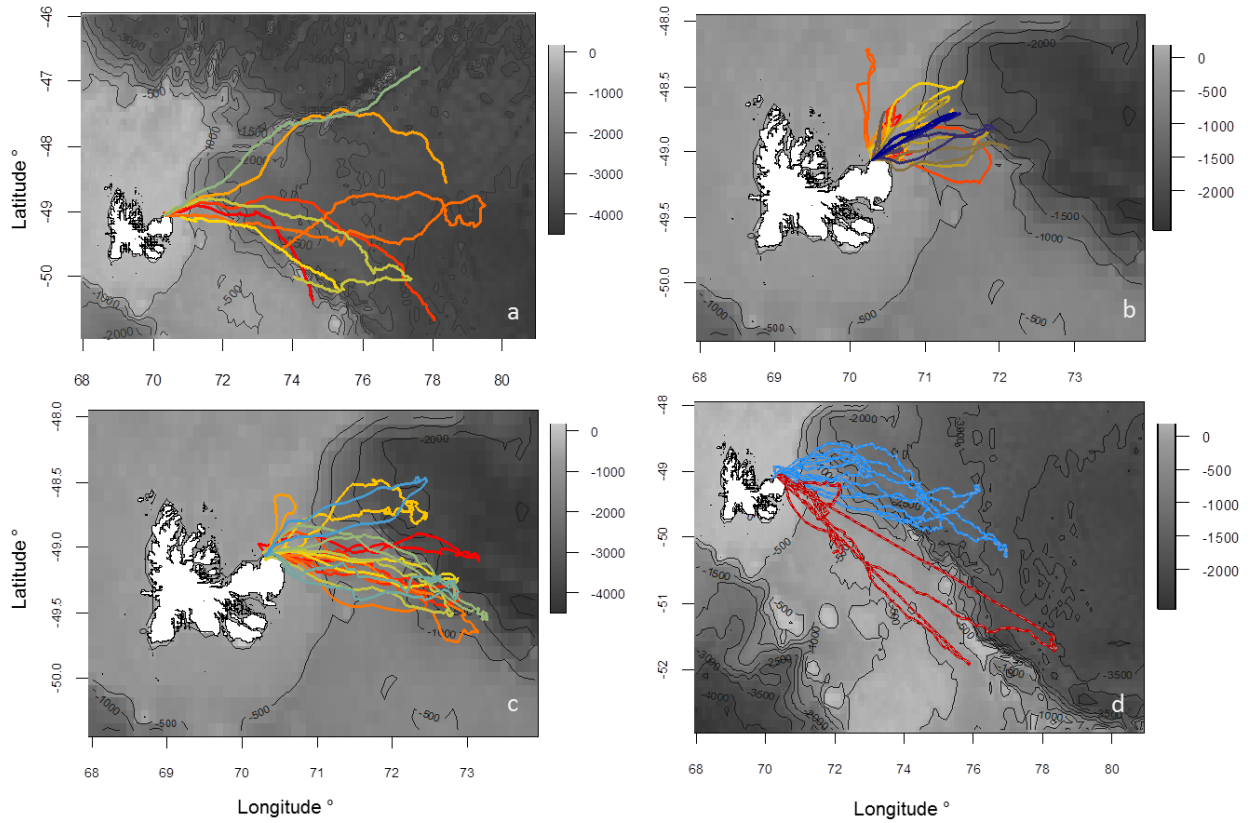


Figure 5.1: Foraging trips of Macaroni penguins at Kerguelen islands. a: Males in incubation stage (2011/2012) b: Brooding females (2011/2012) c: Crècheing females (2014/2015) d: Crècheing males (2011/2012:blue ; 2014/2015: red). The bathymetry scale (m) is represented on the right part of each panel .

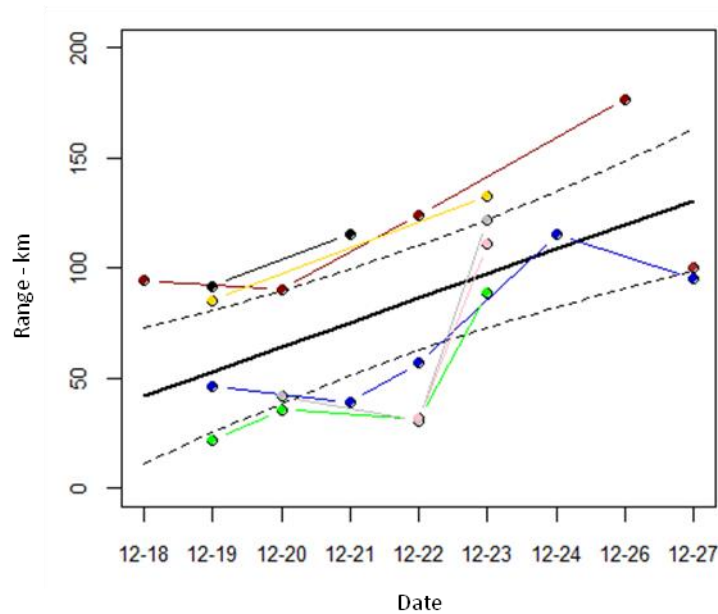


Figure 5.2 : Range of successive trips performed by brooding penguins in relation with departure date at Kerguelen islands.

V. FORAGING STRATEGIES IN CONTRASTED ENVIRONMENTS

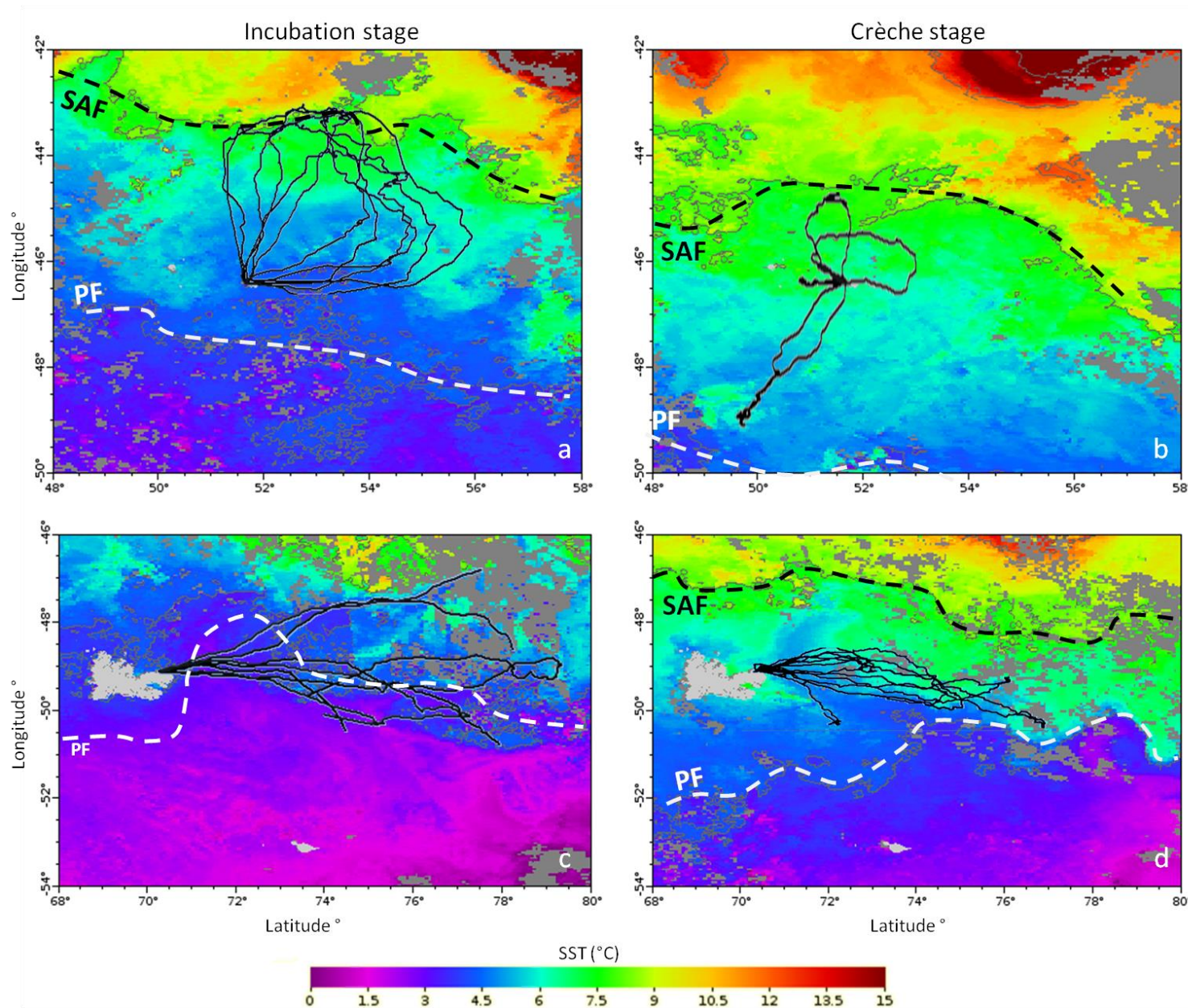


Figure 5.3: Foraging trips of males Macaroni penguins from Crozet (a,b) and Kerguelen islands (c,d) in incubation (a,c) and crèche (b,d). Tracks are overlapped on sea surface temperatures (SST) maps (°C). SubAntarctic Front (SAF, black dotted line) and Polar Front (PF, white dotted line) were estimated from 8°C and 4° surface isotherm (From Park et al. 1993). SST were averaged on 8 days centered on the following dates:
a: 12/01/2012, b: 23/01/2013, c: 24/11/2011, d: 16/01/2012
©Aqua Modis, NPP, 0.05°, Global, Daytime, Science Quality

Relation with oceanographic features.

During all the breeding cycle, both sexes foraged in the Polar Frontal Zone (Figure 5.3).

During the **incubation stage**, males targeted and increased their foraging time (Figure 5.4, Table 4 in paper 3) in areas with relative more turbulence and higher primary productivity described by positive relation with SLA, NPP and EKE. However, the positive relations with turbulence and productivity seem to be independent. We observed that both time spent per cell and NPP increased in a area close of the colony (between 72 and 74°, Figure 3 in paper 3) where EKE is relatively low. Both variation of SSH and SLA suggest the presence of an eddy structure associated there with higher productivity. Farther east, SSH considerably increased as well as EKE (from 77°E), characterizing the border of the border of Polar Front (Figure 5.4). During the **brooding stage**, 57% of performed tracks had a range shorter than 50km from the colony. Females which performed these small trips stayed on the shelf. Concerning more distant trips (>50km), females foraged on the shelf before going further and further on the shelf break (Figure 5.4).

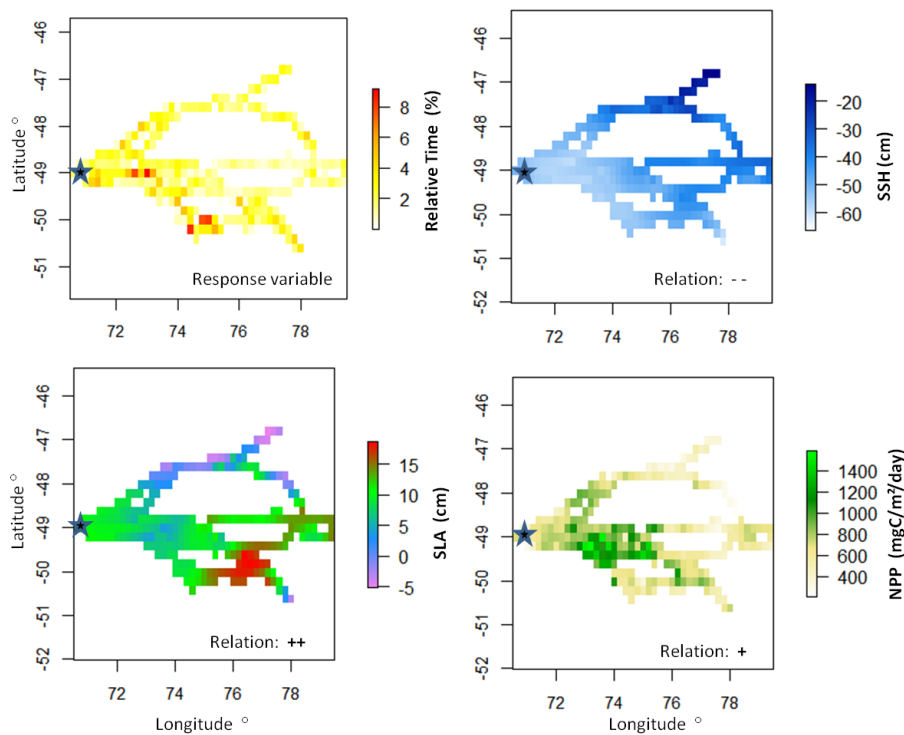


Figure 5.4: Relative variations of oceanographic features within tracks of males at sea, incubation stage. Productivity ; SSH: Sea Surface Height ; SLA: Sea Level Anomaly. Black star: colony. Nature of the relation with the time spent per cell are indicated by the signs - or + in each box.

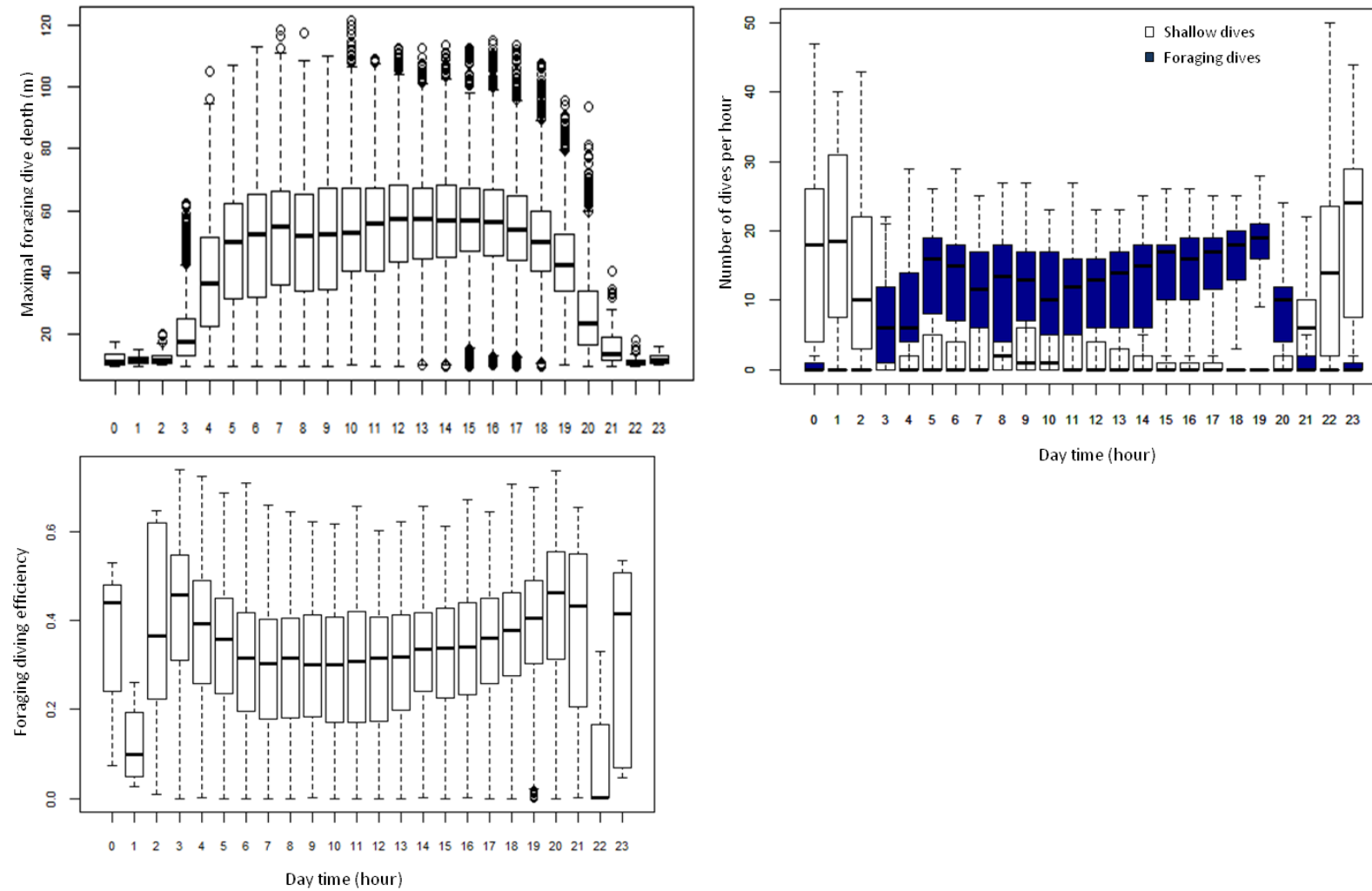


Figure 5.5: Diving parameters in relation with day time from brooding females at Kerguelen Islands.

Diving behaviour.

During the incubation and brood stages, foraging dive depths and dive rate (per hour) followed a quadratic relationship with day time (Table 6, paper 3). During the night, females performed only shallow dives (~15m). By contrast, they dive deeper during the daylight, at mean depth of 50m (Figure 5.5). No individual variation was found on the shape of this relation. On average, the dive rate reached 15 foraging dives per hour during daylight. This number decreased significantly during the brood to 12 dives per hour. However, none difference between the incubation and brood stage was found in terms of foraging dives depth, dive and bottom duration, diving efficiency. Otherwise, during the brood stage, we found an important inter-individual variability in foraging dives depth, duration, bottom duration and diving efficiency. Concerning the bout structures, the majority of foraging dives were included in a bout (85%). The isolated dives were significantly shallower and less efficient.

Body mass variation.

From the start of laying to the end of the first trip of incubation, the **males** increased their body mass of 12% (~4kg to 4.5kg, Figure 5.6). This body mass decreased up to the beginning of brood of 19% (~3.7kg). Body mass of the end of brood stage were not significantly different. However these results must be interpreted with caution as we could not get it during the same year. **Females** decreased their body mass (26%) from the laying of first egg (~3.9kg) to the relieve of incubating duties by males (~3.0kg). During their first foraging trip of the breeding season, females restored their body condition and reached the same level of body mass observed at the laying period (~3.7kg). At the end of December, females reached ~3.6kg ,either a loss of only 4% during the brood stage (Figure 5.6).

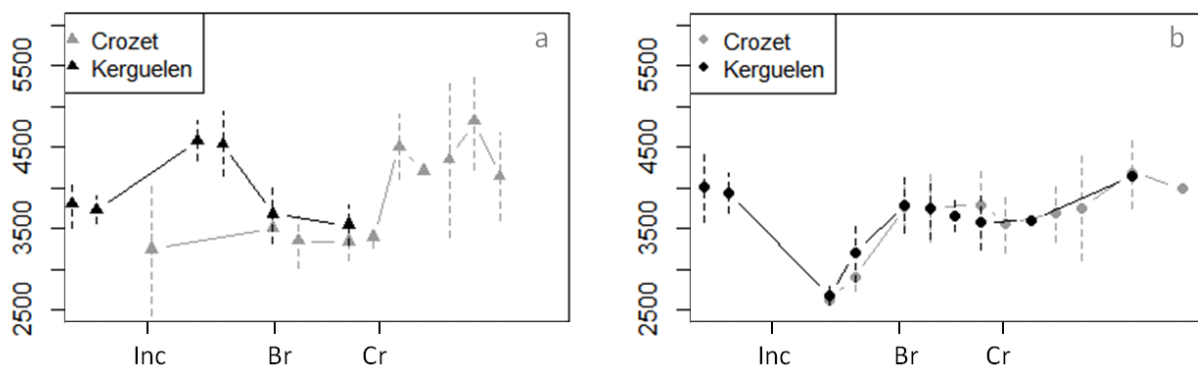


Figure 5.6: Variation of body mass of Macaroni penguins at Crozet and Kerguelen islands. a: Males;b: Females.

Diet composition.

In abundance, the diet was mainly composed of crustaceans (99% of total found items) and the main species of the stomach samples were *Euphausia vallentini*, *Thysanoessa* sp. and *Themisto gaudichaudii* (43.7% %, 28.2%, 27.,0%, respectively). Concerning the meal bulk (1320.4g) , *E. vallentini* was the most important component (45.4%), followed by *T.gaudichaudii* (30.5%), *Krefflichthys anderssoni* (15.7%) and then *Thysanoessa* sp. (8.2%). Finally, an important shift in the diet composition occurred since the proportion of crustaceans part (in biomass) decreased by 36% between the incubation period and the end of the brood stage. In contrast, the myctophids part increased by 20% (*K. anderssoni* : 5.88 to 25.05%).

3.2. Comparisons with the Crozet population

Tracking and Diving behaviour.

– **At the Kerguelen islands, the daily travelled distance as well and range trip** of Macaroni penguins were **higher** than at the Crozet, for each breeding stage and sexe (Figure 5.7). The traveling speed did not differ.

Concerning the **diving data, females from Crozet islands** performed **more foraging dives per hour** whatever the breeding stage (Figure 5.8) suggesting that their foraging effort was more important. However, the **total number of dives per day** did not significantly change between the two localities (Figure 5.8). We investigated the time per hour allocated to other activities than foraging (resting or travelling time) by computing the sum of inter foraging dives duration per hour. A **quadratic relationship** of this variable **with day time** was found for Kerguelen birds with a peak between 6:00 and 9:00 local time. This indicates a decrease of foraging effort during this period. In contrast, **none relation was found for penguins from Crozet**, suggesting that the **surface time is more homogeneously distributed during the day** (Figure 5.9). These results are coherent with the horizontal movements recorded since **penguins from Kerguelen travelled more distance per day**.

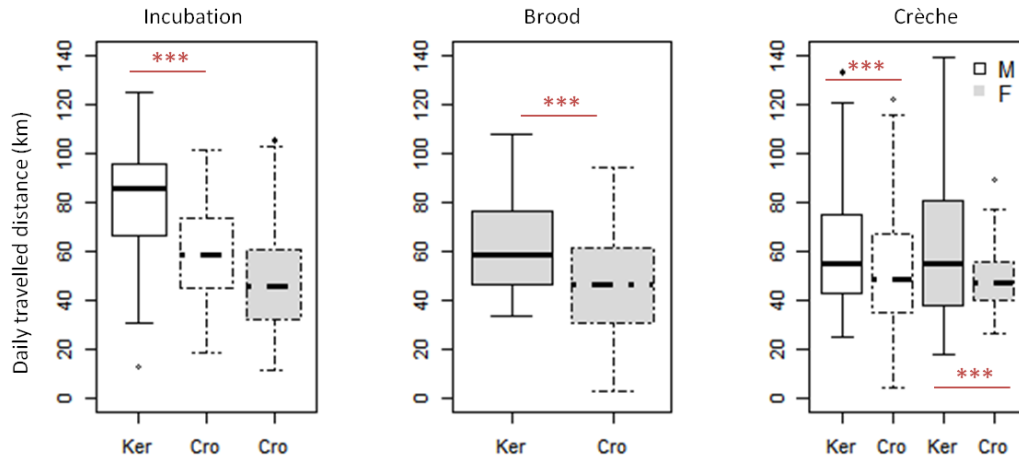


Figure 5.7: Variation of daily travelled distance of Macaroni penguins from Kerguelen and Crozet islands during the breeding season.

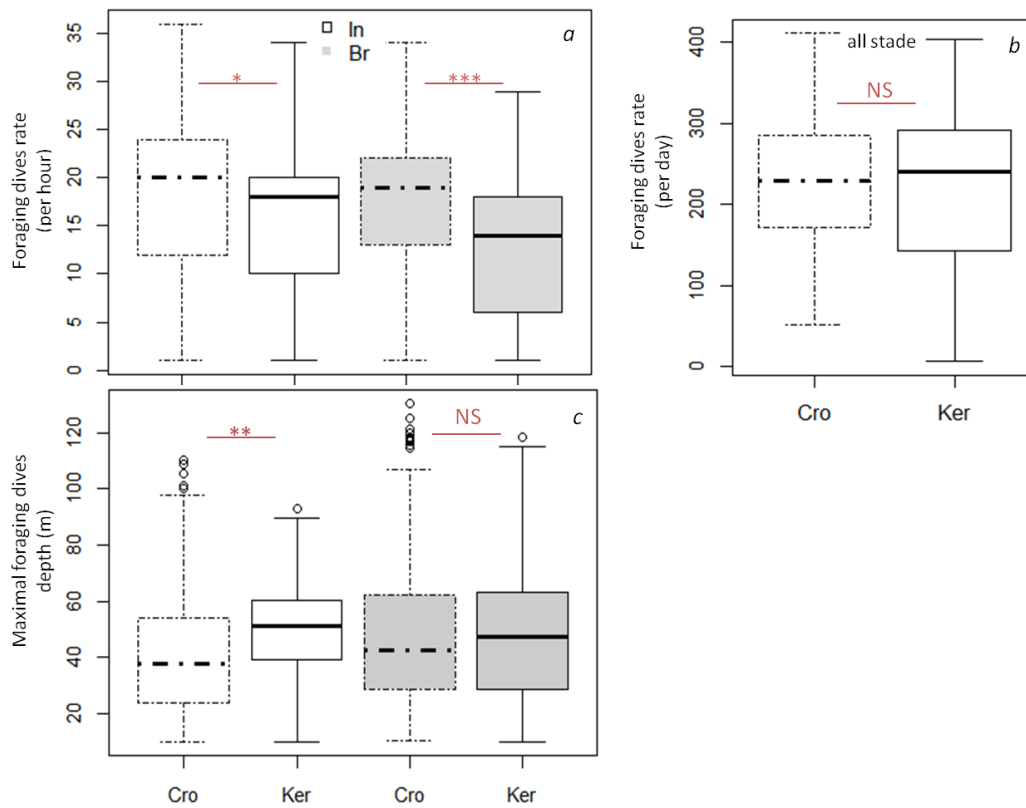


Figure 5.8: Foraging dives rate and depth of females from Crozet and Kerguelen. In : Incubation; Br: Brood. Cro: Crozet ; Ker: Kerguelen. Statistical results are shown in the table 3.3.1 (above). Concerning the **maximal depth**, females from Kerguelen islands dove deeper during the incubation stage than in Crozet (Table 5.1, Figure 5.10). During the brood stage, the maximal depth was not significantly different. Concerning the **bottom time, occurrence and number of wiggles per dives**, these variables were significantly higher in dives performed by birds from Kerguelen (Table 5.1).

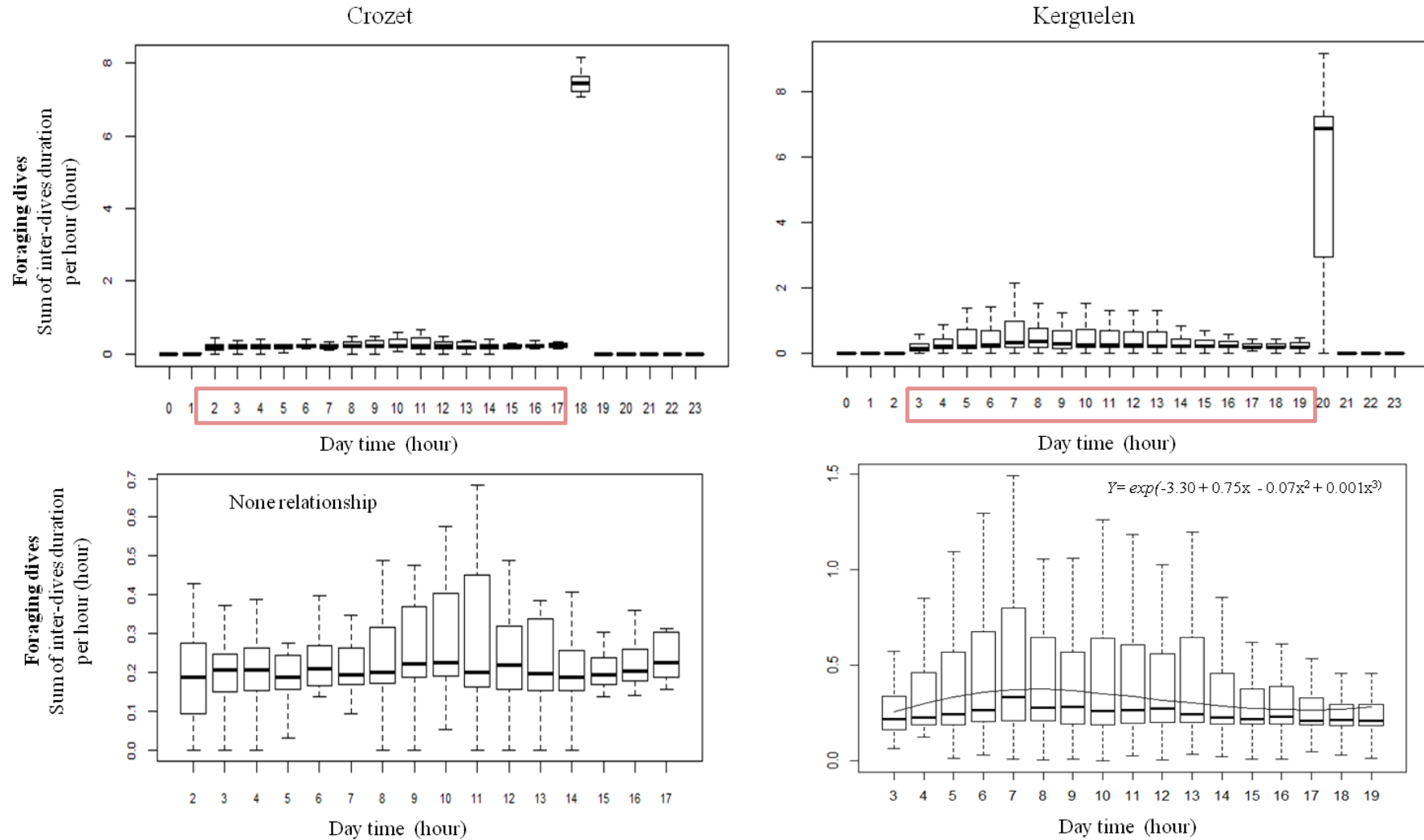


Figure 5.9: Resting or travelling time (sum of inter foraging dives duration per hour) in relation with day time for females of Crozet and Kerguelen islands. The two graphs at the bottom are zoom of those situated above, on the period indicated in the red box. A significant relationship was only found for the Kerguelen case

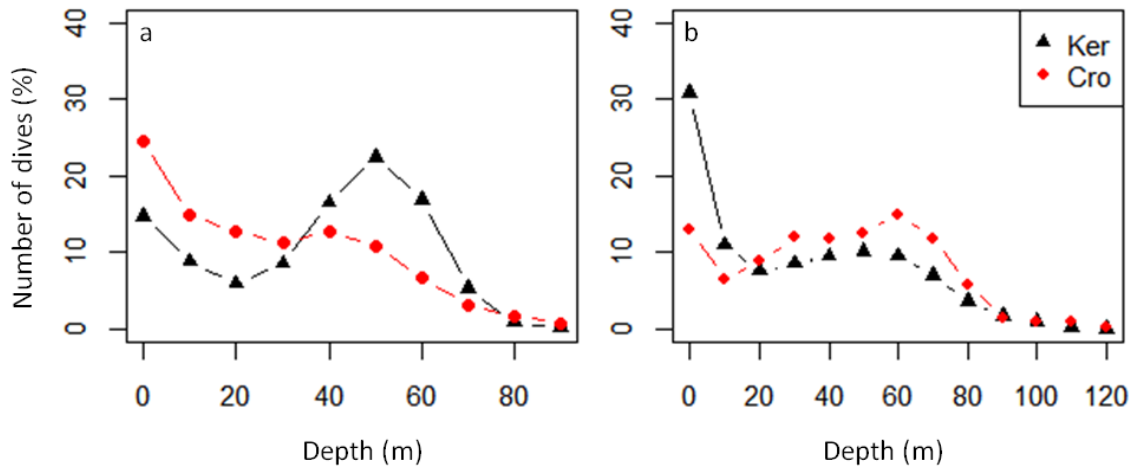


Figure 5.10: Averaged number of dives performed each 10 meters by females in Kerguelen and Crozet waters.

a: incubation ; b: brood. Females of Kerguelen significantly dove deeper only in incubation

Table 5.1: Comparison of foraging dive (>10m) parameters between Kerguelen and Crozet locality for incubation and brood stage. None significant parameters are in grey. Model type is indicated on right. LMM: Linear Mixed Model ; GLMM: Generalized Linear Mixed Model. ΔAIC_{null} indicates the AIC variation from the null model.

	Incubation		Brood		Model
	Coeff $\pm$ SE	ΔAIC_{null}	Coeff $\pm$ SE	ΔAIC_{null}	
Response	Dive rate (per hour)				LMM
Intercept	17.60 $\pm$ 0.58		16.41 $\pm$ 0.62		
Kerguelen	-2.46 $\pm$ 0.73	-5.1	-4.16 $\pm$ 0.69	-20.5	
Random effect: id	1.3 %		3.1 %		
Response	Occurrence (0,1) of wiggles per dive				GLMM Binomial link
Intercept	0.98 $\pm$ 0.17		0.55 $\pm$ 0.19		
Kerguelen	0.77 $\pm$ 0.24	-4.6	NS	-0.7	
Random effect: id	8 %		13 %		
Response	Log (number of wiggles per dive > 0)				LMM
Intercept	1.58 $\pm$ 0.08		1.33 $\pm$ 0.08		
Kerguelen	0.37 $\pm$ 0.10	-6	0.50 $\pm$ 0.09	-16.8	
Random effect: id	4 %		5.7 %		
Response	Log (Maximum depth dive)				LMM
Intercept	3.55 $\pm$ 0.05		3.73 $\pm$ 0.06		
Kerguelen	0.2 $\pm$ 0.06	-6.6	NS	+ 1.4	
Random effect: id	1%		2.5 %		

Oceanographic environment.

Overall during the incubation stage males from Crozet target turbulent waters within the southern limit of the Subantarctic Front (Figure 5.3). We found a strong, positive response of foraging time in relation to the increase of the net primary production and encountered currents speeds. The foraging response of males from Kerguelen is more complex to interpret, especially as most of the tracks were incomplete because of battery failure. However males also positively responded to the net primary production and turbulent waters (EKE and SLA) but with a weaker weight than in Crozet islands. **Trips direction of birds from Kerguelen islands are considerably more variable than in Crozet.** Penguins which foraged to the north and the south encountered waters characterized by very different values of the main studied parameters (Figure 5.4). This observation is supported by the birds identity, found in the mixed model, which is important (bird effect : 26% vs 0.9% in Crozet locality). However, all birds have targeted the Polar Front branch (Figure. 5.3). **In brood**, the main important variable driving the foraging movements is the bathymetry for both localities, followed by the NPP in Kerguelen and bathymetry gradient in Crozet. On the two localities, females used the shelf and shelf break to forage during the first part of the brood stage, before moving toward more pelagic waters. The waters close to Crozet islands were found to be highly productive with important homogeneous values of NPP, in contrast with the Kerguelen situation. This leads to a lack of relationship between the variation of time spent per cell and NPP variable in Crozet.

Body mass differences.

From the beginning to the end of the brooding season, males from Kerguelen were significantly heavier than at Crozet islands ($3656 \pm 334\text{g}$ and $3433 \pm 272\text{g}$ respectively, Mann Withney test, $p < 0.05$). Before their departure at sea, incubating females have the same body mass at Crozet than at Kerguelen ($2971 \pm 386\text{g}$ and $2779 \pm 184\text{g}$, respectively, Mann Whitney test: $W=18.5$, $p=0.48$). The same trend was observed during the brooding period (Crozet: $3747 \pm 366\text{g}$, Kerguelen: $3713 \pm 318\text{g}$) indicating that the lost of weight was similar whatever the locality (Figure 5.6).

Diet variations.

On the two localities, a diet shift in relation to the timing of the season was observed. Thus the crustaceans part decreases and the myctophids part increased. Interestingly, the proportions of the 2 prey categories were also similar. The main species found in the bulk were the same between the two localities indicating penguins have the same diet composition. On Crozet islands, Macaroni penguins feed on a higher proportion of myctophids fish in brooding (17.5%) than during the incubation stage (8.5%) and this trend was similar for Kerguelen birds (5.9 to 25.1%, Table 5.2). Macaroni penguin diving depth at night do not encompass the myctophids depth range (Duhamel 1998). Thus the catch

of myctophids at this time of the year suggest an efficient foraging activity of macaroni penguins during the dawn and dusk period.

Table 5.2: Diet by reconstituted mass (%). Data were get Ridoux (1994) for Crozet (summer 1980/1981) and our study for Kerguelen data (summer 2011/2012).

Site	Incubation		Brood	
	Crozet	Kerguelen	Crozet	Kerguelen
Crustaceans	88	94	77.5	75
Fish	8.9	6	17.5	25
Cephalopods	3.1	0	1.8	0
<i>Sample size</i>	<i>10</i>	<i>12</i>	<i>10</i>	<i>11</i>

V.4. Discussion

This study provided for the first time the foraging strategies of Macaroni penguins from Kerguelen islands over an entire breeding cycle. The bio-logging data allowed us to better assess the different foraging areas as well as the prospected part of the water column during the incubation, brooding and crèche stage. Coupled with oceanographic data, we also brought new information on the oceanographic parameters of the areas prospected by Macaroni penguins. The analysis of contemporaneous diet and body mass data allowed assessing how Macaroni penguins adjust their foraging behavior in relation to the energetic constraints of the breeding cycle.

Foraging strategies in Kerguelen islands.

During the incubation stage, males performed long trips directed eastward of at least 500km. They travelled in pelagic waters with variable oceanographic conditions (Figure 5.1, 5.3). The response of birds to the oceanographic variables is complex since the bird weight (random effect) in the relationships is high (26%) indicating that each bird responded a few differently to the oceanographic features. Although the productive area located close to the colony seems to be harvested, all birds have followed their tracks to the Polar Front characterized by mesoscale and sub-mesoscale structures (eddies, filaments) aggregating patches of resources for top predators (Kostianoy et al. 2003, Pakhomov & McQuaid 1994, Riandey et al. 2005, Landry et al. 2008, Moore & Abott 2002).

During the brood stage, females foraged on areas located north-north east, mainly on the shelf before going further and further on the shelf break, without exceed 150km (Figure 5.1). Their foraging area is considerably smaller than males in incubation indicating that the available stock of resources close to the islands must be high in this period since they have to regularly feed the chicks to ensure its survival.

Each year, a bloom is observed over the Kerguelen plateau, developing from the beginning of November to late January (Mongin et al. 2008) with a peak in mid December, when the brood stage starts. As observed in Crozet islands (Paper 2), there is a good matchtime between the resources availability and the energetic requirements of Macaroni penguins, suggesting that their phenology could have been selected through natural selection process, promoting the breeding success of partners who began the breeding season on the beginning of November. In this period, females may take advantage of the abundant stocks of *T.gaudichaudii*, followed by *Euphausia vallentini* on coastal waters (zone 1, Figure 5.11). These two organisms, carnivorous and grazer, respectively, are considerably advantaged directly or indirectly by the phytoplankton bloom growth over the plateau (Bocher et al. 2001, Bost et al. 1994, Koubbi 1992, Pakhomov 1994).

During the brood stage, females increased their foraging range up to the shelf break characterized by deeper mixed layer unfavourable to the phytoplankton growth (Zone 2, figure 5.11). In this area, there is a northward intrusion of cold Antarctic surface waters along the coast of the Kerguelen Plateau, constituting a bio-geographical barrier to cool fishes, as myctophids (Guinet et al. 2001). In our study, we have found that brooding birds still mainly feed on macro-zooplankton with however higher proportions of copepods (38% *T.gaudichaudii*) and myctophids fish (26% *K. anderssoni*) than in incubation. We suggest that females foraged to the shelf break to increase the proportion of oil-rich myctophids in their diet. These fishes are more nutritive than crustaceans and could be a response of females to the higher energetic requirement of the period (Cherel & Ridoux 1992).

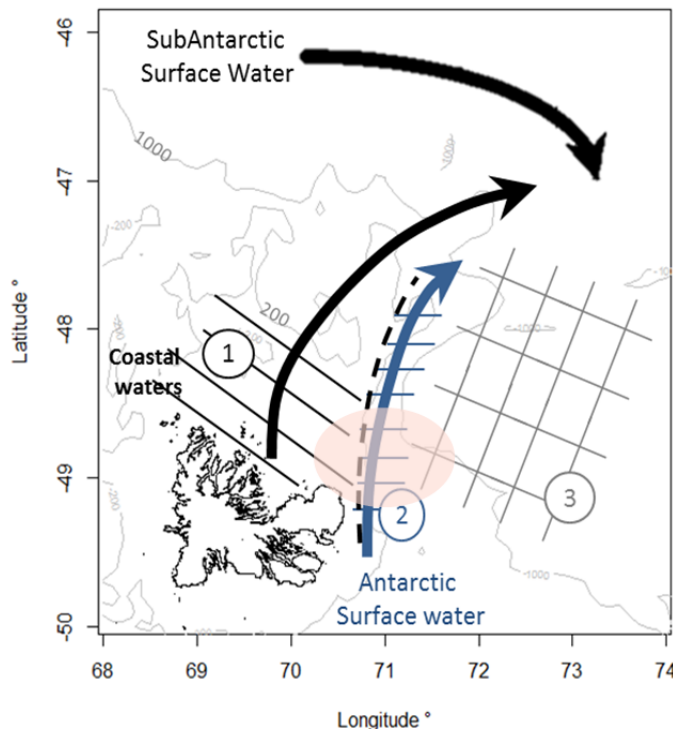


Figure 5.11: Schematic illustration of the circulation of the surface waters northeast of the islands, adapted from Blain *et al.* (2001). Pink area: foraging locations of brooding females. The dotted line is the estimated location of the shelf-break front. The hatched areas show the different biogeochemical systems: Zone 1: High-iron low-biomass case ; Zone2: unfavorable light mixing regime for phytoplankton growth. Zone3: High-iron high-biomass case. Grey lines indicate the 200 and 1000m isobaths.

During the crèche stage, both females and males foraged in the zone 3 located in offshore waters (Figure 5.11). Crèche is a period of high energy expenditure for Macaroni penguins (Green et al. 2009b). In our study, females doubled their foraging range in contrast with the brooding period. During this stage, females more invest themselves in chick feeding since females deliver more meals (59%) than males (41%, Barlow & Croxall 2002b). In contrast, all males equipped before the 10th January have been immediately farther (~400km) before performing shorter trips in late January. These long trips exhibited in crèche seem to be species-foraging strategy in order to build-up the body reserves after the long fasting period. We do not have data on their diet in crèche. However, it has been observed males followed a very similar path than King penguins, foraging to the southeast up to 300 km from their colony, mainly along the eastern edge of the shelf (Charrassin et al. 2002). On this area, the phytoplankton biomass is higher and could be improved by a cold tongue at 100m flow north-westward along the shelf break originating from the south (Park et al. 1998, Charrassin et al. 2002, 2004). The shallow mixed layer (~100m) may provide favorable light-mixing regime to the phytoplankton growth and be attractive to upper trophic levels, as myctophids.

Inter-population comparison.

Overall, during **incubation**, macaroni from the 2 localities rely on **turbulent water masses**, characterized by an higher primary productivity. During the **brood** stage, the diving behavior and effort were broadly the same than during incubation. The main important variable driving the foraging movements of the provisioning females was the **bathymetry** for both localities. However females from Crozet performed much more short trips than the Kerguelen birds. This unexpected result can be related to proximal waters found to be highly productive at a closer distance than at Kerguelen. The cost of travelling are lower for females of Crozet which thus can invest more energy in the diving effort suggesting that their environment is more favorable.

During these shorts trips, the Crozet females foraged however harder in terms of diving effort but birds from Kerguelen dove deeper or at the same depth and always spend higher time at the bottom phase (Table 5.1, Figure 5.10). For a same depth, this suggests that diving behavior of females from Crozet is **less optimal** than in Kerguelen (Houston and Carbone 1992). Otherwise, the number of wiggles is more important in Kerguelen suggesting a better foraging success. Thus, the less optimal behavior could be related to a more dispersive behavior of prey schools in Crozet waters forcing birds to forage in another patch (Watanabe et al. 2014). However, wiggles are not completely representative of foraging success. The study of prey behaviour, dives profiles and prey capture attempts, using for example accelerometers and acoustic methods, could be helpful to understand if the prey behaviour and foraging success differ between the two localities (Pichegru et al. 2011, Watanabe et al. 2014).

Crèching males from Crozet strongly depend to either the SAF, either the Polar Front located 400km south of the colony. In Kerguelen, males display the same strategies than in incubation with long foraging trips southeastward following the shelf break. The higher travelled distance per day could however indicate that the prey distribution is more patchily in Kerguelen water. The lower latitude of Kerguelen islands and the intrusion of cold tongue along the shelf break could favor the presence of cool fishes groups, as myctophids, on the Kerguelen plateau (Hulley 1981, Charrassin et al. 2002). Moreover, the vertical distribution of myctophids is strongly constrained by the waters temperatures, and so the latitude. The vertical distribution varies from 50 and 150 south of the PF to 1000m near the Subtropical Convergence (Hulley 1981). Thus the Kerguelen plateau appears to be highly favorable for *K. anderssoni*, living in the upper offshore water layers (0–200 m) during the day, at depths reachable to Macaroni penguins (Duhamel et al. 2000). The feeding bulk of Macaroni penguins from Kerguelen contains slightly more myctophids (Table 5.2), we can hypothesize that more myctophids could be more accessible in Kerguelen waters than in Crozet waters. The accessibility to more nutritive preys could compensate the higher travelling cost of females, and explain the strong similarities in weight variations.

In the two localities, the females adjusted their diet in relation to the greater energetic needs of chick rearing by increasing the consumption of highly calorific myctophid fish. The trend in body mass change was the same for brooding females provisioning chicks whatever the locality. This strongly suggests that body mass change was an adaptive response to the energetic constraint faced by provisioning females at this critical stage (Salamolard & Weimerskirch 1993, Creswell et al. 2007). Comparing to other studied localities, the mass of the Crozet birds was quite low at the onset of laying. This may suggest a decrease in the body condition of breeders at their return from their migration grounds. A decrease of body condition of rockhopper penguins have been recently pointed out at Marion Island (Crawford et al. 2008). In parallel, long term studies have shown a decrease in population and it has been demonstrated that body condition at the beginning of breeding season strongly influences the breeding success (Chastel et al. 1995, Tveraa et al. 1997, Robinson et al. 2005). The low body mass at the onset of laying highlight the needs to estimate Macaroni penguins population effective in Crozet islands to know if similar process are occurring.

CHAPITRE VI

GENERAL DISCUSSION AND FUTURE RESEARCH



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Les travaux réalisés au cours de cette thèse ont permis de caractériser de manière détaillée les stratégies de recherche alimentaire du gorfou macaroni en période de reproduction dans deux sites d'importance majeure pour l'espèce. Les comptages réalisés au début des années 1980 placent Kerguelen et Crozet parmi les plus grandes populations de gorfou macaroni à l'échelle mondiale. Jusqu'à présent, les connaissances sur leur écologie alimentaire avaient concerné leur régime alimentaire, leur niveau trophique (Ridoux 1994, Cherel et al 2007), leurs migrations hivernales et post-mue (Thiebot, Cherel, et al. 2011a, Thiebot et al. 2013, 2014) et de manière extrêmement limitée leur comportement de recherche alimentaire (Sato 2004, Thiebot et al. 2011). Le comportement alimentaire en période de la reproduction restait donc encore très largement méconnu. Cette lacune était d'autant plus préjudiciable que cette espèce est un des principaux consommateurs aviens (en termes de biomasse, Brooke 2004) et que l'écologie hors période de reproduction (hiver, pré-mue) avait pu être bien documentée malgré la difficulté d'étude (Thiebot et al. 2013, Bost et al. 2009).

Cette étude a tout d'abord permis de combler un manque de connaissances importantes dans le panel des stratégies d'approvisionnement de l'espèce. Au-delà des résultats liés à l'écologie site-spécifique de l'espèce, elle a réussi aussi à mieux cerner les facteurs intrinsèques versus extrinsèques de la plasticité phénotypique dans l'approvisionnement alimentaire chez ce prédateur pélagique. A la suite d'une synthèse des résultats, nous tâcherons de replacer l'ensemble des informations obtenues dans un contexte écologique plus large. Des nouvelles pistes de réflexion et perspectives de recherche seront proposées à l'issue de cette discussion.

VI.1. Stratégies de recherche alimentaire des gorfous macaroni dans l'Océan Austral

1.1. Synthèse des résultats obtenus à Crozet et Kerguelen

En nous appuyant sur les trois articles produits lors de cette thèse, nos travaux ont montré que :

- i) **Entre les sites**, la distribution des gorfous en mer est contrastée, en réponse à des patrons de productivité primaire localement différents. Les caractéristiques physiques des structures visitées restent quant à elles similaires ;
- ii) **Au sein de chaque site**, la même variation de durée et de rayon des voyages d'approvisionnement alimentaire est retrouvée entre les stades de reproduction (incubation, élevage du poussin, et crèche) chez les femelles d'une part, et les mâles d'autre part ;
- iii) **Entre les sexes**, les stratégies d'approvisionnement diffèrent d'un stade reproducteur à l'autre, conformément aux contraintes imposées par la reproduction ;

- iv) **Au sein de chaque sexe, le degré de variabilité** des comportements de recherche alimentaire est plus important chez les mâles que chez les femelles ; il est, de plus, influencé par le site (pour les mâles) et le stade.

Ces résultats mettent en évidence que les stratégies d'approvisionnement observées sont modulées par de multiples facteurs bien précis que nous allons détailler par la suite.

1.1.1. Caractéristiques des traits d'histoire de vie intrinsèques à l'espèce

Au cours du cycle, **les gorfous macaroni partagent des caractéristiques d'histoires de vie communes entre les deux sites, fidèles aux patrons de la reproduction propre à l'espèce, plutôt qu'à des caractéristiques site-spécifiques.**

Ainsi, au début de la période de l'incubation, soit vers la mi-novembre, les mâles vont s'alimenter pendant de longs voyages (~18 jours) dans des **eaux éloignées de la colonie, turbulentes et productives**. Ces dernières sont localisées au sein de grands fronts océanographiques : le **Front Polaire** à Kerguelen et le **Front Subantarctique** à Crozet. Environ 15 à 18 jours plus tard, au retour des mâles, les femelles partent en haute mer dans la même direction mais pendant moins longtemps (~11 jours). A Crozet, les femelles augmentent leur effort d'approvisionnement à la bordure sud du « bloom » phytoplanctonique qui se développe chaque année au nord du plateau, comme nous avons pu le vérifier. Au cours des 3 saisons étudiées, il est intéressant de noter qu'à partir de la période où les mâles étaient en mer, le « bloom » se développe et migre vers le sud : ce rapprochement semble donc très favorable aux femelles qui ciblent ce « bloom » (Figure 4.3, Chapitre IV).

Elevage. Les femelles reviennent aux alentours de la mi-décembre (Crozet : Stahl et al. 1985, Kerguelen : Camprasse et al. *in prep*), soit juste après l'éclosion des poussins. Tandis que le mâle jeûne et garde le poussin pendant près de 3 semaines, les femelles se chargent de l'approvisionnement du poussin pendant tout l'élevage et le début de la période de crèche. Le poussin, très petit à l'éclosion (~116g, Williams 1995), nécessite un nourrissage très fréquent jusqu'à sa mise en crèche, limitant ainsi les femelles dans leur rayon de déplacement. Un tel nourrissage régulier est aussi observé chez d'autres manchots du genre *Eudyptes* où les femelles se chargent seules de l'approvisionnement (Williams 1995). Chez d'autres espèces, plus néritiques (manchot papou) ou pélagiques (manchot royal), les retours à terre du parent parti en mer sont espacés de 1 à 2 jours (papou) ou de 6 à 15 jours (manchot royal) (Bost & Jouventin 1991, Bost et al. 2013) ; chez ces espèces, le parent qui couve a la capacité de régurgiter de la nourriture stockée dans son estomac, parfois jusqu'à 3 semaines (manchot royal, Gauthier-Clerc et al. 2000). Sur les deux sites, **les femelles de gorfou macaroni réalisent des trajets en mer, courts**, restreints aux zones du **plateau et du talus** respectifs des îles.

Crèche. Lors de la mise en crèche du poussin, (généralement autour du 9 janvier), les femelles partent plus loin et plus longtemps qu'en phase d'élevage, sur les deux sites. En parallèle, **leur masse diminue peu pendant cette période**, indicateur d'un effort d'approvisionnement compatible avec les besoins intrinsèques de la femelle et du poussin à ce stade (cette étude, Green et al. 2007).

De manière cohérente, une variation dans la composition du régime alimentaire des femelles a été observée entre les phases d'incubation et d'élevage, sur les deux sites. La part de crustacés majoritaire au début d'incubation (*Euphausia vallentini*, *Themisto gaudichaudii*) diminue au profit de l'augmentation de la proportion de poissons riches en lipides, les myctophidés (dont principalement *Krefftichtys andersonni*) (Article 3, Ridoux 1994). L'éloignement à la côte correspond également ainsi à ce changement de régime, les myctophidés se trouvant dans l'Océan Austral en plus grandes concentrations loin des îles, dans des eaux plus profondes (Perissinotto & McQuaid 1992, Bedford et al. 2015).

En phase de crèche, les mâles réalisent des trajets très longs dirigés vers des eaux turbulentes du Front Polaire à Kerguelen. Les stratégies sont plus variables à Crozet, avec deux grandes directions observées, vers le nord en direction du Front Subantarctique et vers le sud en direction du Front Polaire. La durée élevée de ces trajets semble liée au besoin des mâles de reconstituer leurs réserves corporelles amoindries après ~25 jours de jeûne (Green et al. 2009). De manière cohérente, nous avons observé une prise importante de masse chez les mâles à Crozet au cours du mois de janvier (+33%), confirmant ainsi le bénéfice potentiellement élevé pour ces prédateurs d'exploiter de tels fronts océaniques, connus pour leur forte productivité biologique (Lubimova et al. 1987, Pakhomov et al. 1994, Froneman & Pakhomov 1998).

1.1.2. Variations dans l'effort d'approvisionnement entre les sites

Des différences majeures entre les deux sites

Lors de la recherche alimentaire, **tout organisme serait avantage à optimiser ses déplacements**, c'est à réduire les coûts de transit et maximiser le temps alloué à l'approvisionnement (herbivore) ou la recherche des proies (prédateur : poursuite, capture, ingestion ; (Orians & Pearson 1979, Stephens & Krebs 1986). Au cours du cycle reproducteur, les gorfous se comportent en "*central place forager*", d'autant plus pendant l'élevage en raison du besoin fréquent de revenir à la colonie. La proximité de zones favorables à leur alimentation est donc cruciale. On s'attend ainsi à ce que les stratégies d'approvisionnement aient sélectionné des comportements permettant de minimiser les coûts de transport vers les sites favorables (Ydenberg et al. 1994). Or, au-delà des similarités comportementales

relatives aux stratégies de reproduction de l'espèce, nous avons mis en avant au cours de cette étude **des différences majeures** entre les sites.

1) Entre les deux localités, les oiseaux présentent de fortes différences d'éloignement à la colonie. **Les distances parcourues (par jour, ou totales)** sont toujours nettement supérieures à Kerguelen, pour un stade reproducteur et un sexe donnés (Chapitre 5).

2) En parallèle, l'effort de prospection alimentaire, indiqué par la fréquence de **plongée** par heure (Boyd et al. 1994), est toujours supérieur à Crozet quel que soit le stade reproducteur. Toutefois, les gorfous de Kerguelen plongent soit à la même profondeur, soit plus profondément (en incubation, cf. Chapitre V), mais passent toujours plus de temps au fond des plongées. Le **succès de chasse**, indiqué par le nombre d'ondulations (*wiggles*, Bost et al. 2007) par plongée est aussi plus **important** à Kerguelen (Chapitre V). A profondeur égale, les gorfous de Crozet auraient donc un comportement, **à l'échelle des plongées**, moins optimal car ils passent moins de temps au fond.

A l'échelle des voyages cependant, il semblerait que les gorfous macaroni prospectent dans des couches de proies moins dispersées et plus concentrées qu'à Kerguelen, nécessitant des déplacements horizontaux moins importants et leur permettant de réaliser plus de plongées successives par heure (Boyd et al. 1994).

Ainsi, à l'échelle des voyages, nos résultats suggèrent ainsi que **l'environnement océanique de Crozet serait *a priori* plus favorable pour les gorfous que celui de Kerguelen. Ceci en raison de i) des zones d'alimentations plus proches des points centraux (colonie et surface), et ii) un effort d'approvisionnement (fréquence de plongées) plus important à Crozet, pouvant indiquer une plus disponibilité localisée de proies plus importante.**

3) Cependant, cet avantage ne semble pas aussi évident puisque les **gains et pertes de masses** associées à chaque stade des deux sexes ont été particulièrement similaires entre les deux localités, pour les saisons étudiées. Des données manquent pour confirmer ces résultats (notamment au retour des mâles de leur 1^{er} trajet en mer à Crozet et l'évolution de la masse en crèche à Kerguelen). Cependant, s'il s'avère qu'elles soient bien identiques, ceci indiquerait que ces deux populations très importantes arrivent à extraire une quantité d'énergie suffisante des eaux océaniques au cours du cycle, sans désavantage marqué dans l'une ou l'autre localité.

Ajustement ou environnement réellement plus favorable ?

A Kerguelen, les coûts de déplacement pour les gorfous semblent donc plus importants puisqu'ils vont plus loin, et (en incubation) doivent plonger plus profond. Deux autres causes pourraient expliquer comment les gorfous de Kerguelen arriveraient à compenser des coûts de transport plus importants :

Ajustement du régime.

Tout d'abord, les gorfous consomment plus de poissons (dont l'apport énergétique est supérieur aux crustacés) en période d'élevage à Kerguelen (25% vs 17.5%). Pour autant, ces estimations n'ont pas été faites pendant la même année (Ridoux 1994, notre étude : 2011/2012, chapitre 5). De plus, les signatures isotopiques des gorfous de Crozet en 2009/2010 suggèrent là aussi un régime alimentaire composé **partiellement** de myctophidés (Article 2). Ces éléments montrent qu'il serait intéressant d'étudier finement les variations du régime alimentaire des gorfous macaroni entre les deux sites. Soit lors d'une même année, ou durant des années contrastées sur le plan climatique pour mieux estimer si une légère variation existe dans la composition alimentaire, pouvant expliquer en termes d'énergie l'apparent paradoxe de rentabilité de chasse pour le gorfou macaroni entre ces deux sites.

Ajustement à l'échelle des plongées.

Par ailleurs, étudier en détail le comportement de plongées est un excellent moyen d'obtenir des informations sur le succès d'approvisionnement (Wilson et al. 2005). Au cours de notre étude, nous avons observé qu'à l'échelle de la plongée, **les gorfous de Kerguelen adoptaient un comportement de plongée apparemment plus optimal que ceux de Crozet.**

En plus de devoir se déplacer vers des zones favorables distantes, les manchots doivent effectuer des compromis entre des périodes passées en surface (où ils n'acquièrent pas de nourriture) et des périodes sous l'eau où ils peuvent s'approvisionner mais sous la contrainte de retours réguliers à la surface pour respirer (Wilson 2010). **Ainsi, les modèles théoriques estiment que les prédateurs plongeurs devraient maximiser la proportion de temps passé à des profondeurs favorables et minimiser les temps de transit (descente, remontée)** (Houston & Carbone 1992, Thompson & Fedak 2001). A Crozet, **les gorfous ne maximisent pas la durée disponible pour prospecter** à l'échelle de la plongée, en restant notamment moins longtemps sous l'eau pour une même profondeur. L'accès aux ressources semble être également moins contraignant puisque que les individus plongent moins profondément (Chapitre V).

La remontée régulière à la surface pourrait également indiquer que les femelles de Crozet font face à une **déplétion locale** à très fine échelle des proies lors de leurs plongées, les incitant à remonter à la surface afin de prospecter plus loin. Ce mécanisme pourrait expliquer pourquoi les femelles ne maximisent pas le temps passé au fond des plongées, ce qui paraît surprenant dans des périodes comme l'élevage où les femelles sont extrêmement sollicitées pour la recherche alimentaire.

Pour cette question, il serait intéressant d'étudier le comportement de fuite des proies (dilution, fuite en profondeur) à fine échelle (Watanabe et al. 2014). De plus si les proies ciblées sont différentes, nous pourrions observer des profils de plongées différents en fonction du degré d'agrégation typiquement différent de ces proies (Tremblay & Cherel 2003, Pichegru et al. 2011).

A l'inverse, les gorfous de Kerguelen semblent dépenser plus d'énergie dans la recherche alimentaire qu'à Crozet. Si ce dernier point s'avère exact, ceci conforterait notre hypothèse que **l'environnement océanique de Crozet serait plus favorable aux gorfous femelles en période de reproduction**.

Cependant, l'absence d'ondulations au sein de plongées ne signifie pas forcément que l'animal n'a pas chassé de proies. Un moyen d'affiner cette approche serait d'équiper des gorfous avec des accéléromètres, et/ou des enregistreurs vidéo miniaturisés pour les plongées en eaux peu profondes (Watanabe & Takahashi 2013). En effet, analyser des signaux d'accélération dans les 3 dimensions permettrait d'obtenir des informations précises sur les succès de chasse de ces prédateurs plongeurs (Viviant et al. 2009, Gallon et al. 2013, Carroll et al. 2014), tout en confirmant visuellement la capture effective de proie et la nature de celle-ci.

1.1.3. Le paradoxe de Crozet

Nous avons montré que **sur le plan de l'effort de prospection alimentaire, l'environnement de Crozet serait *a priori* plus favorable pour les gorfous que celui de Kerguelen en raison de zones d'alimentation plus accessibles aux gorfous à la fois sur le plan vertical et horizontal**.

Ceci semble être un **paradoxe**. Kerguelen est situé dans un environnement océanique très productif, **en raison de la présence conjointe d'un plateau très vaste**, de la proximité du Front Polaire à la Péninsule Courbet et le développement printanier du bloom sur Kerguelen (Figure 5.3). De manière contrastée, l'archipel des îles **Crozet** est bordé d'un plateau de faible étendue (~150km dans sa plus grande dimension) s'ouvrant rapidement sur des eaux profondes à priori moins productives que les plateaux, leurs abords ou les fronts, en raison de leurs propriétés *High Nutrients Low Chlorophyll*. La distance aux structures frontales est également plus importante ici (~350km pour le SAF, 450 km pour le PF) qu'à Kerguelen (moins de 100 km pour le PF).

L'archipel des Crozet est situé à distance comparable entre le Front Subantarctique et le Front Polaire, caractérisés tous les deux par une forte productivité biologique. Cependant, l'abondance relative des euphausiacés semble moins importante au niveau du Front Polaire qu'au niveau du Front Subantarctique ; à l'inverse les quantités d'amphipodes et de poissons sont plus abondantes dans le Front Polaire (Pakhomov et al. 1999).

Les manchots royaux, prédateurs spécialistes des myctophidés (Cherel et Ridoux 1992) ciblent le Front Polaire situé au sud (Bost et al. 2015). Les gorfous étant principalement des consommateurs de crustacés, il est possible que le Front Subantarctique soit plus favorable pour l'accès aux crustacés que le Front Polaire. Ainsi, les résultats des observations des oiseaux en mer réalisées lors de campagnes océanographiques dans les secteurs Sud Indien et Sud Atlantique confirment que le secteur du SAF et aussi du Front Sub-tropical abritent les plus grandes diversités et abondances d'oiseaux marins, particulièrement pour les planctonophages (prions) (Abrams 1985).

- Structure hydrologique et accès contrasté à la ressource

Par ailleurs, l'étude de la structuration verticale des masses d'eau apporte également des éléments de réponse.

La couche de mélange est la couche superficielle de l'océan (ou eaux de surface) qui est située au-dessus de la **thermocline**. La thermocline sépare les eaux superficielles des eaux froides d'hiver (eaux d'hiver) et est considérée comme l'un des gradients physico-chimiques les plus importants de l'océan. Ses caractéristiques (changement brusque de température) constituent une barrière importante à la distribution verticale des organismes marins, tels que les myctophidés et le macro-zooplankton (Hulley 1981, Koslov et al. 1991, Perissinotto & McQuaid 1992, Pakhomov et al. 1996). Cette structure a un fort potentiel d'agrégation des proies et est ainsi largement utilisée par les prédateurs plongeurs comme structure océanographique favorable à leur approvisionnement, et ce, de manière prédictible (Boyd & Arnbom 1991, Charrassin & Bost 2001, Biuw et al. 2007, Ropert-Coudert et al. 2009, Scheffer et al. 2012, 2016).

Au nord des îles Crozet (43 et 46°S), le plus faible brassage des eaux de surface induit par des vents moins forts, mais également une augmentation de température liée à la latitude favorise une stratification plus importante des eaux. En conséquence, la couche de mélange est située environ à 60m, ce qui est favorable au développement phytoplanctonique à une profondeur réduite (Venables et al. 2007), et donc accessible pour les gorfous à des eaux modérément profondes.

Au sud de l'île, l'action du vent est plus importante, la couche de mélange plus profonde (~100m) et le régime de productivité dans les eaux superficielles est comparable aux eaux *HNLC* trouvées entre les deux fronts limitrophes de la Zone Polaire Frontale (Banse 1996, Moore, Abbott, et al. 1999, Venables et al. 2007).

A Kerguelen, la couche de mélange située sur le Plateau est plus profonde qu'à Crozet (80-90m, (Roquet et al. 2009). **Ainsi il est très probable que la distribution verticale des euphausiacées soit plus profonde à Kerguelen qu'à Crozet, rendant ainsi la ressource moins accessible pour les gorfous, les conduisant à plonger plus profondément.**

La localisation des îles Crozet, situées à équidistance entre le Front Subantarctique et le Front Polaire, semble donc conférer un avantage aux gorfous macaroni. Les individus ont en effet accès à deux structures ayant des compositions en macro-zooplankton et myctophidés différentes, permettant aux gorfous de cibler l'une ou l'autre structure en fonction de leurs besoins énergétiques. La profondeur de la couche de mélange semble être un facteur très important dans la modulation de l'effort de prospection alimentaire qui mériterait d'être plus amplement étudié pour cette espèce.

1.2. Paramètres océanographiques « clés » des habitats alimentaires utilisés au cours de la reproduction : comparaison des stratégies alimentaires à l'échelle de l'aire de répartition

Selon les espèces, les oiseaux marins présentent un certain degré de plasticité phénotypique leur permettant de palier à l'hétérogénéité de l'environnement et de la distribution des ressources selon les contraintes phylogénétiques (Bost 1991). Cette plasticité peut s'observer entre les différentes phases du cycle annuel où les demandes énergétiques diffèrent (reproduction, mue, migration). Par exemple, les manchots royaux sont connus pour cibler des eaux plus profondes en hiver en raison d'un approfondissement de la thermocline (Charrassin & Bost 2001). Cette plasticité comportementale s'observe également lors de variations interannuelles des conditions environnementales qui peuvent considérablement modifier la localisation géographique des zones d'alimentation (Pinaud et al. 2005, Bost et al. 2015). Dans le même principe, les **conditions régionales** peuvent affecter différemment les populations d'une espèce. Ainsi, deux colonies évoluant dans des environnements contrastés peuvent présenter des stratégies de recherche alimentaire bien différentes. Ces variations ne s'observent pas forcément sur les capacités intrinsèques propres à l'individu (vitesse de nage par exemple), mais plus sur des stratégies globales d'alimentation observables à l'échelle des sites colonisés. Par exemple, la distance totale parcourue ou l'éloignement maximal, l'orientation des voyages, ou encore le degré de variabilité interindividuel peut différer d'une colonie à une autre, aussi bien chez des prédateurs néritiques que pélagiques (*e.g.* Hamer et al. 2001, Watanuki et al. 2002, Lescroël & Bost 2005, Thiebot et al. 2011, 2014). Le régime alimentaire peut également être modifié entre populations (Bost & Jouventin 1990b, Chiaradia et al. 2012).

Le premier facteur écologique pouvant entraîner de telles différences semble être la capacité d'un environnement à fournir des ressources et les rendre accessibles aux prédateurs marins. Ceci est hautement dépendant de la présence ou non de structures océanographiques productives à proximité des colonies (Weimerskirch 2007).

La distribution des gorfous macaroni est quasi-circumpolaire, des côtes du Chili (à l'ouest) à l'île Macquarie (à l'est, sous la forme *E.schlegeli* Christidis and Boles 1994) et de la Péninsule Antarctique (au sud : 65°S) aux îles Crozet au nord (46°S). En conséquence, la vaste répartition (à la fois en latitude et en longitude) de l'espèce expose les colonies à **divers environnements océaniques localement contrastés**. Comme il a déjà été suggéré dans de précédentes études, il était donc attendu d'observer une certaine variation des comportements de recherche alimentaire entre les différentes îles hôtes de l'espèce (Pichegru et al. 2011).

Les localités ayant fait l'objet du plus grand nombre d'études sur l'écologie en mer du gorfou Macaroni sont actuellement celles de la Géorgie du Sud (>1.000.000 couples) et l'île Heard (<1.000.000). Nous avons réalisé un tableau de synthèse regroupant les caractéristiques générales des comportements d'approvisionnements observés dans ces localités en plus des îles Kerguelen et Crozet (Tableau 6.1).

Page suivante:

Table 6.1: Main foraging trip parameters and oceanographic features used by Macaroni penguins from 4 populations according to the breeding stage and gender. Column "variation": increasing or decreasing of both of the of parameters values on the latitudinal gradient, from Crozet to South Georgia. Missing values are indicated by a dash. PF: Polar Front. SAF: SubAntarctic Front. MEB: Maurice Ewing Bank. GB:Georgia Bassin.

VI. DISCUSSION: FORAGING STRATEGIES IN SOUTHERN OCEAN

Stade	Sexe	Foraging parameter		Main colonies on a latitudinal gradient : North - South				Variation
				Crozet	Kerguelen	Heard	South Georgia	
Incubation	Males	Maximal range	km	350 ± 28	530 ± 121	-	572 (510–640)	↗
		Duration	day	18 ± 2	~18	-	~11 to 21	≈
		Total travelled distance	km	1105 ± 135	~ 1400	-	1830 (1550–2160)	↗
		Travel speed	km.h ⁻¹	2.5 ± 1.4 ; GPS	3.2 ± 1.9 ; GPS - PTT	-	4.2 (3.6–5.1) ; PTT	↗
		Targeted features		dynamic waters in SAF	dynamic waters - PF	-	dynamic waters ; reach MEB & PFZ	
		in		Offshore	Kerguelen plateau	-	Georgia Basin north PF	
	Females	Maximal range	km	270 ± 65	-	-	376 (251–486)	↗
		Duration	day	12 ± 2	-	-	12.5 ± 2	≈
		Total travelled distance	km	830 ± 240		-	1240 (974–1608)	↗
		Travel speed	km.h ⁻¹	2.0 ± 1.3 ; GPS-PTT	-	-	4.4 (3.3–5.6) ; PTT	↗
		Targeted features		north phytoplanktonic bloom	toward dynamic waters - PF	-	dynamic waters ; south and north PF	
		in		Offshore waters	Kerguelen plateau	-	Georgia Basin	
Brood	Females	Maximal range	km	32 ± 18	82 ± 41	47 ± 40	38 ± 22	↗↘
		Duration	day	1 ± 1	2 ± 1	0.5 to 1.5	0.6 ± 0.5	↗↘
		Total travelled distance	km	80 ± 50	180 ± 50	110 ± 7	88 ± 71	↗↘
		Travel speed	km.h ⁻¹	2.7 ± 0.9 ; GPS-PTT	3.4 ± 1.8 ; GPS	-		↗
		Targeted features		shelf - slope	shelf - slope	shelf - slope	shelf - slope	
		in		Crozet plateau	Kerguelen plateau	Kerguelen plateau	Georgia Basin south PF	
Crèche	Females	Maximal range	km	80 ± 36	180 ± 45	170 ± 100	59.3 (<80)	↗↘
		Duration	day	3 ± 1	6 ± 1	5 to 8	~2 (<3)	↗↘
		Total travelled distance	km	185 ± 80	420 ± 70	660 ± 140	~200	↗↘
		Travel speed	km.h ⁻¹	2.6 ± 1.6 ; GPS-PTT	3.0 ± 2.0 ; PTT	-	3.5 (0.4–6.9) ; PTT	↗
		Targeted features		shelf - slope - offshore	shelf - slope	toward Fawn Trough Current ?	shelf - slope - beyond	
		in		Crozet plateau	Kerguelen plateau	Offshore waters	Georgia Basin south PF	
	Males	Maximal range	km	245 ± 80	320 ± 187	-	63 (<200)	↗↘
		Duration	day	9 ± 5	17 ± 11	~12	~2.5 (<4)	↗↘
		Total travelled distance	km	485 ± 225	787 ± 443	-	~200	↗↘
		Travel speed	km.h ⁻¹	2.6 ± 1.5 ; GPS-PTT	2.1 ± 1.8 ; PTT	-	3.5 (0.4–6.9) ; PTT	
		Targeted features		Stay in PFZ - toward SAF or PF	shelf - slope - cold water tongue	toward Fawn Trough Current ?	shelf - slope - beyond	
		in		Offshore waters	Kerguelen plateau	Offshore waters	Georgia Basin south PF	
Authors		Bon <i>et al.</i> . 2015 ; this study : Paper A2 - Paper A3; Bost, <i>pers. com</i> for females tracks in incubation at Kerguelen islands			Green <i>et al.</i> . 1998; Deagle <i>et al.</i> 2008; Bedford <i>et al.</i> .2015		Barlow and Croxall 2002b; Green <i>et al.</i> . 2005; Trathan <i>et al.</i> . 2006; Waluda <i>et al.</i> 2009	

1.2.1. Utilisation des structures frontales et abords de plateau

La première observation frappante ressortant de cette synthèse est que mâles et femelles ciblent les mêmes types de structure au cours du cycle, quelle que soit la localité.

En incubation, les mâles de Géorgie du Sud, Kerguelen et Crozet ont ciblé des **eaux dynamiques** localisées dans la **Zone Polaire Frontale**. Les femelles de Kerguelen adoptent aussi ce comportement ; à l'inverse, les femelles de Crozet profitent du rapprochement vers la colonie du bloom phytoplanctonique. Nous y reviendrons plus tard.

Malgré la distance à parcourir pour les atteindre, la durée des voyages vers ces eaux dynamique est **similaire entre les populations** (sur chaque site : ~18jours pour les mâles, et ~12 jours pour les femelles). Cependant, les distances à parcourir pour atteindre les zones d'alimentation varient considérablement (*e.g.* de 350km à Crozet à 570km en Géorgie du Sud pour les mâles). Il s'avère également que les populations qui s'alimentent plus loin ont des vitesses moyennes de déplacement plus importantes au vu des données du *biologging*. Ces observations montrent qu'en incubation, les gorfous macaroni semblent donc extrêmement **dépendants de la productivité associée aux zones frontale pour subvenir à leur besoin et notamment le Front Subantarctique et le Front Polaire**.

Après l'éclosion, l'ensemble des femelles s'alimentent sur le plateau et le talus au cours de voyages courts. **Les voyages les plus longs sont observés chez les oiseaux de Kerguelen**. De la même manière qu'en incubation, lorsque l'éloignement à la colonie augmente, les vitesses de déplacement augmentent aussi. Ainsi, dans des environnements où la ressource est plus éloignée, les adultes ajustent leur comportement ce qui leur permet de garder la même phénologie de leur cycle reproducteur, centré sur l'été austral. Ceci met de nouveau en avant le fait que le comportement de recherche alimentaire de cette espèce est profondément modulé par les contraintes de la reproduction et la nécessité de réussir sa reproduction en une courte période. Dans les TAAF, la perte de poids est faible pendant l'élevage (~3%), en comparaison avec la Géorgie du Sud (16%, Croxall, 1984). En revanche, il est particulièrement frappant de noter qu'à partir des masses initiales différentes, les masses à la fin de l'élevage sont particulièrement proches pour les 3 sites à la fin de l'élevage (3350g et 3550g (cette étude) et 3700g (Croxall, 1984). **Ceci soutient l'hypothèse d'une perte de masse adaptative chez les femelles pendant la saison de reproduction** (Cresswell et al. 2007). Les pertes de masse adaptatives sont des stratégies communes observées chez les oiseaux marins pour faciliter les déplacements. Par exemple, la perte de masse chez les guillemots permet de diminuer la charge alaire et réduire de fait l'énergie nécessaire pour voler au cours de la reproduction (Croll et al. 1991).

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En crèche, les patrons de distribution sont similaires pour les femelles entre les sites, au contraire des mâles. **Les femelles ciblent les abords de plateau** puis des **eaux plus océaniques** de celles exploitées pendant l'élevage, ainsi partent **plus longtemps et plus loin**. Cependant, elles n'atteignent pas de structure frontale, comme en incubation, malgré des directions similaires, vraisemblablement en raison du temps limité imparti pour la recherche des proies. De plus, **les mêmes rapports d'éloignement inter-population** observés en élevage se retrouvent en crèche. **Les populations qui vont le plus loin pendant l'élevage individuel (*brooding period*, Kerguelen et Heard) sont également celles qui vont le plus loin en crèche.** Ceci confirme que la répartition des ressources alimentaires autour des colonies étudiées est probablement différente, comme évoqué dans le chapitre V, induisant des variations dans l'effort de prospection.

Les mâles en crèche montrent des stratégies encore plus variables entre sites que les femelles.

En Géorgie du Sud, tous les mâles effectuent des trajets courts (2 à 3 jours), soit en direction du Front Polaire en restant dans le Bassin de Géorgie à environ 60km des côtes (rayon maximal <200km, aucun gorfou n'atteignant le Front Polaire. A Kerguelen, les individus longent le bord est du Plateau de Kerguelen, voyageant sur de longues distances (~300km) pendant beaucoup plus longtemps (~17 jours). **Enfin à Crozet, les patrons de distribution sont beaucoup plus variables** mais cependant intermédiaires en terme de distance et durée par rapport aux deux autres localités (~9 jours et 250 km). **Les individus de cette population montrent des stratégies diamétralement opposées**, puisque certains vont s'alimenter au sud du Front Subantarctique tandis que d'autres se dirigent vers le Front Polaire.

En crèche, les mâles doivent restaurer leurs réserves après une longue période de jeûne. La variabilité de la durée et des distances parcourues en crèche suggère que la **contrainte de durée des voyages en mer est moins forte** à ce stade du cycle et que chaque individu optimise sa recherche alimentaire propre en fonction de ses besoins intrinsèques et peut-être aussi en fonction de son expérience (Phillips et al. 2005). A l'inverse, la nécessité d'une **reprise de masse** semble être le premier facteur contrôlant leur recherche alimentaire (Green et al. 2007, Chapitre IV).

1.2.2. Influence des courants et de la couche de mélange

Autre localité abritant une population de gorfou macaroni d'importance, l'île Heard est située au nord d'un large sillon profond appelé le fossé de *Fawn Trough*, qui sépare le Plateau de Kerguelen en deux (56°S, 78°E). Ce fossé constitue un véritable **entonnoir** pour le passage de la **quasi-totalité des eaux de l'ACC** trouvées au sud du Front Polaire, soient les eaux du *Fawn Trough Current*, du *Southern Antarctic Circumpolar Current Front* mais également des eaux situées au sud de la Divergence Antarctique (Roquet et al. 2009, Park et al. 2008b). Ces eaux océaniques situées au sud de

l'île de Heard sont **riches en poissons** et intensivement utilisées par les gorfous macaroni en crèche (Bedford et al. 2015).

Une partie de ces eaux froides est transportée le long du talus de *Chun Spur* situé au sud-est de la partie Nord du Plateau. et son écoulement vers le nord est à l'origine de la langue d'eau froide localisée à l'est du Plateau (Charrassin et al. 2004; Park et al. 2008b ; van Wijk et al. 2010). Il est probable que cette advection favorise la concentration d'importantes ressources biotiques, notamment des myctophidés, puisqu'elle est utilisée par de nombreux prédateurs plongeur tels que les otaries à fourrure Antarctique ou les manchots royaux, qui sont spécialistes de ce groupe de proies (Cherel & Ridoux 1992, Bost et al. 2002, Hindell et al. 2011, Charrassin et al. 2004). Nous avons montré dans cette étude que les gorfous macaroni mâles ciblaient également cette langue d'eaux froides en incubation et crèche.

Ces eaux sont associées à de faibles concentrations en chlorophylle *a* mais sont en revanche caractérisées par une **couche de mélange peu profonde** (~80m, Charrassin et al. 2004). Sur le plateau de Kerguelen, la profondeur estimée de cette couche est de 80-90m, et 100 à 110m dans les eaux océaniques (Roquet et al. 2009). La baisse de profondeur de cette couche de mélange sur le Plateau et sur le talus doit très probablement permettre aux prédateurs plongeurs d'accéder à des ressources à plus faibles profondeurs qu'en eaux océaniques, participant de ce fait pour les manchots tels les gorfous macaronis et les manchots royaux à une stratégie de minimisation des coûts de déplacements associés à leur approvisionnement.

1.2.3. Liens avec la productivité primaire

La productivité primaire est un facteur important dans le contrôle de la distribution en mer des gorfous femelles pendant l'élevage et la crèche. Nous avons observé qu'en parallèle du déroulement de la période de reproduction, un « **bloom** » **phytoplanctonique** se développait à proximité des colonies de Kerguelen et Crozet (Chapitre IV et V) et qu'un important chevauchement existait entre le pic de concentration de chlorophylle-*a* et la période d'élevage.

En **Géorgie du Sud**, il s'avère qu'un bloom phytoplanctonique se développe également. La Géorgie du Sud constitue également une barrière importante à l'ACC, de par sa position géographique. Le Front Polaire est dévié au nord de l'île (Moore et al. 1999) tandis que la limite sud du courant circumpolaire (SACCF, Southern ACC Front) passe au sud, remonte en direction du Bassin de Géorgie (*Georgia Basin*) puis reprend sa course vers l'est (Orsi et al. 1995, Thorpe et al. 2002). Cette configuration permet à un bloom de se développer au nord-ouest de l'île dans les eaux très profondes (3500-4000m) du Bassin de Géorgie (Borrione & Schlitzer 2013, Figure 6.1). Le pic saisonnier de ce bloom coïncide également avec la période d'élevage des femelles (10 janvier - 20 Février, Figure 6.1) en Géorgie du Sud.

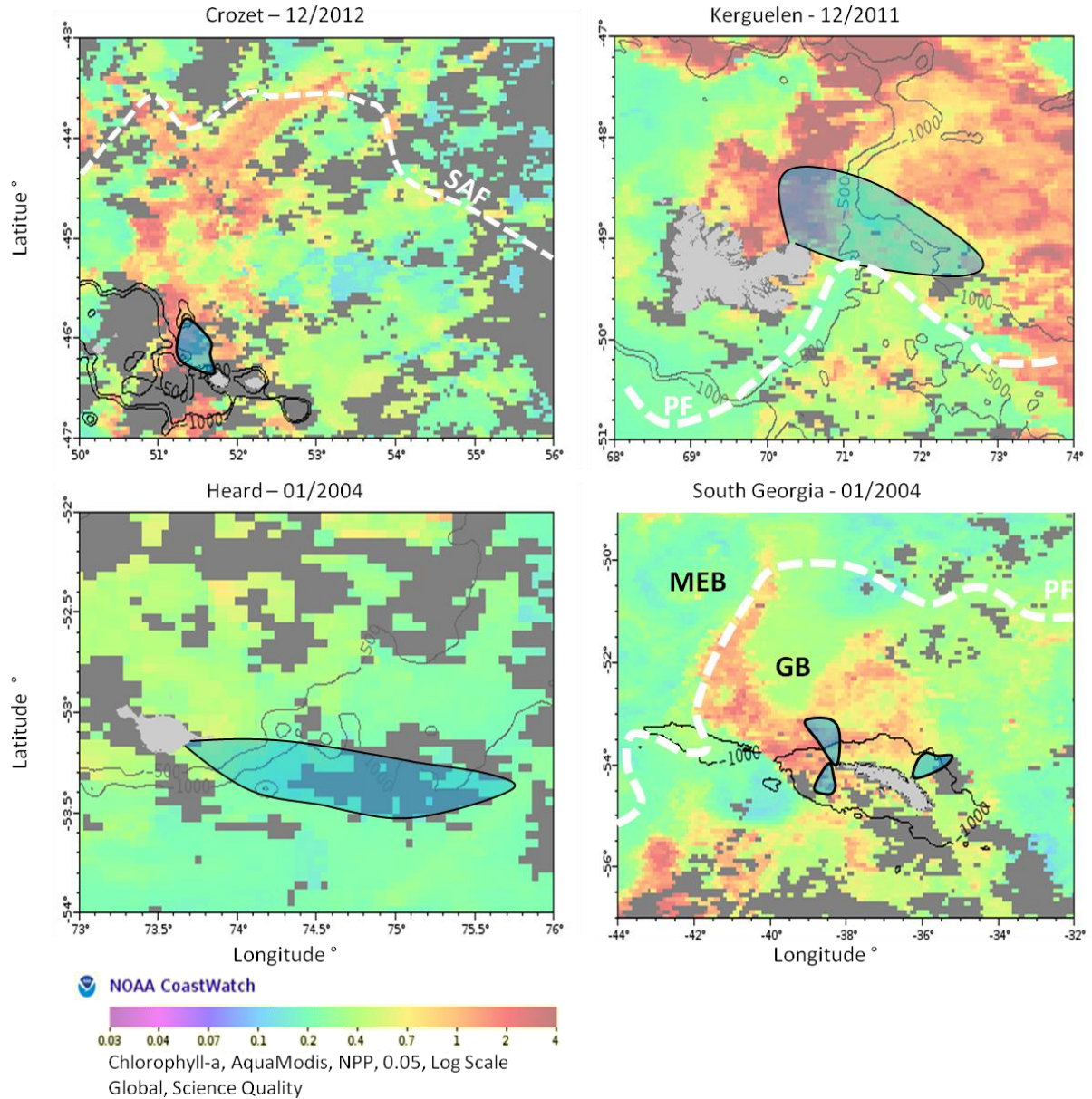


Figure 6.1: Overlap of brooding Macaroni penguins trips (blue) on temporal matched maps of Chlorophyll-a. Chlorophyll-a values were monthly averaged. Tracks data were get from: Crozet: chapter 4. Kerguelen: chapter 5. Heard: Deagle et al. 2008. South Georgia: Trathan et al. 2006; The PF bordure (Polar Front) was defined on the 4°C isotherm. SAF: SubAntarctic Front (8°C). MEB: Maurice Ewing Bank. GB: Georgia Bassin. Black lines indicate the 500 and 1000m isobaths.

A Heard, l'association est beaucoup moins claire, du fait notamment de chaînes trophiques plus complexes qu'en Georgie du sud. Au nord de l'île s'étend le « bloom » sur le Plateau de Kerguelen (Mongin et al. 2008) mais les gorfous n'y vont pas et restent à proximité du plateau au sud de Heard. Nous ne pouvons exclure l'hypothèse que les eaux situées à la limite sud du Plateau soient chargées en zooplancton ayant tiré profit du « bloom » situé plus au nord.

Sur les trois îles, les blooms phytoplanctoniques se développent au minimum depuis début octobre (Venables et al. 2007, Mongin et al. 2008, Borrione & Schlitzer 2013). Il a été observé que les

concentrations de biomasses de zooplancton pouvaient considérablement augmenter sur le Plateau de Kerguelen entre mi-octobre et mi-novembre, à la même période de développement du « bloom », en contraste avec les eaux océaniques où aucune variation n'était observée (Carlotti et al. 2015).

Prédictabilité de la disponibilité de la ressource : aspects évolutifs

Il est très probable que la croissance et l'attraction des organismes brouteurs (krill, copepodes, microzooplancton) soient suffisamment progressives au cours de la croissance du « bloom » (Hosie et al. 2003) sur le Plateau pour permettre à la zone exploitée par les gorfous femelles de devenir particulièrement favorable en période d'élevage et de crèche, ceci de façon prédictible.

Ce couplage de la croissance du bloom et de la période d'élevage que nos résultats mettent en avant correspond bien aux concepts de "Match/Mismatch hypothesis" évoquées par Cushing (1969,1990) où le pic de demande énergétique du prédateur est ajusté sur le pic de disponibilité en proies (revue Durant et al. 2007, Chapitre IV). Il est établi que la période d'élevage du jeune poussin est critique sur le plan des besoins énergétiques pour le gorfou macaroni (Green et al.2007) comme pour beaucoup d'oiseaux marins (Ricklefs 1983). A l'échelle communautaire, d'autres prédateurs marins en période de reproduction ciblent les zones phytoplanctoniques évoquées pendant les mêmes périodes (Weimerskirch et al. 1993, 1997, Charrassin et al. 2002, Lea & Dubroca 2003, Louzao et al. 2011, Weimerskirch et al. 1989).

Sur le plan écologique, **cette relation étroite entre la disponibilité des ressources et la phénologie du cycle reproducteur est caractéristique des milieux saisonniers**. La saisonnalité est plus marquée aux hautes latitudes et se traduit par des variations cycliques de facteurs abiotiques, comme la température, précipitations ou pression de vent qui vont affecter la production biologique (e.g. cycle annuel du zooplankton, Varpe 2012)). La **photopériode** sera ainsi le principal activateur des fonctions reproductrices (via les gonades) des oiseaux (Wingfield et al. 1992, Gwinner 1996).

La variation saisonnière de la photopériode étant fixe, les oiseaux situés en milieu tempéré sont moins plastiques à l'activation des fonctions physiologiques reproductrices que des espèces situées en milieu tropical où la variation de lumière annuelle est plus faible. De plus, au cours du cycle annuel, les oiseaux doivent effectuer différentes activités, dont certaines ne peuvent pas s'effectuer en même temps (par exemple : la mue et la reproduction) en raison d'un coût physiologique trop important. En conséquence, la périodicité de ces activités aurait été sélectionnée à travers l'évolution, notamment sous le joug de compromis entre la disponibilité des ressources, la demande énergétique des activités, et leur valeur sélective (Lack 1968, Perrins 1970, Newton 2008).

La **reproduction** étant l'activité ayant une importante valeur sélective, il apparaît normal que celle-ci soit située temporellement à une période où le succès reproducteur sera maximisé, par une meilleure accessibilité aux ressources, pendant l'élevage des jeunes ou leur émancipation (Lack 1968).

Pour les gorfous macaroni, la **dépense énergétique lors de la recherche alimentaire est maximale lors de la recherche alimentaire pendant la période de reproduction et lors des voyages d'hyperphagie précédant la mue** qui se situent toutes deux en été austral (Green et al. 2009). Des estimations effectuées sur le succès d'approvisionnement (g/min submergé) ont montré que les gorfous macaroni avaient une prise alimentaire supplémentaire lors des voyages d'incubation (~5g.min) et de pré-mue (~7g.min) par rapport à la période d'élevage (~3g.min) (Green et al. 2009). Lors des voyages pré-mue (~12jours), les adultes doivent être capables d'accumuler suffisamment de réserves pour effectuer la mue complètement (~24jours) avant de partir en migration hivernale. La période juste après la mue est celle présentant la plus grande mortalité des adultes chez les manchots (*e.g.* Dann 1991) indiquant de très grandes contraintes physiologiques à cette période.

Cependant, nous pouvons nous demander si la phénologie du gorfou macaroni ne montrerait pas un **compromis évolutif** effectué entre la période du voyage pré-mue, en fin d'été, qui est d'une importance cruciale pour la survie de l'individu et la période de l'élevage du poussin, réalisée avant la mue. Les coûts associés à l'effort d'approvisionnement sont plus importants qu'en reproduction en raison d'une plus grande distance à parcourir pour aller s'alimenter (Green et al. 2009, Thiebot et al. 2014). Ils sont compensés par l'assurance d'acquérir des ressources énergétiquement profitables dans la zone polaire frontale pendant une période où les oiseaux peuvent s'absenter plus longtemps. La chronologie de la période d'élevage serait particulièrement adaptative puisque les distances à parcourir sont réduites en raison d'une proximité des ressources alimentaires, permettant des apports réguliers au poussin. La proximité des ressources en été est certainement un facteur déterminant dans la mise en place de la phénologie des stratégies d'approvisionnement de cette espèce comme l'exemple de Crozet le démontre.

1.2.4. Compétition potentielle à l'échelle interspécifique

Les îles de l'Océan Austral hébergent une **biomasse très importante d'oiseaux marins** jouant un rôle trophique important (environ 400 millions d'individus, Croxall 1984, Brooke 2004) et de nombreux pinnipèdes (Jouventin et al. 1984). Ces espèces sont également considérées comme des prédateurs à place centrale, dépendant des îles pour se reproduire pendant l'été austral (Weimerskirch 2007). Ainsi nous pourrions nous attendre à observer une **forte compétition interspécifique** pour les ressources, particulièrement pendant la période d'élevage des juvéniles où les demandes énergétiques sont importantes (Hamer et al. 2001). Cette situation a été observée en Géorgie du Sud où les gorfous macaroni seraient en compétition directe avec les otaries à fourrure Antarctique pour leur ressource commune, le krill Antarctique *Euphausia superba*. Ce processus serait d'ailleurs considéré comme l'une des causes principales de leur déclin (Trathan et al. 2012).

Dans les TAAF, l'étude des comportements d'approvisionnement chez les prédateurs marins démontre que certains mécanismes de ségrégation spatiaux, temporels ou trophiques se sont mis en place afin de pallier à cette compétition comme observé en Géorgie du Sud (Croxall et al. 1997).

Ainsi, les **otaries à fourrures** s'alimentent en grande partie des myctophidés *Gymnoscopelus nichols*, *G. piabilis*, *Electrona superba* et du poisson des glaces *Champsocephalus gunnari* (Cherel et al. 1997, Guinet et al. 2001) qui sont des espèces différentes de celles ciblées par les gorfous macaroni, indiquant une **ségrégation trophique** importante entre les deux espèces.

Les **manchots royaux** sont également spécialistes des myctophidés, mais s'alimentent essentiellement d'*Electrona superba*, *K. anderssoni* ainsi que de *Protomyctophum tenisoni* (Bost et al. 1997). Le régime alimentaire des royaux qui se recoupe partiellement avec les macaroni sur *K. anderssoni* est compensé par une **ségrégation verticale** des zones d'alimentation. En effet, les manchots royaux plongent à des profondeurs bien plus élevées que les gorfous macaroni en moyenne à 150m, et jusqu'à 400 m (Charrassin et al. 1998, Charrassin, Le Maho, et al. 2002).

Les **manchots papous** quant à eux s'alimentent également de crustacés, essentiellement *E.vallentini* suivi de *T.gaudichaudii* mais aussi de petits poissons néritiques (Bost et al. 1994, Lescroel et al. 2004). La ségrégation avec les gorfous macaroni s'opère sur le plan **spatial et temporel**. En effet, les manchots papous sont côtiers et s'alimentent dans les eaux néritiques. Ils ne s'éloignent rarement pas plus de 50km de la colonie et voyagent en général moins d'une journée (Lescroël & Bost 2005). Sur le plan temporel, le régime alimentaire diffère lors de l'arrivée des gorfous macaroni, avec une augmentation accrue des poissons néritiques consommés (Crozet, Ridoux 1994).

Les **gorfous sauteurs** s'alimentent des mêmes types de proies du macro-zooplankton, *Thysanoessa gregaria* et *E. vallentini*. En revanche, ils plongent à des **profondeurs plus faibles** que celles atteintes par les gorfous macaroni (30-40m) lors de voyages courts effectués sur les plateaux sous-marins (Tremblay & Cherel 2003) et leur cycle reproducteur est décalé de 3 semaines en retard. Ce décalage dans la phénologie joue un rôle considérable : il leur permet d'exploiter les ressources proches du front sub-antarctique lorsque les gorfous macaroni femelles restent cantonnés sur le plateau en élevage. A l'inverse, lors de la crèche, les gorfous sauteurs exploitent le sud du plateau lorsque les macaronis en crèche partent plus au sud dans la zone polaire frontale riche en myctophides (Crozet : Bost et al. *in prep*) .

Ainsi, la variété des stratégies alimentaires des prédateurs marins du sud de l'océan Indien et la gamme des habitats océanographiques à Crozet et Kerguelen permettent donc la coexistence de nombreux prédateurs marins (Ridoux 1994). La **compétition interspécifique** entre les gorfous macaroni et d'autres prédateurs marins dans ces deux écosystèmes existe potentiellement mais est limitée par des mécanismes de ségrégations trophiques et reproducteurs.

1.2.5. Effet « *Ahsmole* » à proximité des colonies

Une caractéristique commune aux gorfous macaroni est l'augmentation de la distance à la colonie pendant l'élevage et la crèche (étude, Barlow et Croxall 2002b, Deagle et al. 2008). Cet éloignement constant peut aussi révéler un processus sous-jacent majeur lié à l'activité de vastes colonies d'oiseaux marins: une **déplétion des ressources** à proximité des colonies (Ashmole 1963).

Plusieurs avantages sont conférés à la reproduction en **colonie**, comme par exemple l'échange potentiel d'informations sur la localisation des ressources, des mécanismes efficaces de défense contre les prédateurs ou l'augmentation du succès reproducteur individuel (Danchin & Wagner 1997, Brown & Brown 2001, Danchin et al. 1998). Cependant, ces regroupements importants de prédateurs sont également associés à des coûts, comme une augmentation de la charge parasitaire (*e.g.* Mangin et al. 2003) et l'augmentation du risque d'infidélité (Moller & Birkhead 1993).

Ces regroupements peuvent également provoquer une **déplétion** des ressources à proximité des colonies en raison d'une importante **compétition intra-spécifique**. Ce processus forcerait les individus à voyager plus loin pour retrouver des ressources, ce qui pourrait de manière ultime limiter leur succès reproducteur et à long terme la taille de population ("*Ashmole halo*", Ahsmole, 1963). Par exemple, en considérant deux colonies de tailles différentes de fous masqués, *Sula dactylatra*, Oppel et al. (2015) ont observé que la plus petite population allait s'alimenter moins loin, dépensait moins d'énergie et avait un meilleur taux de survie du poussin au nid.

Au-delà d'un certain seuil, le temps supplémentaire passé à prospecter sur des zones éloignées peut se refléter dans la fréquence d'approvisionnement du poussin. Ces mécanismes de déplétion des ressources constitueraient également ainsi une partie des pressions de **sélection** à l'origine de la taille de ponte réduite et des taux de croissance plus faible observés chez les oiseaux marins (Lack 1968).

Du fait de l'importance parfois de leurs colonies à l'échelle d'une même localité, il est fort probable que les gorfous macaroni subissent une **déplétion locale** à proximité de la colonie, bien qu'elle ne soit pas de la même intensité entre les différents sites.

En conséquence, les éloignements plus importants entre l'élevage et la crèche dans les sites étudiés de l'Océan Indien seraient la conséquence d'une **compétition intra-spécifique** qui serait d'autant plus importante que les effectifs augmentent. Les **tailles de populations** connues vont dans le sens de cette hypothèse. En Georgie du sud, la distance à la côte des reproducteurs double pratiquement entre la phase de garde et la crèche. En effet, la Géorgie du Sud héberge actuellement environ 1.000.000 de couples après avoir subi un déclin considérable (Crossin et al. 2013). A Kerguelen, la dernière estimation effectuée datant de 1985 estime que la population est de 1.8 million de couples. La distance parcourue entre la phase de garde et la crèche est plus que doublée. A l'inverse de la tendance mondiale, la population de Kerguelen (colonies de la Péninsule Courbet) tend à

augmenter depuis les années 1960 (taux de croissance: 1%, C. Barbraud, Pers. Com). Elle serait donc d'une importance similaire à celle de la Géorgie du Sud.

A Crozet, les dernières estimations datent de 1985 où la population de gorfous macaroni était considérée comme la plus importante au monde (>2.000.000) mais de nouvelles estimations seraient nécessaires.

Par ailleurs, les gorfous macaroni de Géorgie du Sud montrent un patron d'éloignement faible au regard des autres sites et seraient pourtant en compétition directe avec les otaries à fourrures. Ceci suggère que **l'abondance du krill antarctique** en Géorgie du Sud doit être plus importante à proximité des colonies en élevage et en crèche que l'abondance des ressources ciblées par les gorfous macaroni de Kerguelen et Crozet.

La situation à Heard est un cas à part avec la taille de population inférieure à 1.000.000 de couples (Crossin et al. 2013), soit moins qu'en Géorgie, et l'éloignement des gorfous en crèche est plus importante. Une étude plus approfondie serait nécessaire pour connaître les raisons d'un tel éloignement, (compétition inter ou intra spécifique, et/ou disponibilité des ressources moins importantes).

Dans tous les cas, le moyen d'obtenir plus de précisions sur les mécanismes en œuvre serait d'estimer de manière fiable le succès reproducteur et les tailles des colonies étudiées sur le long terme, mais également le degré de proximité d'autres colonies de la même espèce. En effet, la déplétion peut être accentuée en raison d'une compétition inter colonie plus importante, à condition qu'elles s'alimentent sur les mêmes zones géographiques, comme observé chez les mouettes tridactyles ou les manchots Adélie (Ainley et al. 2004, Ford et al. 2007). Il est surtout déterminant d'obtenir des informations sur la dynamique de l'ensemble des colonies de chaque localité, ce qui reste une tâche considérable.

VI.2. Rôle du sexe dans les stratégies de recherche alimentaire

Les **oiseaux marins** sont caractérisés par une **maturité sexuelle tardive, une faible fécondité annuelle, une reproduction itéropare, des soins parentaux partagés et une longévité importante**. Le caractère indispensable d'une coopération entre les partenaires pour garantir le succès reproducteur serait la première raison de la **monogamie** observée chez ce groupe (Lack 1968, Orians 1969).

Les 18 espèces de manchots partagent des caractéristiques communes concernant la période de reproduction. Tous se reproduisent de manière plus ou moins synchrone au sein de chaque site de reproduction (à l'exception des espèces du genre *Spheniscus* : *e.g.* manchot des Galápagos). Les adultes se relaient entre séjours en mer et garde/approvisionnement du poussin et possèdent la capacité de maintenir des périodes longues de jeûne (Ancel et al. 2013). Il est connu que la **fidélité au partenaire** permet d'améliorer le succès reproducteur. Connaître son partenaire permettrait en effet de diminuer les coûts associés à la recherche d'un partenaire, d'un nid et d'avoir une meilleure coordination en raison de la familiarité entre les deux adultes (Bradley et al. 1990).

Chez les manchots, l'échec d'un épisode reproducteur peut considérablement influencer la décision d'un divorce (*review* dans Choudhury 1995) et c'est notamment **la femelle qui initie le plus souvent la séparation**. Dans ce cas là, **la probabilité pour les femelles de retrouver un partenaire la saison suivante est plus élevée** (94%) que chez les mâles (40%, Williams & Croxall 1991, Williams & Rodwell 1992).

En effet, chez les manchots, plusieurs espèces (*Megadyptes antipode*, *Pygoscelis adeliae* et *P.papua*, *Eudyptula minor*, *Eudyptes chrysolophus*) présentent un **sex-ratio non équilibré en faveur des mâles** (Marchant et al.1990). Le **nombre de mâles étant plus important, la compétition entre mâles est favorisée pour l'accès aux femelles**. Un divorce entraîne ainsi un risque important pour le mâle de ne pas pouvoir se reproduire à la saison suivante (Williams & Rodwell 1992). **La fidélité des mâles à la femelle semble donc est une stratégie importante pour les mâles afin de pouvoir d'augmenter leur probabilité de se reproduire , et donc augmenter leur valeur sélective**.

Cette fidélité au partenaire se traduit avant tout par une fidélité au nid.

A la fin de leur migration hivernale, les mâles réalisent en effet une réelle course pour arriver le plus tôt possible sur la colonie (Thiebot et al. 2014). Les mâles arrivent ainsi en avance à la colonie, en moyenne une semaine plus tôt que les femelles (Williams, 1995). Ceci leur permet **de pouvoir prendre possession du nid dans les sites favorables** et de maximiser les rencontres avec la femelle. La **fidélité au nid entre les deux sexes est similaire** et de la même manière, les femelles retournent d'abord sur le nid de l'ancienne saison. Si le mâle est déjà présent, alors la **chance d'un appariement avec son ancien partenaire est maximisée**. Si le mâle est absent, elles peuvent aller s'associer avec le mâle non apparié le plus proche (Davis & Speirs 1990).

Ces comportements sous-entendent que les **pressions pour se reproduire** exercée sur les mâles sont plus importantes que pour les femelles. La **capacité d'attraction des mâles** envers les femelles, essentiellement reliée à leur **qualité individuelle**, va être ainsi primordiale. Généralement, les femelles pondent des œufs plus lourds et plus grands quand elles sont appariées avec des mâles plus attractifs (Reyer et al. 1999, Cunningham & Russell 2000, Kolm 2001, Horvathova et al. 2012). Ceci semble se répercuter sur la masse, la croissance et la survie du poussin, augmentant de cette manière la valeur sélective des adultes (Hutchings 1991, Williams 1994, Styrsky et al. 1999). De plus, chez les espèces nidicoles ou semi-nidicoles (e.g. *Eudypetes*), les femelles pourraient moduler les ressources allouées aux œufs par rapport à leur **perception des capacités du mâle à être un bon père** (Poisbleau et al. 2013).

Les signaux de bonne qualité des mâles sont principalement reliés à la **masse** des individus et à la capacité de défense du territoire (comportements d'avertissements, agressivité envers les conspécifiques) (Williams 1995, Trivers 1972) bien que les caractéristiques **ornementales** (intensité de la couleur des plumes oranges) doivent également jouer un rôle (Hill 1991, Keddar et al. 2015).

Afin de maximiser leur pouvoir d'attraction envers les femelles et l'accomplissement des tâches parentales (défense du nid, approvisionnement du poussin en crèche), les mâles ont tout intérêt à être performants dans la recherche alimentaire. Cette performance peut être mesurée au cours du cycle reproducteur à travers l'étude des stratégies de recherche alimentaire et des variations de masse.

Une des conséquences de la sélection sexuelle chez les gorfous macaroni sera la mise en place d'un dimorphisme sexuel marqué, caractéristique observée chez de nombreux taxa d'oiseaux marins.

Conséquences du dimorphisme sexuel sur les stratégies alimentaires

Les causes de la divergence de niches entre les sexes suite au dimorphisme sont toujours très discutées (Shine 1989, Blanckenhorn 2005). Chez les oiseaux marins, les mécanismes de ségrégation spatiales entre sexes sont souvent associés à des mécanismes de compétition interindividuelles (e.g. Phillips et al. 2004) ou encore des variations d'efficacité d'approvisionnement (Cook et al. 2007). Ainsi le dimorphisme pourrait être un facteur favorisant la **ségrégation de niche entre sexe**, et permettrait en conséquence de **limiter la compétition intraspécifique** lors de certaines périodes. Chez les manchots, le dimorphisme en faveur des mâles est bien observable à l'échelle du bec (Szekely et al. 2007). Une taille de bec différente permettrait de capturer de proies de différente taille (e.g. manchot papou, Volkman et al. 1980 ; manchot Adélie, Ainley & Emison 1972). Les oiseaux les plus lourds ont accès à des profondeurs plus importantes, principalement en raison d'une capacité de stockage de l'oxygène plus importante (e.g. (Bethge et al. 1997, Halsey et al. 2006). Il pourrait également jouer un

rôle dans la ségrégation spatiale des zones d'alimentation (e.g. Weimerskirch et al. 2000, 2009, Lewis et al. 2005). Chez les gorfous macaroni et les gorfous de Schlegel, **les mâles ont un bec 14% plus grands que les femelles et sont plus lourds d'environ 15 à 20%** (Crossin et al. 2013). Le poids plus important des mâles leur permet d'une part de **nager plus vite et d'exploiter des zones d'alimentation situées à des profondeurs plus importantes** que celles atteintes par les femelles dans la colonne d'eau (Green et al. 2005).

2.1 Différence sexuelle dans l'effort d'approvisionnement au cours du cycle

Au cours du cycle reproducteur du gorfou macaroni, les deux sexes exhibent deux stratégies différentes en raison de devoirs parentaux bien distincts. Après la ponte et l'incubation où les deux partenaires alternent la garde de l'œuf, les mâles sont considérés comme des "*capital breeders*" pendant la phase d'élevage puisqu'ils doivent assurer la garde du nid et du poussin pendant environ 25 jours uniquement à partir de leurs réserves. Les stratégies de reproduction des femelles sont à la fois du type "*capital*" et "*income breeders*" puisqu'elles alimentent la progéniture avec la nourriture obtenue de voyages réguliers en mer, mais utilisent également leur propre réserves corporelles comme ressources d'énergie (Green et al. 2007).

Nous avons pu montrer que les trajets en mer effectués par chaque sexe reflètent les contraintes liées aux différentes phases du cycle. En revanche, un **certain degré de ségrégation spatiale entre les sexes existe selon le stade (incubation et crèche) et le site considéré.** Très peu d'espèces de manchots ayant pu être étudiées au cours de la totalité du cycle montrent ainsi des différences aussi radicales entre les sexes sur le plan spatial (Borboroglu & Boersma 2013).

Nous avons comparé l'effort de recherche alimentaire entre les sexes, au cours du cycle et selon la localité. L'effort de recherche alimentaire ou d'approvisionnement peut être indiqué par la distance totale parcourue au cours des voyages en mer. Le ratio de cette variable entre les deux sexes peut donc être considéré comme un indice des différences d'effort entre les mâles et les femelles. Cette différence d'approvisionnement est illustrée dans la figure 6.2.

Premièrement, **les mâles effectuent toujours des voyages plus longs que les femelles** pour les deux phases étudiées. Depuis l'arrivée à la colonie, les mâles ont jeûné pendant au minimum 24 jours (jusqu'à la ponte) puis 8 à 12 jours (incubation partagée de l'œuf) jusqu'au départ des mâles pour le 1^{er} long voyage en mer (Williams 1995). La durée des voyages des mâles au stade incubation varie entre 11 et 18 jours (Barlow et Croxall 2002b, Williams 1995, cette étude) et ce voyage est essentiellement destiné à la restauration des réserves corporelles mais également à la préparation du long jeûne de l'élevage à venir. En conséquence, le gain de masse des mâles lors de ce voyage est

important (~60% de prise de masse, d'après Croxall 1984). Les femelles partent ensuite en mer pour une durée d'environ 12 jours. Elles prennent relativement moins de poids lors de ce voyage (~26%). Cependant, elles ont moins jeûné que les mâles et doivent assurer l'élevage par la suite. Une prise de poids trop importante pourrait notamment engendrer des coûts supplémentaires à leur mouvements en mer (Chaurand & Weimerskirch 1994). **La ségrégation spatiale observée en incubation entre les sexes est une conséquence directe de la chronologie des tâches parentales, entraînant une ségrégation temporelle et spatiale dans la disponibilité des proies entre les périodes d'approvisionnement des deux sexes.**

En crèche, l'effort des mâles est encore plus important et témoigne d'une stratégie essentiellement dédiée à la restauration des réserves corporelles.

Les demandes énergétiques des poussins varient au cours du cycle, augmentent entre 100 à 400g.j⁻¹ jusqu'au début de la crèche, puis diminuent progressivement jusqu'au départ en mer. En crèche, il a été estimé que seulement 22.3% de la nourriture ingérée par les adultes est destinée au poussin, avec un investissement plus important des femelles (16.7%) que les mâles (10.2%) (Green et al. 2007). Ceci indique **que la majorité des ressources consommées est allouée aux besoins énergétiques propres de l'adulte. La variation de cet indice qui est très important entre les sites reflète bien les patrons de déplacement observés à l'échelle spatiale. Ceci confirme à nouveau que les stratégies adoptées par les mâles en crèche sont hautement site dépendantes.**

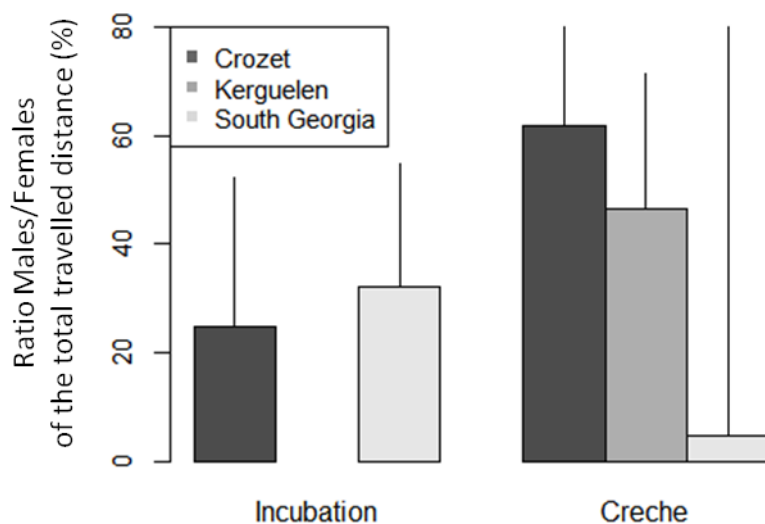


Figure 6.2: Ratio of total travelled distance per trip between males and females (%) in incubation and crèche, per site. During the brooding, female is the only gender who feed on the chick and this phase was therefore not included. Crozet, Kerguelen : this study. South Georgia: Barlow et Croxall, 2002b. The large standard deviation in crèche for South Georgia comes from the lack of accuracy on travelled distance per each sexe.

A Kerguelen et à Crozet, les zones d'alimentation des mâles sont en moyenne plus éloignées que celles des femelles, tandis que les vitesses de nages sont relativement similaires, voire moins élevées pour les femelles. Plusieurs trajets observés en crèche sont localisés dans la même zone d'alimentation des femelles à Kerguelen comme à Crozet (Chapitre V,VI). Les mâles sont capables d'exploiter des profondeurs plus importantes que les femelles en raison de leur poids plus important (Green et al. 2005b). Il serait toutefois intéressant d'étudier en détail le comportement de plongée afin de savoir si il n'existerait pas une ségrégation verticale des hauteurs d'eau exploitées.

Cette **ségrégation verticale existe en Géorgie du Sud** où les zones d'alimentation se recoupent (Barlow et Croxall 2002b). A ce stade, les femelles plongent plus profondément que les mâles (Green et al.2005b). Il a été suggéré que durant cette phase, la distribution spatiale des proies oblige les deux sexes à s'approvisionner en sympatrie. En conséquence, les **mâles pourraient exclure les femelles** par compétition et les contraindre à plonger plus profondément pour s'alimenter. Cette hypothèse semble cependant peu plausible car elle ne tient pas compte d'une recherche de proies énergétiquement plus rentables.

A l'échelle des T.A.A.F., il apparaît que les **zones exploitées par les femelles aux abords des colonies de Crozet et Kerguelen ne sont pas favorables aux mâles**. Cette différence de degré de ségrégation pourrait également s'expliquer en grande partie par le régime alimentaire.

En résumé, chez les gorfous macaroni, il semble que la ségrégation de niche entre sexes soit relativement faible au regard d'autres espèces. Ainsi, chez le manchot Adélie, les adultes assurent la période d'élevage du poussin de manière équilibrée. Les adultes exploitent des niches écologiques différentes puisque le régime alimentaire, les zones d'approvisionnement et la durée des trajets diffèrent entre les sexes (Clarke et al. 1998). Chez les gorfous sauteurs (*E chrysocome chrysocome*), les mâles s'alimentent en plus grande proportion de poissons tandis que les femelles s'alimentent principalement de krill et de calmars (Dehnhard et al. 2011).

Les gorfous macaroni de Géorgie du Sud s'alimentent majoritairement de **krill Antarctique**, et ceci pendant toutes les phases du cycle. Dans l'océan Indien, les individus en crèche ciblent une plus grande quantité de **myctophidés** qui sont connus pour vivre dans des eaux océaniques éloignées des eaux côtières (Bedford et al. 2015), aux abords et dans les zones frontales. La composition des réseaux **trophiques associés à chaque site** semble ainsi être un **facteur majeur gouvernant la distribution en mer des gorfous macaroni**, et par conséquence, limite la compétition entre les deux sexes à Kerguelen et Crozet.

2.2. Variation interindividuelle chez les mâles

Au cours de cette étude et de la discussion, nous avons observé que :

- i) les **patrons de distribution les plus variables à l'échelle du cycle concernent les voyages des mâles en crèche, avec d'importantes variations inter- et intra- sites. Ceci indique une importante plasticité comportementale** à ce stade.
- ii) la prise de masse diffère à ce stade entre la Géorgie du Sud (24%) et Crozet (33%).
- iii) les fortes variations interindividuelles observées sur une même colonie (Crozet) suggèrent également une **spécialisation individuelle** qui pourrait être reliée aux **fortes pressions de compétition sexuelle entre mâles**.

Concernant les patrons de distribution observés chez les mâles, plusieurs hypothèses pourraient expliquer un tel niveau de ségrégation interindividuelle (observé surtout à Crozet).

Premièrement, la plasticité comportementale permet aux individus d'acquérir des connaissances sur les caractéristiques de l'environnement au cours de leur développement (Danchin et al. 2005). Chez une espèce longévive comme le gorfou macaroni, les mâle **pourraient avoir acquis des stratégies de recherche d'approvisionnement individuelles par rapport aux habitats choisis** au cours de la crèche. Ces différences pourraient s'expliquer par la contrainte majeure de reconstituer des réserves corporelles plus élevée que chez les femelles.

De plus, avoir une certaine plasticité comportementale permettrait aussi de **limiter la compétition entre les individus qui ne cibleraient pas les mêmes sites en priorité** au cours de leur développement (par exemple: habitats nord et sud de Crozet).

Les patrons actuels de distribution pourraient être également la résultante d'une qualité différente **entre mâles**. Certains individus pourraient s'être installés dans des **zones attractives tandis que d'autres auraient ciblé des zones moins productives mais moins convoitées**. De cette manière, ces variations de distributions peuvent également refléter des **degrés différents de motivation** pour la reproduction (Danchin et al. 2005).

La question ultime est de savoir si ces **différents comportements ont effectivement des conséquences sur leur valeur sélective**.

Il est possible que le **comportement d'approvisionnement des mâles en crèche ait une conséquence indirecte sur le succès reproducteur de l'année suivante**. En effet, une récente étude a montré que les événements survenant lors d'une reproduction pouvait affecter la prochaine saison à travers des "*carry-over effects*" (Shoji et al. 2015). Chez les gorfous macaroni, comme chez le plupart des autres manchots, les voyages alimentaires en crèche précèdent la fin de l'élevage et la phase de

pré-mue. La période de crèche est déterminante pour les gorfous mâles qui doivent restaurer leurs réserves du jeûne de l'élevage. Après la crèche, les oiseaux partent en voyage pré-mue qui est une période cruciale d'hyperphagie pour les gorfous macaroni (Thiebot et al. 2014). Chez les gorfous, une mauvaise récupération des pertes de masse liées au jeûne de l'élevage pourrait avoir des conséquences sur la capacité du mâle à s'alimenter en période d'hyperphagie, ce qui pourrait *in finit* diminuer ses probabilités de mener à terme la mue, et ainsi diminuer sa valeur sélective. Cette hypothèse reste à vérifier par une approche énergétique sur le long terme.

Les gorfous macaroni étant des animaux longévifs, il est attendu que les individus ajustent leur comportement parental de **manière à maximiser l' aptitude phénotypique** (Williams 1966).

En cas de ressources limitées dans l'environnement lors d'un épisode reproducteur, les individus devront effectuer un compromis entre leur propre survie et celle du poussin (Stearns 1976 ; Ricklefs 1991). Chez les organismes longévifs à stratégie lente (faible fécondité, organismes itéropares), la survie de l'adulte est un paramètre démographique déterminant pour la dynamique des populations, plus important que le succès reproducteur à un épisode t (Stearns & Kawecki 1994, Saether & Bakke 2000).

Chez les manchots, la **période de mue étant cruciale** pour la survie des adultes, il serait intéressant de mesurer le **degré d'investissement des mâles en crèche** et lors des voyages d'hyperphagie sur des années variables de disponibilité alimentaire. Ceci nous permettrait d'estimer de manière plus précise si la période de crèche répond à la fois à une **restauration des réserves corporelles** mais également à une **préparation en amont de la mue**. Ainsi une telle étude permettrait de répondre à la question suivante : en cas de mauvaise année, la **restauration des réserves en crèche s'effectue-t-elle au détriment de l'approvisionnement du poussin ?**

Une telle étude permettrait d'identifier quelle activité gouverne le cycle annuel du gorfou macaroni : La période d'élevage du poussin, hautement synchronisée avec une pic d'abondance des ressources et reliée au succès reproducteur, ou la période de la mue, déterminante pour la survie des adultes (Brown 1989) ?

VI.3. Plasticité phénotypique chez le gorfou macaroni

La plasticité phénotypique se traduit par la capacité d'un même génotype à donner différents phénotypes dans différents environnements. La plasticité phénotypique permet aux organismes de modifier les réponses comportementales aux variations climatiques saisonnières mais également interannuelles qui peuvent considérablement modifier la distribution et la localisation des ressources.

La plasticité phénotypique peut avoir un caractère adaptatif, en étant favorisée par la sélection naturelle lorsqu'elle permet aux individus d'une population de s'ajuster efficacement à la variabilité environnementale qu'ils peuvent rencontrer au cours de leur vie (Danchin et al. 2005). Cette plasticité est directement reliée à l'aptitude phénotypique des individus, c'est à dire la capacité d'un phénotype à produire des descendants matures. Il existe cependant certains coûts pour assurer un tel niveau de flexibilité aux organismes (DeWitt 1998) et la plasticité phénotypique reste limitée. **La flexibilité des comportements d'approvisionnement du gorfou macaroni observés entre les différents sites /stades de notre étude relève de ce concept.**

3.1. Degré de plasticité des gorfous macaroni dans l'Océan Austral

Au cours de cette étude, **nous avons mis en évidence que les gorfous macaroni de l'océan Indien étaient flexibles dans la recherche alimentaire au cours du cycle de reproduction, que ce soit au niveau des stratégies comportementales qu'au niveau du choix des proies. La réponse comportementale des individus aux contraintes du cycle varie également entre localités indiquant un certain degré de flexibilité comportementale de l'espèce.**

Les variations comportementales observables à l'échelle de l'Océan Austral peuvent être résumées de la manière suivante :

Suite à la reproduction, les gorfous macaroni s'engagent dans la période de préparation de la mue. Cet épisode où les gorfous renouvellent leur plumage, extrêmement critique pour la survie des oiseaux, est précédée d'un voyage en mer d'hyperphagie (Williams 1995). Chez le gorfou macaroni, cette durée est de 12 à 21 j seulement en Géorgie du Sud, alors qu'elle dépasse 50 jours à Crozet avec un rayon maximal compris entre 0 et 1000km. La masse corporelle des gorfous macaroni aura augmenté de 2.5kg, soit un gain net de 50–70% (Williams 1995, Green et al. 2009b).

En migration hivernale, les oiseaux de Crozet et Kerguelen partent entre mi avril et mi mai et migrent à environ 2400 ± 1000 km (en 3mois et demi) dans des zones où le régime alimentaire sera similaire à la reproduction, soit principalement des crustacés. Par contre, les aires d'alimentations sont

complètement ségréguées entre les deux populations, l'une complètement à l'est de l'île d'origine (Kerguelen) et l'autre à l'ouest (Crozet) (Bost et al. 2009, Thiebot et al. 2011).

En Géorgie du Sud, de 1977 à 1996, pendant la reproduction, le régime alimentaire des gorfous macaroni était essentiellement composé de krill Antarctique (96%) pendant la saison de reproduction (Croxall et al. 1997) mais de nouvelles études montrent que le régime serait actuellement plus mixte (55% de krill, Waluda et al. 2012).

Sur l'île Heard, la proportion de poissons est plus importante que sur les autres îles, et augmente au cours de la période de reproduction (Green et al. 1998). Sur l'île Marion, les gorfous macaroni s'alimentent en grande majorité du crustacé *Thysanoessa vicina* (83% de la masse totale) et du myctophidé *K.anderssoni* (9.2%). L'euphausiacé *E.vallentini* représente seulement 3% de la masse de crustacés ingérés. A Macquarie, le régime alimentaire du gorfou de Schlegel, sous espèce du gorfou macaroni, reste constant (Hull 1999). En revanche, les manchots s'alimentent toujours dans des eaux océaniques (>2000m) durant toutes les phases du cycle (Hull et al. 1997) alors que les gorfous de Kerguelen, Crozet et Géorgie du Sud s'alimentent sur des eaux néritiques pendant la phase d'élevage (cette étude, Barlow et Croxall 2002b). De plus, des variations importantes sont observées sur le temps alloué aux plongées pendant les phases du cycle (Hull 2000).

Une telle plasticité est observée chez d'autres espèces, avec néanmoins des degrés variables (*e.g.* gorfou sauteur : Tremblay & Chérel 2003; manchot adélie: Rodary et al. 2000, Ropert-Coudert et al. 2002, Kato et al. 2003, manchot royal : Moore, Wienecke, et al. 1999, Charrassin & Bost 2001 ; manchot papou : Bost & Jouventin 1991, Lescroël & Bost 2005 ; puffin cendré : Paiva et al. 2010 ; Guillemot de Brünnich : Benvenuti et al. 2002).

Les gorfous macaroni de l'ensemble des sites étudiés présentent des stratégies de recherche alimentaire variables en réponse aux contraintes de la reproduction, chacune spécialisée aux caractéristiques biogéographiques de leur environnement. La durée, distances et caractéristiques des zones alimentaires ciblées varient entre les sites. En revanche, le degré de plasticité comportementale d'un point de vue phénologique et synchronisation intra site de la reproduction est relativement faible au regard de ce qui est observé chez d'autres espèces d'oiseaux marins.

Par exemple, les manchots papous, qui vivent en sympatrie avec les gorfous macaroni, présentent un degré de plasticité phénotypique bien plus important sur de nombreux traits d'histoire de vie (Bost & Jouventin 1990b). La saison de reproduction est étalée sur de nombreux mois (jusqu'à 5) dans la partie nord de leur aire de répartition (îles Crozet et Macquarie), alors que la ponte des œufs des populations situées dans la partie sud (Péninsule Antarctique) est contractée sur 2 à 3 semaines au début du printemps (Williams 1980, Bost & Jouventin 1990a,b). Opportunistes, leur régime alimentaire est varié et peut inclure une diversité de poissons, crustacés et céphalopodes variant d'une année à l'autre

(Bost and Jouventin 1990, Croxall et al. 1999). Les papous des îles sub-Antarctiques consomment principalement des poissons, des calamars et des amphipodes (Robinson & Hindell 1996, Pütz et al. 2001, Lescroel et al. 2004). Au contraire, les gorfous des îles de Géorgie du Sud et Falklands mangent principalement du krill Antarctique (Pütz et al. 2001, Croxall et al. 1999).

En conclusion, bien que les degrés de flexibilité comportementales varient entre les sites observables notamment par des variations de distances et durée de prospection alimentaire allouées à certaines phases du cycle annuel (par exemple, incubation, crèche, pré-mue), la période d'élevage des gorfous macaroni semble être relativement peu flexible à l'échelle de l'Océan Austral et phénologiquement bien adaptée à la saisonnalité de la production des ressources. Les gorfous macaroni montrent des différences d'effort de prospection entre localités à cette période (*e.g.* Kerguelen versus Crozet), cependant **les limites de cette plasticité peuvent-elles être atteintes dans le cas de changements trop extrêmes dans l'environnement, comme par exemple lors d'une délocalisation importante des ressources à court et à long terme ?**

3.2. Quelles réponses face aux changements globaux ?

Importance des changements globaux à court et long terme dans l'océan Austral

L'Océan Austral est soumis à d'importantes variations climatiques selon des processus atmosphériques à large échelle. Le couplage des phénomènes atmosphériques tels que l'oscillation atmosphérique australe (*Southern Oscillation*) et le Mode Annulaire Austral (*Southern Annular Mode*, SAM) (Trathan & Murphy 2002, Meredith et al. 2004, Meredith & Hogg 2006) a des conséquences indirectes et directes sur les écosystèmes de l'Océan Austral. Lors d'évènements *El Niño*, les anomalies chaudes de température peuvent affecter les processus de formation de glace de mer (Yuan 2004) ou la localisation des fronts océanographiques. Par exemple, 1°C d'augmentation de température d'eau de surface peut provoquer une migration vers le sud de 130km du Front Polaire, induisant une augmentation de la distance à parcourir pour les prédateurs marins dépendants de ce front pour s'alimenter (Bost et al. 2015).

Les dernières décennies ont démontré l'importance des conséquences des changements globaux à l'échelle l'océan Austral. Ainsi la circulation atmosphérique dans l'Océan Austral est affectée : les anomalies dues à mode annulaire Austral (SAM) tendent à devenir de plus en plus positives, induisant une augmentation de 15 à 20% des vents d'ouest autour de l'Antarctique, une augmentation de la température et une diminution de l'étendue de la glace de mer sur la côte ouest de l'Antarctique (Marshall 2003). Les évènements *El Niño* deviennent plus fréquents et les anomalies de températures

associées plus élevées (Solomon et al. 2007). La température de l'air a augmenté de 0.2°C depuis la fin du XIX^e siècle, avec une tendance plus prononcée en Péninsule Antarctique. Les 1000 premiers mètres de l'Océan Austral se sont substantiellement réchauffés entre les années 1930 et 2000 à toutes les profondeurs, et le réchauffement est concentré au sein de l'ACC (0.9°C par décennie depuis les années 1980 (Levitus et al. 2000, 2009, Gille 2002, 2008). Ces changements ont de profondes modifications sur la productivité biologique. Par exemple, un déclin de 38 à 80% des stocks de krill Antarctique a été observé depuis le milieu des années 1970 (Atkinson et al. 2004). Ce déclin serait probablement lié à une augmentation importante de la température de l'eau de surface en Géorgie du Sud (2.3°C dans les 150 premiers mètres depuis 80ans (Trathan et al. 2007) et d'un réchauffement local de la Péninsule Antarctique (Murphy et al. 1998). Les eaux de surface de l'Océan Austral Indien ont globalement augmenté entre les années 1960 et 2000 (Alory et al. 2007). Une migration généralisée vers le pôle sud des fronts océanographiques du Courant Circumpolaire Antarctique a été observée grâce à la mesure satellitaire des hauteurs d'eau (Sokolov & Rintoul 2009) bien que les mouvements des structures frontales soient plus complexes et hétérogènes entre les différents bassins hydrologiques (Pacifique, Atlantique, Indien, Aoki et al. 2015). Selon les différents scénarios climatiques, la signature de surface du Front Polaire dans l'Océan Austral Indien tendrait à migrer vers le sud de 24.9 à 40km par décennie, soit s'éloigner jusqu'à 800km au sud de Crozet d'ici 2100 (Péron et al. 2012).

Dans les prochaines décennies, il faut s'attendre à observer une augmentation de la fréquence des événements climatiques extrêmes (ECE, *Extrem Climatic Event*, Jentsch et al. 2007), telle une plus grande occurrence et intensité des événements *El Niño*.

De nombreux exemples existent sur l'influence négative des ECE sur la dynamique des populations d'oiseaux marins (*e.g.* Jenouvrier et al. 2009, Ainley et al. 2010, Jenouvrier 2013). Ces changements s'opèrent notamment à travers de profondes modifications de l'accessibilité aux ressources dans le temps et l'espace (Atkinson et al. 2004). L'éloignement ou l'appauvrissement des zones d'alimentation lors d'ECE peut ainsi contraindre les individus à intensifier l'effort de recherche alimentaire (distance à parcourir par exemple) de manière considérablement plus importante qu'en conditions environnementales normales. En période de reproduction, un éloignement des zones d'alimentation à la colonie peut ainsi provoquer des baisses drastique du succès reproducteur puisque les adultes mettent trop de temps pour revenir nourrir leur progéniture (Bohec et al. 2008, Bost et al. 2015, Ropert-Coudert et al. 2014, Péron et al. 2012). De manière générale, à partir des modèles démographiques, il est attendu que le réchauffement climatique affecte les populations de prédateurs marins dans l'Océan Austral (Ainley et al. 2010, Jenouvrier 2013).

Depuis une vingtaine d'années, une baisse dramatique des effectifs de gorfous macaroni et sauteurs est observée (Crawford et al. 2006, 2009, Cuthbert et al. 2009, Crossin et al. 2013) avec cependant des tendances variables entre les populations. D'après les récents comptages, les gorfous

macaroni font face à une baisse généralisée de leurs effectifs (30% sur les 30 dernières années en Géorgie du Sud et sur l'île Marion). En revanche, la population de Kerguelen tend à augmenter (1% par an depuis les années 1960, Barbraud et al. en préparation). La tendance est méconnue pour Crozet.

La réponse des gorfous macaroni face aux changements à venir est difficile à prévoir mais quelques pistes sont à explorer.

En Géorgie du Sud, la diminution de la population pourrait être reliée à un réchauffement local de la Péninsule Antarctique d'où proviennent les stocks de krill Antarctique dont sont extrêmement dépendantes les populations de prédateurs marins (Aktison et al. 2004, Trivelpiece et al. 2011). Les populations de gorfous macaroni feraient également face à une compétition accrue pour les ressources avec les otaries à fourrure antarctique et les baleines, qui voient leurs populations se reconstituer depuis l'arrêt de leur exploitation commerciale (Trathan et al. 2012). Une pression de prédation importante de la part des pétrels géants existerait également sur les gorfous juvéniles (Trathan et al. 2012, Horswill et al. 2014).

Le réchauffement local n'affecterait pas uniquement la localisation des zones alimentaires mais également la répartition spatiale des gorfous macaroni. Ainsi, il est attendu que la fonte des glaces permette aux manchots non dépendants de la glace de l'Atlantique Sud (*e.g.* gorfou macaroni, papou, à jugulaire) de migrer le long de la Péninsule Antarctique et coloniser de nouvelles localités. Concernant les espèces dépendantes de la glace (*e.g.* manchot Adélie), il est prédit qu'elles migrent de plus en plus vers le sud, et *a fortiori* voient leurs effectifs diminuer (Forcada et al. 2006, Forcada & Trathan 2009).

Dans le Sud de l'Océan Indien, la migration vers le sud du Front Polaire pourra avoir des impacts néfastes sur les populations de manchots royaux qui sont hautement spécialistes d'un seul type de proies, les myctophidés (Péron et al. 2012, Bohec et al. 2008, Bost et al. 2015). Il est probable que le réchauffement des eaux de surface affecte également les myctophidés ciblés par les gorfous macaroni de ce secteur. En revanche, les gorfous macaroni de Crozet continuent d'aller s'alimenter vers le Front Subantarctique, alors que les manchots royaux n'y vont plus depuis 15 ans (C.A. Bost pers. Com.). Ceci suggère que les stocks de crustacés ne sont pas pour l'instant affectés de la même manière que les myctophidés. Sur l'île Marion, dans l'océan Indien la masse des gorfous sauteurs femelles à l'arrivée de la reproduction a diminué d'environ 20% sur les 15 dernières années (Crawford et al. 2008). Les gorfous sauteurs ont diminué comme les gorfous macaroni sur cette localité et il est suggéré que la productivité des zones hivernales serait diminuée. Nous ne savons pas si la masse corporelle des gorfous de Crozet et Kerguelen a baissé dans la même proportion. En Géorgie du Sud, la diminution des stocks de krill Antarctique pourrait rapidement devenir un facteur extrêmement limitant pour les populations du sud de l'Océan Atlantique.

Dans le cas des changements globaux, la plasticité phénotypique est une des réponses permettant aux organismes de s'ajuster aux changements climatiques (Davis et al. 2005).

Les gorfous macaroni semblent avoir une phénologie peu plastique et sont extrêmement contraints en période d'élevage du poussin. Si les stocks de ressources à proximité des côtes pendant l'élevage venaient à diminuer ou disparaître en raison des changements globaux, les populations seraient considérablement affectées, que ce soit dans l'Océan Austral Atlantique ou Indien. En revanche, si la distribution des ressources varie temporellement, un ajustement phénologique est envisageable. Ces processus sont déjà en cours autant en milieu marin que terrestre (Chambers et al. 2013). Par exemple, la ponte des gorfous de Schlegel aurait été avancée de 3 jours en 30 ans sur l'île Macquarie en relation avec une augmentation de la température (Hindell et al. 2012).

Le gorfou macaroni est une espèce dont le degré de spécialisation du régime alimentaire varie entre les populations, et entre les stades de la reproduction. La spécialisation pourrait être une stratégie de réponse à un environnement relativement stable (ressources prédictibles) en permettant aux individus d'optimiser leur comportement de recherche des proies. De cette manière, la spécialisation individuelle sur de courtes périodes peut conférer des avantages au succès reproducteur des oiseaux, particulièrement pour ceux ayant une période de reproduction courte (Ceia & Ramos 2015). En revanche, il est suggéré que les **animaux utilisant des niches alimentaires plus larges pourraient être avantagés face aux variations environnementales.** Ainsi, plus flexibles dans leur phénologie et leur régime alimentaire, les manchots papous apparaissent actuellement moins affectés par les variations interannuelles des stocks de krill Antarctique au contraire de leur congénères. Leurs populations restent pour l'instant stable, voir en augmentation dans plusieurs sites de la Péninsule Antarctique (Lynch 2013).

Les îles Crozet et Kerguelen sont situées au sein de la Zone Polaire Frontale et permettent aux gorfous macaroni d'avoir accès à des régions océaniques plus diversifiées et un spectre de proies plus grandes qu'en Géorgie du Sud. La superficie et la gamme des environnements pourraient de cette manière leur conférer un avantage plus important quant à l'exploitation d'habitats marins possibles. De cette manière, les populations des TAAF pourraient être avantagées face aux, changement globaux, sur un court terme, par rapport aux populations de la Géorgie du Sud.

IV.4. Conclusion et perspectives

Cette thèse s'est concentrée sur la **description et la comparaison des stratégies de recherche alimentaires** en période de reproduction d'une **espèce épipélagique** dont le rôle dans l'écosystème marin est considérable. Au cours de ce travail, une comparaison multifactorielle a été réalisée, notamment par la prise en compte des contraintes énergétiques liées au stade reproducteur, le genre des individus et l'environnement océanographique dans lesquels les animaux s'alimentaient. Ainsi, le rôle de structures **hydrologiques** précises a été démontrée dans l'utilisation de l'habitat, **organisées** hiérarchiquement dans l'espace, **dynamiques** dans le temps et **prédictibles** périodiquement. De plus, un important **ajustement** des **déplacements**, de **l'effort d'approvisionnement** et du **régime alimentaire** a été démontré au cours du cycle en réponse aux contraintes imposées par les traits d'histoire de vie de l'espèce. Par ailleurs, l'approche comparative entre deux environnements océanographiques contrastés a démontré une **flexibilité insoupçonnée** des comportements de prospection alimentaire et pose de multiples questions sur la **valeur sélective** de ces stratégies à l'échelle individuelle, mais également sur ses conséquences sur les **paramètres démographiques** des populations étudiées. Enfin, cette flexibilité renvoie à une question majeure du **potentiel adaptatif de l'espèce** face aux nombreux changements climatiques et écosystémiques prévus au cours des futures décennies.

4.1. Apport de l'étude

Avant cette thèse, le comportement de recherche alimentaire au cours de la reproduction était complètement méconnu sur deux des plus grandes populations au monde du gorfou macaroni. Maintenant, ces lacunes sont comblées et ont permis d'apporter une meilleure vision des facteurs primordiaux à la recherche alimentaire de l'espèce. Ce travail est l'un des rares ayant couvert **l'ensemble d'un cycle de reproduction** chez les manchots, et il souligne le degré important des variations de comportement de recherche alimentaire pouvant survenir entre les différentes phases d'un cycle reproducteur.

Nous avons observé que les stratégies de recherche alimentaires étaient **reliées** dans le temps au cours du cycle à travers l'évolution des conditions océanographiques affectant le développement de la production primaire. Premièrement, la présence et l'abondance du phytoplancton semblent être un très bon indicateur de la profitabilité d'une zone pour les gorfous macaroni. Deuxièmement, nous avons mis en avant que la phénologie, le pic de demande énergétique et le comportement alimentaire pouvaient être bien corrélés à la croissance phytoplanctonique. Plusieurs échelons trophiques existent entre les proies des prédateurs et le niveau primaire, mais ces résultats indiquent que pour être

accessibles en si grande quantité aux abords des colonies, l'**agrégation** et le **développement** des ressources intermédiaires doit s'effectuer sur un temps relativement rapide autour des blooms saisonniers.

Cette étude a également mis en avant l'importance des **approches comparatives entre plusieurs localités, ceci est essentiel** pour mieux entrevoir la **diversité des comportements** qu'une espèce peut adopter pour s'ajuster aux environnements qu'elle rencontre. La spécificité propre à chaque localité peut être remarquable, telle observée à Crozet pendant la période de crèche. C'est la première fois, à notre connaissance, qu'un tel niveau de **ségrégation interindividuel** au sein d'une même colonie et d'un même stade reproducteur est observé chez les manchots. De plus, effectuer une approche comparative à l'échelle de l'Océan Austral nous a permis d'observer que les gorfous macaroni présentaient un **degré de plasticité phénotypique insoupçonné** pour une espèce pélagique, au contraire de ce qui avait été démontré pour des espèces néritiques (*e.g.* manchot papou, Lynch 2013). Ces comparaisons permettent de mieux visualiser la gamme des habitats et des niches trophiques utilisées par une espèce pour vivre. Cette notion est essentielle dans la construction des modèles d'habitats à des vues de conservations. En effet, la prise en compte d'une seule localité pourrait considérablement sous-estimer les aires propices à l'approvisionnement d'une espèce, et induire des erreurs sur la cartographie des zones à protéger.

Cette étude était complémentaire au projet EU-BEST coordonné par le BAS (*British Antarctic Survey*) en partenariat avec le CEBC et BirdLife International. Ce projet avait pour vocation de modéliser les habitats des gorfous macaroni à l'échelle de l'Océan Austral. Ainsi, notre étude a permis d'apporter des éléments sur l'utilisation de l'habitat des populations des TAAF.

4.2. Limites de l'étude

Une première limite de l'étude réside simplement dans le fait que les déploiements s'effectuent sur un nombre limité d'oiseaux, et la question de la **généralisation** possible des résultats à l'ensemble de la population se pose.

Il est vrai qu'un certain degré de variabilité interindividuelle a été observée au cours de cette étude, notamment pendant la période de crèche, entre les années mais surtout à l'échelle des plongées (variations de profondeurs exploitées entre individus d'un même stade). Cependant, l'effet de l'individu et l'année ont été pris en compte dans la modélisation statistique et des **réponses communes** aux paramètres océanographiques ont été trouvées. Ceci suggère que nos résultats sont vraisemblablement **généralisables** à l'ensemble des populations étudiées.

Par ailleurs, le déploiement des appareils s'est effectué sur les oiseaux se reproduisant dans les premiers rangs de la colonie, ceci pour éviter de déranger au maximum les oiseaux. Ce protocole peut être à l'origine d'un biais relatif à la **qualité individuelle** des oiseaux. Dans les colonies, la localisation du nid peut refléter des variations de succès reproducteur. Selon un des modèles théoriques sur les conséquence de la reproduction coloniale, (« *central-periphery distribution hypothesis* », Coulson 1968), les oiseaux situés au centre des colonies seraient de meilleur qualité et subiraient une pression de prédation moins importante qu'en périphérie. En conséquence, leur succès reproducteur et leur aptitude phénotypique seraient plus élevés (Coulson 1968, Hamilton 1971, Aebischer & Coulson 1990). Dans les faits, ces hypothèses sont moins évidentes à démontrer car la distance aux zones d'alimentation, le risque de charge parasitaire sont également des facteurs à prendre en compte (Regehr et al. 1998, Liljesthröm et al. 2007, Descamps et al. 2009). De plus, des associations spatiales entre des couples de différente qualité pourrait également s'effectuer (« *central-satellite distribution hypothesis* » Danchin & Wagner 1997, Velando & Freire 2001).

Chez les gorfous macaroni, la pression de prédation des skuas subantarctiques, des goélands des pétrels géants est importante aux abords des colonies (Crossin et al. 2013, Horswill et al. 2014). Les mâles les plus compétiteurs (aggressifs et territoriaux) et de meilleur condition corporelle (meilleur succès de chasse) arriveraient probablement plus tôt à la colonie, et nidifieraient au centre de la colonie là où la pression de prédation est la moins forte. Ceci étant, il est fort probable que les variations de qualité individuelle aient joué sur les paramètres comportementaux quantitatifs de notre étude, telles que la durée des temps passés en mer, l'effort et l'efficacité de plongée ou les gains de masse obtenus. Le déploiement et le suivi d'animaux situés sur d'autres endroits de la colonie seraient un bon moyen de modérer de biais si l'on désire étudier à fine échelle les stratégies de recherche alimentaire.

Par ailleurs, un effet des appareils est également probable puisque une augmentation des durées des trajets entre le lot d'oiseaux équipés et le lot témoin a été notée, surtout en période d'élevage. Le manque d'hydrodynamisme des appareils, notamment les GCDC (marque d'accéléromètres) ou des Fastloc II peut entraîner un effet de traîne qui peut gêner l'hydrodynamisme des manchots. Cependant, les nouveaux développements technologiques et la miniaturisation toujours croissante vont permettre de réduire considérablement cet impact. Par exemple, des GPS de moins de 10 grammes sont disponibles pour les oiseaux volants (GiPSy-2, Technosmart Italy, 8 – 9.5g). La contrainte de la pressions sous marine est encore le premier obstacle à la miniaturisation des appareils.

4.3. Perspectives d'études

Ces travaux ouvrent de multiples pistes de réflexion et certaines seraient extrêmement intéressantes et pertinentes à réaliser au cours des prochaines années.

Une première problématique de nouveau liée à l'environnement serait particulièrement intéressante, mais cette fois, menée dans la dimension verticale. Depuis plusieurs années, l'utilisation des structures hydrologiques est de plus en plus étudiée chez les prédateurs plongeurs (Charrassin, Park, et al. 2002, Scheffer et al. 2012, 2016, Jaud et al. 2012, Guinet et al. 2014). Les manchots, comme les pinnipèdes ou les cétacés, évoluent dans un milieu structuré dans les 3 dimensions. La prise en compte de la variation de la composition de la colonne d'eau (*e.g.* thermocline, isopycnes, quantité de lumière) entre les différentes phases du cycle du gorfou macaroni est très importante pour

- i) apporter des éléments inconnus sur l'environnement utilisé en profondeur chez cette espèce,
- ii) caractériser les conditions oceanographiques les plus importantes pour leur succès d'approvisionnement (quelle température ? quelle salinité ? etc.)
- iii) obtenir de nouvelles informations sur la biologie de leurs proies qui est encore assez peu connue.

Le développement des techniques de suivi comportemental (accélérométrie, caméra miniaturisé ou TDR) et d'échosondage permettrait d'associer des **mesures directes** (embarquées : tentatives de captures de proies, reconstitution des profils physico-chimique de la colonne d'eau, Vacquié-Garcia et al. 2012, Watanabe & Takahashi 2013) et **indirectes** (estimation des profondeurs et l'abondance des bancs de zooplankton, Bedford et al. 2015). Ces études sont ambitieuses mais restent cependant le meilleur moyen d'obtenir de compléter la compréhension des stratégies de recherche alimentaire.

D'un point de vue **évolutif**, une étude intéressante serait d'étudier le lien entre les différentes stratégies d'approvisionnement observées pendant cette thèse et leurs conséquences sur le succès reproducteur des individus. Cette aptitude phénotypique pourrait se mesurer grâce à un suivi individuel du taux de croissance du poussin jusqu'à son départ en mer. Cette idée repose sur la question suivante: **Est-ce que certaines stratégies sont plus efficaces que d'autres ?** Cet aspect permettrait de mieux percevoir le potentiel adaptatif des différents comportements de recherche alimentaire.

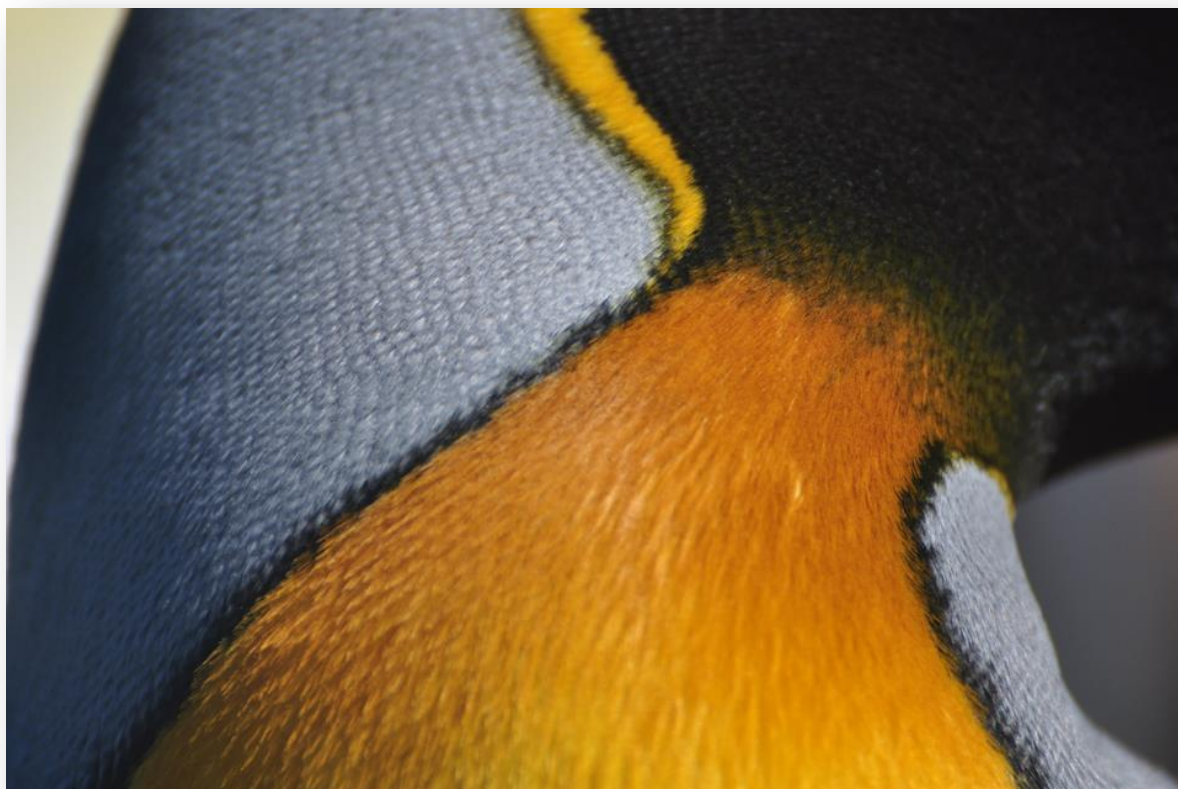
Pour ce travail, un suivi du couple (équipement successif des partenaires à leur départ en mer) pendant au minimum la période d'élevage et la crèche serait essentiel pour obtenir des données sur l'investissement parental des adultes quand le poussin a éclos. En parallèle, une pesée régulière des poussins pourrait être effectuée, tandis que le régime alimentaire pourrait être estimé par des prises de sang sur les adultes, puis analysées par la méthode des isotopes stables. L'équipement proposé serait

un couplage entre un accéléromètre (dépense énergétiques et mesure des tentatives de captures de proies) et un TDR (environnement prospecté).

Cette étude permettrait également d'aborder une autre question passionnante: **existe-il un ajustement des soins parentaux entre les deux partenaires du couple lorsque les deux individus présentent des degrés d'efficacité de recherche alimentaire différents ?**

A l'échelle **populationnelle**, estimer les tailles de populations et leur **paramètres démographiques** (taux de croissance, survie des juvéniles et adultes, succès reproducteur) est bien sûr une étude essentielle pour définir l'état de santé actuel des populations de gorfous macaroni dans les AAF. Une telle étude permettrait d'apporter des éléments de réponse déterminants pour conforter ou réfuter notre hypothèse sur **l'avantage de l'environnement océanographique des îles Crozet**. Face aux différents scénarios climatiques, une étude des traits démographiques associée à un suivi à long terme des déplacements en mer permettrait de mieux prédire l'avenir des populations de l'Océan Austral.

LIST OF FIGURES



LIST OF FIGURES

Figure 1.1: Ocean Chlorophyll Concentrations (Southern Hemisphere) during the southern summer 2011/2012).....	11
Figure 1.2: Vertical characteristics of the water column.....	13
Figure 1.3: Maps of filamentary structures (A) and phytoplakton distribution (B) at the confluence of the Brazil and Malvinas currents	14
Figure 1.4: Schema of <i>central place foraging</i> behaviour in diving predators.....	16
Figure 2.1: Circumpolar distribution of the Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF), Southern ACC Front (SACCF).....	27
Figure 2.2: Localisation of Crozet and Kerguelen islands in the Indian Basin	28
Figure 2.3 : Macaroni penguins.....	30
Figure 2. 4 : Distribution and abundance of Macaroni penguins populations.....	31
Figure 2.5: Estimated size of Macaroni penguins population from Crozet islands	32
Figure 2.6: Estimated size of Macaroni penguins population from Kerguelen islands.....	32
Figure 2.7: Studied colony of Macaroni penguins at Cap Cotter, Kerguelen Archipelago.....	33
Figure 2.8: Annual cycle of Macaroni penguins from Crozet Islands	36
Figure 2.9: Two main preys of Macaroni penguin	37
Figure 2.10: Some aspects of field work.....	39
Figure 2.11: PTT Kiwisat used in this PhD (Sirtrack)	41
Figure 2.12: GPS Fastloc II used in this PhD.....	42
Figure 2.13: Temperature depth recorder (TDR) devices with external fast-responding temperature sensor, used in this PhD	43
Figure 2.14: Effect of equipment on at-sea trips duration and time spent on land in brooding Macaroni penguins, Kerguelen Island.....	44
Figure 2.15: Time spent at sea after the different returns to the colony where birds were weighed in comparison with a control group	45
Figure 2.16: Schematic path recorded by GPS and Argos devices	46
Figure 2.17: Interpolation of GPS track to the sampling rate of Argos tags	47
Figure 2.18: ARS behaviours found on a track of male Macaroni penguin in incubation stage.....	48

LIST OF FIGURES

Figure 2.19: Relative time spent per cell for a Macaroni penguin from Kerguelen Island (crèche stage)	49
Figure 2.20: Schema of dive cycle structure composed of four main phases : descent, bottom, ascent and post-dive phases.....	50
Figure 2.21: Distribution of maximal depth dive for individuals from A. Kerguelen and B. Crozet.....	51
Figure 2.22: Altimetry method components.....	53
Figure 2.23: Root mean square of the Sea level Anomalies (SLA) over the whole Jan 1993-March 2010 period.....	53
Figure 3.1: Trips and travel speed of six incubating macaroni penguins presented on a bathymetry map around the Crozet islands	64
Figure 3.2: The positions of one bird overlaid on oceanographic features	65
Figure 4.1: Tracks of females and males during the breeding season at Crozet islands	73
Figure 4.2: Range of successive trips in brooding females from Crozet Islands	74
Figure 4.3: Evolution of net primary production north of Crozet Islands during the breeding season	74
Figure 4.4: Relation of maximal diving depth and dive rate with day time	75
Figure 4.5: Variation of foraging dive depth, duration and inter-foraging dives durations over the breeding season	75
Figure 4.6: Variation of body mass during the breeding season of Macaroni penguins at Crozet islands	77
Figure 4.7: Smoothed variation of body mass of Macaroni penguins during the breeding season in Crozet islands and in South Georgia	79
Figure 5.1: Foraging trips of Macaroni penguins at Kerguelen islands	86
Figure 5.2 : Range of successive trips performed by brooding penguins in relation with date at Kerguelen islands.....	86
Figure 5.3: Foraging trips of males Macaroni penguins from Crozet (a,b) and Kerguelen islands (c,d) in incubation (a,c) and crèche (b,d). Tracks are overlapped on sea surface temperatures (SST) maps	87
Figure 5.4: Relative variations of oceanographic features within tracks of males at sea, incubation stage.....	88
Figure 5.5: Diving parameters in relation with day time from brooding females at Kerguelen Islands.....	89
Figure 5.6: Variation of body mass of Macaroni penguins at Crozet and Kerguelen islands	90

LIST OF FIGURES

Figure 5.7: Variation of daily travelled distance of Macaroni penguins from Kerguelen and Crozet islands during the breeding season.....	92
Figure 5.8: Foraging dives rate and depth of females from Crozet and Kerguelen.....	92
Figure 5.9: Resting or travelling time (sum of inter foraging dives duration per hour) in relation with day time for females of Crozet and Kerguelen islands	93
Figure 5.10: Averaged number of dives performed each 10 meters by females in Kerguelen and Crozet waters.....	94
Figure 5.11: Schematic illustration of the circulation of the surface waters northeast of the islands.....	97
Figure 6.1: Overlap of brooding Macaroni penguins trips (blue) on temporal matched maps of Chlorophyll	115
Figure 6.2: Ratio of total travelled distance per trip between males and females (%) in incubation and crèche, per site	124

LIST OF TABLES

Table 2.1: Number of instrumented Macaroni penguins studied in this PhD.....	39
Table 2.2 : Locations class from Argos system.....	41
Table 2.3: Biological and physical meanings of oceanographic variables used in habitat use investigation	54
Table 4.1: Results of models of the body mass of brooding females in relation with date	76
Table 5.1: Comparison of foraging dive (>10m) parameters between Kerguelen and Crozet locality for incubation and brood stage	94
Table 5.2: Diet by reconstituted mass (%)	96
Table 6.1: Main foraging trip parameters and oceanographic features used by Macaroni penguins from 4 populations according to the breeding stage and gender	111

BIBLIOGRAPHY



- Abrams RW (1985) Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean. *J Biogeogr* 5:473–492
- Aebischer NJ, Coulson JC (1990) Survival of the Kittiwake in Relation to Sex, Year, Breeding Experience and Position in the Colony. *J Anim Ecol* 59:1063–1071
- Ainley DG (2002) *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press
- Ainley DG, Ribic CA, Ballard G, Heath S, Gaffney I, Karl BJ, Barton KJ, Wilson PR, Webb S (2004) Geographic structure of adélie penguin populations: overlap in colony-specific foraging areas. *Ecol Monogr* 74:159–178
- Ainley DG, Blight LK (2009) Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish Fish* 10:13–38
- Ainley D, Russell J, Jenouvrier S, Woehler E, Lyver PO, Fraser WR, Kooyman GL (2010) Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecol Monogr* 80:49–66
- Akaike H (1981) Likelihood of a model and information criteria. *J Econom* 16:3–14
- Akesson S, Hedenström A (2007) How migrants get there: migratory performance and orientation. *BioScience* 57:123–133
- Alerstam T (2006) Conflicting evidence about long-distance animal navigation. *Science* 313:791–794
- Alory G, Wijffels S, Meyers G (2007) Observed temperature trends in the Indian Ocean over 1960–1999 and associated mechanisms. *Geophys Res Lett* 34(2)
- Anel A, Petter L, Groscolas R (1998) Changes in egg and body temperature indicate triggering of egg desertion at a body mass threshold in fasting incubating blue petrels (*Halobaena caerulea*). *J Comp Physiol B* 168:533–539
- Anel A, Beaulieu M, Gilbert C (2013) The different breeding strategies of penguins: a review. *C R Biol* 336:1–12
- Anderson DR, Burnham KP, Gould WR, Cherry S (2001) Concerns about finding effects that are actually spurious. *Wildl Soc Bull*:311–316
- Anderson OR, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O, Black A (2011) Global seabird bycatch in longline fisheries. *Endanger Species Res* 14:91–106
- Angel MV (1968) The thermocline as an ecological boundary. *Sarsia* 34:299–312
- Angelier F, Moe B, Weimerskirch H, Chastel O (2007) Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *J Anim Ecol* 76:1181–1191
- Aoki S, Mizuta G, Sasaki H, Sasai Y, Rintoul SR, Bindoff NL (2015) Atlantic–Pacific asymmetry of subsurface temperature change and frontal response of the Antarctic Circumpolar Current for the recent three decades. *J Oceanogr* 71:623–636
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473

- Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Baar HJW de, Jong JTM de, Bakker DCE, Löscher BM, Veth C, Bathmann U, Smetacek V (1995) Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373:412–415
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J Range Manag* 49:386–400
- Bailey DW (2009) Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endanger Species Res* 10:93–106
- Bailleul F, Charrassin J-B, Monestiez P, Roquet F, Biuw M, Guinet C (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philos Trans R Soc B Biol Sci* 362:2169–2181
- Bailleul F, Cotté C, Guinet C (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Mar Ecol Prog Ser* 408:251–264
- Bailleul F, Lesage V, Hammill MO (2010) Spherical First Passage Time: A tool to investigate area-restricted search in three-dimensional movements. *Ecol Model* 221:1665–1673
- Baker AJ, Pereira SL, Haddrath OP, Edge K-A (2006) Multiple gene evidence for expansion of extant penguins out of Antarctica due to global cooling. *Proc R Soc B Biol Sci* 273:11–17
- Banse K (1996) Low seasonality of low concentrations of surface chlorophyll in the Subantarctic water ring: underwater irradiance, iron, or grazing? *Prog Oceanogr* 37:241–291
- Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. *Nature* 411:183–186
- Barbraud C, Marteau C, Ridoux V, Delord K, Weimerskirch H (2008) Demographic response of a population of white-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch. *J Appl Ecol* 45:1460–1467
- Barlow K, Boyd I, Croxall J, Reid K, Staniland I, Brierley A (2002) Are penguins and seals in competition for Antarctic krill at South Georgia? *Mar Biol* 140:205–213
- Barlow KE, Croxall JP (2002a) Provisioning behaviour of Macaroni Penguins *Eudyptes chrysolophus*. *Ibis*. 144:248–258
- Barlow KE, Croxall JP (2002b) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Prog Ser* 232:291–304
- Bedford M, Melbourne-Thomas J, Corney S, Jarvis T, Kelly N, Constable A (2015) Prey-field use by a Southern Ocean top predator: enhanced understanding using integrated datasets. *Mar Ecol Prog Ser* 526:169–181
- Begon M, Townsend CR, Harper JL (2006) *Ecology: from individuals to ecosystems*, 4th ed. Blackwell Pub, Malden, MA

- Bell GP (1980) Habitat use and response to patches of prey by desert insectivorous bats. *Can J Zool* 58:1876–1883
- Benvenuti S, Dall'Antonia L, Falk K (2002) Diving behaviour differs between incubating and brooding Brünnich's guillemots, *Uria lomvia*. *Polar Biol* 25:474–478
- Bethge P, Nicol S, Culik BM, Wilson RP (1997) Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). *J Zool* 242:483–502
- BirdLife International (2016) Species factsheet: *Eudyptes chrysolophus*. Downloaded from <http://www.birdlife.org> on 16/01/2016.
- Biro D, Meade J, Guilford T (2004) Familiar route loyalty implies visual pilotage in the homing pigeon. *Proc Natl Acad Sci USA* 101:17440–17443
- Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin J-B, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y, McDonald B, Park Y-H, Rintoul SR, Bindoff N, Goebel M, Crocker D, Lovell P, Nicholson J, Monks F, Fedak MA (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proc Natl Acad Sci U S A* 104:13705–13710
- Blain S, Tréguer P, Belviso S, Bucciarelli E, Denis M, Desabre S, Fiala M, Martin Jézéquel V, Le Fèvre J, Mayzaud P, others (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep Sea Res Part Oceanogr Res Pap* 48:163–187
- Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111:977–1016
- Block WM, Brennan LA (1993) The habitat concept in ornithology. In: *Current ornithology*. Springer, p 35–91
- Bocher P, Cherel Y, Labat J-P, Mayzaud P, Razouls S, Jouventin P, others (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser* 223:251–260
- Boggs CL (1992) Resource Allocation: Exploring Connections between Foraging and Life History. *Funct Ecol* 6:508–518
- Bohec CL, Durant JM, Gauthier-Clerc M, Stenseth NC, Park Y-H, Pradel R, Grémillet D, Gendner J-P, Maho YL (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci* 105:2493–2497
- Borrione I, Schlitzer R (2013) Distribution and recurrence of phytoplankton blooms around South Georgia, Southern Ocean. *Biogeosciences* 10:217–231
- Bost CA, Jouventin P (1990a) Laying asynchrony in Gentoo Penguins on Crozet Islands: causes and consequences. *Ornis Scand* 21:63–70
- Bost C-A, Jouventin P (1990b) Evolutionary ecology of gentoo penguins (*Pygoscelis papua*). In: *Penguin biology*. L.Davis and J.Darby, San Diego, p 85–112

- Bost CA, Jouventin P (1991) The breeding performance of the Gentoo Penguin *Pygoscelis papua* at the northern edge of its range. *Ibis* 133:14–25
- Bost CA, Koubbi P, Genevois F, Ruchon L, Ridoux V (1994) Gentoo penguin *Pygoscelis papua* diet as an indicator of planktonic availability in the Kerguelen Islands. *Polar Biol* 14:147–153
- Bost CA, Georges J-Y, Guinet C, Cherel Y, Putz K, Charrassin JB, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33
- Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. *Mar Ecol Prog Ser* 227:51–61
- Bost CA, Handrich Y, Butler PJ, Fahlman A, Halsey LG, Woakes AJ, Ropert-Coudert Y (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
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Bost CA, Delord C, Barbraud C, Cotté C, Peron C, Weimerskirch H (2013) The King Penguin : Life History, current status and priority conservation action. In: *Penguins: Natural History and Conservation*, P. G. Borboroglu and P. D. Boersma (eds). University of Washington Press, Seattle, p 7-21
- Bost CA, Cotté C, Terray P, Barbraud C, Bon C, Delord K, Gimenez O, Handrich Y, Naito Y, Guinet C, Weimerskirch H (2015) Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat Commun* 6:8220
- Boyd IL, Arnborn T (1991) Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biol* 11:259–266
- Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging Behaviour of Antarctic Fur Seals During Periods of Contrasting Prey Abundance. *J Anim Ecol* 63:703–713
- Boyd IL (1996) Temporal Scales of Foraging in a Marine Predator. *Ecology* 77:426–434
- Boyd IL (1997) The behavioural and physiological ecology of diving. *Trends Ecol Evol* 12:213–217
- Bracco A, Provenzale A, Scheuring I (2000) Mesoscale vortices and the paradox of the plankton. *Proc R Soc B Biol Sci* 267:1795–1800
- Bradley JS, Wooller RD, Skira IJ, Serventy DL (1990) The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *J Anim Ecol*:487–496
- Bradshaw CJ, Hindell MA, Sumner MD, Michael KJ (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim Behav* 68:1349–1360

- Bregnballe T, Frederiksen M (2006) Net-entrapment of great cormorants *Phalacrocorax carbo sinensis* in relation to individual age and population size. *Wildl Biol* 12:143–150
- Brower L (1996) Monarch butterfly orientation: missing pieces of a magnificent puzzle. *J Exp Biol* 199:93–103
- Brown CR (1989) Energy requirements and food consumption of *Eudyptes* penguins at the Prince Edward Islands. *Antarct Sci* 1:15–21
- Brown CR, Brown MB (2001) Avian coloniality - Progress and problems. In: *Current Ornithology*, Vol 16. Kluwer Academic/Plenum Publ, New York, p 1–82
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media
- Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Calenge C (2011) Analysis of Animal Movements in R: the adehabitat LT Package. R Found Stat Comput Vienna Austria
- Camprasse E, Passerault M, Lacombe T, Bost CA, *in preparation*. Some aspects of the breeding biology of the Macaroni penguins, *Eudyptes chrysolophus*, at Kerguelen islands, South Indian Ocean.
- Carbone C, Houston AI (1996) The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Anim Behav* 51:1247–1255
- Carlotti F, Jouandet M-P, Nowaczyk A, Harmelin-Vivien M, Lefevre D, Richard P, Zhu Y, Zhou M (2015) Mesozooplankton structure and functioning during the onset of the Kerguelen phytoplankton bloom during the KEOPS2 survey. *Biogeosciences* 12:4543–4563
- Carroll G, Slip D, Jonsen I, Harcourt R (2014) Supervised accelerometry analysis can identify prey capture by penguins at sea. *J Exp Biol* 217:4295–4302
- Ceia FR, Ramos JA (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar Biol* 162:1923–1938
- Cezilly F, Benhamou S (1996) Les stratégies optimales d’approvisionnement.
- Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont LJ, Crawford RJ, Durant JM, Hughes L, Keatley MR, Low M, others (2013) Phenological changes in the Southern Hemisphere. *PloS One* 8:e75514
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136
- Charrassin J-B, Bost CA, Pütz K, Lage J, Dahier T, Zorn T, Le Maho Y (1998) Foraging strategies of incubating and brooding king penguins *Aptenodytes patagonicus*. *Oecologia* 114:194–201
- Charrassin JB, Bost CA (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar Ecol Prog Ser* 221:285–297

- Charrassin J-B, Kato A, Handrich Y, Sato K, Naito Y, Ancel A, Bost C-A, Gauthier-Clerc M, Ropert-Coudert Y, Maho YL (2001) Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proc R Soc Lond B Biol Sci* 268:151–157
- Charrassin J-B, Park Y-H, Maho YL, Bost C-A (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecol Lett* 5:317–319
- Charrassin J-B, Le Maho Y, Bost C-A (2002) Seasonal changes in the diving parameters of king penguins (*Aptenodytes patagonicus*). *Mar Biol* 141:581–589
- Charrassin J-B, Park Y-H, Le Maho Y, Bost C-A (2004) Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep Sea Res Part Oceanogr Res Pap* 51:2091–2103
- Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246
- Chaurand T, Weimerskirch H (1994) The Regular Alternation of Short and Long Foraging Trips in the Blue Petrel *Halobaena caerulea*: A Previously Undescribed Strategy of Food Provisioning in a Pelagic Seabird. *J Anim Ecol* 63:275–282
- Cherel Y, Ridoux V (1992) Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–127
- Cherel Y, Guinet C, Tremblay Y (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croix, Kerguelen. *Polar Biol* 17:87–90
- Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol* 76:826–836
- Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- 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 Ecol* 37:610–619
- Choudhury S (1995) Divorce in birds: a review of the hypotheses. *Anim Behav* 50:413–429
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998a) Sex differences in Adélie penguin foraging strategies. *Polar Biol* 20:248–258
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press
- Cook TR, Cherel Y, Bost C-A, Tremblay Y (2007) Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. *Antarct Sci* 19:55–63
- Costa DP (1991) Reproductive and Foraging Energetics of High Latitude Penguins, Albatrosses and Pinnipeds: Implications for Life History Patterns. *Am Zool* 31:111–130

- Cotté C, Park Y-H, Guinet C, Bost C-A (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B Biol Sci* 274:2385–2391
- Cotté C, D'Ovidio F, Dragon A-C, Guinet C, Lévy M (2015) Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Prog Oceanogr* 131:46–58
- Coulson JC (1968) Differences in the Quality of Birds nesting in the Centre and on the Edges of a Colony. *Nature* 217:478–479
- Cowie RJ (1977) Optimal foraging in great tits (*Parus major*). *Nature* 268:137–139
- Crawford RJM, Cooper J, Dyer BM (2003) Population of the Macaroni Penguin *Eudyptes Chrysolophus* at Marion Island, 1994/95–2002/03, with Information on Breeding and Diet. *Afr J Mar Sci* 25:475–486
- Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L (2006) The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biol Conserv* 132:119–125
- Crawford RJM, Makhado AB, Upfold L, Dyer BM (2008) Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. *Afr J Mar Sci* 30:185–188
- Crawford RJM, Whittington PA, Upfold L, Ryan PG, Petersen SL, Dyer BM, Cooper J (2009) Recent trends in numbers of four species of penguins at the Prince Edward Islands. *Afr J Mar Sci* 31:419–426
- Cresswell K, Tarling GA, Trathan P (2007) Weight loss during breeding is adaptive for female macaroni penguins, *Eudyptes chrysolophus*. *Evol Ecol Res* 9:1053–1076
- Croll DA, Gaston AJ, Noble DG (1991) Adaptive loss of mass in thick-billed murre. *Condor* 93:496–502
- Crossin G, Trathan PN, Crawford RJM (2013) Macaroni Penguin (*Eudyptes chrysolophus*) and Royal Penguin (*Eudyptes schlegeli*). In: *Penguins: Natural History and Conservation*, P. G. Borboroglu and P. D. Boersma (eds). University of Washington Press, Seattle, p 185–208
- Croxall JP (1984) Seabirds. In: *Antarctic Ecology*, Cambridge University Press, Cambridge, p 531–616
- Croxall JP, Prince PA, Reid K (1997) Dietary segregation of krill-eating South Georgia seabirds. *J Zool* 242:531–556
- Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177:115–131
- Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. *Antarct Sci* 16:569–584
- Cunningham EJA, Russell AF (2000) Egg investment is influenced by male attractiveness in the mallard. *Nature* 404:74–77

- Cushing DH (1969) The regularity of the spawning season of some fishes. *J Cons* 33:81–92
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Cuthbert R, Cooper J, Burle M-H, Glass CJ, Glass JP, Glass S, Glass T, Hilton GM, Sommer ES, Wanless RM, others (2009) Population trends and conservation status of the Northern Rockhopper Penguin *Eudyptes moseleyi* at Tristan da Cunha and Gough Island. *Bird Conserv Int* 19:109–120
- Cuthill IC, Houston AI (1997) Managing time and energy In: *Behavioural Ecology*, fourth edition, K, J R., D & B N. (eds). Blackwell, Oxford, p 97 - 120
- Danchin E, Wagner RH (1997) The evolution of coloniality: the emergence of new perspectives. *Trends Ecol Evol* 12:342–347
- Danchin É, Giraldeau L-A, Cézilly F (2005) *Écologie comportementale - Cours et questions de réflexion*. Dunod
- Dann P (1991) Distribution, Population Trends and Factors Influencing the Population Size of Little Penguins *Eudyptula minor* on Phillip Island, Victoria. *Emu* 91:263–272
- Davies NB, Krebs JR, West SA (2012) *An introduction to behavioural ecology*. John Wiley & Sons
- Davis LS, Speirs EA (1990) Mate choice in penguins. In: *Penguin Biology*, L.S. Davies and J.T. Darby (eds). Academic Press, San Diego. p 377–397
- Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. *Ecology* 86:1704–1714
- Deagle BE, Gales NJ, Evans K, Jarman SN, Robinson S, Trebilco R, Hindell MA (2007) Studying seabird diet through genetic analysis of faeces: a case study on macaroni penguins (*Eudyptes chrysolophus*). *PLoS One* 2:e831
- Deagle BE, Gales NJ, Hindell MA (2008) Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. *Mar Ecol Prog Ser* 359:295–309
- Dehnhard N, Voigt CC, Poisbleau M, Demongin L, Quillfeldt P (2011) Stable isotopes in southern rockhopper penguins: foraging areas and sexual differences in the non-breeding period. *Polar Biol* 34:1763–1773
- Dejours P (1987) Water and air physical characteristics and their physiological consequences. In: *Comparative physiology: life in water and on land*. Dejours P, Bolis L, Taylor CR, Weibel ER, Fidia Research Series, Livinia Press, Padova
- Della Penna A, De Monte S, Kestenare E, Guinet C, d' Ovidio F (2015) Quasi-planktonic behavior of foraging top marine predators. *Sci Rep* 5:18603

- Delord K, Besson D, Barbraud C, Weimerskirch H (2008) Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. *Biol Conserv* 141:1840–1856
- Delord K, Barbraud C, Bost CA, Cherel Y, Guinet C, Weimerskirch H (2013) Atlas of top predators from French Southern Territories in the Southern Indian Ocean. CEBC-CNRS
- Delord K, Barbraud C, Bost C-A, Deceuninck B, Lefebvre T, Lutz R, Micol T, Phillips RA, Trathan PN, Weimerskirch H (2014) Areas of importance for seabirds tracked from French southern territories, and recommendations for conservation. *Mar Policy* 48:1–13
- Demer DA, Hewitt RP (1995) Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration. *Deep Sea Res Part Oceanogr Res Pap* 42:455–475
- Descamps S, Bohec CL, Maho YL, Gendner J-P, Gauthier-Clerc M (2009) Relating Demographic Performance to Breeding-Site Location in the King Penguin. *The Condor* 111:81–87
- DeWitt TJ (1998) Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *J Evol Biol* 11:465–480
- D’Ovidio F, Fernández V, Hernández-García E, López C (2004) Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophys Res Lett* 31
- D’Ovidio F, Isern-Fontanet J, López C, Hernández-García E, García-Ladona E (2009) Comparison between Eulerian diagnostics and finite-size Lyapunov exponents computed from altimetry in the Algerian basin. *Deep Sea Res Part Oceanogr Res Pap* 56:15–31
- D’Ovidio F, De Monte S, Alvain S, Dandonneau Y, Lévy M (2010) Fluid dynamical niches of phytoplankton types. *Proc Natl Acad Sci* 107:18366–18370
- D’Ovidio F, De Monte S, Penna AD, Cotté C, Guinet C (2013) Ecological implications of eddy retention in the open ocean: a Lagrangian approach. *J Phys Math Theor* 46:254023
- Dugger KM, Ballard G, Ainley DG, Barton KJ (2006) Effects of flipper bands on foraging behavior and survival of adélie penguins (*pygoscelis adeliae*). *The Auk* 123:858–869
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biol* 23:106–112
- Durant JM, Hjermann DØ, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol Lett* 8:952–958
- Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res* 33:271–283
- El-Sayed SZ (1988) Productivity of the Southern Ocean: a closer look. *Comp Biochem Physiol Part B Comp Biochem* 90:489–498
- Emlen JM (1966) The role of time and energy in food preference. *Am Nat*:611–617
- Falkowski PG, Raven JA (2013) Aquatic photosynthesis. Princeton University Press

- Fauchald P (1999) Foraging in a Hierarchical Patch System. *Am Nat* 153:603–613
- Fauchald P, Tveraa T (2003) Using First-Passage Time in the Analysis of Area-Restricted Search and Habitat Selection. *Ecology* 84:282–288
- Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. *Mar Ecol Prog Ser* 391:139–151
- Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Glob Change Biol* 12:411–423
- Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Change Biol* 15:1618–1630
- Ford RG, Ainley DG, Brown ED, Suryan RM, Irons DB (2007) A spatially explicit optimal foraging model of Black-legged Kittiwake behavior based on prey density, travel distances, and colony size. *Ecol Model* 204:335–348
- Friesen VL (2015) Speciation in seabirds: why are there so many species...and why aren't there more? *J Ornithol* 156:27–39
- Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proc R Soc Lond B Biol Sci* 270:1143–1148
- Froneman PW, McQuaid CD, Perissinotto R (1995) Biogeographic structure of the microphytoplankton assemblages of the south Atlantic and Southern Ocean during austral summer. *J Plankton Res* 17:1791–1802
- Froneman P, Perissinotto R (1996) Microzooplankton Grazing in the Southern Ocean: Implications for the Carbon Cycle. *Mar Ecol* 17:99–115
- Froneman PW, Pakhomov EA (1998) Biogeographic study of the planktonic communities of the Prince Edward Islands (Southern Ocean). *J Plankton Res* 20:653–669
- Gales R, Brothers N, Reid T (1998) Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biol Conserv* 86:37–56
- Gallon S, Bailleul F, Charrassin J-B, Guinet C, Bost C-A, Handrich Y, Hindell M (2013) Identifying foraging events in deep diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers. *Deep Sea Res Part II Top Stud Oceanogr* 88-89:14–22
- Gaston AJ, Hipfner J (2006) Adult Brünnich's guillemots *Uria lomvia* balance body condition and investment in chick growth. *Ibis* 148:106–113
- Gauthier-Clerc M, Le Maho Y, Clerquin Y, Drault S, Handrich Y (2000) Ecophysiology: Penguin fathers preserve food for their chicks. *Nature* 408:928–929
- Gentry RL, Kooyman GL (1986) Fur seals: maternal strategies on land and at sea. Princeton University Press
- Gille ST (2002) Warming of the Southern Ocean Since the 1950s. *Science* 295:1275–1277

- Gille ST (2008) Decadal-scale temperature trends in the Southern Hemisphere ocean. *J Clim* 21:4749–4765
- Glorioso PD, Piola AR, Leben RR (2005) Mesoscale eddies in the Subantarctic Front-Southwest Atlantic. *Sci Mar* 69:7–15
- Godø OR, Samuelsen A, Macaulay GJ, Patel R, Hjøllø SS, Horne J, Kaartvedt S, Johannessen JA (2012) Mesoscale Eddies Are Oases for Higher Trophic Marine Life. *PLoS ONE* 7:e30161
- Goodman D (1975) The theory of diversity-stability relationships in ecology. *Q Rev Biol* 50:237–266
- Green JA (2005) Do seasonal changes in metabolic rate facilitate changes in diving behaviour? *J Exp Biol* 208:2581–2593
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during year-round foraging in macaroni penguins. *Mar Ecol Prog Ser* 296:183–196
- Green JA, Boyd I, Woakes A, Green C, Butler P (2007) Feeding, fasting and foraging success during chick rearing in macaroni penguins. *Mar Ecol Prog Ser* 346:299–312
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009a) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538
- Green K, Williams R, Green MG (1998) Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. *Mar Ornithol* 26:27–34
- Grether GF, Palombit RA, Rodman PS (1992) Gibbon foraging decisions and the marginal value model. *Int J Primatol* 13:1–17
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarct Sci* 8:23–30
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonadonna F, Donnay JP (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Guinet C, Vacquié-Garcia J, Picard B, Bessigneul G, Lebras Y, Dragon A, Viviant M, Arnould J, Bailleul F (2014) Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. *Mar Ecol Prog Ser* 499:285–301
- Gurney LJ, Froneman PW, Pakhomov EA, McQuaid CD (2002) Diel feeding patterns and daily ration estimates of three subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep Sea Res Part II Top Stud Oceanogr* 49:3207–3227
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. *Ibis* 138:47–63
- Halsey LG, Butler PJ, Blackburn TM (2006) A phylogenetic analysis of the allometry of diving. *Am Nat* 167:276–287

- Halsey LG, Bost C-A, Handrich Y (2007) A thorough and quantified method for classifying seabird diving behaviour. *Polar Biol* 30:991–1004
- Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Mar Ecol Prog Ser* 224:283–290
- Hamer KC, Humphreys EM, Magalhães MC, Garthe S, Hennicke J, Peters G, Grémillet D, Skov H, Wanless S (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *J Anim Ecol* 78:880–889
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Handrich Y, Bevan RM, Charrassin J-B, Butler PJ, Ptz K, Woakes AJ, Lage J, Maho YL (1997) Hypothermia in foraging king penguins. *Nature* 388:64–67
- Hanuis N, Bost C-A, Huin W, Auber A, Halsey LG, Handrich Y (2010) Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. *J Exp Biol* 213:3874–3880
- Hanuis N, Bost C-A, Handrich Y (2013) Optimization of transit strategies while diving in foraging king penguins. *J Zool* 290:181–191
- Haskell DG (1997) Experiments and a model examining learning in the area-restricted search behavior of ferrets (*Mustela putorius furo*). *Behav Ecol* 8:448–449
- Hassell MP, May RM (1973) Stability in Insect Host-Parasite Models. *J Anim Ecol* 42:693–726
- Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339
- Hindell MA, Lea M-A, Bost C-A, Charrassin J-B, Gales N, Goldsworthy S, Page B, Robertson G, Wienecke B, O'Toole M, others (2011) Foraging habitats of top predators, and areas of ecological significance, on the Kerguelen Plateau. *Kerguelen Plateau Mar Ecosyst Fish Société Fr D'Ichtyologie Paris*:203–215
- Hindell MA, Bradshaw CJA, Brook BW, Fordham DA, Kerry K, Hull C, McMahon CR (2012) Long-term breeding phenology shift in royal penguins. *Ecol Evol* 2:1563–1571
- Hirshfield MF, Tinkle DW (1975) Natural selection and the evolution of reproductive effort. *Proc Natl Acad Sci* 72:2227–2231
- Hoeting JA, Madigan D, Raftery AE, Volinsky CT (1999) Bayesian model averaging: a tutorial. *Stat Sci* 14:382–417
- Horswill C, Matthiopoulos J, Green JA, Meredith MP, Forcada J, Peat H, Preston M, Trathan PN, Ratcliffe N (2014) Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *J Anim Ecol* 83:1057–1067
- Horvathova T, Nakagawa S, Uller T (2012) Strategic female reproductive investment in response to male attractiveness in birds. *Proc R Soc B-Biol Sci* 279:163–170

- Hosie GW, Fukuchi M, Kawaguchi S (2003) Development of the Southern Ocean continuous plankton recorder survey. *Prog Oceanogr* 58:263–283
- Houston AI, Davies NB (1985) The evolution of cooperation and life history in the Dunnock, *Prunella modularis*.
- Houston AI, Carbone C (1992) The optimal allocation of time during the diving cycle. *Behav Ecol* 3:255–265
- Hull CL, Hindell MA, Michael K (1997) Foraging zones of royal penguins during the breeding season, and their association with oceanographic features. *Mar Ecol Prog Ser* 153:217–228
- Hull CL (1999) The foraging zones of breeding royal (*Eudyptes schlegeli*) and rockhopper (*E. chrysocome*) penguins: an assessment of techniques and species comparison. *Wildl Res* 26:789
- 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. *Can J Zool* 78:333–345
- Hulley PA (1981) Results of the research cruises of FRV Walther Herwig to South America. LVIII. Family *Myctophi- dae* (Osteichthyes, Myctophiformes). *Arch FischWiss* 31:1–300
- Hunt G, Mehlum F, Russell RW, Jones D, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: N. J. Adams & R. H. Slotow, Johannesburg: BirdLife International South Africa
- Hunter S (1983) The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *J Zool* 200:521–538
- Hutchings JA (1991) Fitness Consequences of Variation in Egg Size and Food Abundance in Brook Trout *Salvelinus fontinalis*. *Evolution* 45:1162–1168
- Hutto RL (1985) Habitat Selection by Nonbreeding, Migratory Land. In: Habitat selection in bird, M.L. Cody (eds). New York: Academic Press. p 455-476.
- Jacquet N, Whitehead H, Lewis M (1997) Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. *Mar Ecol Prog Ser* 145:1-10
- Jaud T, Dragon A-C, Garcia JV, Guinet C (2012) Relationship between Chlorophyll a Concentration, Light Attenuation and Diving Depth of the Southern Elephant Seal *Mirounga leonina* (A Fahlman, Ed.). *PLoS ONE* 7:e47444
- Jenouvrier S, Caswell H, Barbraud C, Holland M, Strove J, Weimerskirch H (2009) Demographic models and IPCC climate projections predict the decline of an emperor penguin population (vol 106, pg 1844, 2009). *Proc Natl Acad Sci U S A* 106:11425–11425
- Jenouvrier S (2013) Impacts of climate change on avian populations. *Glob Change Biol* 19:2036–2057
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* 5:365–374

- Jones KM, Ruxton GD, Monaghan P (2002) Model parents: is full compensation for reduced partner nest attendance compatible with stable biparental care? *Behav Ecol* 13:838–843
- Jonsen ID, Myers RA, Flemming JM (2003) Meta-analysis of animal movement using state-space models. *Ecology* 84:3055–3063
- Jouventin P, Stahl JC, Weimerskirch H, Mougin JL (1984) The seabirds of the French subantarctic islands and Adélie Land, their status and conservation. *Status Conserv Worlds Seab Camb UK Int Counc Bird Preserv Techn Publ* 2:609–625
- Kacelnik A (1984) Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *J Anim Ecol* 53:283–299
- Kai ET, Rossi V, Sudre J, Weimerskirch H, Lopez C, Hernandez-Garcia E, Marsac F, Garçon V (2009) Top marine predators track Lagrangian coherent structures. *Proc Natl Acad Sci* 106:8245–8250
- Kareiva P, Odell G (1987) Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Am Nat* 130:233–270
- Kato A, Watanuki Y, Naito Y (2003) Annual and seasonal changes in foraging site and diving behavior in Adélie penguins. *Polar Biol* 26:389–395
- Keddar I, Altmeyer S, Couchoux C, Jouventin P, Dobson FS (2015) Mate Choice and Colored Beak Spots of King Penguins. *Ethology* 121:1048–1058
- Kirkwood R, Robertson G (1997) Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. *Mar Ecol Prog Ser* 156:205–223
- Klages NTW, Gales RP, Pemberton D (1989) Dietary segregation of macaroni and rockhopper penguins at Heard Island. *Wildl Res* 16:599–604
- Kohlmann SG, Risenhoover KL (1998) Effects of resource distribution, patch spacing, and preharvest information on foraging decisions of northern bobwhites. *Behav Ecol* 9:177–186
- Kokubun N, Kim J-H, Shin H-C, Naito Y, Takahashi A (2011) Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. *J Exp Biol* 214:3760–3767
- Kolm N (2001) Females produce larger eggs for large males in a paternal mouthbrooding fish. *Proc R Soc Lond B Biol Sci* 268:2229–2234
- Kooyman GL, Castellini MA, Davis RW, Maue RA (1983) Aerobic diving limits of immature Weddell seals. *J Comp Physiol* 151:171–174
- Kooyman G, Kooyman T (1995) Diving Behavior of Emperor Penguins Nurturing Chicks at Coulman Island, Antarctica. *Condor* 97:536–549
- Kooyman GL, Ponganis PJ (1998) The physiological basis of diving to depth: birds and mammals. *Annu Rev Physiol* 60:19–32
- Kooyman GL (2004) Genesis and evolution of bio-logging devices: 1963–2002. *Mem Natl Inst Polar Res* 58:148–154

- Koslov AN, Shust KV, Zemsky AV (1991) Seasonal and interannual variability in the distribution of *Electrona carlsbergi* in the Southern Polar Front area. *Sel Sci Pap SC-CAMLR-SSP7 Comm Conserv Antarct Living Resour Hobart*:337–367
- Kostianoy AG, Ginzburg AI, Lebedev SA, Frankignoulle M, Delille B (2003) Fronts and mesoscale variability in the southern Indian Ocean as inferred from the TOPEX/POSEIDON and ERS-2 altimetry data. *Oceanol CC Okeanol* 43:632–642
- Kotler BP, Gross JE, Mitchell WA (1994) Applying patch use to assess aspects of foraging behavior in Nubian ibex. *J Wildl Manag* 58:299–307
- Kramer DL (1988) The behavioral ecology of air breathing by aquatic animals. *Can J Zool* 66:89–94
- Kuhn CE, Johnson DS, Ream RR, Gelatt TS (2009) Advances in the tracking of marine species: using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar Ecol Prog Ser* 393:97–109
- Lack DL (1968) *Ecological Adaptations for Breeding in Birds*. Methuen
- Lea MA, Dubroca L (2003) Fine-scale linkages between the diving behaviour of Antarctic fur seals and oceanographic features in the southern Indian Ocean. *Ices J Mar Sci* 60:990–1002
- Lea M-A, Johnson D, Ream R, Sterling J, Melin S, Gelatt T (2009) Extreme weather events influence dispersal of naive northern fur seals. *Biol Lett* 5:252–257
- Landry MR, Decima M, Simmons MP, Hannides CC, Daniels E (2008) Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep Sea Res Part II Top Stud Oceanogr* 55:1378–1388
- Laubscher RK, Perissinotto R, McQuaid CD (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biol* 13:471–481
- Le Corre M, Pellerin M, Pinaud D, Van Laere G, Fritz H, Saïd S (2008) A multi-patch use of the habitat: testing the First-Passage Time analysis on roe deer *Capreolus capreolus* paths. *Wildl Biol* 14:339–349
- Lescroël A, Ridoux V, Bost CA (2004) Spatial and temporal variation in the diet of the gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. *Polar Biol* 27:206–216
- Lescroël A, Bost C-A (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Mar Ecol Prog Ser* 302:245–261
- Levitus S, Antonov JJ, Boyer TP, Locarnini RA, Garcia HE, Mishonov AV (2009) Global ocean heat content 1955-2008 in light of recently revealed instrumentation problems: Global ocean heat content. *Geophys Res Lett* 36: L07608
- Levitus S, Antonov JJ, Boyer TP, Stephens C (2000) Warming of the World Ocean. *Science* 287:2225–2229
- Lévy M, Klein P, Treguier A-M (2001) Impact of sub-mesoscale physics on production and subduction of phytoplankton in an oligotrophic regime. *J Mar Res* 59:535–565

- Lévy M (2003) Mesoscale variability of phytoplankton and of new production: Impact of the large-scale nutrient distribution. *J Geophys Res Oceans* 108:3358
- Lévy M, Ferrari R, Franks PJS, Martin AP, Rivière P (2012) Bringing physics to life at the submesoscale: *Frontier. Geophys Res Lett* 39
- Lewis SUE, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S, Hamer KC (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* 147:408–414
- Liljeström M, Emslie SD, Frierson D, Schiavini A (2007) Avian predation at a Southern Rockhopper Penguin colony on Staten Island, Argentina. *Polar Biol* 31:465–474
- Limmer B, Becker PH (2009) Improvement in chick provisioning with parental experience in a seabird. *Anim Behav* 77:1095–1101
- Louzao M, Pinaud D, Peron C, Delord K, Wiegand T, Weimerskirch H (2011) Conserving pelagic habitats: seascape modelling of an oceanic top predator. *J Appl Ecol* 48:121–132
- Louzao M, Aumont O, Hothorn T, Wiegand T, Weimerskirch H (2013) Foraging in a changing environment: habitat shifts of an oceanic predator over the last half century. *Ecography* 36:57–67
- Lowther AD, Lydersen C, Biuw M, De Bruyn PJN, Hofmeyr GJG, Kovacs KM (2014) Post-breeding at-sea movements of three central-place foragers in relation to submesoscale fronts in the Southern Ocean around Bouvetøya. *Antarct Sci* 26:533–544
- Lubimova TG, Shust KV, Popkov VV (1987) Specific features in the ecology of Southern Ocean mesopelagic fish of the family Myctophidae. *Biol Resour Arct Antarct Nauka Press Mosc*:320–337
- Luque SP, Guinet C (2007) A maximum likelihood approach for identifying dive bouts improves accuracy, precision and objectivity. *Behaviour* 144:1315–1332
- Lynch HJ, Naveen R, Trathan PN, Fagan WF (2012) Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93:1367–1377
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609
- Mangin S, Gauthier-Clerc M, Frenot Y, Gendner J-P, Le Maho Y (2003) Ticks *Ixodes uriae* and the breeding performance of a colonial seabird, king penguin *Aptenodytes patagonicus*. *J Avian Biol* 34:30–34
- Marshall GJ (2003) Trends in the Southern Annular Mode from Observations and Reanalyses. *J Clim* 16:4134–4143
- Martin JH (1990) Glacial-interglacial CO₂ change. *Paleoceanography* 5:1–13
- Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. *Nature* 345:156–158
- McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct Sci* 4:393–398

- McCullagh P, Nelder JA (1989) Generalized Linear Models, no. 37 in Monograph on Statistics and Applied Probability. Chapman & Hall.
- McGillicuddy DJ, Robinson AR, Siegel DA, Jannasch HW, Johnson R, Dickey TD, McNeil J, Michaels AF, Knap AH (1998) Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394:263–266
- McGillicuddy DJ, Anderson LA, Bates NR, Bibby T, Buesseler KO, Carlson CA, Davis CS, Ewart C, Falkowski PG, Goldthwait SA, Hansell DA, Jenkins WJ, Johnson R, Kosnyrev VK, Ledwell JR, Li QP, Siegel DA, Steinberg DK (2007) Eddy/Wind Interactions Stimulate Extraordinary Mid-Ocean Plankton Blooms. *Science* 316:1021–1026
- McNamara J (1982) Optimal patch use in a stochastic environment. *Theor Popul Biol* 21:269–288
- McNamara JM, Houston AI (1996) State-dependent life histories. *Nature* 380:215–221
- Mech SG, Zollner PA (2002) Using body size to predict perceptual range. *Oikos* 98:47–52
- Meredith MP, Woodworth PL, Hughes CW, Stepanov V (2004) Changes in the ocean transport through Drake Passage during the 1980s and 1990s, forced by changes in the Southern Annular Mode. *Geophys Res Lett* 31:L21305
- Meredith MP, Hogg AM (2006) Circumpolar response of Southern Ocean eddy activity to a change in the Southern Annular Mode. *Geophys Res Lett* 33:L16608
- Moller AP, Birkhead TR (1993) Cuckoldry and Sociality: A Comparative Study of Birds. *Am Nat* 142:118–140
- Mongin M, Molina E, Trull TW (2008) Seasonality and scale of the Kerguelen plateau phytoplankton bloom: A remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* 55:880–892
- Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive depths of breeding king penguins at Heard Island. *Polar Biol* 21:376–384
- Moore JK, Abbott MR, Richman JG, Smith WO, Cowles TJ, Coale KH, Gardner WD, Barber RT (1999) SeaWiFS satellite ocean color data from the Southern Ocean. *Geophys Res Lett* 26:1465–1468
- Moore JK, Abbott MR (2002) Surface chlorophyll concentrations in relation to the Antarctic Polar Front: seasonal and spatial patterns from satellite observations. *J Mar Syst* 37:69–86
- Mori Y (1998) The Optimal Patch Use in Divers: Optimal Time Budget and the Number of Dive Cycles During Bout. *J Theor Biol* 190:187–199
- Mori Y (2002) Optimal diving behaviour for foraging in relation to body size. *J Evol Biol* 15:269–276
- Mori Y, Boyd IL (2004) Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? *Mar Ecol Prog Ser* 275:241–249
- Mori Y, Boyd IL (2004b) The behavioral basis for nonlinear functional responses and optimal foraging in antarctic fur seals. *Ecology* 85:398–410

- Mori Y, Mitani Y, Watanabe Y, Sato K (2007) A Behavioral Indicator of Prey Patch Richness Derived From Diving Behavior: the Proportion of Residence Time to the Standard Time. *Isr J Ecol Evol* 53:347–354
- Mougin J-L (1984) La ponte du Gorfou macaroni *Eudyptes chrysolophus* de l’archipel Crozet. *Oiseau Rev Francaise Ornithol* 54:281–291
- Mueller T, Fagan WF (2008) Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos* 117:654–664
- Murphy EJ, Watkins JL, Reid K, Trathan PN, Everson I, Croxall JP, Priddle J, Brandon MA, Brierley AS, Hofmann E (1998) Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish Oceanogr* 7:381–390
- Murray TE, Bartle JA, Kalish SR, Taylor PR (1993) Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988-1992. *Bird Conserv Int* 3:181–210
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Newton I (2010) The sparrowhawk. A&C Black
- Oaten A (1977) Optimal foraging in patches: a case for stochasticity. *Theor Popul Biol* 12:263–285
- Oppel S, Beard A, Fox D, Mackley E, Leat E, Henry L, Clingham E, Fowler N, Sim J, Sommerfeld J, Weber N, Weber S, Bolton M (2015) Foraging distribution of a tropical seabird supports Ashmole’s hypothesis of population regulation. *Behav Ecol Sociobiol* 69:915–926
- Orians GH (1969) On the evolution of mating systems in birds and mammals. *Am Nat*:589–603
- Orians G., Pearson N (1979) On the theory of central place foraging. In: *Analysis of Ecological System*. D.J. Horn, G.R. Stairs and R.D. Mitchell, Ohio State University Press, Colombu, p 155–177
- Orsi AH, Whitworth III T, Nowlin Jr. WD (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res Part Oceanogr Res Pap* 42:641–673
- Paiva VH, Geraldès P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010) Oceanographic characteristics of areas used by Cory’s shearwaters during short and long foraging trips in the North Atlantic. *Mar Biol* 157:1385–1399
- Pakhomov EA, Perissinotto R, McQuaid CD (1994) Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar Ecol Prog Ser Oldendorf* 111:155–169
- Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol* 16:271–286
- Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar Ecol Prog Ser Oldendorf* 134:1–14

- Pakhomov EA, Perissinotto R, Froneman PW (1999) Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. *J Mar Syst* 19:47–64
- Pakhomov EA, Froneman PW (1999) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Mar Biol* 134:501–515
- Park Y-H, Gamberoni L, Charriaud E (1993) Frontal structure, water masses, and circulation in the Crozet Basin. *J Geophys Res Oceans* 1978–2012 98:12361–12385
- Park Y-H, Charriaud E, Fieux M (1998) Thermohaline structure of the Antarctic surface water/winter water in the Indian sector of the Southern Ocean. *J Mar Syst* 17:5–23
- Parkes KC (1992) Review of Distribution and Taxonomy of Birds of the World. B. L. Monroe, Jr. *J Field Ornithol* 63:228–235
- Pauly D, Christensen V, Dalgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860–863
- Peck DR, Congdon BC (2006) Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *J Avian Biol* 37:245–251
- Pennycuik CJ, Croxall JP, Prince PA (1984) Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Ornis Scand* 15:145–154
- Perissinotto R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean Archipelago. *Mar Ecol Prog Ser* Oldendorf 80:15–27
- Péron C, Weimerskirch H, Bost C-A (2012) Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc R Soc Lond B Biol Sci* 279:2515–2523
- Perrins CM (1970) The Timing of Birds' Breeding Seasons. *Ibis* 112:242–255
- Perruche C, Rivière P, Lapeyre G, Carton X, Pondaven P (2011) Effects of surface quasi-geostrophic turbulence on phytoplankton competition and coexistence. *J Mar Res* 69:105–135
- Phillips RA, Silk JR, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* 86:2386–2396
- Pichegru L, Ropert-Coudert Y, Kato A, Takahashi A, Dyer BM, Ryan PG (2011) Diving patterns of female macaroni penguins breeding on Marion Island, South Africa. *Polar Biol* 34:945–954
- Pinaud D, Cherel Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Mar Ecol Prog Ser* 298:295–304

- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9–19
- Pinaud D (2008) Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. *J Appl Ecol* 45:91–99
- Poisbleau M, Dehnhard N, Demongin L, Parenteau C, Quillfeldt P, Eens M (2013) Females Paired with New and Heavy Mates Reduce Intra-Clutch Differences in Resource Allocation. *PLoS ONE* 8:e72136
- Pollard RT, Venables HJ, Read JF, Allen JT (2007) Large-scale circulation around the Crozet Plateau controls an annual phytoplankton bloom in the Crozet Basin. *Deep Sea Res Part II Top Stud Oceanogr* 54:1915–1929
- Ponganis PJ, Kooyman GL, Starke LN, Kooyman CA, Kooyman TG (1997) Post-dive blood lactate concentrations in emperor penguins, *Aptenodytes forsteri*. *J Exp Biol* 200:1623–1626
- Ponganis PJ, Kooyman GL (2000) Diving physiology of birds: a history of studies on polar species. *Comp Biochem Physiol A Mol Integr Physiol* 126:143–151
- Posada D, Buckley TR (2004) Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Syst Biol* 53:793–808
- Pütz K, Ropert-Coudert Y, Charrassin JB, Wilson RP (1999) Foraging areas of King penguins *Aptenodytes patagonicus* breeding at Possession Island, southern Indian Ocean. *Mar Ornithol* 27:77–84
- Pütz K, Ingham RJ, Smith JG, Croxall JP (2001) Population trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. A review. *Polar Biol* 24:793–807
- Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Regehr HM, Rodway MS, Montevecchi WA (1998) Antipredator benefits of nest-site selection in Black-legged Kittiwakes. *Can J Zool* 76:910–915
- Reins T, Adelung D (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
- Reyer HU, Frei G, Som C (1999) Cryptic female choice: frogs reduce clutch size when amplexed by undesired males. *Proc R Soc B Biol Sci* 266:2101–2107
- Riandey V, Champalbert G, Carlotti F, Taupier-Letage I, Thibault-Botha D (2005) Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep Sea Res Part Oceanogr Res Pap* 52:2029–2048

- Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. *Stud Avian Biol* 8:84–94
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Mar Ornithol* 22:1–192
- Ridoux V (1995) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Oceanogr Lit Rev* 12:1128
- Robinson SA, Hindell MA (1996) Foraging ecology of gentoo penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. *Ibis* 138:722–731
- Robinson S, Chiaradia A, Hindell MA (2005) The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis* 147:483–489
- Rodary D, Wienecke BC, Bost CA (2000) Diving behaviour of Adélie penguins (*Pygoscelis adeliae*) at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. *Polar Biol* 23:113–120
- Roitberg BD (1990) Optimistic and pessimistic fruit flies: evaluating fitness consequences of estimation errors. *Behaviour* 114:65–82
- Roitberg BD, Mangel M, Lalonde RG, Roitberg CA, Alphen JJ van, Vet L (1992) Seasonal dynamic shifts in patch exploitation by parasitic wasps. *Behav Ecol* 3:156–165
- Roport-Coudert Y, Kato A, Bost C-A, Rodary D, Sato K, Le Maho Y, Naito Y (2002) Do Adélie penguins modify their foraging behaviour in pursuit of different prey? *Mar Biol* 140:647–652
- Roport-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Environ* 3:437–444
- Roport-Coudert Y, Chiaradia A, Kato A (2006) An exceptionally deep dive by a little penguin, *Eudyptula minor*. *Mar Ornithol* 34:71–74
- Roport-Coudert Y, Kato A, Wilson RP, Cannell B (2006) Foraging strategies and prey encounter rate of free-ranging Little Penguins. *Mar Biol* 149:139–148
- Roport-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 R Soc Lond B Biol Sci* 276:4105–4109
- Roport-Coudert Y, Kato A, Meyer X, Pellé M, MacIntosh AJJ, Angelier F, Chastel O, Widmann M, Arthur B, Raymond B, Raclot T (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* 38:111–113
- Roquet F, Park Y-H, Guinet C, Bailleul F, Charrassin J-B (2009) Observations of the Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals. *J Mar Syst* 78:377–393
- Saether B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653

- Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Funct Ecol* 7:643–652
- Sanial V, Beek P van, Lansard B, d'Ovidio F, Kestenare E, Souhaut M, Zhou M, Blain S (2014) Study of the phytoplankton plume dynamics off the Crozet Islands (Southern Ocean): A geochemical-physical coupled approach. *J Geophys Res Oceans* 119:2227–2237
- Sato K, Naito Y, Kato A, Niizuma Y, Watanuki Y, Charrassin JB, Bost C-A, Handrich Y, Maho YL (2002) Buoyancy and maximal diving depth in penguins. *J Exp Biol* 205:1189–1197
- Sato K (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J Exp Biol* 207:4057–4065
- Scheffer A, Bost CA, Trathan PN (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Mar Ecol Prog Ser* 465:281–297
- Scheffer A, Trathan PN, Edmonston JG, Bost C-A (2016) Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Prog Oceanogr* 141:1–16
- Schneider DC (1991) The role of fluid dynamics in the ecology of marine birds. *Oceanogr Mar Biol Annu Rev* 29:487–521
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- Schooley RL, Wiens JA (2003) Finding habitat patches and directional connectivity. *Oikos* 102:559–570
- Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q Rev Biol* 64:419–461
- Shoji A, Aris-Brosou S, Culina A, Fayet A, Kirk H, Padget O, Juarez-Martinez I, Boyle D, Nakata T, Perrins CM, Guilford T (2015) Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biol Lett* 11:20150671
- Shoji A, Aris-Brosou S, Fayet A, Padget O, Perrins C, Guilford T (2015) Dual foraging and pair coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. *J Exp Biol* 218:2116–2123
- Smith HG, Kallander H, Nilsson J-A (1989) The trade-off between offspring number and quality in the great tit *Parus major*. *J Anim Ecol* 58:383–401
- Sokolov S, Rintoul SR (2009) Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 2. Variability and relationship to sea surface height. *J Geophys Res Oceans* 114:1978–2012
- Solomon S, Qin D, Manning M, Chen Z (2007) Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC. Cambridge University Press

- Stahl J-C, Derenne P, Jouventin P, Mougin JL, Teulieres L (1985) Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le gorfou macaroni et *Eudyptes chrysocome*, le gorfou sauteur. Oiseau Rev Francaise Ornithol 55:27 – 43
- Stearns SC (1989) Trade-offs in life-history evolution. *Funct Ecol* 3:259–268
- Stearns SC (1992) The evolution of life histories. Oxford University Press
- Stearns SC, Kawecki TJ (1994) Fitness sensitivity and the canalization of life-history traits. *Evolution* 48:1438–1450
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan K-S, Lima M (2002) Ecological Effects of Climate Fluctuations. *Science* 297:1292–1296
- Stephens DW, Krebs JR (1986) Foraging Theory. Princeton University Press
- Styrsky JD, Eckerle KP, Thompson CF (1999) Fitness-related consequences of egg mass in nestling house wrens. *Proc R Soc B Biol Sci* 266:1253
- Suryan RM, Sato F, Balogh GR, Hyrenbach KD, Sievert PR, Ozaki K (2006) Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep Sea Res Part II Top Stud Oceanogr* 53:370–386
- Szekely T, Lislevand T, Figuerola J (2007) Sexual size dimorphism in birds. In: Sex, size and gender roles, Blanckenhorn W, Fairbairn D, Székely T, (eds). Oxford University Press; Oxford. p27–37
- Tanton JL, Reid K, Croxall JP, Trathan PN (2004) Winter distribution and behaviour of gentoo penguins *Pygoscelis papua* at South Georgia. *Polar Biol* 27:299–303
- Taupier-Letage I, Puillat I, Millot C, Raimbault P (2003) Biological response to mesoscale eddies in the Algerian Basin. *J Geophys Res Oceans* 108:1978–2012
- Thiebot J-B (2011) Déplacements et sélection d'habitat chez les animaux non contraints par la reproduction: une étude de l'écologie en mer des Manchots durant les phases d'immaturité et inter-nuptiale. Université Pierre et Marie Curie-Paris VI
- Thiebot J-B, Lescroël A, Pinaud D, Trathan PN, Bost C-A (2011) Larger foraging range but similar habitat selection in non-breeding versus breeding sub-Antarctic penguins. *Antarct Sci* 23:117–126
- Thiebot J-B, Cherel Y, Trathan P, Bost C (2011a) Inter-population segregation in the wintering areas of macaroni penguins. *Mar Ecol Prog Ser* 421:279–290
- Thiebot J-B, Cherel Y, Trathan PN, Bost C-A (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93:122–130
- Thiebot J-B, Cherel Y, Crawford RJM, Makhado AB, Trathan PN, Pinaud D, Bost C-A (2013) A Space Oddity: Geographic and Specific Modulation of Migration in *Eudyptes* Penguins (EJ Woehler, Ed.). *PLoS ONE* 8:e71429

- Thiebot J-B, Cherel Y, Acqueberge M, Prudor A, Trathan PN, Bost C-A (2014) Adjustment of pre-moult foraging strategies in Macaroni Penguins *Eudyptes chrysolophus* according to locality, sex and breeding status. *Ibis* 156:511–522
- Thiebot J-B, Delord K, Barbraud C, Marteau C, Weimerskirch H (2015) 167 individuals versus millions of hooks: bycatch mitigation in longline fisheries underlies conservation of Amsterdam albatrosses. *Aquat Conserv Mar Freshw Ecosyst*
- Thomas LN, Lee CM (2005) Intensification of ocean fronts by down-front winds. *J Phys Oceanogr* 35:1086–1102
- Thompson D, Fedak MA (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav* 61:287–296
- Thorpe SE, Heywood KJ, Brandon MA, Stevens DP (2002) Variability of the southern Antarctic Circumpolar Current front north of South Georgia. *J Mar Syst* 37:87–105
- Trathan PN, Murphy EJ (2002) Sea surface temperature anomalies near South Georgia: relationships with the Pacific El Nino regions. *J Geophys Res Oceans* 107:SOV-2
- Trathan PN (2006) Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Mar Ecol-Prog Ser* 323:239–251
- Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philos Trans R Soc B Biol Sci* 362:2351–2365
- Trathan PN, Ratcliffe N, Masden EA (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. *Ecography* 35:983–993
- Tréguer P, Jacques G (1993) Review Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Pol Biol* 12:149–162
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Prog Ser* 204:257–267
- Tremblay Y, Cherel Y (2003) Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Mar Ecol Prog Ser* 251:279–297
- Tremblay Y, Bertrand S, Henry R, Kappes M, Costa D, Shaffer S (2009) Analytical approaches to investigating seabird–environment interactions: a review. *Mar Ecol Prog Ser* 391:153–163
- Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci* 108:7625–7628
- Trivers R (1972) Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871-1971*, B. Campbell. Aldine-Atherton, Chicago, p 136–179
- Tuck GN, Polacheck T, Bulman CM (2003) Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biol Conserv* 114:1–27

- Tukey JW (1980) We need both exploratory and confirmatory. *Am Stat* 34:23–25
- Turchin P (1997) Quantitative analysis of animal movements in congregations. Cambridge University Press, New York
- Tveraa T, Lorensten S-H, Sæther B-E (1997) Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). *Behav Ecol* 8:465–469
- Vacquié-Garcia J, Royer F, Dragon A-C, Viviant M, Bailleul F, Guinet C (2012) Foraging in the darkness of the Southern Ocean: influence of bioluminescence on a deep diving predator. *PLoS One* 7:e43565
- Valone TJ (1991) Bayesian and prescient assessment: foraging with pre-harvest information. *Anim Behav* 41:569–577
- Van Franeker JA, Bathmann UV, Mathot S (1997) Carbon fluxes to Antarctic top predators. *Deep Sea Res Part II Top Stud Oceanogr* 44:435–455
- Varpe Ø (2012) Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *J Plankton Res* 34:267–276
- Velando A, Freire J (2001) How general is the central-periphery distribution among seabird colonies? Nest spatial pattern in the European Shag. *The Condor* 103:544–554
- Venables HJ, Pollard RT, Popova EE (2007) Physical conditions controlling the development of a regular phytoplankton bloom north of the Crozet Plateau, Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* 54:1949–1965
- Viviant M, Trites AW, Rosen DAS, Monestiez P, Guinet C (2009) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biol* 33:713–719
- 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
- Vleck CM, Vleck D (2002) Physiological condition and reproductive consequences in Adélie penguins. *Integr Comp Biol* 42:76–83
- Von Frisch K (1974) Decoding the language of the bee. *Science* 185:663–668
- Walsh PD (1996) Area-restricted search and the scale dependence of path quality discrimination. *J Theor Biol* 183:351–361
- Waluda CM, Collins MA, Black AD, Staniland IJ, Trathan PN (2010) Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. *Mar Biol* 157:99–112
- Waluda C, Hill S, Peat H, Trathan P (2012) Diet variability and reproductive performance of macaroni penguins *Eudyptes chrysolophus* at Bird Island, South Georgia. *Mar Ecol Prog Ser* 466:261–274
- Warham J (1996) The behaviour, population biology and physiology of the petrels. Academic Press

- Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. *Proc Natl Acad Sci* 110:2199–2204
- Watanabe YY, Ito M, Takahashi A (2014) Testing optimal foraging theory in a penguin–krill system. *Proc R Soc Lond B Biol Sci* 281:20132376
- 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 Biol* 17:296–304
- Watanuki Y, Kato A, Sato K, Niizuma Y, Bost CA, Maho YL, Naito Y (2002) Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biol* 25:672–681
- Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. *Emu* 89:15–29
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993a) Foraging Strategy of Wandering Albatrosses Through the Breeding-Season - a Study Using Satellite Telemetry. *Auk* 110:325–342
- Weimerskirch H, Mougey T, Hindermeier X (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behav Ecol* 8:635–643
- Weimerskirch H, Brothers N, Jouventin P (1997) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biol Conserv* 79:257–270
- Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* 67:99–109
- Weimerskirch H, Barbraud C, Lys P (2000) Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. *Ecology* 81:309–318
- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc R Soc Lond B Biol Sci* 267:1869–1874
- Weimerskirch H, Zimmermann L, Prince PA (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behav Ecol* 12:22–30
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Pinaud D, Pawlowski F, Bost C-A (2007) Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Albatross. *Am Nat* 170:734–743
- Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K, Aurioles D (2009) Species-and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar Ecol Prog Ser* 391:267–278

- Weimerskirch H, Louzao M, De Grissac S, Delord K (2012) Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211–214
- Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L (2014) Lifetime foraging patterns of the wandering albatross: Life on the move! *J Exp Mar Biol Ecol* 450:68–78
- Whitehead TO, Kato A, Ropert-Coudert Y, Ryan PG (2016) Habitat use and diving behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins during the critical pre-moult period. *Mar Biol* 163:1–20
- Wijk EM van, Rintoul SR, Ronai BM, Williams GD (2010) Regional circulation around Heard and McDonald Islands and through the Fawn Trough, central Kerguelen Plateau. *Deep-Sea Res Part -Oceanogr Res Pap* 57:653–669
- Williams AJ (1980) Aspects of the breeding biology of the Gentoo Penguin, *Pygoscelis papua* [at Marion Island in the Prince Edward archipelago Antarctic areas; Atlantic and Indian Oceans; chick mortality, food availability]. *Gerfaut*
- Williams TD, Croxall JP (1991) Annual variation in breeding biology of macaroni penguins, *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J Zool* 223:189–202
- Williams TD, Rodwell S (1992) Annual variation in return rate, mate and nest-site fidelity in breeding gentoo and macaroni penguins. *Condor* 94:636–645
- Williams TD (1994) Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol Rev Camb Philos Soc* 69:35–59
- Williams TD (1995) *The penguins : Spheniscidae*. Oxford University Press, Oxford ; New York
- Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am Nat* 100:687–690
- Wilson RP, Cooper J, Plötz J (1992) Short Communication: Can We Determine When Marine Endotherms Feed? A Case Study With Seabirds. *J Exp Biol* 167:267–275
- Wilson R, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar Biol* 140:17–27
- Wilson RP, Scolaro JA, Grémillet D, Kierspel MAM, Laurenti S, Upton J, Gallelli H, Quintana F, Frere E, Müller G, Straten MT, Zimmer I (2005) How do magellanic penguins cope with variability in their access to prey? *Ecol Monogr* 75:379–401
- Wilson RP (2010) Resource partitioning and niche hyper-volume overlap in free-living *Pygoscelid penguins*. *Funct Ecol* 24:646–657
- Wiltschko R, Wiltschko W (2006) Magnetoreception. *Bioessays* 28:157–168
- Wingfield J, Hahn T, Levin R, Honey P (1992) Environmental Predictability and Control of Gonadal Cycles in Birds. *J Exp Zool* 261:214–231

- Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by western grebes: An optimal foraging approach. *J Theor Biol* 139:437–447
- Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G (1994) Time and energy constraints and the relationships between currencies in foraging theory. *Behav Ecol* 5:28–34
- Yoder JA, Aiken J, Swift RN, Hoge FE, Stegmann PM (1993) Spatial variability in near-surface chlorophyll a fluorescence measured by the Airborne Oceanographic Lidar (AOL). *Deep Sea Res Part II Top Stud Oceanogr* 40:37–53
- Yuan X (2004) ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. *Antarct Sci* 16:415–425
- Zacharias MA, Roff JC (2001) Use of focal species in marine conservation and management: a review and critique. *Aquat Conserv Mar Freshw Ecosyst* 11:59–76
- Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2008) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biol* 31:229–243
- Zollner PA, Lima SL (1999) Orientational data and perceptual range: real mice aren't blind. *Oikos* 84:164–166
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media

ANNEXES



King penguins, it started there © Cécile Bon

ANNEXE 1	175
BON et al. (2015) Influences of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. <i>Mov Ecol</i> 3:32-42	
ANNEXE 2	187
BON et al. Foraging strategies of Macaroni penguins at Crozet Islands during the breeding season. <i>Marine Ecology Progress Series</i> , <i>to be submitted</i>	
ANNEXE 3	209
BON et al. Foraging strategies of Macaroni penguins at Kerguelen Islands during the breeding season. <i>Marine Ecology Progress Series</i> , <i>in preparation</i>	
ANNEXE 4	233
BOST et al. (2015) Large-scale anomalies affect marine predator foraging behaviour and demography. <i>Nature Communications</i> 6:8820	
ANNEXE 5	243
LOISEL et al. (2015) Diving behaviour in Eastern rockhopper penguins <i>Eudyptes</i> <i>chrysocome filholi</i> during incubation. <i>Marine Biology</i> , <i>to be submitted</i>	



RESEARCH

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Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands

Cecile Bon^{1*}, Alice Della Penna², Francesco d'Ovidio³, John Y.P. Arnould⁴, Timothée Poupart¹ and Charles-André Bost¹**Abstract**

Background: In the open ocean, eddies and associated structures (fronts, filaments) have strong influences on the foraging activities of top-predators through the enhancement and the distribution of marine productivity, zooplankton and fish communities. Investigating how central place foragers, such as penguins, find and use these physical structures is crucial to better understanding their at-sea distribution. In the present study, we compared the travel heading and speed of the world's most abundant penguin, the Macaroni penguin (*Eudyptes chrysolophus*), with the distribution of surface physical structures (large-scale fronts, eddies and filaments).

Results: The study was performed during December 2012 in the Crozet Archipelago (46.42° S; 51.86° E), South Indian Ocean. Six males at incubation stage were equipped with GPS loggers to get their trajectories. We used Eulerian and Lagrangian methods to locate large-scale fronts, mesoscale eddies (10–100 km) and part of the sub-mesoscale structures (<10 km, filaments) at the surface of the ocean. By comparing the positions of birds and these structures, we show that Macaroni penguins: i) target the sub Antarctic Front; ii) increase their foraging activity within a highly dynamic area, composed of eddy fields and filamentary structures; and iii) travel in the same direction as the predominant currents.

Conclusions: We show that penguins adjust their travel speed and movement during their whole trips in relation with the oceanographic structures visited. At a large scale, we hypothesize that Macaroni penguins target the sub Antarctic Front to find profitable patches of their main prey. At finer scale, Macaroni penguin may adopt a horizontal drifting behavior in strong currents, which could be a way to minimize costs of displacement.

Background

In the open ocean, the distribution and abundance of marine organisms is related to physical processes at different spatial and temporal scales [1]. Many studies have provided evidence of strong relationships between the foraging movements of top-predators and the distribution of mesoscale (10–100 km), predictable oceanographic structures such as large fronts and eddies (e.g. [2–4]). Recently, the relationships between marine top-predators and sub-mesoscale (<10 km) features (e.g. filamentary structures) have also received growing interest and have triggered the development of new Eulerian (observations at a given time, in the “non-moving” frame

of reference of the bathymetry) and Lagrangian diagnostics (from the frame of reference of flowing water particle). Lagrangian diagnostics enable the analysis of the temporal and spatial variability of oceanographic features to identify physical structures like eddies, fronts, and part of the filament variability. Such structures have been shown to affect the distribution and growth of phytoplankton because their lateral and vertical transport properties influence the supply and retention of nutrients in the euphotic layer from deeper waters [5, 6]. Correspondingly, such aggregations of primary production can influence food web dynamics due to their profitability for all species from grazers to top predators [1, 7, 8]. Indeed, it has been shown that several top predators use eddies (e.g. [9, 10]), currents and associated filaments to forage (e.g. [8, 11]).

Relatively, few studies have focused on penguins [10, 11] despite their key role in marine food webs [12]. These

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non-flying, diving predators are highly constrained in their foraging range because of their low travelling speed and high cost of transport. It might be expected, therefore, that oceanic penguins should target sub-meso and mesoscale structures during their at-sea activities to maximise their foraging efficiency [10].

Consequently, we investigated the at-sea foraging movements of the Macaroni penguin (*Eudyptes chrysolophus*) in a highly dynamic marine environment: the waters around the Crozet Archipelago in the South Indian Ocean. The Macaroni penguin is a pelagic predator, diving within the mixed layer to mean depths of 50 m (up to 163 m, [13]) to capture crustaceans and myctophid fish [14–16]. The species exhibits large flexibility in its foraging range, exploiting frontal structures or the shelf area according to the breeding requirements [17, 18]. While the world population is currently decreasing [19, 20], it is still the most abundant penguin species and the largest marine biomass consumer among seabirds [12]. The Crozet Archipelago is a breeding stronghold for the species [19].

Our aim was to identify how Macaroni penguins use oceanic structures to forage at different spatial scales, from large-scale (front) to meso- (eddies) and sub-mesoscale filamental structures [21]. We attempted to answer the following questions: i) do Macaroni penguins adjust their spatial movements with the regional circulation of currents?; and ii) how do they adjust their foraging behavior within meso- and sub-mesoscale structures? We address these questions by investigating the relationships between the spatial behavior of penguins and: i) the presence of persistent, large-scale frontal structures; ii) the

occurrence of eddies and filamentary structures; and iii) the adjustment of their travel speed with the encountered currents. We hypothesize that penguins would target these structures, reducing travel speed within eddies and filamentary structures to foraging intensively, as such behaviors should be advantageous with respect to travel costs.

Results

After their foraging trips (18 ± 2 days), all the instrumented penguins were re-captured upon returning to their colony having increased their body mass (subsequently, all pairs successfully fledged their chicks). Data from one GPS were lost due to technical failure and thus six tracks were analyzed in the present study. Individuals performed long clockwise looping trips, heading north towards the SAF, up to 388 km in a region encompassing positive and negative eddies, before returning to the colony (Fig. 1a). The central phase of their trips were longer (435.7 ± 69.9 km; 9.66 ± 1.35 d) than the outward (280.8 ± 38.9 km; 3.80 ± 0.47 d) and inward phases (237.6 ± 72.8 km; 9.66 ± 1.35 d, Kruskal-Wallis test on duration: $X^2 = 11.94$, $df = 2$, $p < 0.01$, Table 1).

The distance travelled every 6 h was on average 15.2 ± 12.7 km. The travel speed was significantly lower within the central phase (outward: 3.57 ± 1.25 km · h⁻¹, central: 1.93 ± 1.05 km · h⁻¹, inward: 3.30 ± 1.30 km · h⁻¹, Kruskal-Wallis test: $X^2 = 103.97$, $df = 2$, $p < 0.0001$, Table 1, Fig. 1b).

There was a gradient in SST encountered by penguins during their trip from $\sim 4^\circ\text{C}$ at the colony to 8°C at the lowest latitudes visited ($\sim 43^\circ\text{S}$, Fig. 2a). The SST was

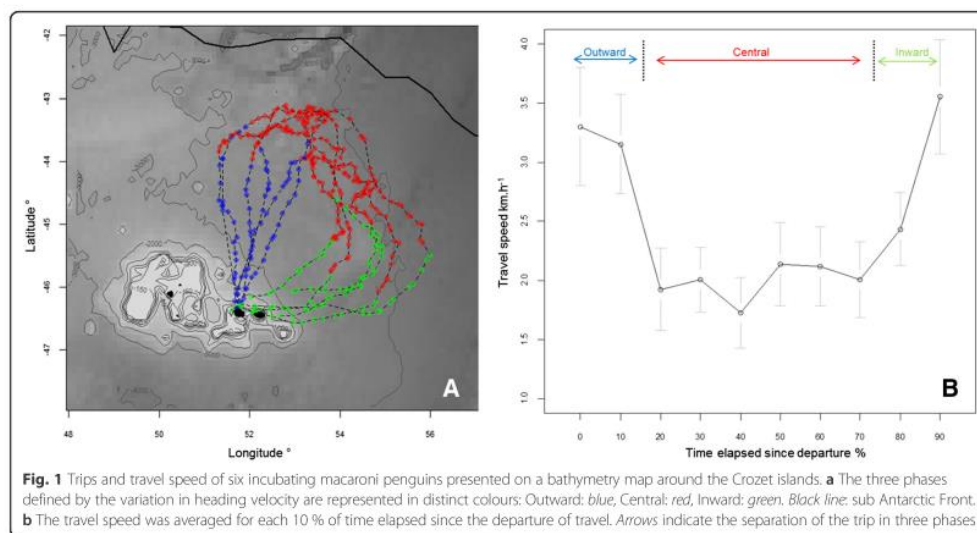


Table 1 Main characteristics of foraging trips of six Macaroni penguins

Trip phase	Duration (j)	Travel speed (km.h ⁻¹)	Heading velocity (km.h ⁻¹)	Current speed (km h ⁻¹)	Animal direction °	Current direction °
Outward <i>n</i> = 86	3.8 ± 0.5	3.6 ± 1.3	3.5 ± 1.3	0.2 ± 0.2	11.4 ± 22.4	61.4 ± 97.8
Central <i>n</i> = 233	9.7 ± 1.4	1.9 ± 1.1	1.7 ± 0.9	0.9 ± 0.4	141.4 ± 68.8	118.1 ± 37.9
Inward <i>n</i> = 96	3.8 ± 1.1	3.3 ± 1.3	3.2 ± 1.3	0.3 ± 0.1	233.2 ± 45.0	246.3 ± 101.0

n number of gps localisations

highly positively correlated with the current speed. This suggests that the warmer waters encountered by penguins located at the lowest latitudes were also in the strongest currents visited (Spearman correlation test: 7068809, $R^2 = 0.40$, $p < 0.001$).

Penguin and mesoscale eddies

During the central phase of their trips, Macaroni penguins foraged at the edge of two large eddies, situated in

the vicinity of the SAF (Fig. 2b). These two eddies were located to the south of a large eddy field which was not used by the birds. Overall, 63 % of the locations associated with an eddy were within the central phase whereas 11 and 26 % were within the outward and inward phases, respectively (Table 2). This indicates that the main eddy activity was observed within the central phase where the penguins had reduced swimming speed. Indeed, the degree of association with eddies was 37 % in

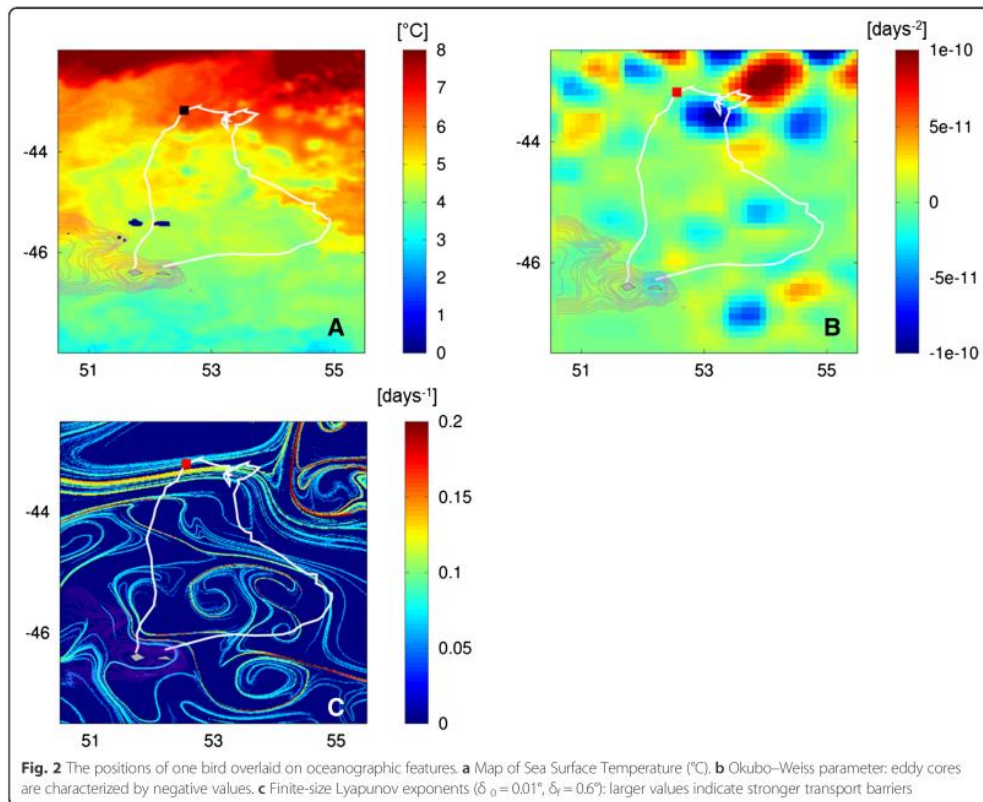


Table 2 Distribution of eddies and filaments within trips of six macaroni penguins

Trip Phase	n_{locs} averaged on individuals	Eddies		Filaments	
		Distribution of eddy locations %– n_{locs}	Degree of association within phase %– n_{locs}	Distribution of filaments %– n_{locs}	Degree of association within phase %– n_{locs}
Outward	14 ± 4	11 %–15	17 %–3 ± 1	20.8 %–22	21.7 %–3.0 ± 1.0
Central	38 ± 5	63 %–87	37 %–15 ± 6	66.7 %–61	27.6 %–9.6 ± 6.0
Inward	16 ± 4	26 %–36	38 %–6 ± 3	12.5 %–10	12.5 %–2.0 ± 1.0

n_{locs} number of locations. Mean ± SD Number of locations within eddies/filaments averaged within each phase for each individual

the central phase, 17 % in the outward phase and 38 % in the inward phase (Table 2).

Examination of time spent within eddies (successive locations in an eddy) indicates penguins spent more time within eddies in the central phase (43 ± 25 h, 11 cases) than in the transit phases (25 ± 10 h, 10 cases, Mann-Whitney: $U = 81.5$, $P = 0.066$). The retention parameter was small for eddies in the central phase (9.7 ± 15 d, $n = 60$ locations) since 80 % of water parcels had been recirculating within the eddy for less than 8 d. In transit phases, the retention parameter of eddies was significantly higher (16 ± 15 d, $n = 32$ locations, Mann-Whitney test: $U = 658$, $P = 0.013$). Finally, the three mixed models built for each phase indicated that penguins significantly slowed down when they were inside eddies in the inward phase, contrary to that observed in the two other phases (Table 3 models M1, M2, M3, Fig. 3a).

Penguin movements and filaments

Filaments identified by the FSLE method were present over the whole area prospected by the penguins (Fig. 2c). At the trip scale, we observed high inter-individual variation in the level of association with filaments (n_{locs} within filaments/ n_{locs} total) (from 5.6 to 35.9 %). Across all trips, 66.7 % of the locations associated with filaments were located within the central phase of the foraging trip where penguins reduced travel speed (20.8 and 12.5 % in outward and inward phases, respectively, Table 2). The degree of association was significantly higher in the central

phase since 27.6 % of locations were within filaments. In the two others phases, the number of locations within filaments were significantly lower (Kruskal-Wallis test: $X^2 = 6.976$, $df = 2$, $p < 0.05$, Table 2). FSLE values of the filaments were significantly higher at the central phase (0.20 ± 0.05 d⁻¹) than at the outward (0.15 ± 0.04 d⁻¹) and inward (0.12 ± 0.02 d⁻¹) phases (Kruskal-Wallis test: $X^2 = 18.603$, $df = 2$, $p < 0.001$). Once individuals were inside the filaments, they slowed down more when FSLE values were higher (Table 3 model M4, Fig. 3b).

Penguin movements and currents

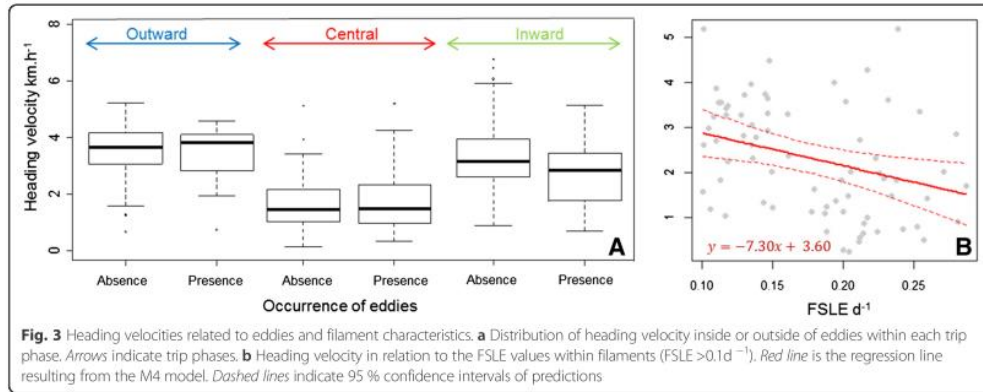
At the whole-trip scale, at-sea movements of individuals seem to be strongly modified by the currents encountered. Firstly, travel speed was negatively correlated with the current speed indicating that penguins decelerated when they encountered stronger currents (Table 3 model M5). Indeed, during the outward phase, the current speed was generally low and no clear relationship was observed between the penguins and direction of the current (Table 1, Fig. 4).

In the central phase, penguins shifted toward a south-eastern direction ($141.40 \pm 68.78^\circ$) with a travelling speed significantly lower than during the two other trip phases (Kruskal-Wallis test: $X^2 = 103.9734$, $df = 2$, $p < 0.001$). At that time the currents were significantly faster than during the two other phases (Kruskal-Wallis test: $X^2 = 169.90$, $df = 2$, $p < 0.001$), up to $1.6 \text{ km} \cdot \text{h}^{-1}$, and mainly oriented in the same direction as the penguins' headings ($118.10 \pm 37.86^\circ$, Fig. 4). A strong correlation between the directions

Table 3 Influence of the occurrence of eddies, filaments and current speed on heading velocity

HV ~ OW category	Intercept	Presence of eddy	$P_{\text{intercept}}/P_{\text{variable}}$	$\Delta\text{AIC}_{\text{Null}}$
M1 – Outward phase	3.57 ± 0.20	–0.14 ± 0.40	<0.0001/NS	+1.87
M2 – Central phase	1.62 ± 0.11	0.12 ± 0.16	<0.0001/NS	+3.30
M3 – Inward phase	3.43 ± 0.25	–0.635 ± 0.29	<0.0001/< 0.05	–2.14
HV ~ FSLE (>0.1)	Intercept	FSLE (>0.1)	$P_{\text{intercept}}/P_{\text{variable}}$	$\Delta\text{AIC}_{\text{Null}}$
M4 – Whole trip	3.60 ± 0.51	–7.29 ± 2.78	<0.001/< 0.05	–6.40
TV ~ Current speed	Intercept	Current speed	$P_{\text{intercept}}/P_{\text{variable}}$	$\Delta\text{AIC}_{\text{Null}}$
M5 – Whole trip	3.51 ± 0.19	–1.51 ± 0.24	<0.001/<0.001	–27.38

Linear mixed models were independently built with individual bird included as a random effect ($n = 6$) for each explanatory variable. Response variables are heading velocity (HV) and travel velocity (TV). The Okubo-Weiss parameter is a binary factor coding for the occurrence of eddies (0: absence, 1: presence). Current speed and FSLE are continuous variables. Only FSLE values $>0.1 \text{ d}^{-1}$ were selected to test for the influence of filaments on HV when penguins were within a filament. Significant coefficients (mean ± se) are in bold. P value, NS non-significant. $\Delta\text{AIC}_{\text{Null}}$ shows the AIC deviation from AIC of the null model

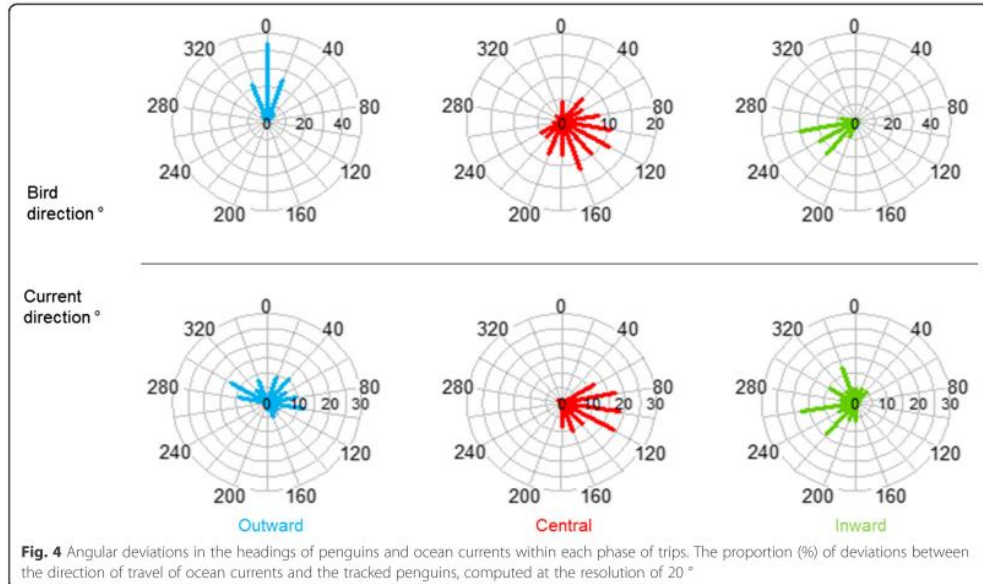


of the penguins and currents were also found (circular Pearson test: 5.78, $R^2 = 0.40$, $p < 0.001$). A substantial proportion (25.3 %) of heading velocities was $< 1 \text{ km} \cdot \text{h}^{-1}$ indicating displacement close to that of the current speed suggesting a possible drifting behavior by the birds.

During the inward phase, the penguins moved quickly back to the colony and their paths were mostly orientated south-westerly (Fig. 4). The weak currents were also oriented south-westerly and positively correlated with the penguins' main direction (circular Pearson test: 4.55, $R^2 = 0.50$, $p < 0.001$).

Discussion

The salient findings of this study can be summarized as follows. Firstly, tracked Macaroni penguins performed long looping trips north of Crozet towards a predictable large-scale frontal structure, the SAF. The similarity in their swimming direction strongly suggests a common use of oceanographic features. Secondly, during the central phase of their trip, the penguins slowed down and foraged inside large eddies, following a northeast flow. Overall, in accordance with our assumptions, the penguins adjusted their travel



speed and movement throughout their trips in relation to the oceanographic structures visited.

Use of large-scale circulation around the Crozet Archipelago

The foraging movements of Macaroni penguins toward the SAF demonstrate these diving predators use predictable, large-scale physical feature in agreement with our first assumption. This is consistent with the highest mean seabird species richness and diversity in the South Indian Ocean having been reported at the SAF [22]. This diversity and abundance is driven by the high concentration of chlorophyll-*a* and macro-zooplankton within the SAF, resulting from increased water column stability and availability of nutrients [23].

Recent *in situ* oceanographic sampling and remote sensing data [24] have shown that a predictable phytoplankton bloom occurs north of Crozet [25] each year in early September. North of Crozet, the SAF deviation creates a closed area with long residence time which allows dissolved iron from land or sediments of the Crozet plateau to fertilize the water during winter. These conditions enhance the development of the phytoplankton bloom [26, 27] which reaches a peak in late October i.e. during the period before the at-sea sojourns of incubating males tracked in our study. During this time, Macaroni penguins mainly feed on euphausiids, (primarily *Euphausia valentini* and *Thysanoessa macrura*), amphipods (*Themisto gaudichaudii*) and myctophid fish (*Krefflichthys anderssoni* spp.) [15, 16], which have been found in high concentrations within the PFZ [28-30].

Foraging behavior in meso- and sub-mesoscale structures

At a fine scale, individuals modified their swimming behavior when entering meso- (eddies) and sub-mesoscale (filaments) structures. In agreement with other diving predators [9, 10, 31], Macaroni penguins slowed down, suggesting they undertook more intensive foraging activity, during this phase characterized by an important eddy field. The greater relative abundance of young eddies in this phase compared to the two other phases confirms that the central phase is located in a branch of the SAF characterized by an important mixing activity [32]. Numerous studies have shown that several trophic levels of organism can aggregated within eddies [33, 34] and, through a cascading effect, many predators could benefit from this [10, 31, 35]. In addition, in this study, penguins showed no difference in heading velocity within and outside of eddies in the central phase, whereas currents were stronger and filamentary activity higher than in the other phases. We suggest that the prey field was extended at the spatial scale of the branch of the SAF and this hypothesis is coherent with the spatial structure of the annual phytoplankton bloom [36]. While it is

reasonable to assume that local variations of prey density exist at finer scale, at the sub-mesoscale, the sampled distance between locations (tens of km) was too large to detect variations in heading velocity responding to such prey distributions.

During outward and inward phases, penguins did not respond in the same way to the presence of eddies. Eddies were not visited in the outward phase since no changes of heading velocity were observed. However, a significant slow-down was shown in the inward phase within an eddy. As suggested by Cotté et al. [31], all eddies are not used and it would depend on their life-time and history. In our study, eddies in transit phases presented a retention time significantly higher than in the central phase. As eddy cores present a relatively poorly mixing environment [37], they retain nutrients and thus probably enhance biological productivity and prey aggregation. The weak currents inside the eddy cores may also explain the reduced travelling speed of individuals as they foraged inside these structures. Thus, the behavioral changes observed in the eddy during the inward phase could indicate that the eddy is profitable.

Concerning the sub-mesoscale activity, the central phase was also the area where the filamentary structure was the highest, confirming the dynamic character of the area. This is to be expected as filaments are mostly formed from eddy-eddy interactions [38]. Furthermore, once individuals were inside filaments, they slowed down more as the horizontal stirring increased. This is consistent with the trapping characteristics of these structures retaining chlorophyll and thus attracting species in the upper trophic levels [6, 39]. However, no difference was detected in swimming behavior inside and outside the filaments, in contrast to that observed with eddies. This may be due to several factors.

Firstly, crustaceans and fish are mobile in comparison to the phytoplankton patches which are transported by currents, which could induce a more dispersed spatial distribution outside the filaments. Secondly, these transport barriers are mostly located at eddy edges [37]. Thus, Macaroni penguins may have responded to the productivity associated with eddy characteristics and not to the filament properties (i.e. at a finer scale). Finally, any adjustment of movements by penguins to filament characteristics may not have been detected due to the spatial resolution of the datasets used (i.e. altimetry data at 0.33 ° and 1 week, GPS locations limited to 6 h intervals, tens of km).

Currents

Throughout the different phases of their foraging trips, Macaroni penguins exhibited marked shifts in their travel speed in relation to the current directions encountered. The heading velocities (HV) were generally much greater

than the fastest encountered currents ($>0.8 \text{ km} \cdot \text{h}^{-1}$). However, in areas where currents were fastest, 30 % of trip segments were associated with an HV of less than $1 \text{ km} \cdot \text{h}^{-1}$. This indicates a travel speed close to the current speed which strongly suggests individuals were drifting horizontally.

In marine predators, surface drift behaviors have been explained as a consequence of different processes. Firstly, current speeds may be similar to the swimming ability of the studied species. This results from the current's influence on the animals' trajectories [40]. Secondly, drift behavior could occur at night in daytime foragers resting during multi-day trips [17]. Thirdly, horizontal drift behaviors could be indicative of an increase in vertical foraging activity.

Finally, the maximum swimming speed of Macaroni penguins (up to $10 \text{ km} \cdot \text{h}^{-1}$ [41]) is high compared to the current speed. Hence, the low HV observed at the central phase of the foraging trips in the present study could correspond to an increase in diving activity resulting in passive horizontal movement (drift).

Association with the local currents could be a good way to minimize transports costs. Indeed, from the start of the breeding cycle until the creching phase, males have to endure two extended fasting periods. The first lasts ~35 d (i.e. from the arrival of the birds at the colony until their departure after the first long incubation period) and the second occurs at the end of their first post-incubating trip until the end of brooding (i.e. ~35 days [42, 43]). Thus, during their first post-incubation trip, males are highly energetically constrained as they have to restore their body condition and acquire enough reserves to prepare for the next fasting event. Consequently, individuals would gain significant energetic advantages by adopting behaviors that avoided swimming against currents. Our results support this hypothesis. Such behavior has been observed in other oceanic penguins (e.g. king penguins *Aptenodytes patagonicus*, Magellanic penguins *Spheniscus magellanicus*) at a time when they also need to quickly progress to favorable foraging areas [10, 44].

Conclusions

This work confirms the high dependence of Macaroni penguins on large-scale frontal zones such as the SAF in the Crozet area, a key breeding area for the species. This is the first demonstration of such strong dependence to the SAF for the Crozet Macaroni population. In addition, our study highlighted the role of currents and eddy activity on the foraging behavior of a diving predator. In future studies, the adjustment of movement behavior to filaments should be tackled at a finer scale with a more precise overlap between predator movements and the location of frontal structures. Investigating diving success in these structures would

be also of special interest. Furthermore, analysis of whether the drift behavior is actually associated with more intensive foraging should be undertaken, potentially using 3D movement data. Finally, it would also be important to know if such behavior is exhibited during other periods where penguins are subjected to other major energetic constraints such the creche phase or pre-moulting period [45].

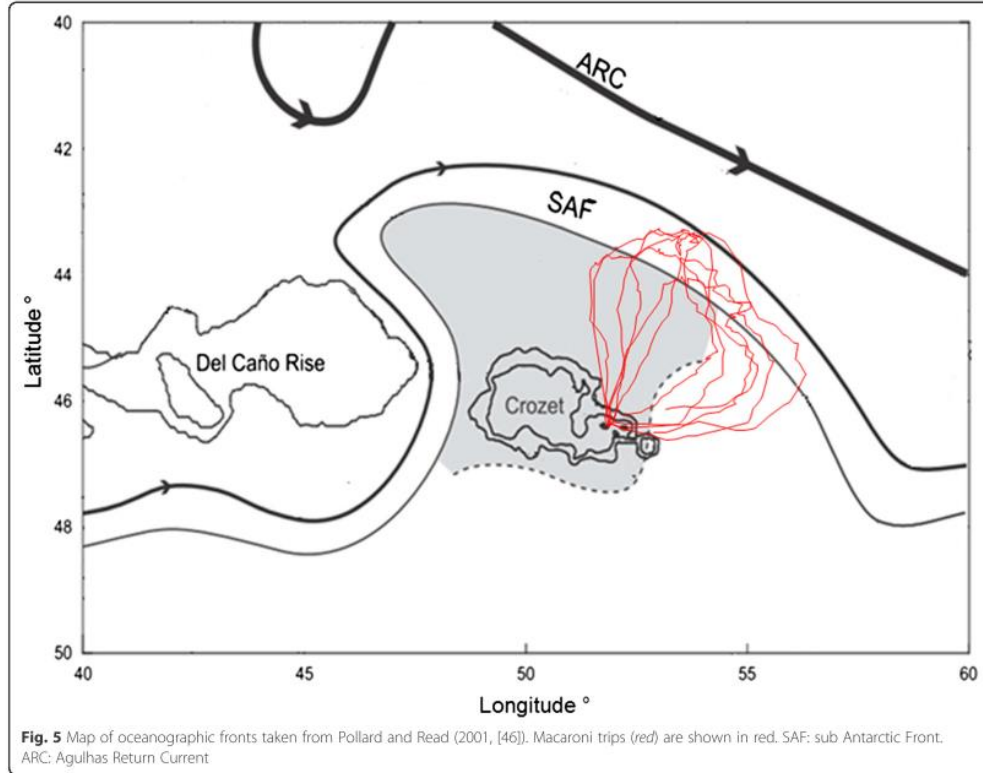
Methods

The study was carried out at the Jardin Japonais colony, Possession Island ($46^{\circ}21' \text{ S}$, $51^{\circ}43' \text{ E}$), Crozet Archipelago (hereafter, referred to as Crozet). The archipelago lies on the Crozet Plateau ($45\text{--}47^{\circ} \text{ S}$, $49\text{--}51^{\circ} \text{ E}$) (150 km of width, less than 500 m deep) and at the northern extent of the eastward flowing Antarctic Circumpolar Current (ACC) [36]. The Crozet Plateau deflects one of the current's major branches, the sub Antarctic Front (SAF), to the south of the Del Caño Rise before flowing northward under the influence of the local bathymetry. North of the plateau, it turns eastward under the influence of the Agulhas Return Current and the SubTropical Front [36]. The SAF is associated with strong eastward currents, located between 42 and 43° S , whereas a weak circulation dominates between the Crozet shelf and 44° S [25] (Fig. 5, [46]).

During the 2012 Austral summer, a total of 7 adult breeding males (incubation stage) were captured (20–21 November) before the departure for their first long trip. The penguins were instrumented with a GPS logger (Fastloc 2, Sirtrack, Havelock North, N.Z.) when leaving their colony. The devices were programmed to record location every 15 min. Each logger was attached to the lower dorsal feathers along the central mid-line, to minimize drag effects [47], with instantaneous cyanoacrylate glue (Loctite 401 Prism, Instant Adhesive, Hempstead, Hertfordshire, HP2 4RQ UK) and waterproof tape (Tesa 4651, Tesa Tape, Quickborn str 24, Hamburg 20253, Germany), and further secured by two cables ties. The duration of the instrumentation procedure lasted <15 min. All the birds were recaptured upon their return to the colony and the equipment removed.

Oceanographic data

Altimetry maps were obtained from the CNES/CLS AVISO website [48] with spatial and temporal resolutions of 0.33° and 1 week, respectively [49]. Altimetry was used to compute the velocity of horizontal currents and to identify sub- and mesoscale physical structures. The currents' velocities were compared with the velocity of penguins, called travelling velocity (TV), determined from GPS tracking, by computing the heading velocity (HV) [50], which is defined as: $V_{(\text{heading})} = V_{(\text{tracking})} - V_{(\text{currents})}$.



To identify sub- and mesoscale structures, we used Eulerian and Lagrangian diagnostics: the Okubo-Weiss (OW) parameter to identify eddies, the Finite Size Lyapunov Exponent (FSLE) to identify filaments, and the Retention Parameter (RP) to quantify for how long the water parcels within an eddy have been recirculating:

The Okubo-Weiss parameter OW [37, 51] is defined as:

$$W = sn^2 + ss^2 - \omega^2$$

where sn and ss are the normal and shear components of strain and ω is the relative vorticity of the flow. The sign of this parameter locates eddies as regions with negative OW parameters (vorticity is dominant) and background as oceanic regions of small negative and positive OW parameters (strain is dominant, absence of eddies). Following Bailleul et al. [9], we used the $W_o = 0.2\sigma_w$ (σ_w is the standard deviation of W in the whole domain) threshold to separate vorticity-dominated ($W < -W_o$, presence of eddy) regions from strain-dominated regions ($W \geq W_o$, absence of eddy) and the background field ($|W| \leq W_o$).

The Finite Size Lyapunov Exponents (FSLE) method provides a direct measure of the amount of local stirring by mesoscale currents. It can be used to identify transport barriers along which water parcels are stretched into elongated structures (hereafter, termed filaments), typically in the region between eddies [38]. The FSLE computes the backward-in-time divergence (i.e. convergence) of particles initially in close proximity to each other and is commonly used as an indicator of frontal activity and stirring intensity [52].

It is computed as:

$$\lambda(x, t, \delta_0, \delta_f) = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0}$$

Where δ_0 represents the initial separation of water parcels, and τ the time taken for the water parcels to reach a separation δ_f . For the present study, the parameters used for the calculation were $\delta_f = 0.6$ degrees, $\delta_0 = 0.01$ degrees and τ had a maximum limit of 100 days.

Highest FSLE values are associated to formerly distant water masses, whose confluence creates a transport front [52]. Here, we used $FSLE > 0.1 \text{ d}^{-1}$ as indicators of the presence of a transport front. FSLE ridges can represent the edges of mesoscale eddies but also the convoluted boundaries of sub-mesoscale filaments.

The Retention Parameter (RP) computes the backward trajectories of simulated water parcels from negative OW regions (i.e. eddies) and measures for how long each water parcel has been within the same OW negative patch. This quantity corresponds to the time the water has been recirculating within the eddy [37].

The SAF was identified as the 8°C sea surface isotherm during the period corresponding to the measured trajectories (22/11/2012–11/12/2012) [53, 54]. Sea Surface Temperature (SST) was obtained from the G1SST (Global 1-km Sea Surface Temperature) Level 4 product from GHRSSST (Group for High Resolution Sea Surface Temperature [55]). In addition, to provide context for primary production in the regions explored by the tracked penguins, we used sea-surface chlorophyll-*a* concentration data from GlobColour [56] with a daily average resolution of 9 km^2 .

Tracks analysis

A speed filter was applied on locations to delete speed data higher than $10 \text{ km} \cdot \text{h}^{-1}$, which is the maximum travel speed previously recorded by Macaroni penguins [41]. The temporal resolution of the oceanographic data limited us to subsample the tracks at four points per day. Therefore, we chose to keep locations closest to 04:00 h, 10:00 h, 16:00 h and 22:00 h (local time) which provided a 24 h cycle divided into $4 \times 6 \text{ h}$ periods.

It has been shown that penguins decrease their horizontal movements when increasing their foraging activity, especially during the central phase of their trip [3, 57]. Thus, trips were split into three phases according to the smoothed relation between the heading velocity and the elapsed time relative to the departure. First, the outward phase, indicating the journey between the island and the central phase, was defined as the initial contiguous period where the smoothed heading velocities were higher than the average heading velocity during the whole trip ($2.2 \pm 1.4 \text{ km} \cdot \text{h}^{-1}$, Table 1). Second, the central phase was defined as the period where the heading velocities were below the mean heading velocity. Finally, the inward phase, from the central phase to the colony, corresponded to an increase of the heading velocity. In addition, as Macaroni penguins forage less at night [13, 58], we excluded from the analyses the velocities between 22:00 and 03:00 which, respectively, correspond to local dusk and dawn [59]. Directions of penguins and currents they experienced (varying from 0 to 360°) were then computed

for each location using the Great Circle distance (*bearing* function, “geosphere” package).

The distribution of sub-mesoscale structures were investigated in two ways. Firstly, we looked at “the distribution of eddies within each trip phase” computed as $\frac{n_{\text{locs-eddies in trip phase}}}{n_{\text{locs-eddies on the whole trip}}} \times 100$ for each trip phase respectively. $n_{\text{locs-eddies}}$ indicates the number of locations within an eddy. Secondly, we looked at the “degree of association with eddies” computed as $\frac{n_{\text{locs-eddies}}}{n_{\text{locs in trip phase}}} \times 100$, for each trip phase respectively. Same ratios were computed for investigating filaments distributions.

Statistical analysis

All analyses were conducted in the R statistical environment [60]. We used circular statistics (“circular” package) to determine the average bearing of currents and animals within each phase and assess the correlations between currents and animal directions. A Mann–Whitney *U* test (“stats” package) was used to compare the behavior of penguins within and outside of eddies or filaments. Following these descriptive analyses, different linear mixed effects models (*lme* function, “nlme” package) were constructed. For all models, individuals were included as a random effect as each location within individuals was not independent. The autocorrelation of residuals was tested (*acf* function) and consequently an autoregressive term of order 1 (coAR1) was included.

The best model was selected using the Akaike criterion (AIC [61]). Firstly, to investigate the response behavior to occurrence of eddies within each trip phase, three mixed models (one by trip phase, called M1, M2, M3) were built with the heading velocity as response variable and the factor “occurrence of eddies” (explanatory binary variable: absence or presence). Secondly, another model was built to link the variation of heading speed to the occurrence of frontal structures (explanatory binary variable: absence or presence). This model (not presented) had an AIC higher than the null model and the weak number of filaments within the outward and inward phases prevented us from building one model per trip phase. Thus, we looked at the relation of heading velocity (response variable) with the FSLE values (explanatory variable) when penguins were inside filaments ($FSLE > 0.1$, model called M4). Finally, we tested the influence of currents (explanatory variable) on the travelling speed (response variable, model called M5). The different studied parameters are presented as Mean $\pm$ Standard Deviation (SD) whereas coefficients of models are presented as Mean $\pm$ SE (Standard Error). AIC deviations of tested models from the null models are shown. Results were considered significant at $P < 0.05$.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

CB analysed the trajectories, performed the statistical analysis and drafted the manuscript. AD handled the oceanographic products, created the oceanographic maps and assisted with the analyses. FO helped in obtaining oceanographic products, helped design the study and to draft the manuscript. JA provided devices, participated in discussion of the results and helped to draft the manuscript. TP participated in the field work and data processing. CAB conceived of the study, helped develop the design, coordinated the study and helped to draft the manuscript. All authors read and approved the final manuscript.

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References

- Hunt GJ, Mehlum F, Russell R, Irons D, Decker M, Becker P. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Proceedings of the 22th International Ornithological Congress, vol. 22. Durban: Adams, NJ, Slotow RH; 1999. p. 2040–56.
- Tew Kai E, Marsac F. Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Prog Oceanogr*. 2010;86:214–23.
- Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, et al. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser*. 1997;150:21–33.
- Tynan CT. Cetacean distributions and oceanographic features near the Kerguelen Plateau. *Geophys Res Lett*. 1997;24:2793–6.
- Lévy M, Ferrari R, Franks PJS, Martin AP, Rivière P. Bringing physics to life at the submesoscale: FRONTIER. *Geophys Res Lett*. 2012;39:L14602.
- d' Ovidio F, De Monte S, Alvain S, Dandonneau Y, Lévy M. Fluid dynamical niches of phytoplankton types. *Proc Natl Acad Sci*. 2010;107:18366–70.
- Bradshaw CJ, Higgins J, Michael KJ, Wotherspoon SJ, Hindell MA. At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES J Mar Sci J Cons*. 2004;61:1014–27.
- Cotté C, d' Ovidio F, Chaigneau A, Lévy M, Taupier-Letage I, Mate B, et al. Scale-dependent interactions of Mediterranean whales with marine dynamics. *Limnol Oceanogr*. 2011;56:219–32.
- Bailleul F, Cotté C, Guinet C. Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Mar Ecol Prog Ser*. 2010;408:251–64.
- Cotté C, Park Y-H, Guinet C, Bost C-A. Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B Biol Sci*. 2007;274:2385–91.
- Lowther AD, Lydersen C, Biuw M, de Bruyn PJJ, Hofmeyr GJG, Kovacs KM. Post-breeding at-sea movements of three central-place foragers in relation to submesoscale fronts in the Southern Ocean around Bouvetøya. *Antarct Sci*. 2014;26:533–44.
- Mde Brooke L. The food consumption of the world's seabirds. *Proc R Soc B Biol Sci*. 2004;271:5246–8.
- Green K, Williams R, Green MG. Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. *Mar Ornithol*. 1998;26:27–34.
- Pichegru L, Robert-Coudert Y, Kato A, Takahashi A, Dyer BM, Ryan PG. Diving patterns of female macaroni penguins breeding on Marion Island, South Africa. *Polar Biol*. 2011;34:945–54.
- Cherel Y, Hobson KA, Guinet C, Vanpe C. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol*. 2007;76:826–36.
- Ridoux V. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Oceanogr Lit Rev*. 1995;12:1128.
- Barlow KE, Croxall JP. Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Prog Ser*. 2002;232:291–304.
- Thiebot J-B, Cherel Y, Trathan PN, Bost C-A. Inter-population segregation in the wintering areas of macaroni penguins. *Mar Ecol Prog Ser*. 2011;421:279–90.
- Crossin G, Trathan P, Crawford R. Macaroni Penguin (*Eudyptes chrysolophus*) and Royal Penguin (*Eudyptes schlegelii*). In: Boersma PD, Borboroglu PG, editors. *Penguins: Natural History and Conservation*. Seattle: University of Washington Press; 2013. p. 185–208.
- Reid K, Croxall JP. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc R Soc B Biol Sci*. 2001;268:377–84.
- Tew Kai E, Rossi V, Sudre J, Weimerskirch H, Lopez C, Hernandez-Garcia E, et al. Top marine predators track Lagrangian coherent structures. *Proc Natl Acad Sci*. 2009;106:8245–50.
- Abrams RW. Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean. *J Biogeogr*. 1985;12:473–92.
- Venables HJ, Pollard RT, Popova EE. Physical conditions controlling the development of a regular phytoplankton bloom north of the Crozet Plateau, Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr*. 2007;54:1949–65.
- Pollard R, Sanders R, Lucas M, Statham P. The Crozet Natural Iron Bloom and Export Experiment (CROZEX). *Deep Sea Res Part II Top Stud Oceanogr*. 2007;54:1905–14.
- Sanial V, van Beek P, Lansard B, d' Ovidio F, Kestenare E, Souhaut M, et al. Study of the phytoplankton plume dynamics off the Crozet Islands (Southern Ocean): A geochemical-physical coupled approach. *J Geophys Res Oceans*. 2014;119:2227–37.
- Pollard RT, Lucas MJ, Read JF. Physical controls on biogeochemical zonation in the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr*. 2002;49:3289–305.
- Planquette H, Statham PJ, Fones GR, Charette MA, Moore CM, Salter I, et al. Dissolved iron in the vicinity of the Crozet Islands, Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr*. 2007;54:1999–2019.
- Pakhomov EA, McQuaid CD. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol*. 1996;16:271–86.
- Pakhomov EA, Froneman PW. Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Mar Biol*. 1999;134:501–15.
- Koubbi P. Influence of the frontal zones on ichthyoplankton and mesopelagic fish assemblages in the Crozet Basin (Indian sector of the Southern Ocean). *Polar Biol*. 1993;13:557–64.
- Cotté C, d' Ovidio F, Dragon A-C, Guinet C, Lévy M. Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Prog Oceanogr*. 2014;131:46–58.
- Kostianoy AG, Ginzburg AI, Lebedev SA, Frankignoulle M, Delille B. Fronts and mesoscale variability in the southern Indian Ocean as inferred from the TOPEX/POSEIDON and ERS-2 altimetry data. *Oceanology*. 2003;43:632–42.
- Riandey V, Champalbert G, Carlotti F, Taupier-Letage I, Thibault-Botha D. Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep Sea Res Part Oceanogr Res Pap*. 2005;52:2029–48.
- Landy MR, Decima M, Simmons MP, Hannides CC, Daniels E. Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep Sea Res Part II Top Stud Oceanogr*. 2008;55:1378–88.
- De Monte S, Cotté C, d' Ovidio F, Lévy M, Le Corre M, Weimerskirch H. Frigatebird behaviour at the ocean-atmosphere interface: integrating animal behaviour with multi-satellite data. *J R Soc Interface R Soc*. 2012;9:3351–8.

36. Pollard RT, Venables HJ, Read JF, Allen JT. Large-scale circulation around the Crozet Plateau controls an annual phytoplankton bloom in the Crozet Basin. *Deep Sea Res Part II Top Stud Oceanogr.* 2007;54:1915–29.
37. d' Ovidio F, De Monte S, Penna AD, Cotté C, Guinet C. Ecological implications of eddy retention in the open ocean: a Lagrangian approach. *J Phys Math Theor.* 2013;46:254023.
38. Lapeyre G, Klein P. Impact of the small-scale elongated filaments on the oceanic vertical pump. *J Mar Res.* 2006;64:835–51.
39. Lévy M. The modulation of biological production by oceanic mesoscale turbulence. In: *Transport and Mixing in Geophysical Flows*. Berlin Heidelberg: Springer; 2008. p. 219–61.
40. Gaspar P, Georges J-Y, Fossette S, Lenoble A, Ferraroli S, Le Maho Y. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc R Soc B Biol Sci.* 2006;273:2697–702.
41. Brown CR. Traveling Speed and Foraging Range of Macaroni and Rockhopper Penguins at Marion Island (Velocidad de Movimiento y Extensión de las Áreas de Forrajeo de los Pinguinos Eudyptes chrysolophus y E. chrysocome). *J Field Ornithol.* 1987;118–125.
42. Williams TD, Croxall JP. Annual variation in breeding biology of macaroni penguins, *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J Zool.* 1991;223:189–202.
43. Stahl J-C, Derenne P, Jouventin P, Mougín J-L, Teulieres L, Weimerskirch H. Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le gorfou macaroni et *Eudyptes chrysocome*, le gorfou sauteur. *Oiseau Rev Française Ornithol.* 1985;55:27–43.
44. Raya Rey A, Bost C-A, Schiavini A, Pütz K. Foraging movements of Magellanic Penguins *Spheniscus magellanicus* in the Beagle Channel, Argentina, related to tide and tidal currents. *J Ornithol.* 2010;151:933–43.
45. Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ. Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol.* 2009;40:529–38.
46. Pollard RT, Read JF. Circulation pathways and transports of the Southern Ocean in the vicinity of the Southwest Indian Ridge. *J Geophys Res Atmospheres* 2001, 106:2881–2898.
47. Bannasch R, Wilson RP, Culik B. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol.* 1994;194:83–96.
48. AVISO 2013 Ssalto/Duacs User Handbook: M(SLA) and M(ADT) Near-Real Time and Delayed-Time Products, Edition 3.4 (www.aviso.oceanobs.com).
49. Le Traon PY, Nadal F, Ducet N. An improved mapping method of multisatellite altimeter data. *J Atmos Ocean Technol.* 1998;15:522–34.
50. Girard C, Sudre J, Benhamou S, Roos D, Luschi P. Homing in green turtles *Chelonia mydas*: oceanic currents act as a constraint rather than as an information source. *Mar Ecol Prog Ser.* 2006;322:281–9.
51. Weiss J. The dynamics of enstrophy transfer in two-dimensional hydrodynamics. *Phys Nonlinear Phenom.* 1991;48:273–94.
52. d' Ovidio F, Fernández V, Hernández-García E, López C. Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophys Res Lett.* 2004;31:L17203.
53. Orsi AH, Whitworth T, Nowlin WD. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res Part Oceanogr Res Pap.* 1995;42:641–73.
54. Park Y-H, Gamberoni L, Charriaud E. Frontal structure, water masses, and circulation in the Crozet Basin. *J Geophys Res Oceans* 1978–2012. 1993;98:12361–85.
55. Group for High Resolution Sea Surface Temperature (www.ghrsst.org)
56. GlobColour (www.globcolour.info)
57. Pütz K, Ropert-Coudert Y, Charrassin JB, Wilson RP. Foraging areas of King penguins *Aptenodytes patagonicus* breeding at Possession Island, southern Indian Ocean. *Mar Ornithol.* 1999;27:77–84.
58. Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD. Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J Zool.* 1993;230:31–47.
59. Sun or Moon Rise/Set Table for One Year (http://aa.usno.navy.mil/data/docs/RS_OneYear.php)
60. The R Foundation for Statistical Computing 2013 (www.r-project.org)
61. Burnham KP, Anderson DR. Multimodel inference understanding AIC and BIC in model selection. *Sociol Methods Res.* 2004;33:261–304.

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ANNEXE A2

Foraging strategies of Macaroni penguins at Crozet islands during the breeding season

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Abstract

Although penguins are major consumers of the marine resources, few studies have investigated their foraging strategies over the whole breeding cycle, relative to the constraints imposed by breeding on their at-sea foraging behaviour. Macaroni penguin is still considered as the main abundant penguin of the world and the largest marine biomass consumer. Although Crozet archipelago (46.42° S; 51.86° E) is a strong hold location for the species, knowledge of their foraging strategies during the breeding season is still poorly known. In this study, we characterized at-sea distribution, diving activity, and trophic level of Macaroni penguins in relation with the environmental features and the energetic requirements imposed by the breeding stage (incubation, brood and crèche). Data concern breeding birds equipped with GPS or TDRs over 3 breeding seasons (2009/2010, 2012/2013, 2013/2014). First we showed during the incubation period, males performed long looping trips directed toward the sub Antarctic Front. Females realized shorter directed trips linked with the net primary productivity distribution. During the brood period, females performed short successive trips between the shelf and mesopelagic waters. During the crèche, they increased their foraging range and dived deeper. Inter-individual variability of trips was especially important in males. This study highlighted how the oceanographic factors drive the penguins foraging strategies of males. Females seem to be more driven by the breeding duties. The adjustment of foraging strategies and the distribution of the annual phytoplanktonic bloom occurring north of Crozet according to the breeding stage are discussed.

Introduction

Marine resources are distributed heterogeneously in space and time, and are generally related to spatial heterogeneity in physical, chemical and bathymetric features of the marine environment (Hunt et al. 1999). Because marine productivity is not uniformly distributed, prey distribution is patchy and the

predictability of the patches depends on the physical processes responsible for their formation at different spatial and temporal scales (Hunt & Schneider 1987). Thus, the distribution of prey will strongly affect the predators at-sea distribution and their related foraging behavior and costs (*e.g.* Weimerskirch et al. 2005, Grémillet et al. 2008). Seabirds are central place foragers and the separation of their foraging at-sea zones and

breeding colonies is one of their fundamental life-history constraints (Pennycuik et al. 1984, Weimerskirch 2007). Effectively locate favorable areas is thus crucial during the breeding season because seabird must limit their transit time to favorable patches.

This especially concerns non-flying, diving predators such penguins which are highly constrained because of their limited foraging range (Costa 1991). Such these predators strongly depend of predictable prey distribution (Cotté et al. 2007, Bost et al. 2009) during the breeding season when the energetic requirements are the highest (Ricklefs 1983, Green et al. 2007, 2009). Despite their major role in the food webs of the Southern ocean (Brooke 2004), a limited number of studies have concerned penguins foraging strategies over the whole breeding cycle (Kirkwood & Robertson 1997, Charrassin & Bost 2001, Barlow & Croxall 2002a, Zimmer et al. 2008) and the constraints imposed by breeding on their at-sea distribution and foraging behavior (Green et al. 2005).

Macaroni penguin (*Eudyptes chrysolophus*) is still considered as the most abundant of penguins (Crossin et al. 2013) and the largest marine biomass consumer (Brooke 2004). Their foraging strategies have been extensively studied in the South Atlantic (South Georgia: Green et al. 1998, 2005, 2007, 2009, Barlow & Croxall 2002a, PN Trathan 2006), South Indian ocean (Marion island: Pichegru et al. 2011), Heard (Klages et al. 1989, Green et al. 1998, Trebilco 2004, Deagle et al. 2008), Bouvet (Blanchet et al. 2013). All these studies have shown a strong effect of breeding constraints on the penguins' foraging behavior and energetic balance predicting an high dependence to profitable foraging areas. Indeed, it has been shown that energetic constraints are high concerning females during the chick rearing period since the feeding rate has to be increased and foraging ranges restricted. However few studies have been able to describe the detailed aspects of the foraging movements, diving activity and prey choice over the whole breeding cycle.

Although Crozet islands may host more than 35% of the world population (Crossin et al. 2013), at sea foraging behavior during the breeding period has not been investigated yet and the only available data concern the diet and trophic level during the chick rearing period (Ridoux 1995, Cherel et al. 2007).

During incubation (~35days), both sexes successively undertake long foraging trips (~13days) while the partner stayed on land incubates. After hatching (15-21th December), females regularly returns to the colony to feed the chick whereas males fast and guard it (brooding phase, ~25 days). Once chick emancipate (~9 January), females continue to regularly feed them. Males undertake long trips at sea to build up their fat reserves and then start to feed on the offspring until the end of February. The rearing period last about 70 days at Crozet (Stahl et al. 1984). In this context, we investigate for the first time the at-sea foraging strategies of Macaroni penguins at Crozet Islands during the entire breeding season in relation with the environmental features.

Our aim was first to describe and estimate at sea distribution and diving activities of breeding macaroni penguins in relation with the energetic requirements imposed by the breeding stage (incubation, brood and crèche). Secondly, we investigated which oceanographic areas are targeted by the birds in order to understand how their foraging strategies are adjusted to the marine environmental features, which play a role in marine productivity, at several temporal and spatial scales.

We predicted that i) Macaroni penguins will adjust their foraging movements in relation to the foraging time (distant and long trips in incubation and crèche, short range trips during the brooding phase as observed in other localities: ii) Macaroni penguins will target predictable areas of different profitability as shelf break, large eddies or frontal zones according to breeding time and their own energetic needs, i.e. deal with the balance between the body condition and the chick provisioning, iii) Finally, we predict a temporal adjustment between the at-sea movements of penguins and the phytoplankton bloom from year to year.

Methods

Study site. The study was carried out at Jardin Japonais, Possession Island (46°21' S, 51°43' E), Crozet Archipelago, hereafter referred to as Crozet. Deployments were carried out from November to February over three breeding seasons, 2009/2010, 2012/2013 and 2013/2014 season (Table 1). Adult

penguins relieved from breeding duties were captured before their departure at sea.

To investigate the foraging movements, a total of 64 deployments were instrumented either with a GPS (49 individual, Fastloc 2, Sirtrack, Havelock North, N.Z.) either with a PTT 15 individuals, Kiwisat 202, Sirtrack, Havelock North, N.Z.). The PTTs had a transmission interval of 45 s. GPS were programmed to record location every 15 minutes. The total number of individuals trips used here was 45 because of technical failures or data download problems (32% of individuals equipped in incubation and brooding, 15% in crèche). To investigate the diving behavior, another group of birds was equipped with a time-depth recorder (MK9, Wildlife Computers, Redmond, WA, USA, 64Mb, sampling rate: 1s, accuracy: 0.1m) in 2009/2010 (n=6: 3 incubating and 3 brooding) and 2012/2013 (n=3, 1 brooding and 2 in brooding and crèche) season, respectively. Detailed information on the birds equipped (year, sex, breeding stage) is summarized in table 1. Each logger was attached to the lower dorsal feathers along the central mid-line to minimize drag effects (Bannasch et al. 1994) that have deleterious effect on penguins energetic balance (Wilson et al. 1986). The instruments were glued on the penguins' back with instantaneous cyano-acrylate glue (Loctite 401 Prism, Instant Adhesive, Hempstead, Hertfordshire, HP2 4RQ UK) and waterproof tape (Tesa Tape, Quickborn str 24, Hamburg 20253, Germany) and securized by two cables ties. The duration of the instrumentation procedure did not exceed 15 min. All the birds were recaptured upon their return to the colony and the equipment removed.

The variation of mass was investigated using weight of penguins from a control group. These birds were marked by a small black number on the chest (*Loréal* hair dye). Over the three seasons, a total of 213 weights were obtained between the 20th november and the 17th February.

Data processing and tracks analysis. All following analysis were conducted on the R environment (Version 3.1.2, "The R Foundation for Statistical Computing 2013"). All class Z locations were removed from ARGOS datasets. Then, tracks were speed filtered (function *speedfilter* , package 'trip') with a criterion of $8 \text{ km} \cdot \text{h}^{-1}$ which is maximum travel

speed previously recorded by Macaroni penguins (Whitehead et al. 2016). Some locations were not deleted by the speed filter although the associated travel speed was higher than the criterion (up to $15 \text{ km} \cdot \text{h}^{-1}$ less than 0.45% of locations, $n_{\text{locs}_{\text{total}}} = 16741$). We removed these locations in order to ensure that locations with large error were removed. Two types of loggers were used but it is known that trips characteristics might be biased by the logger system (Kuhn et al. 2009). Excepted some 5 GPS records containing lag > 10h, the time lag between ARGOS location was longer (84.3 ± 190.2 mins, range: 2 – 4089 mins) than GPS time lag (23.2 ± 32.0 mins, range: 3-860). Thus, we re-sampled GPS locations to the interval sampling of PTT loggers which encompass 80% of locations (either 100mins). A bias of logger type has been demonstrated on the travel speed estimation which disappears when computed on a single daily location (Kuhn et al. 2009) and so the travel speed was daily estimated.

Descriptive comparisons of the trips characteristics (range, travelling speed, travelled distance, duration, directions) were performed, when available, between years and sexes within each breeding stage. All distances from the colony refer to great circle distances. Elongation coefficient (EC) was computed for each trip using the ratio: $\text{EC} = \frac{\text{standardized (range)}}{\text{standardized (surface area)}}$ with range the maximal distance from the colony (km). As Range and surface areas were very variable between breeding stages, we standardized them at the trip scale using the mean and standard deviation of the appropriated breeding stage. The surface area was estimated by creating a convex hull on all the locations (function *hull*, package 'grDevices') then transformed in a polygon (function *SpatialPolygons*, package 'sp') taking account of the spatial projection. Surface area unit is km^2 . EC varies between 0.4 and 14. More EC tend to 0, the more the trip is circular.

Trip comparisons between years were performed on incubating females since tracks of males were available on one single year. Inter-annual comparisons were not possible during brooding as the timing of deployment differed between years. Deployments on brooding birds were performed from 15th to 17th December in 2009, from 18th to 20th December 2012 and from 17th to 21th December

2013. The analysis of the at-sea departure of a control group of females showed that the brood phase was extended from 12th December to 3th January for the three years. Equipment in season 09 was done on birds with very small chicks whereas the others periods were realized when chicks were bigger. As macaroni penguins potentially increase their foraging range in relation to chick growth (Barlow & Croxall, 2002b), the observed difference in range was probably skewed by the timing of the equipment. Thus, we analyzed the range' variation considering the 3 years as a single brooding season.

Dives analysis. Diving data were analyzed using Multi Trace-Dive (©Jensen Software Systems, Laboe, Germany). The threshold value to detect dive events was 3m. The distribution of maximal dives depths (n= 127626) was nearly bimodal and break point was estimated at 12m (function *segmented*). In order to be able to compare foraging diving behavior with other localities, we choose the very close threshold of 10m (Pichegru et al. 2011). We used this criteria to distinguish shallows dives (<10m) considered as travelling dives and deep dives (>10m) considered as foraging dives. In this study, we only focused on foraging dives (n=60855). Several parameters were determined such as maximal depth, descent phase, bottom phase (time within the dive spent between 75 and 100% of the maximum dive depth and have to last more than 15% of the total dive duration), ascent phase, post-foraging dive surface intervals, number of wiggles (*i.e.* deviation of the dive profile during which at three points the vertical speed passes below 0m s⁻¹) (Tremblay & Cherel 2000, Halsey et al. 2007). Concerning the sequential structures of deep dives (called thereafter bouts), 90% of the distribution of post-dives surface intervals values were normally distributed under 60s. By contrast, the scope was very large beyond this threshold (up to 10000s). Thus, a period of 60s was used as threshold to define diving bouts.

Oceanographic data. Oceanographic data are collected over a broad area (km or more) whereas GPS instruments have accuracy of the order of the meter. In consequence, all tracks were re-sampled at the main sampling interval of ARGOS data, either 100min (80% of the value). Tracks were then gridded on cells of 0.2°×0.2° in order to calculate time spent

per cell which is a reliable proxy of foraging success (Bost et al. 1997).

The selected non-correlated environmental variables included in our habitat models were bathymetry, seafloor slope, sea surface height (SSH), geostrophic currents and primary production. Sea surface height and geostrophic currents were quantified through an altimetry multi-satellite global product (Delayed Time Maps of Sea Surface Height products, All Satellites, daily resolution) developed by CNES/CLS Aviso (<http://www.aviso.oceanobs.com>). Net primary production (NPP) was determined using the Vertical Generalized Production Model (VGPM, standard product available Ocean Productivity). NPP is computed with the following equation:

$$NPP = Chl \times Pb_{opt} \times day_length \times f(par) \times z_{eu}$$

with *NPP* are milligrams of carbon fixed per day per unit volume, *Chl* the chlorophyll *a* concentration, *z_{eu}* the euphotic layer depth, *day_length* the number of hours of daylight at the location of interest, *f(par)* the ratio of realized water column integrated NPP to themaximum potential NPP if photosynthetic rates were maintained at maximum levels (*Pb_{opt}*) and *Pb_{opt}* the daily net primary production found within a given water column (photosynthetic efficiency). *Pb_{opt}* is described as a function of sea surface temperature (SST).

SST was included in the original set of environmental variables considered for the habitat models, but eliminated from the dataset due to high correlations with SSH. We choose to keep SSH as a predictor in our models as it allows direct interpretation in terms of frontal zones of the Antarctic Circumpolar Current (Sokolov & Rintoul 2009, Venables et al. 2012). Distance from the colony was included as a model parameter to take into account the constraints of central-place foragers travelling from the colony for foraging, making distant habitats more costly to reach in terms of travel time and energy. All products were determined with a 0.2° resolution and then averaged on the periods of each track.

In order to investigate the spatial and temporal evolution of NPP (net primary productivity) values with time, NPP values was averaged each 0.2° between 46.3° and 42° S on 3° of longitude (50° and

54°E, Figure 3, grey box). We then investigated the variation of NPP values with distance from the colony on this segment within 4 successive periods: 1- from 20th November to 12th December 2012 (males at sea foraging) , 2- from 7th to 20th December 2012 (females at sea foraging), 3 from 20th December 2012 to 3th January 2013 (brooding period) and 4: from 4th January to 15th January 2013 (crèching females at-sea foraging) .

Statistical analysis.

Tracks and dives. In order to compare the characteristics of trips and dives between sexes or years within each breeding stage, parametric (one-way analysis of variance) or non-parametric (Kruskal-Wallis test, Mann-Whitney test) were used by respect of normality and homoscedasticity hypothesis (package "Stats"). Circular statistics were used to deal with directions and angles variables (package "Circular"). Coefficient variation ($CV = \frac{s}{|x|} \times 100$ with s standard deviation and x the mean EC of the individual) was used to investigate the repeatability of trips, only realized on individual with multiple trips available (>2) in the dataset (in brood or crèche stage). The differences of mass over the breeding season were investigating using Wilcoxon signed-ranked tests. The different studied parameters are presented as Mean $\pm$ Standard Deviation (SD).

Relation with oceanographic features. Mixed models (function *lme*) were built to put in relation the time spent (response variable) per cell with oceanographic variables (covariables) using the package "nlme". Generalized additive models were tested but curves were almost linear, thus linear mixed model were preferred. Response variable was squared-transformed to correspond to the normal distribution. Covariates were standardized at the trip scale in order to compare coefficients within the model. A model was built per breeding stage and sex in order to point out the relationships with oceanographic environment. The following procedure was realized for each case: before including covariables in the full model, we tested the correlation between them (Spearman correlation test). If R^2 was superior to 0.8, we removed the less pertinent covariable to avoid multi-collinearity. All

combinations were realized and models were ranked using their AICc (package "MuMIn"). AICc has a correction term for small samples but converges to AIC when sample size is large (Burnham & Anderson 2004). Once models were ranked, variation of AICc was used to select the best model. In all cases, we get more than one best model (with a variation of $AICc < 2$). We used therefore the model averaging procedure on all models with an Akaike weight (probability for each model to be selected as best model) inferior to 0.95. This procedure allows to calculate the mean of the coefficient for all models weighted by their Akaike weight (Burnham & Anderson 2004). Any mean of coefficients inferior to its standard error was indicated it as non-significant (NS).

Random effects were included since each location within individuals and trips were not independent. When we get successive trips for one individual (brood and crèche stages), we tested a nested effect (trips within individual). However, the individual variance was always very low (close to 0) in comparison to trip effect. Thus, only trip was considered as random effect. Nested effect of trips within year was added when necessary. Validation of model was realized by graphical examination of residuals, and relation with covariables. Results were considered significant when $p < 0.05$.

RESULTS

Trips characteristics.

Incubation. Equipped males left the colony on 22th November in 2012 and 2013 seasons during at-sea trips lasting on average 18.33 ± 2.2 days . Males exhibited long, remote and looping trips headed toward the north, very similar between birds (Figure 1). After relieved by males, instrumented females started to leave the colony on the 29 November in 2009/2010, 7th December in season 2012 and 2013 . They foraged during 11.8 ± 2.1 days, performing trips relatively directional (Figure 1). Males distributed at greater distance than females ($F_{1,11} = 8.6, p < 0.05$) during longer trips ($W = 36, p < 0.001$), and had an higher traveling speed (Mann-Whitney $W = 524784, p < 0.001$, Table 2). Elongation coefficient of males were smaller than for females in relation to

the circular shape of their trips ($W=41$, $p<0.01$, Table 2).

Females range was similar between 2009/2010 and seasons 2012, 2013 ($X^2=2.75$, $df=2$, $p=0.25$). Likewise the total travelled distance did not differ ($F_{2,4}=2.08$, $p=0.24$), as well trip duration ($X^2=1.35$, $df=2$, $p=0.50$) travelling speed (Mann-Whitney $W=352622$, $p=0.68$) and directions ($W_{atson-wheeler}=6.81$, $df=4$, $p=0.15$).

Brooding. Instrumented females started to leave on about the 12th December in 2009/2010 and on 20th December in the two other seasons (2012/2013, 2013/2014). Brooding females foraged at a mean maximal distance of 31.6 ± 18.4 from the colony (range: 3 - 97.7km) during trips lasting 1.2 ± 0.8 days. A quadratic relation of the distance from colony with time was observed, increasing from the 12th to 26th December (Spearman test: $R^2=0.73$, $p<0.001$) and then decreasing up to the 3th January (Spearman test: $R^2=-0.64$, $p<0.001$). Travel speed of females was significant higher than during the incubation stage (Wilcoxon test $W=232207$, $p<0.001$). The distribution of trips directions was not uniform (Watson's Test for circular uniformity: $p<0.05$) and their directions were broadly similar between birds ($325.5 \pm 27.7^\circ$, $n_{trips}=51$).

Elongation coefficient was significantly smaller than during incubation ($X^2=6.0$, $p<0.05$; Post-hoc Multiple comparison test: $EC_{brood} \neq EC_{incubation}$) and did not differ significantly between birds ($X^2=7.05$, $p=0.32$).

For each bird having performed several consecutive trips (>2), we computed the coefficient variation (CV) to estimate the dispersion of the coefficient elongation around the mean. CV differed a lot between birds (range: 43– 115%) suggesting that each bird performed successively different forms of trips (Kruskal-Wallis $X^2=11.21$, $p=0.08$).

Crèche. The first penguins were equipped on average on the 3rd January on the three studied years. Females foraged at greater distance than during the brood phase (79.5 ± 35.5 km, range: 20.69 - 130.13km, Mann-Whitney $W=188$, $p<0.001$) with same pattern ($X^2=15.8$, $p<0.001$; Post-hoc Tukey test: $EC_{brood}=EC_{crèche}$, $p=0.87$, Table 2). EC did not

significantly differ between birds which performed successive trips (Kruskal-Wallis $X^2=1.0$, $p=0.62$).

By contrast, males performed very different trips according to the individuals. Three patterns occurred: i) short trips headed north ($n=5$, direction: $296.4 \pm 16.6^\circ$, mean: 52.8 ± 11.4 km, range: 40.3-68.0 km), ii) northern long trips ($n=3$, direction: $48.4 \pm 43.8^\circ$, mean: 234.2 ± 140.8 km, range: 119.5-391.3km), and southern headed trips ($n=6$, direction: $210.2 \pm 5.6^\circ$, mean 251.2 ± 49.8 km, range: 198.6 - 332.9 km, Figure 1). Long trips were all performed at the beginning of crèche. Long south trips ($EC=4.6 \pm 2.67$) were the most directional trips with respect to the others (Kruskal-Wallis $X^2=10.0$, $p<0.05$; Post-hoc test: $EC_{north\ long} \neq EC_{sud}$).

Distribution of marine productivity.

The map of NPP distribution over the breeding season and contemporaneous penguins' tracks is presented in Figure 2 (Season 2012/2013). The highest values of NPP in period 1 (incubation, males at-sea) and 2 (incubation, females at-sea) were between 250 and 450 km (323.5 ± 33.3 mgC/m²/day, Spearman $R^2=0.90$, $p<0.001$). These values were considerably higher in period 2 (459.14 ± 84.52 mgC/m²/day, Mann-Whitney $W=0$, $p<0.001$, Figure 3). This indicates a southward migration of the bloom. NPP distribution was different according to the year. Thus in 2009/2010, NPP was homogeneously distributed north of Crozet and was considerably higher (twice higher) than those recorded in the two other seasons (Kruskal-Wallis $X^2=3484.7$, $p<0.001$).

A significant increase of NPP occurred in the first 150km close to colony ($F_{2,18}=10.6$, $p<0.001$) within period 3 (brood) and 4 (crèche). Concerning the two other seasons (2009/2010 and 2012/2013), there was also a significant increase of NPP in the first 150km of the colony during the seasons (Season 09: $F_{2,18}=94.4$, $p<0.001$; Season 13: $F_{2,18}=148$, $p<0.001$).

Relation between oceanographic features and penguins tracks

Incubation. Final mixed models of the time spent per cell with oceanographic variables are summarized in

the table 3. In incubation stage, time spent per cell of males was positively related with the increase of NPP values, currents speed indicating that they targeted frontal structures. Females strongly increased their foraging time with the increase of SSH and gradient of NPP. For the both sexes, the time spent per cell was positively correlated with the bathymetry, which was highly correlated with distance from the colony (not included in the models).

Brood period. Bathymetry and its gradient had the most important effect on time spent per cell, following by the distance from the colony. Birds increased their foraging time with these variables and it was maximal when bathymetry was of $1200 \pm 830\text{m}$. A relative homogeneity of NPP values occurred on areas prospected by penguins (Season 2009/2010: $1105.14 \pm 40.26 \text{ mgC/m}^2/\text{day}$; Season 2012/2013: $359.52 \pm 15.340 \text{ mgC/m}^2/\text{day}$; Season 2013/2014: $480.42 \pm 55.92 \text{ mgC/m}^2/\text{day}$, Figure 2).

Crèche. The bathymetry was the only variable which had an effect on the time spent per cell for females. Males performing short trips increased their foraging time with the increase of depth and NPP gradients. Males which performed long headed north trips responded positively to the increase of bathymetry but individual effect was important (33.4%). This suggests that each individual had its own response with the oceanographic variables. Finally, concerning the trips headed south, relationships with bathymetry, NPP and SSH were all negative. This contrasts with the previous stages. In this case, all birds have increased their foraging time in the most southern part of their tracks, whatever the NPP distribution. This latest was higher near the colony than in offshore waters.

Diving behavior.

Dive scale. Diving behavior did not differ according to the three breeding stage in terms of bottom duration, diving efficiency, number of diver per hour and averaged number of foraging dives per day (table 4). Dive depth followed a quadratic relationship with day hour with shallow depths performed at night (All dives: 26.7 ± 26.5 , Deep dives: 42.6 ± 25.2) and deeper dives during day (All dives: dawn: $44.5 \pm 28.3\text{m}$ day: $39.5 \pm 25.3\text{m}$ dusk :

$5.2 \pm 2.0 \text{ m}$; Deep dives: dawn: $49.3 \pm 26.4\text{m}$ day: $46.3 \pm 22.2\text{m}$, dusk : $10.3 \pm 0.2 \text{ m}$, Figure 5a). In parallel, deep dive rate was also the most important during dusk and at the end of daylight (Figure 5b).

Bout and day scales. The number of foraging dives realized during daylight per day no significantly change according to the breeding stage (incubation= 193 ± 80 , brood= 177 ± 78 , crèche= 163 ± 60) whereas more foraging dives were performed at night in brood and crèche (incubation= 22 ± 11 , brood= 45 ± 27 , crech= 41 ± 23 , Kruskal-Wallis $X^2=20.11$, $p<0.001$, Post hoc multiple comparisons : Dive rate_{incubation} $\neq$ Dive rate_{brood & crèche}). Likewise the dives were deeper and longer with the advance of the breeding season, from $41.77+19.56\text{m}$ ($118+26\text{s}$) in incubation to $49.9+22.41 \text{ m}$ ($133+27\text{s}$) in crèche (Model A, B, Figure 5c, table 5). The majority of deep dives were mostly included in bouts for the three stages, (incubation: 96.5% brood: 95.2% crèche:94.5 %). In brood and crèche, females realized less bouts per day than during incubation (Model C, table 5). The diving bouts were significantly longer (Model D, table 5) with a trend to have more dives but it was not significant.

Trip scale. We observed that depth dive (Y) followed a quadratic relation with time spent since departure(x) (regression equation of a linear mixed model: $Y = 34.36 + 2.47x - 0.14x^2$, $p<0.001$, $\Delta_{\text{AIC.null}} = -110.18$, $n_{\text{obs}}=8358$, random effect: individual) with averaged depth which varies from $34.39 \pm 13.92\text{m}$ at the beginning and end of trips to $52.90 \pm 18.72\text{m}$ in the middle of the trip.

Body mass changes. Body mass changes are summarized in the table 2. Just before leaving the colony, incubating females weighted $2778 \pm 176\text{g}$ ($n=10$, 3th – 7th December). During their at-sea trips, they gained $\sim 985\text{g}$ (BM: $3763 \pm 346\text{g}$, $n=67$, 15-23th December), i.e. $\sim 35\%$ of body mass. From the beginning of brood stage, there was a significant increase of the BM during the first 6 days and then a decrease up to the start of the crèche stage (Linear mixed model: $Y=3433+116x-8x^2$, $\Delta_{\text{AIC2ndModel}}=-7.9$, $n_{\text{obs}}=99$, year effect: 22%, x: days since the start of brood stage). Close to the starting of crèche, females had a body mass of 3555 ± 367 corresponding to a loss of about 5.5% from the brood start ($n=20$, 3rd – 8th January). After the 8th January, the body mass

tend to increase with time, up to 8% , but the difference with the end of brood stage was not significant (BM: $3835 \pm 409\text{g}$, $n=10$, January: 14th Jan – 8th February). Moreover, a significant year effect was found since all females were heavier in 2009/2010 at the beginning of brood ($> 300\text{g}$) and crèche stage ($>400\text{g}$) than in 2012/2013 and 2013/2014 (Kruskal Wallis test: Brood start: $\chi^2=11.64$, $p < 0.01$, Crèche start: $\chi^2=7.56$, $p < 0.05$).

When leaving the colony to forage, males relieved for incubation duties weighted $3243 \pm 188\text{ g}$ ($n=16$, 20-22th November). No data could be obtained concerning their at-sea return. At the beginning of brood stage, males had an increased body mass ($3465 \pm 305\text{g}$, $n=30$, 17-22th December) and lost weight (~3%) up to the start of crèche ($3354 \pm 285\text{g}$, $n=12$, 3-8th January). From the beginning of crèche to the end of January, males increased their body mass by about 33% (BM: 4477 ± 626 , $n=48$, 13 – 31st January). Females were significantly heavier than males at the end of brood stage (Mann Withney $W = 234$, $p < 0.05$, 30th December – 8th January). This relation reversed during the crèche (Mann Withney $W = 89.5$, $p < 0.01$, 13th January – 02nd February).

Isotopical signature. The nitrogen isotopic signatures of males was of $8.3 \pm 0.4\text{‰}$ ($n=4$) at the incubation stage and was significantly higher at the crèche stage, $8.8 \pm 0.1\text{‰}$ ($n=3$, $F_{1,5}=6.82$, $p < 0.05$). Females had no higher nitrogen signature ($8.7 \pm 0.2\text{‰}$, $n=7$) during the incubation and brood stages ($n = 17$, $F_{1,22}=0.28$, $p=0.60$).

DISCUSSION

This study has been focused on the foraging behaviors exhibited by Macaroni penguins during an entire breeding cycle on Crozet archipelago. We studied tracking and diving data get from Argos, GPS and time depth recorder loggers deployed on males and females on three different years. Coupled with oceanographic data, masses and isotopic signatures, it allowed us to better understand how they adjust their foraging behavior to the oceanographic features in face to their energy constraints. These dataset allowed us to improve our knowledge about breeding foraging strategies of Macaroni penguins in one of the most important breeding locality.

Phenology

At sea departure dates of breeding macaroni penguin observed in our study is coherent with findings from previous studies performed during the eighties on the Crozet islands (Stahl et al. 1984). Variations of hatching date between season 09 and the two others correspond to the time range ever already observed (15 – 21 December). The delay is surely the consequence of the laying period which lasts 16 days on Crozet Island (Stahl et al. 1984). This suggests that this timing difference between seasons is more due the date of presence of fieldworker and not the consequence of any inter-annual variation

Comparisons of foraging trips between incubation, brood and crèche

Incubation. At the incubation stage, Macaroni penguins performed long and remote trips from colony; all headed North West, toward the sub Antarctic Front (SAF). They slowed during the central part of their trips in an area dominated by strong eastward currents coming from the SAF, as demonstrated in previous studies (Bon et al. 2015, Pollard, Venables, et al. 2007a). Females also travelled toward the SAF but stayed in the polar frontal zone (PFZ) without reaching the SAF for the three studied seasons. From November to mid-December, the NPP values increased, being higher at lower latitudes, close to the SAF, suggesting that penguins target productive areas going north (Figure 2,3).

This at-sea distribution is consistent the predictable and phytoplankton bloom which occurs north of Crozet (Pollard, Sanders, et al. 2007, Sanial et al. 2014) each year in early September. The Crozet plateau features constitutes a physical barrier to the Antarctic Circumpolar current, inducing a deviation of the sub-Antarctic front (SAF) that leads to the creation of a closed area with long residence time. During winter, waters are fertilized by dissolved iron or sediments from land or of the Crozet plateau (Pollard, Sanders, et al. 2007, Pollard, Venables, et al. 2007a, Sanial et al. 2014). This sustains a phytoplankton bloom with variable concentrations observed from September to January (Venables et al. 2007). The North of Crozet seems thus an highly productive area during the summer as indicated by

its attractiveness for several top predators such as albatrosses (Weimerskirch et al. 1993, Delord et al. 2013).

Importantly the progression of the productive area from the northern to the southern latitudes is consistent with adjustment of the penguins at-sea movements from the beginning to the end of the incubation period. We indeed observed a southward displacement of the bloom from mid-November (long trips of males), to mid-December (long but shorter incubation trips of females, Figure 3). The advection of productivity close to the colony is mainly due to an anti-cyclonic flow around the Crozet plateau which advects chl-*a* around the western side of the plateau (Pollard, Venables, et al. 2007a, Venables et al. 2007). These annual increase of primary production provides an important food resources for herbivores and predators, which could see their growth rates considerably increase in this period (Alonzo et al. 2002), conferring to the area a strong attractive power for the upper trophic levels. Moreover, chl-*a* was significantly correlated to zooplankton abundance on the SAF on Prince Edward Islands confirming that these waters should be very attractive for crustaceans eater (Froneman & Pakhomov 1998).

Otherwise, males have responded positively to the increase of geostrophic currents indicating they increase their foraging activity in frontal areas with high turbulence (Figure 4). The SAF is characterized by an important mixing activity (Kostianoy et al. 2003) characterized by mesoscale and sub-mesoscale structures (eddies, filaments) aggregating patches of resources for top predators (Pakhomov & McQuaid 1996, Riandey et al. 2005, Landry et al. 2008). At the incubation stage, females dived on average at depths of 42±20m during day time with some variations between the beginning and central part of trips (from 34m to 52m). The main foraging part of penguins are generally located during the central phase of their trips (Bon et al. 2015, Charrassin & Bost 2001, Bost et al. 1997). Thus, favorable areas targeting spatially by Macaroni penguins could also be areas where preys are at the deeper depths. Going closest to the SAF, waters masses become warmer with a driving of cold waters (Park et al. 1993) which could influence also the

vertical distribution of their prey. Macaroni penguins from Crozet island foraged on average at 42m in incubation. Their foraging depths are similar to those of the Marion Island situation where penguins encompass similar environmental conditions at the northern part of their area (Pichegru et al. 2011), *i.e.* deeper than dives performed in South Georgia, Heard and Kerguelen islands which are located further south in colder waters (Sato 2004, Green et al. 2005, Deagle et al. 2008).

In incubation, macaroni penguins from Crozet mainly feed on euphausiids (primarily *Euphausia valentini* and *Thysanoessa macrura*), amphipods (*Themisto gaudichaudii*) and in smaller proportion, myctophid fish (*Krefftichthys anderssoni*, Cherel et al. 2007, Ridoux 1995) which are resources found in high concentrations within the SAF and the PFZ (Pakhomov & McQuaid 1996, Pakhomov & Froneman 1999, Koubbi et al. 2011). Vertical distribution of myctophids fishes, which mainly feed on copepods, euphausiids and hyperiid amphipods (Pakhomov et al. 1996), is highly correlated with the latitude. For example, *K. anderssoni* was found between 50 and 150 south of the PF whereas it is not caught before 1000m near the Subtropical Convergence (Hulley 1981). As the Crozet islands are further north than most other colonies, this could explain why Macaroni penguins have to dive deeper here. Referring to trawl studies realized in Prince Edward sector, the most important abundance of *E. valentini* and *T. gaudichaudii* (>150m) were deeper than the maximum depth observed in our study (135m) (Perissinotto & McQuaid 1992). However, recent acoustic cruise have found that zooplankton could be found at lower depth, in the top 100m, but with low densities, confirming that these preys are spread along a gradient beginning on depths foraged by penguins (Bedford et al. 2015). Moreover, these preys show a clear patterns of diel vertical migration with exploited depths of 100 and 250m in daytime and <100m at night with a dense abundance of *E. valentini* between 20 and 50m at dusk (Perissinotto & McQuaid 1992, Pakhomov et al. 1994). Macaroni penguins from Crozet islands all exhibited a diel vertical migration pattern which begins before dawn and end after the dusk (Figure 5a). Dive rate was also the most important between 4 and 8:00 and just before the dusk (21-22:00)

whereas it was nearly null at night (Figure 5). This confirms their daily adjustment to the daily migrations of crustaceans and myctophids schools.

Brood. After hatching (12 – 20th December), females performed multi short and highly directional trips close to the colony, all headed north-west. This characteristic of shorter, closer trips at chick hatching hatch is common in most of the penguins (Williams & Rothery 1990, Bost et al. 1997, Croxall & Davis 1999, Collins et al. 1999, Barlow & Croxall 2002a, PN Trathan 2006, Deagle et al. 2008).

In comparison to incubation, females have to regularly feed the chicks to ensure his survival. They are highly temporally constrained to find food in depend of their body condition since they lose weight and travel significantly faster than in incubation. This suggests that energy expended by females was greater than the energy content of the diet, after subtraction of food to fed to the chick (Green et al. 2007). This constraint is also shown by their diving behavior since they performed longer bouts than in incubation, which last more than 30 minutes and were composed of twice as many dives than during incubation.

All females foraged in North West and respond negatively to bathymetry and associated gradient (Figure 1). Maximal bathymetry of areas prospected varied between 68m and 3200m indicating foraging activities realized as on the shelf than in pelagic waters. No response to NPP values was detected but the distribution of NPP was homogeneous and high on the visited area for the 3 years studied, in response to the southward migration of bloom located northern in incubation (Figure 2,3). Brooding birds still mainly fed on macro-zooplankton with however higher proportions of myctophids fish (17.5%) than in incubation (8.5%) (Ridoux 1995). Isotope analysis showed that Macaroni penguins here studied (2009/10 breeding season) have however a nitrogen signature (8.7 ± 0.2 ‰) more relevant of myctophids diet (~ 7.5 ‰ Cherel et al. 2010). There is a discrepancy between nitrogen signature and crustaceans proportions found in stomach sample in previous studies which exceeds 70% of the bulk (Ridoux 1995, Cherel et al. 2007). This signature could be due to different environmental conditions which lead to a more

important availability of myctophids. Such variations of diet composition have ever been observed in other localities and are coherent with the species adjustment abilities (Klages et al. 1989, Green et al. 1998, Crawford et al. 2003).

In this work, an important range of bathymetry was exploited indicating that birds foraged from the shelf to pelagic waters. We suggest that bloom movements and spreading close to the islands could advect important stocks of resources close to the island shelf. At Prince Edward Is., it has been hypothesized that that strong wind action on Ekman layer could rapidly advects surface water on shelf, bringing with it the pelagic fish and crustaceans which were located near the surface at night. As wind is relatively strong on Crozet islands (Weimerskirch et al. 2012), we can hypothesize that similar process appear near the Crozet shelf.

Crèche. When crèche begins, females continue to intensively forage for chicks and continue to exhibit directional trips, north headed, and in averaged twice as far than in brood (Figure 1). Only response to bathymetry was positive. This appears obvious since this variable is fixed features and highly correlated with the distance from the colony. No other relationship with oceanographic features was found. As during the brooding stage, area foraged by females exhibits values of NPP with a weak variation (Figure 2). NPP values were significantly more important in the 100km north of Crozet than during brooding, still suggesting an important availability of food to top predators (Figure 3). From incubation to crèche, Macaroni penguins shifted from a mainly crustaceans diet to a more fish-diet, mainly composed of myctophids which dive deeper than crustaceans (Ridoux 1994) which could explain why dive depth increases with the season. Although these preys are epi- and mesopelagic (Croxall et al. 1985, Fraser et al. 1989, Duhamel et al. 2000), there are accessible when they vertically migrate in the water column, at dawn and dusk (Perissinotto & McQuaid 1992).

Changes in range and diving behavior in response to variability in diet or season is common in penguins. At Marion and Heard islands, Macaroni penguins have increased the proportions of fish and squids in their diet with the breeding season whereas they

dive deeper and foraged further from the colony (Brown & Klages 1987, Green et al. 1998, Deagle et al. 2008).

As brooding period, crèche is a period of high energy expenditure and food intake (Green et al. 2009). In crèche, females continue to intensively feed on chicks which have more important energetic requirement in reason to his growth. Moreover, although the male is at sea, females still deliver more meals (59%) to the chick than males (41%, Barlow & Croxall 2002b). Thus, females seem to adjust their foraging behavior by performing successive short trips and diving deeper to catch more calorific preys (myctophids, Croxall et al. 1984, Cherel & Ridoux 1992). This adjustment may both ensure the energy requirement of the chick and maintain a body condition on a basal level. However we observed that females have increased their body mass just at the beginning of crèche whereas their loss of body mass during the brood stage was very low (5%). These observations contrast with the weight variation observed in South Georgia, where females considerably lose weight during brood and the beginning of crèche in contrast with other localities (Croxall 1984, Green et al. 2009). This indicates that the stocks of resources close to Crozet islands at this period is probably very important and highly profitable for females.

Males did not adopt the same strategy. After a 25 days fast, males started long trips leaving their crèched chick. They performed very different trips according to the individuals, looping to the north or long headed trips. Concerning the long north trips, responses to environments features were different between the three birds. This could be explained by the important difference in prospected areas which suppose that encountered oceanographic environment differed. However, the three studied birds targeted areas with relative important values of geotropic currents indicating they both target meanders of the SAF (Figure 5). In contrast, the birds which traveled toward the south presented very similar trips all directed toward the Antarctic polar front (Figure 1) and seem to target the same foraging area. These birds negatively respond to SSH and NPP when they are far from colony indicating that they may respond to other oceanographic features, not

detected such eddies. It has been shown that King penguins used actively eddies in this region (Cotté et al. 2007). Otherwise, Macaroni penguins come closer to the Polar Front. The Polar Frontal Zone and PF provide high concentrations of myctophids where they are at lower depth than near the SAF (Hulley 1981, Pakhomov et al. 1994). Antarctic fur seals and King penguins which are myctophids specialist eater also target the PF during their breeding seasons (Bost et al. 1997, Guinet et al. 2001, Cherel et al. 2007). Males could adopt such behaviour, *i.e.* long trips directed to frontal areas, to respond to their need to recover their body condition after a long fast period. This area seems very profitable for Macaroni penguins since they strongly forage south of this area during the pre-moult hyperphagic trip (Thiebot et al. 2014, Whitehead et al. 2016).

Five trips were performed very close to the colony. These behaviors are similar to those exhibited by females at this stage. These short trips show that resources are still available near the colony, but probably in preys with lower nutritive values than myctophids, as crustaceans, since fishes are mostly found over deeper waters, further from the islands (Perissinotto & McQuaid 1992). Acoustic analyses have shown that zooplankton stocks remain consistent between brood and crèche in the column water suggesting that there were no depletion of resources near the islands (Bedford et al. 2015). In Crozet, occurrence of shorts trips (males and females) and long ones appear to have to respond to two different constraints. Long foraging trips might involved in reserves recovery, with a foraging behaviour concentrated on nutritive preys located in meso-pelagic waters. The short trips could be related to provisioning the chick.

However, we observed a increase of range (3 to 130km) with the advance in chick-rearing stage. As Macaroni penguins are highly synchronous in their breeding cycle (Stahl et al. 1984), this suggest that the gradual distance from the colony could be a response of females to avoid inter-individual competition on a stock of resources which may decreases near the colony ("*ashmole halo*", Ashmole 1963). However, if short trips of males are mainly devoted to provisioning the chick, it indicates that resources are still available close the colony. Thus,

females could increase their foraging range in order to increase their probability to hunt myctophids which are found in higher stock far from the island. The number of individual is too low to get a clear answer and we cannot exclude this hypothesis that the two mechanisms (hunting strategy and individual competition pressure very close to the colony) are both acting.

Variability inter–intra birds. During the brooding, EC were very variable within individuals suggesting that females exhibited trips which were successively different. In parallel, we observed a loss of weight, characteristic of the species at this stage (Green et al. 2009), confirming that this period is also costly for females from Crozet Island. Different successive trips could be a strategy for females to minimize competition between birds which all forage in a small area. Green et al. (2009) has estimated that foraging success of brooding penguins from Bird Island would be lower than in crèche. In Crozet, the mean range travelled is similar to those observed in Bird island. If the foraging success of Crozet penguins is also lower than for trips performed in crèche, females may change of locations between trips in order to limit competition, and increase their chance of find more food (Barlow & Croxall 2002b, Trathan et al. 2006).

In contrast, in incubation, males and all females, excepted one, display the same sexual pattern whereas their trips were conducted in offshore areas. Estimated foraging success is high at this period (Green et al. 2009). As Macaroni penguins from Crozet island also gain significantly mass during this period and forage same areas, we can suggest that competition between birds is low in incubation when birds target distant areas of high marine productivity.

Adjustment to marine productivity

At the incubation stage, males performed highly circular trips whereas females, excepted one, travelled more directly and less far. Males have to recover from the pre-incubation period and prepare one other. Males may minimize foraging costs by using the currents associated to the SAF to drift and minimize costs of swim (Bon et al. 2015).

Two hypothesis dealing with the difference of trips exhibited by males and females in incubation can be done. First, as females swim slower than males, it could be more costly to reach the same foraging areas than males and take too much time in regards to the breeding constraints. Otherwise, males can dive deeper than females (Green et al. 2005). It could be less costly for them to go to warmer waters where preys may be deeper.

Another hypothesis could be associated with the southward migration of the annual bloom occurring north of Crozet (Pollard, Venables, et al. 2007b). Interestingly, the NPP values in the most northern areas foraged by females (between 200 and 350km north of Possession island) have considerably increased, up to 1.5 times in comparison with the NPP observed when males were at-sea (Figure 3). This southward migration of bloom could be an advantage for females which have not to forage as far as males since preys are available closer and which have lower swimming abilities. Moreover, since the beginning of incubation, NPP values near the colony are maximal when the brood stage starts. We observed at Crozet Island a very good match between spatial productivity and trips destination.

The Match hypothesis (Cushing 1969, 1990, see Durant et al. 2007), hypothesize that recruitment in a population (*i.e.* of predator) will be high if the most energetically part of the breeding season occurs at the same time as the peak availability of the lower trophic level (*i.e.* preys).

Transcript to spatial scale, the hypothesis assumes that reducing the distance to forage increase the food availability per units time since travel time is decreased (Durant et al. 2007). Macaroni chicks hatch when the NPP values are the highest close to the colony, corresponding to a relative good synchronicity between productivity and energetic constraints of adults. This adjustment of breeding phenology to spatial distribution of marine resources is well known in seabirds (*e.g.* Ashmole 1963, Lack 1969 Durant et al. 2004). At Crozet islands, the bloom has, in part, physical origin and is annually predictable (Venables et al. 2007). This suggests that inter-annual environmental variations would not too much affect its development. To our knowledge, time lag between a bloom of chlorophyll and the

development/growth/attraction of upper trophic levels is weak. However, in Crozet, we know that adults of the euphausiid *E.vallentini* mate from mid-August to late December with maximum breeding activity from mid-September to late November (Ridoux 1988). It was hypothesized that post-furciliac stages (body length: 10mm) could be reached in two months whereas sub-adults (body length: 21.5mm) stage 4.5 months after mating. These stages are mainly found from December to late January. *E.vallentini* juveniles are mainly herbivorous whereas adults seem to be more omnivorous (Gurney et al. 2002) and they probably take advantage of the biological productivity. During breeding season, Macaroni penguins mainly feed on preys with sizes between 10 and 50mm and this corresponds to juveniles and adults sizes of *E.vallentini* (Ridoux 1988, 1995). We observe there a very good temporal synchronicity between the bloom development, the population growth of *E.vallentini* and then the timing of at-sea foraging trips of Macaroni penguins. The mismatch between the development bloom and the beginning of incubating trips is coherent with the *Euphausiid* growth observed by Ridoux (1994). Although Macaroni penguins do not exclusively feed on *E.vallentini*, we can hypothesize that other crustaceans, as *T.gaudichaudii* benefit of the bloom development and the grazers associated.

Conclusion

On Crozet islands, Macaroni penguins foraging strategies show a strong adjustment with the oceanic productivity at the spatial and temporal scale. The birds target specific areas depending of the season and their breeding requirements with some shifts in their diets as in other localities. Macaroni penguin foraging provide a fruitful study case model of temporal relation between time of primary resources production and the breeding phenology of a top marine predator. We also can hypothesize that Macaroni penguins which have started their breeding season when preys abundance was maximal had a better breeding success. Bloom development and associated biotic productivity could have been factors involved in actual breeding phenology through natural selection mechanisms which could have advantaged penguins starting to breed early November. Besides that, global warming leads to an increase of temperatures of sea surface waters. On long term, this may not provide a viable

environment for zooplankton and fishes and may probably have consequences on their distribution in the Crozet basin, and thus on the foraging success of Macaroni penguins (Peron et al. 2012)

Bibliography

- Alonzo F, Mayzaud P, Razouls S, Bocher P, Cherel Y (2002) Seasonal changes in biomass, growth rates and production of subantarctic calanoid copepods in the Bay of Morbihan, Kerguelen Islands. *Mar Biol* 142:525–536
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473
- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- Barlow KE, Croxall JP (2002b) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Prog Ser* 232:291–304
- Barlow KE, Croxall JP (2002c) Provisioning behaviour of Macaroni Penguins *Eudyptes chrysolophus*. *Ibis* 144:248–258
- Bedford M, Melbourne-Thomas J, Corney S, Jarvis T, Kelly N, Constable A (2015) Prey-field use by a Southern Ocean top predator: enhanced understanding using integrated datasets. *Mar Ecol Prog Ser* 526:169–181
- Blanchet M-A, Biuw M, Hofmeyr GG, Bruyn PN de, Lydersen C, Kovacs KM (2013) At-sea behaviour of three krill predators breeding at Bouvetoya-Antarctic fur seals, macaroni penguins and chinstrap penguins. *Mar Ecol Prog Ser* 477:285–302
- Bohec CL, Durant JM, Gauthier-Clerc M, Stenseth NC, Park Y-H, Pradel R, Grémillet D, Gendner J-P, Maho YL (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci* 105:2493–2497
- Bon C, Della Penna A, Ovidio F d', Y.P. Arnould J, Poupart T, Bost C-A (2015) Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. *Mov Ecol* 3:32
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33
- Brooke M de L (2004) The food consumption of the world's seabirds. *Proc R Soc Lond B Biol Sci* 271:S246–S248

- Brown CR (1987) Traveling Speed and Foraging Range of Macaroni and Rockhopper Penguins at Marion Island (Velocidad de Movimiento y Extensión de las Áreas de Forrajeo de los Pingüinos *Eudyptes chrysolophus* y *E. chrysocome*). *J Field Ornithol* 58:118–125
- Brown CR, Klages NT (1987) Seasonal and annual variation in diets of Macaroni (*Eudyptes chrysolophus*) and Southern rockhopper (*E. chrysocome*) penguins at sub-Antarctic Marion Island. *J Zool* 212:7–28
- Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Charrassin JB, Bost CA (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar Ecol Prog Ser* 221:285–297
- Cherel Y, Fontaine C, Richard P, Labatc J-P (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol Oceanogr* 55:324–332
- Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol* 76:826–836
- CHEREL Y, RIDOUX V (1992) Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–127
- Collins M, Cullen JM, Dann P (1999) Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. *Wildl Res* 26:705–721
- Costa DP (1991) Reproductive and Foraging Energetics of High Latitude Penguins, Albatrosses and Pinnipeds: Implications for Life History Patterns. *Am Zool* 31:111–130
- Cotté C, Park Y-H, Guinet C, Bost C-A (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B Biol Sci* 274:2385–2391
- Crawford RIM, Cooper J, Dyer BM (2003) Population of the Macaroni Penguin *Eudyptes Chrysolophus* at Marion Island, 1994/95–2002/03, with Information on Breeding and Diet. *Afr J Mar Sci* 25:475–486
- Crossin G, Trathan P, Crawford R (2013) Macaroni Penguin (*Eudyptes chrysolophus*) and Royal Penguin (*Eudyptes schlegeli*). In: *Penguins: Natural History and Conservation*, University of Whashington Press. P.D. Boersma and P.G. Borboroglu, Seattle, p 185–208
- Croxall JP (1984) Seabirds. In: *Antarctic Ecology*, Cambridge University Press, Cambridge, p 531–616
- Croxall JP, Davis LS (1999) Penguins: paradoxes and patterns. *Mar Ornithol* 27:1–12
- Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW (1985) Fur Seal Diving Behaviour in Relation to Vertical Distribution of Krill. *J Anim Ecol* 54:1–8
- Croxall JP, Ricketts C, Prince PA (1984) Impact of Seabirds on Marine Resources, Especially Krill, of South Georgia Waters. In: Whittow GC, Rahn H (eds) *Seabird Energetics*. Springer US, p 285–317
- Cushing DH (1969) The regularity of the spawning season of some fishes. *J Cons* 33:81–92
- Cushing D (1990) Plankton Production and Year-Class Strength in Fish Populations - an Update of the Match Mismatch Hypothesis. *Adv Mar Biol* 26:249–293
- Deagle BE, Gales NJ, Hindell MA (2008) Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. *Mar Ecol Prog Ser* 359:295–309
- Delord K, Barbraud C, Bost CA, Cherel Y, Guinet C, Weimerskirch H (2013) Atlas of top predators from French Southern Territories in the Southern Indian Ocean. CEBC-CNRS
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biol* 23:106–112
- Durant JM, Anker-Nilssen T, Hjermann DO, Stenseth NC (2004) Regime shifts in the breeding of an Atlantic puffin population. *Ecol Lett* 7:388–394
- Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res* 33:271–283
- Fraser WR, Pitman RL, Ainley DG (1989) Seabird and fur seal responses to vertically migrating winter krill swarms in Antarctica. *Polar Biol* 10:37–41
- Froneman PW, Pakhomov EA (1998) Biogeographic study of the planktonic communities of the Prince Edward Islands (Southern Ocean). *J Plankton Res* 20:653–669
- Green JA, Boyd IL, Woakes AJ, Green CJ, Butler PJ (2007) Feeding, fasting and foraging success during chick rearing in macaroni penguins. *Mar Ecol Prog Ser* 346:299–312
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during year-round foraging in macaroni penguins. *Mar Ecol Prog Ser* 296:183–196
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538
- Green K, Williams R, Green MG (1998) Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. *Mar Ornithol* 26:27–34
- Grémillet D, Lewis S, Drapeau L, Der Linden CD van, Huggett JA, Coetzee JC, Verheye HM, Daunt F, Wanless S, Ryan PG (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *J Appl Ecol* 45:610–621
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonadonna F, Donnay J-P (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-

- p>dependent approach using geographic information systems.
- Mar Ecol Prog Ser*
- 219:251–264
- Gurney LJ, Froneman PW, Pakhomov EA, McQuaid CD (2002) Diel feeding patterns and daily ration estimates of three subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep Sea Res Part II Top Stud Oceanogr* 49:3207–3227
- Halsey LG, Bost C-A, Handrich Y (2007) A thorough and quantified method for classifying seabird diving behaviour. *Polar Biol* 30:991–1004
- Hulley PA (1981) Results of the research cruises of FRV Walther Herwig to South America. LVIII. Family *Myctophidae* (Osteichthyes, Myctophiformes). *Arch Fischwiss* 31:1–300
- Hunt GJ, Mehlum F, Russell R, Irons D, Decker M, Becker P (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proceedings of the 22th International Ornithological Congress*. Adams, NJ, Slotow RH, Durban, p 2040–2056
- Hunt GL, Schneider DC (1987) Scale-dependent processes in the physical and biological environment of marine birds. *Seab Feed Ecol Role Mar Ecosyst*:7–41
- Kirkwood R, Robertson G (1997) Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. *Mar Ecol Prog Ser* 156:205–223
- Klages N, Gales R, Pemberton D (1989) Dietary Segregation of Macaroni and Rockhopper Penguins at Heard Island. *Wildl Res* 16:599–604
- Kostianoy AG, Ginzburg AI, Lebedev SA, Frankignoulle M, Delille B (2003) Fronts and mesoscale variability in the southern Indian Ocean as inferred from the TOPEX/POSEIDON and ERS-2 altimetry data. *Oceanology* 43
- Koubbi P, Moteki M, Duhamel G, Goarant A, Hulley P-A, O'Driscoll R, Ishimaru T, Pruvost P, Tavernier E, Hosie G (2011) Ecoregionalization of myctophid fish in the Indian sector of the Southern Ocean: Results from generalized dissimilarity models. *Deep Sea Res Part II Top Stud Oceanogr* 58:170–180
- Kuhn CE, Johnson DS, Ream RR, Gelatt TS (2009) Advances in the tracking of marine species: using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar Ecol Prog Ser* 393:97–109
- Landry MR, Decima M, Simmons MP, Hannides CC, Daniels E (2008) Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep Sea Res Part II Top Stud Oceanogr* 55:1378–1388
- L. Brooke M de (2004) The food consumption of the world's seabirds. *Proc R Soc B Biol Sci* 271:S246–S248
- Lescroël A, Bost C-A (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Mar Ecol Prog Ser* 302:245–261
- Pakhomov EA, Froneman PW (1999) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Mar Biol* 134:501–515
- Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol* 16:271–286
- Pakhomov EA, Perissinotto R, McQuaid CD (1994) Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar Ecol Prog Ser Oldendorf* 111:155–169
- Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar Ecol Prog Ser Oldendorf* 134:1–14
- Park Y-H, Gamberoni L, Charriaud E (1993) Frontal structure, water masses, and circulation in the Crozet Basin. *J Geophys Res Oceans* 1978–2012 98:12361–12385
- Pennycuik CJ, Croxall JP, Prince PA (1984) Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Ornis Scand*:145–154
- Perissinotto R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean Archipelago. *Mar Ecol Prog Ser Oldendorf* 80:15–27
- Peron C, Weimerskirch H, Bost C-A (2012) Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc R Soc B Biol Sci* 279:2515–2523
- Pichegru L, Ropert-Coudert Y, Kato A, Takahashi A, Dyer BM, Ryan PG (2011) Diving patterns of female macaroni penguins breeding on Marion Island, South Africa. *Polar Biol* 34:945–954
- Pinaud D, Cherel Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Mar Ecol Prog Ser* 298:295–304
- PN Trathan CG (2006) Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Mar Ecol-Prog Ser* 323:239–251
- Pollard R, Sanders R, Lucas M, Statham P (2007) The Crozet Natural Iron Bloom and Export Experiment (CROZEX). *Deep Sea Res Part II Top Stud Oceanogr* 54:1905–1914
- Pollard RT, Venables HJ, Read JF, Allen JT (2007a) Large-scale circulation around the Crozet Plateau controls an annual phytoplankton bloom in the Crozet Basin. *Deep Sea Res Part II Top Stud Oceanogr* 54:1915–1929
- Pollard RT, Venables HJ, Read JF, Allen JT (2007b) Large-scale circulation around the Crozet Plateau controls an annual phytoplankton bloom in the Crozet Basin. *Deep Sea Res Part II Top Stud Oceanogr* 54:1915–1929

- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Riandey V, Champalbert G, Carlotti F, Taupier-Letage I, Thibault-Botha D (2005) Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep Sea Res Part Oceanogr Res Pap* 52:2029–2048
- Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. *Stud Avian Biol* 8:84–94
- Ridoux V (1988) Subantarctic krill, *Euphausia vallentini* Stebbing, preyed upon by penguins around Crozet Islands (Southern Indian Ocean): population structure and annual cycle. *J Plankton Res* 10:675–690
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Mar Ornithol* 22:1–192
- Ridoux V (1995) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Oceanogr Lit Rev* 12:1128
- Sanial V, Beek P van, Lansard B, Ovidio F d', Kestenare E, Souhaut M, Zhou M, Blain S (2014) Study of the phytoplankton plume dynamics off the Crozet Islands (Southern Ocean): A geochemical-physical coupled approach. *J Geophys Res Oceans* 119:2227–2237
- Sato K (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J Exp Biol* 207:4057–4065
- Sokolov S, Rintoul SR (2009) Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 1. Mean circumpolar paths. *J Geophys Res Oceans* 114:1978–2012
- Stahl J-C, Derenne P, Jouventin P, Mougin J-L, Teulieres L, Weimerskirch H (1985) Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le gorfou macaroni et *Eudyptes chrysocome*, le gorfou sauteur. *Oiseau Rev Francaise Ornithol* 55:27–43
- Thiebot J-B, Cherel Y, Acqueberge M, Prudor A, Trathan PN, Bost C-A (2014) Adjustment of pre-moult foraging strategies in Macaroni Penguins *Eudyptes chrysolophus* according to locality, sex and breeding status. *Ibis* 156:511–522
- Trathan PN, Green C, Tanton J, Peat H, Poncet J, Morton A (2006) Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Mar Ecol Prog Ser* 323:239–251
- Trebilco R (2004) Macaroni penguin (*Eudyptes chrysolophus*) foraging ecology at Heard Island: behaviour and environmental influences. University of Tasmania
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Prog Ser* 204:257–267
- Venables H, Meredith MP, Atkinson A, Ward P (2012) Fronts and habitat zones in the Scotia Sea. *Deep Sea Res Part II Top Stud Oceanogr* 59:14–24
- Venables HJ, Pollard RT, Popova EE (2007) Physical conditions controlling the development of a regular phytoplankton bloom north of the Crozet Plateau, Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* 54:1949–1965
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86:2611–2622
- Weimerskirch H, Louzao M, De Grissac S, Delord K (2012) Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211–214
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging Strategy of Wandering Albatrosses Through the Breeding-Season - a Study Using Satellite Telemetry. *Auk* 110:325–342
- Whitehead TO, Kato A, Ropert-Coudert Y, Ryan PG (2016) Habitat use and diving behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins during the critical pre-moult period. *Mar Biol* 163:1–20
- Williams TD, Rothery P (1990) Factors Affecting Variation in Foraging and Activity Patterns of Gentoo Penguins (*Pygoscelis papua*) During the Breeding Season at Bird Island, South Georgia. *J Appl Ecol* 27:1042–1054
- Wilson RP, Grant WS, Duffy DC (1986) Recording Devices on Free-Ranging Marine Animals: Does Measurement Affect Foraging Performance? *Ecology* 67:1091–1093
- Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2008) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biol* 31:229–243

Competing interests

The authors declare that they have no competing interests.

Tables

Table 1: Number of available tracks and diving file from monitored Macaroni penguins in 3 different breeding seasons at Crozet Island

Logger Stage	2009			2012			2013			Total of id and trips
	GPS	ARGOS	TDR	GPS	ARGOS	TDR	GPS	ARGOS	TDR	
Incubation $n_{init}:19$	-	3♀	3♀	2♀ - 6♂	-	-	2♀	-		7♀ - 6♂ 13 trips
Brood $n_{init}:25$	4♀	4♀	3♀	4♀	-	3♀	2♀	3♀		17♀ 51 trips
Crech $n_{init}:20$	-	3♂	-	3♀ - 4♂	-	2♀	1♀ - 2♂	2♂	-	4♀ - 11♂ 32 trips
Total number	11♀ - 3♂		-	9♀ - 10♂		-	8♀ - 4♂		-	45 id – 96 trips

The initial number n_{init} of deployment is shown under the breeding stage. Gender of individuals is indicated by ♀: female and ♂: male. The total of available tracks is shown in the last column without taking account of the diving data recorded by TDR. As individuals may have performed several trips during the equipment time, the number of trips is higher than individuals number in brood and crèche stade. id: individual.

Table 2: Trips characteristics of Macaroni penguins during each breeding stage.

Trips parameters	Sexe	Incubation	Brood	Crèche
Range - km	♀	274.3 ± 65.2	31.6 ± 18.4	79.5 ± 35.5
	♂	358.6 ± 28.1	-	186.3 ± 92.0
Travelled distance - km	♀	825.6 ± 242.7	80.0 ± 52.8	184.7 ± 82.0
	♂	1104.8 ± 135.0	-	484.7 ± 225.0
Duration - day	♀	11.9 ± 2.1	1.2 ± 0.8	3.1 ± 1.4
	♂	18.1 ± 2.1	-	8.8 ± 4.5
Direction °	♀	18.4 ± 9.0	325.5 ± 27.7	317.4 ± 36.0
	♂	65.2 ± 14.5	-	254.8 ± 75.8
Travelling speed km.h ⁻¹	♀	1.98 ± 1.25	2.7 ± 0.9	2.6 ± 1.6
	♂	2.53 ± 1.35	-	2.6 ± 1.5
Elongation Coefficient	♀	5.1 ± 2.8	2.9 ± 2.1	2.7 ± 2.3
	♂	1.0 ± 0.3	-	4.0 ± 3.5
Masse - g	♀ start	2778 ± 176	3763 ± 346	3555 ± 367
	♀ end	-	-	3835 ± 409
	♂ start	3243 ± 188	3465 ± 305	3354 ± 285
	♂ end	3685 ± 227	-	4477 ± 626

Table 3: Results of linear mixed models of time spent per cell of Macaroni penguins in relation with oceanographic variables during the breeding season

	Incubation				Brood		Crèche							
	♂		♀		♀		♀		north - short trips		north - long trips		south trips	
	Coeff + SE	w	Coeff + SE	w	Coeff + SE	w	Coeff + SE	w	Coeff + SE	w	Coeff + SE	w	Coeff + SE	w
Fixed effects:														
Intercept	1.14 + 0.03		1.44 + 0.07	-	4.24 + 0.29	-	3.16 + 0.14	-	3.36 + 0.25	-	1.47 + 0.20	-	1.57 + 0.08	-
Distance	NI		NI		0.26 + 0.23	0.44	NS	-	NS	-	NI	-	NI	-
NPP	0.05 + 0.03	0.83	NS	1	NS	-	NS	-	NS	-	NS	-	-0.11 + 0.05	0.85
Geostrophic currents	0.10 + 0.03		NS	-	NS	-	NS	-	NS	-	NS	-	NS	-
SSH	NI	-	0.10 + 0.04	0.95	NI	-	NS	-	NS	-	NS	-	-0.28 + 0.08	1
Bathymetry	0.04 + 0.03	0.45	0.09 + 0.04	0.72	0.43 + 0.20	0.75	0.65 + 0.12	1	NS	-	0.43 + 0.20	0.75	-0.11 + 0.08	0.44
Gradient of NPP	NS	-	0.11 + 0.04	0.98	NS	-	NS	-	0.35 + 0.29	0.35	NS	-	NS	-
Gradient of bathymetry	-0.05 + 0.02	0.73	-0.06 + 0.05	0.46	0.40 + 0.15	0.96	NS	-	0.41 + 0.28	0.44	-0.03 + 0.02	0.02	NS	-
Random effects:														
Sd - residual		0.41		0.61		1.75		1.24		1.5		0.48		0.63
Sd - year	NI		0.11		0.55		NS		NI		NI		0.11	
Sd - trip	0.04		NI		0.48		0.38		NS		0.34		NS	

Table 4: Main diving parameters of Macaroni penguins during the breeding season

Breeding stage		Shallow dives		Foraging Dives							Foraging Bout		
		Dives Rate		Dives Rate		Maximal depth	Dive duration	Bottom duration	DE	Wiggles	Bout rate	Duration	Number of dives
		per day		per day	per hour	m	s	s	-	-	per day	min	per bout
Incubation	n=3	75 ± 81		231 ± 71	21.2 ± 6.3	41.8 ± 19.6	118.0 ± 25.5	52.8 ± 18.9	0.40 ± 0.2	4.1 ± 3.4	10.7 ± 5.2	46.3 ± 62.0	19.6 ± 23.9
Brood	n=6	49 ± 57		230 ± 83	19.0 ± 4.9	54.2 ± 19.2	135.3 ± 21.9	51.5 ± 20.3	0.3 ± 0.1	2.9 ± 2.7	7.6 ± 4.2	67.3 ± 94.3	38.7 ± 44.9
Crèche	n=2	67.8 ± 91		211 ± 66	18.7 ± 5.3	49.9 ± 22.4	132.9 ± 26.8	54.0 ± 24.9	0.3 ± 0.2	4.2 ± 4.3	7.9 ± 4.1	67.0 ± 99.1	28.0 ± 40.3

Table 5: Results of linear mixed models of diving parameters of Macaroni penguins in relation with the breeding stage.

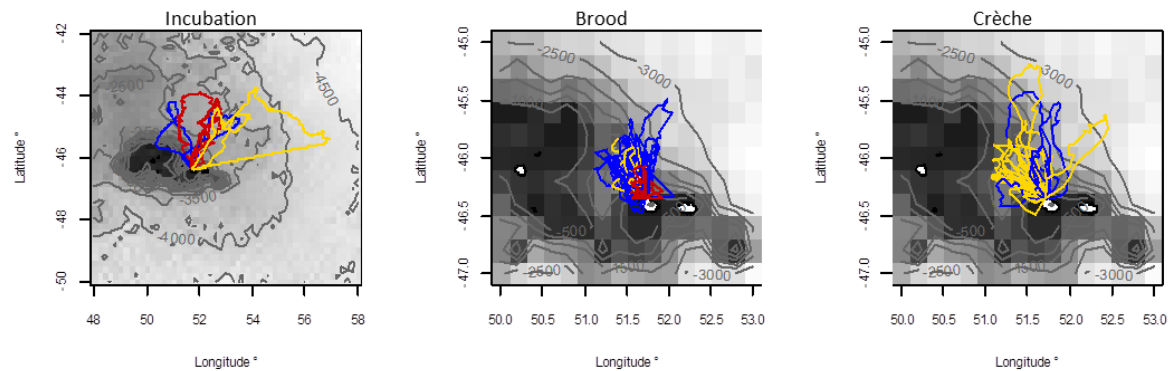
Model	A		B		C		D	
Response variable	Log (Maximum depth)		Dive Duration		Number of bouts per day		Log (Bout Duration)	
Predictors	Coeff + SE	ΔAIC_{null}	Coeff + SE	ΔAIC_{null}	Coeff + SE	ΔAIC_{null}	Coeff + SE	ΔAIC_{null}
Intercept	3.82 ± 0.07	-2.01	132.12 ± 0.96		8.90 ± 0.60		3.53 ± 0.06	
Incubation	-0.23 ± 0.11	Random effect	-14.33 ± 1.32	-12.62	2.42 ± 0.84	-10.3	-0.32 ± 0.08	-16.69
Crèche	-0.02 ± 0.12	5.9%	1.05 ± 1.5		-0.66 ± 0.86		-0.01 ± 0.09	

Coefficient and SE were estimated in comparison to the brood stage values. Model A: Linear mixed model was realized on the absolute maximum depth. Model B, C, D: Individual effect had no weight and linear model were performed. Significant coefficients are in bold.

Figures

Figure 1: Foraging trips of males and females Macaroni penguins during the breeding at Crozet Islands; Trips are overlaid on bathymetry maps. red: season 09 ; gold: season 12 ; blue: season 13.

Females



Males

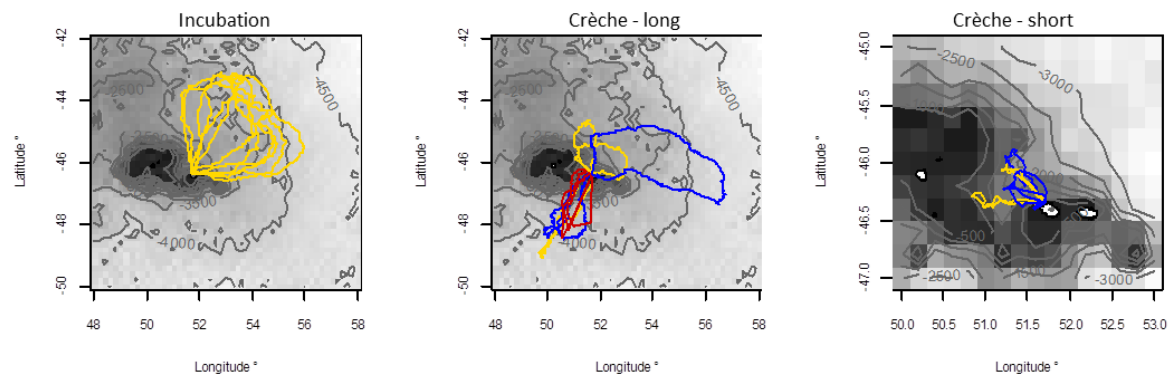


Figure 2: Foraging trips and distribution of net primary production during the breeding season 2012/2013 of Macaroni penguins at Crozet Islands. NPP units are in mgC/m²/day. Red: females, blue: males. a-b : incubation c:brood d: crèche.

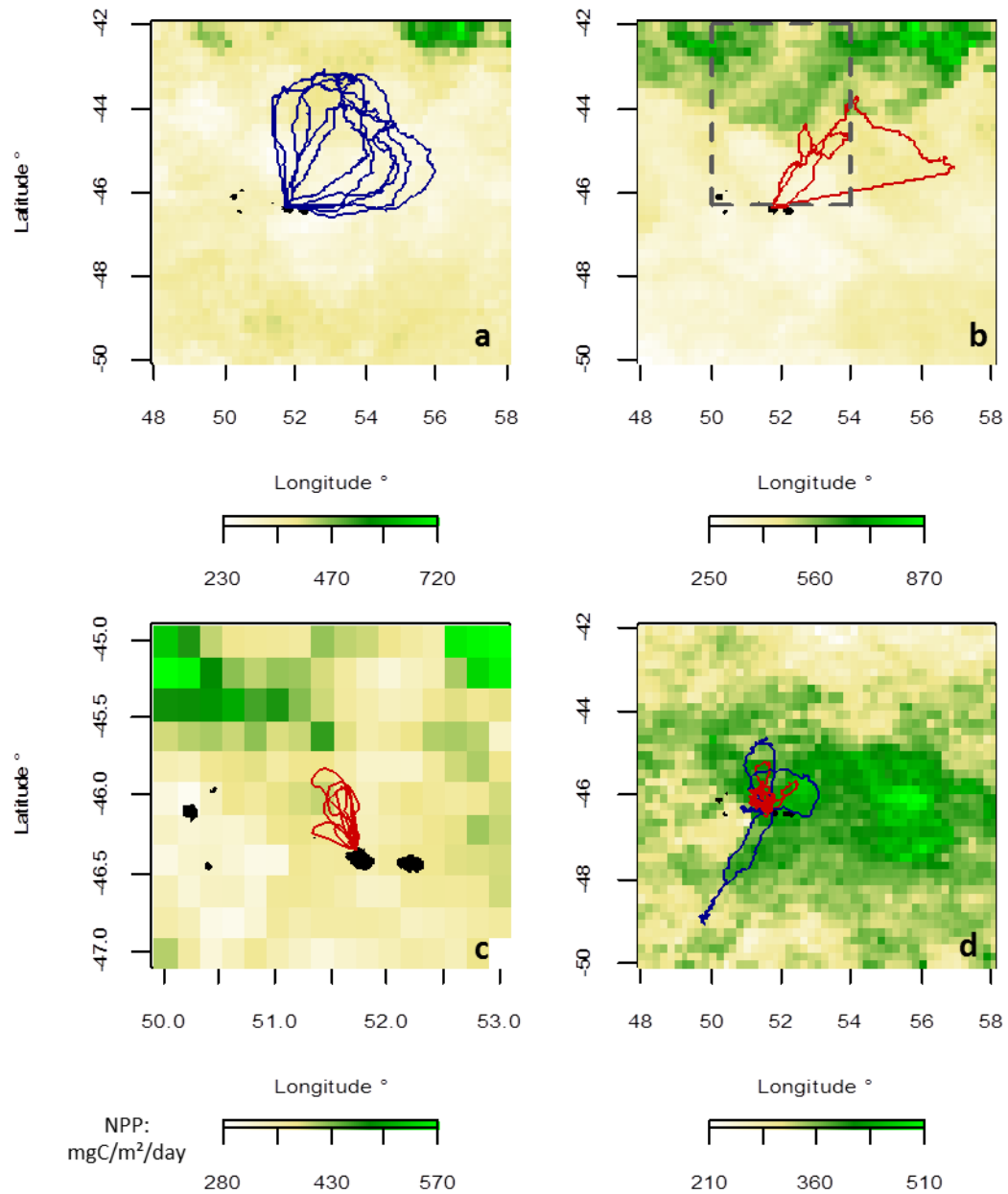


Figure 3: Evolution of net primary production north of Crozet Islands during the breeding season. A- Mean NPP values were computed every 0.2° of latitude (46.3 and 42°S) between 50 and 54° East (see grey box in figure 3 b). Dashed lines indicate standard deviations. Horizontal lines above the horizontal axis indicate the mean maximal range of Macaroni penguins during each period. Period 1: 20th November - 12th December 2012 (at-sea incubating males) ; Period 2: 7th - 20th December 2012 (at sea incubating females) ; Period 3: 20th December - 3th January 2013 (brood) ; Period 4: 4th January - 15th January 2013 (beginning of crèche).

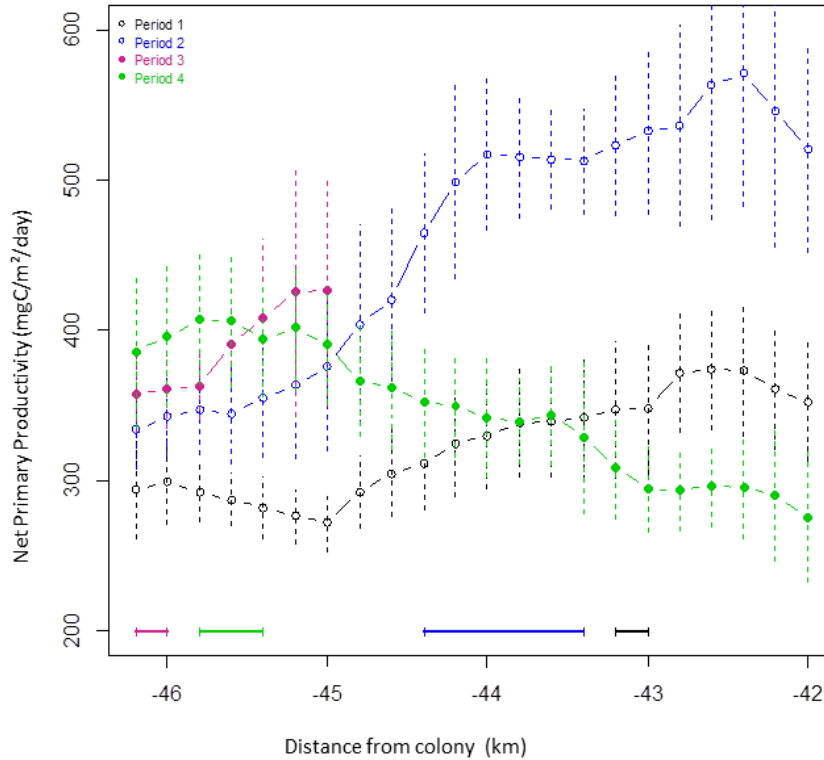
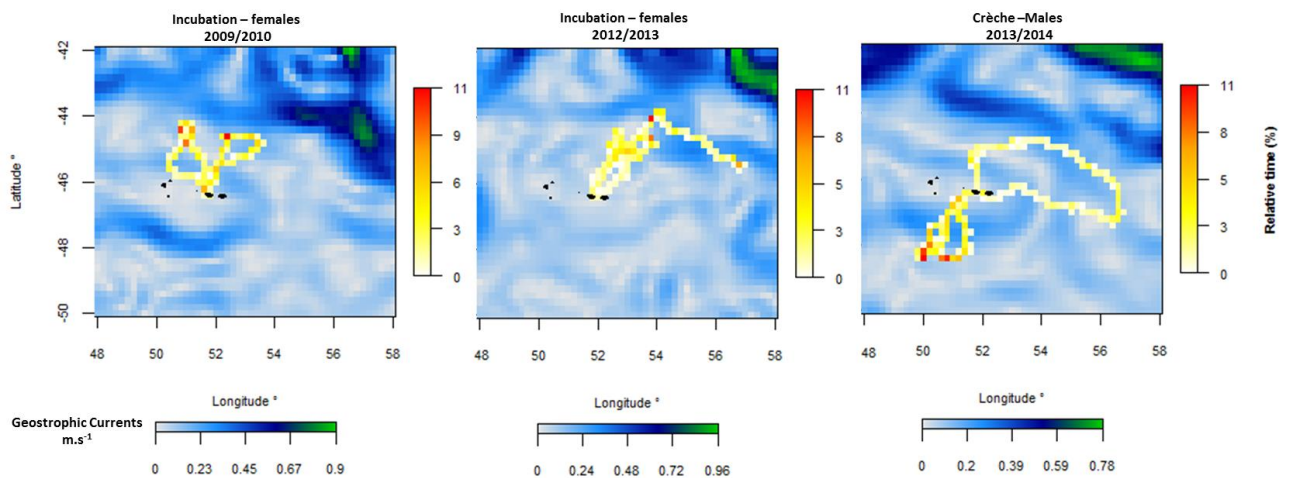


Figure 4 : Foraging trips and frontal structures (SSHg) during the breeding season 2013/2014 at Crozet Islands. Geostrophic currents units are m.s^{-1} . Trips were gridded on cells and relative time per cell is presented.



Foraging strategies of Macaroni penguins during the breeding season at Kerguelen islands

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Introduction

In the open marine environment, physical process aggregate preys at different temporal and spatial scales, driven by several abiotic and biotic factors (Hunt & Schneider 1987, Fauchald et al. 2000). The distance to profitable prey patches and their availability are major constraints for seabird especially during the breeding season. During this period, seabirds behave as central place foragers and are highly time and space limited in foraging ranges (Orians & Pearson 1979). Diving predators, such penguins, travel at a much important energy cost and slower than flying birds (Costa 1991). In consequence, the use of predictable areas of resources is considered as an important part of their foraging strategy (Weimerskirch 2007).

In the Southern ocean, the role of bathymetric features, as edges of island shelves, sea floor has been highlighted in foraging strategies of several marine predators (Tremblay & Cherel 2000). Several main oceanographic, dynamic structures laying a role in foraging strategies are now well identified for the most studied marine predators. Oceanographic fronts, as the Polar Front or Sub

Antarctic front, and eddies (Cotté et al. 2007, Bailleul et al. 2010) are targeted by several diving

and flying species during the breeding season (Bost et al. 2009). However, regional environmental conditions can shape the foraging strategies of the populations at the specific level. Indeed, to overcome to the heterogeneity of environments, seabirds can exhibit a certain degree of plasticity. For example, strong differences in range, bearings and degree of inter-individual variability between two contrasted sites have been observed in seabirds (*e.g.* Adélie penguin Watanuki et al. 1994, Northern gannet: Hamer et al. 2001, Gentoo penguin: Lescroël & Bost 2005, crested penguins: (Tremblay & Cherel 2000, Thiebot, Cherel, et al. 2011a, Thiebot et al. 2013). Primary ecological drivers to such differences seem to be the availability and distribution of distinct prey in each site. Prey availability at the population scale are driven by productivity gradients of each site depending of oceanographic features, as regional sea ice extend, oceanographic fronts feature and bathymetry landscape (*e.g.* Paiva et al. 2010). Macaroni penguins are pelagic foragers, broadly distributed on the Southern Ocean with 55

breeding sites located along the ACC between 37°S and 62°S. The South Indian population host major populations of the world effectives especially the Crozet is (2.2Mo pairs) and the Kerguelen is.(1.8Mo pairs, Jouventin et al. 1984).This region is strongly influenced by the Antarctic Circumpolar Current, flowing eastward and comprising a latitudinal succession of fronts (Park et al. 2009). Crozet archipelago is located northern than Kerguelen islands, within the Polar Frontal Zone between the Subantartic front (~43°S) and the Polar Front (~50°S) (Park et al. 1993). Part of a plateau of 150-km-wide, the two main islands have a small shelf around them and bathymetry steeply drops to over 2000m (Venables et al. 2007). These bathymetric characteristics highly contrast with the Kerguelen case. Kerguelen lies close to the Polar Front, on a very large shallow shelf, in an dynamic oceanic area dominated by the presence of the Polar front and the ACC. However, these two localities seem to provide very favorable conditions to Macaroni penguins since they both host 50% of the world population (Crossin et al. 2013).

Until now, the at-sea foraging strategies of Macaroni penguins from these localities have been only studied in Crozet sector during the breeding season (Bon et al. 2015). Concerning Kerguelen archipelago, the foraging movements has been investigated during the crèche period (Thiebot, Lescroël, et al. 2011) and diving information are available for the brooding period from one studied season (Sato 2004). Available information indicate that the breeding cycle is very similar to the other localities. After their winter migration, the males arrive the first at the colony followed by the female. After the courtship and laying starts the incubation (~35 days). Both sexes successively undertake long foraging trips (~13days) while the partner stayed on land incubates . After hatching (15-21th December), females regularly returns to the colony to feed the chick whereas males fast and guard it (brooding phase, ~25 days). Once chick emancipate (~9 January), females continue to regularly feed them. Males undertake long trips at sea to build up their fat reserves and then start to feed on the offspring until the end of February. The rearing period last about 70 days at Crozet (Stahl et al. 1984). In this study, we investigated the

foraging strategies of Macaroni penguins of Kerguelen islands during an entire breeding season. Firstly, we characterized the at-sea distribution and diving behavior of males and females during each breeding stage. In order to characterize the main oceanographic conditions driving the foraging habitat we put in relation the spatial distribution of birds with pertinent oceanographic features. Through the use of body mass changes and diet data, we tried to identify how macaroni penguins respond to the energetic constraints of the breeding duties. We did the following assumptions: i) gender-specific foraging strategies occur, with long, distant foraging trips for males in incubation and crèche in contrast to short and small trips performed by females during the brooding stage and crèche start because of the chick provisioning. ii) Macaroni penguins especially use the shelf area and break shelf during the brooding season and the close Polar front during the crèche period in response with highest energetic requirements (build up of fat reserves in incubation and body condition recovery in crèche).

Secondly, we compared the foraging behavior at the Kerguelen breeders to the close Crozet archipelago located at the northern limit of the range (Bon et al. to be submitted) by highlighting the common and the different foraging behaviors. This second part of the work allowed to point out the flexibility range in the species foraging behavior. We hypothesized that regional characteristics of the two archipelago localizations will affect the foraging patterns of the species by the productivity characteristics of the sector.The following assumptions were made: i) the more important productivity surrounding Kerguelen islands coupled with the proximity of the PF will advantage Macaroni penguins by involving a decrease of their foraging range to reach the resources patches ii) in consequence, the lose of body mass of brooding femalesin Kerguelen islands should be lower.

Methods

Study site. Kerguelen islands. The study was carried out at Cap Cotter, Péninsule Courbet, Kerguelen Archipelago, hereafter referred to as

Kerguelen. Deployments were carried out from November to February over two breeding seasons. All incubating and brooding birds were equipped in 2011/2012. In crèche, the 11 dataset on females were from the 2014/2015 season, 4 males on 7 were get on the 2014/2015 season (Table 1). Adult breeding penguins were captured before their departure at sea. To investigate the foraging movements, a total of 45 deployments were made either with a GPS (23 individual, Fastloc 2, Sirtrack, Havelock North, N.Z.) either with a PTT (22 individuals, Kiwisat 202, Sirtrack, Havelock North, N.Z.). The PTTs had a transmission interval of 45s. GPS were programmed to record location every 15 minutes. To investigate the diving behavior, another group of birds was equipped with a time-depth recorder (MK9, Wildlife Computers, Redmond, WA, USA, 64Mb, sampling rate: 1s, accuracy: 0.1m) in 2011/2012 (n=9: 5 incubating and 4 brooding) and 2013/2014 (n=15, brood stage) season, respectively. The variation of mass was investigated using weight of penguins from a control group. These birds were marked by a small black number on the chest (*Loréal* hair dye). Over the three seasons, a total of 90 weight were get between the beginning of november and January.

Crozet islands. The study was carried out at Jardin Japonais, Possession Island (46°21' S, 51°43' E), Crozet Archipelago, hereafter referred to as Crozet. Deployments were carried out from November to February over three breeding seasons, 2009/2010, 2012/2013 and 2013/2014 season. Adult penguins relieved from breeding duties were captured before their departure at sea. To investigate the foraging movements, a total of 64 deployments were instrumented either with a GPS (49 individual, Fastloc 2, Sirtrack, Havelock North, N.Z.) either with a PTT 15 individuals, Kiwisat 202, Sirtrack, Havelock North, N.Z.). The PTTs had a transmission interval of 45 s. GPS were programmed to record location every 15 minutes. The total number of individuals trips used here was 45 because of technical failures or data download problems (32% of individuals equipped in incubation and brooding, 15% in crèche). To investigate the diving behavior, another group of birds was equipped with a time-depth recorder (MK9, Wildlife Computers, Redmond, WA, USA,

64Mb, sampling rate: 1s, accuracy: 0.1m) in 2009/2010 (n=6: 3 incubating and 3 brooding) and 2012/2013 (n=3, 1 brooding and 2 in brooding and crèche) season, respectively

Each logger was attached to the lower dorsal feathers along the central mid-line to minimize drag effects (Bannasch et al. 1994) that have deleterious effect on penguins energetic balance (Wilson et al.1986, Ecology). The instruments were glued on the penguins' back with instantaneous cyano-acrylate glue (Loctite 401 Prism, Instant Adhesive, Hempstead, Hertfordshire, HP2 4RQ UK) and waterproof tape (Tesa 4651, Tesa Tape, Quickborn str 24, Hamburg 20253, Germany) and securized by two cables ties. The duration of the instrumentation procedure did not exceed 15 min. All the birds were recaptured upon their return to the colony and the equipment removed.

Diet.Food samples from 23 females Macaronipenguins were collected by stomach lavage following Gales (1987) and Bocher et al. (2000) during two periods (S1: 27/11/2011 to 24/12/2011, start of incubation to hatching and S2: 25/12/2011 au 01/01/2012, brood stage). Birds were flushed 1 time. No individual bird was sampled more than once. Samples collected by flushing were then drained to remove excess water. All the samples were immediately frozen at -20°C and returned to Chizé, France, for analysis. In the laboratory, each sample was thawed, drained, weighed and placed in a flat-bottomed tray. Fresh remains were divided into broad prey classes (crustaceans, fish and other organisms), which were weighed to estimate their proportions by fresh mass in the diet. Total numbers of common and rare prey items were counted in each individual sample. Prey were identified using published keys and by comparison with material held in our own reference collection. Frequency of occurrence (number of samples containing one species as a percent of total number of samples) and its percentage by number (number of one species as a percent of total number of prey in the pooled samples) was computed for main species found in the bulk. Contribution by mass of a prey taxon in a sample was given by the number

of individuals and the mean body mass of this taxon in the sample.

Data processing and tracks analysis. All following analysis were conducted on the R environment (Version 3.1.2, “The R Foundation for Statistical Computing 2013”). All class Z locations were removed from ARGOS datasets. Then, all tracks were speed filtered (function *speedfilter*, package ‘trip’) with a criterion of $8 \text{ km}\cdot\text{h}^{-1}$ which is maximum travel speed previously recorded by Macaroni penguins. Two types of loggers were used but it is known that trips characteristics might be biased by the logger system (Kuhn et al. 2009). Thus, we re-sampled GPS locations to the interval sampling of PTT loggers which encompass 80% of locations (either 100 mins). Descriptive comparisons of the trips characteristics (range, travelling speed, travelled distance, duration, directions) were performed, when available, between years and sexes within each breeding stage. All distances from the colony refer to great circle distances.

Dives analysis. Diving data were analyzed using Multi Trace-Dive (©Jensen Software Systems, Laboe, Germany). The threshold value to detect dive events was 3m. The distribution of maximal dives depths ($n=64088$) was nearly bimodal and break point was estimated at 14m (function “segmented”). In order to be able to compare foraging diving behavior with other localities, we choose the very close threshold of 10m (Pichegru et al. 2011). We used this criteria to distinguish shallows dives ($<10\text{m}$) considered as travelling dives and deep dives ($>10\text{m}$) considered as foraging dives. In this study, we only focused on foraging dives ($n=46918$). Several parameters were determined such as maximal depth, descent phase, bottom phase (time within the dive spent between 75 and 100% of the maximum dive depth and have to last more than 15% of the total dive duration), ascent phase, post-foraging dive surface intervals, number of wiggles (i.e. deviation of the dive profile during which at three points the vertical speed passes below 0 m s^{-1}) (Tremblay & Cherel 2000, Halsey et al. 2007). Dive efficiency was computed as bottom duration/(dive duration + post-dive interval duration) (Green 2005).

Oceanographic data. Oceanographic data are collected over a broad area (km or more) whereas GPS instruments have accuracy of the order of the meter. In consequence, all tracks were re-sampled at the main sampling interval of ARGOS data, either 100min (80% of the value). Tracks were gridded on cells of $0.2\times 0.2^\circ$ in order to calculate time spent per cell which is a reliable proxy of foraging success (Bost et al. 1997).

The selected non-correlated environmental variables included in our habitat models were bathymetry, seafloor slope, sea surface height (SSH), sea level anomaly (SLA) and primary production. Sea surface height and sea level anomaly were quantified through an altimetry multi-satellite global product (Delayed Time Maps of Sea Surface Height products, All Satellites, daily resolution) developed by CNES/CLS Aviso (<http://www.aviso.oceanobs.com>). Net primary production (NPP) was determined using the Vertical Generalized Production Model (VGPM, standard product available Ocean Productivity). NPP is computed with the following equation:

$$NPP = Chl \times Pb_{opt} \times day_length \times f(par) \times z_{eu}$$

with *NPP* are milligrams of carbon fixed per day per unit volume, *Chl* the chlorophyll *a* concentration, *z_{eu}* the euphotic layer depth, *day_length* the number of hours of daylight at the location of interest, *f(par)* the ratio of realized water column integrated NPP to the maximum potential NPP if photosynthetic rates were maintained at maximum levels (*Pb_{opt}*) and *Pb_{opt}* the daily net primary production found within a given water column (photosynthetic efficiency). *Pb_{opt}* is described as a function of sea surface temperature (SST).

SST was included in the original set of environmental variables considered for the habitat models, but eliminated from the dataset due to high correlations with SSH. We choose to keep SSH as a predictor in our models as it allows direct interpretation in terms of frontal zones of the Antarctic Circumpolar Current (Sokolov & Rintoul 2009; Venables et al. 2012). Distance from the colony was included as a model parameter to take

into account the constraints of central-place foragers travelling from the colony for foraging, making distant habitats more costly to reach in terms of travel time and energy. All products were determined with a 0.2° resolution and then averaged on the periods of each track.

Tracks and dives. In order to make multicomparison (between sexes /stages), comparison of foraging parameters were realized by parametric (one-way analysis of variance) or non-parametric (Kruskal-Wallis test, Mann-Whitney test) by respect of normality and homoscedasticity hypothesis (package "Stats"). Circular statistics were used to deal with directions and angles variables (package "Circular"). The differences of mass over the breeding season were investigating using Mann Whitney. The different studied parameters are presented as Mean $\pm$ Standard Deviation (SD).

Relation with oceanographic features. Mixed models (function *lme*) were built to put in relation the time spent (response variable) per cell with oceanographic variables (covariables) using the package "nlme". Generalized additive models were tested but curves were almost linear, thus linear mixed model were preferred. Response variable was squared-transformed to correspond to the normal distribution. Covariates were standardized at the trip scale in order to be able to compare coefficients within the model. A model was built per breeding stage and sex in order to point out the relationships with oceanographic environment. Then the following procedure was realized for each case: before including covariables in the full model, we tested the correlation between them (Spearman correlation test). If R^2 was superior to 0.8, we removed the less pertinent covariable to avoid multi-collinearity.

All combinations were realized and models were ranked using their AICc (package *MuMIn*, Barton 2012). AICc has a correction term for small samples but converges to AIC when sample size is large (Burnham & Anderson 2004). Interactions were tested but no difference was found within AIC and we didn't add it in models. Quadratic relation were tested for each variable and only retained when selected by AIC ranking.

Once models were ranked, variation of AICc was used to select the best model. In all cases, we get more than one best model (with a variation of AICc < 2). We used therefore the model averaging procedure on all models with an Akaike weight (probability for each model to be selected as best model) inferior to 0.95. This procedure allows to calculate the mean of the coefficient for all models weighted by their Akaike weight (Burnham & Anderson 2004). Any mean of coefficients inferior to its standard error was indicated it as non-significant (NS).

Random effects were included as each location within individuals and trips were not dependant. When we get successive trips for one individual (brood and crèche stages), we tested a nested effect (trips within individual). However, the individual variance was always very low (close to 0) in comparison to trip effect. Thus, only trip was considered as random effect. Nested effect of trips within year was added when necessary. Validation of model was realized by graphical examination of residuals, and relation with covariables. Results were considered significant at $p < 0.05$.

Results

Trips characteristics.

Incubation—In 2011/12, Departures of equipped males on the beginning of incubation occurred between the 13th and 18th November. Once at sea, males travelled during 8 ± 4 days and foraged as far as 530 ± 121 km ($n=7$, 671 and 523km for two birds which have begun the return and reached, Figure 1 a). Males travelled a mean distance of 49.0 ± 24.6 km per day and exhibited a travel speed higher during daylight than at night. Directions of birds were not uniform (Watson's Test for Circular Uniformity, $p < 0.05$) and bearing were ranged between 73° and 107° (mean: $94.2 \pm 62.2^\circ$).

Brood —In 2011/12, the mean hatching dates was on the 16th December and the brooding period was extended up to the 9th January 2012 (Camprasse et al. *in prep.*). A total of 8 foraging trips were obtained from brooding females instrumented with GPS. The mean foraging range

was 81.8 ± 41.4 and did not differ among birds ($F_{6,15}=1.88$, $p=0.15$). All females studied during 2 or 3 consecutive trips increased their distance from the colony (Table 3-M1) with an average increase of 35.9 ± 22.1 km per trip (Figure 2). Bearing of trips were not uniformly distributed (Watson's Test for Circular Uniformity, $p < 0.05$) and birds foraged in an area located north-north east (mean: $63 \pm 30^\circ$, figure 1b). The total travelled distance (mean: 173.4 ± 83.9 km) was strongly related with the foraging range (Pearson test $r^2=0.96$, $p < 0.001$) and ranged y between 45 and 290km. Distance travelled was different during daylight compared with night. Thus, distances travelled per day were on average 56.6 ± 8.8 km and 18.3 ± 3.4 per night and females exhibited a significant lower travel speed during night (Table 3-M2). Travel speed significantly differed between birds ($F_{7,727}=6.01$, $p < 0.001$).

Crèche-In 2014/15, a total of 11 tracks were successfully recorded from 5 females between the 1st and the 20th January. The maximal foraging range and total travelled distance (427.0 ± 109.5 km) were significantly extended in comparison to the brood stage (Table 3-M3) but did not differ between birds (range: Kruskal-Wallis = 5.4, df = 4, $p = 0.25$; mean: total travelled distance: Kruskal-Wallis = 1.7, df = 4, p-value = 0.80). The trip range of successive trips increased with time (Spearman correlation test : $R^2 = 0.85$, $p < 0.001$, Figure courbe-tracks) with an average increase of 42.6 ± 38.8 km. Trips were mostly oriented eastward than in brood ($88.9 \pm 71.3^\circ$, Watson Wheeler Test $W = 8.1$, $p < 0.05$, figure 1 c). The penguins travelled on average 50.7 ± 24.4 km per day and 10.5 ± 17.1 km per night but no difference was found in terms of traveling speed between day and night (2.7 ± 0.7 km.h⁻¹).

A total of 4 tracks was obtained from 3 males equipped in January 2012 and of 7 tracks from 5 males equipped in January 2015. Trips realized in 2012 were slightly more directed south than in 2015 ($113.8 \pm 6^\circ$ versus $95.40 \pm 4.5^\circ$, Watson-Wheeler test $W = 7.4$, df=2, $p < 0.05$; Figure 1 d). No difference was found between the two breeding seasons (Mann Whitney test $W = 11$, $p = 0.65$). However we observed a strong inter-individual

variability (50.9-600km). Males travelled further (319.0 ± 186.5 km) than females (Table 3-M4).

Relation with oceanographic features

Incubation. The time spent per cell of males was the most influenced by the increase of the distance from the colony, SLA and the decrease of SSH, respectively (Table 4). NPP and EKE had a weaker effect on the response variable. On the longitudinal gradient, we observed that both time spent per cell and NPP increased in the same area (between 72 and 74°) which may explain the positive relationship between the two variables. In parallel, the SSH and SLA firstly decreased before increased (Figure 3). The variation of SLA suggests the presence of a eddy structures associated there with higher productivity. Farther east, the SSH considerably increased as well as EKE (from 77° E), characterizing the border of a frontal structure (Figure 3). Otherwise, trips direction of birds from Kerguelen islands are highly variable. These pattern associated with the variability of the studied oceanographic parameters makes the relationships more difficult to define as shown by the random effect (26%). This support the fact that birds differently respond to the oceanographic variables (Table 4)

Brood -At the beginning of the brooding phase (19th-22 December), 57% of performed tracks were shorter than 50km from the colony. Birds which performed these small trips stayed on the shelf since the bathymetry did not exceed 123m (mean: 96.5 ± 15 m). Later in the brooding phase, a strong positive relationship was observed between the foraging time and the bathymetry as well its gradient (Table 4). The used bathymetry depended of the range of trips but varied between 167.9 and 1801.7m (mean: 888.1 ± 424.8 m). Another mixed model with the distance from the colony (correlated with bathymetry, not shown here) also indicate that birds increased their foraging effort in the furthest part of their trips. The NPP had also a positive effect on time spent per cell. Mean of NPP did not significantly differ between incubation and brood on areas prospected (Mann Whitney test, $W=27359$, $p=0.10$, Incubation : $707 + 270$ mgC/m²/day, Brood: $692 + 289$ mgC/m²/day).

Diving behaviour

Incubation. Diving characteristics are summarized in the table 5. The foraging dive frequency was the most the important during daylight (240 ± 73), following by the dawn (18 ± 6) and then both dusk (7 ± 6) and night (6 ± 5 , Kruskal Wallis $X^2=137.2$, $df=3, p<0.001$). No individual effect was observed concerning the diving frequency with respect to the timing of the day. The foraging dive depth (range: 10 - 118.2 m) also followed a quadratic relation with day time (Table 5, Figure 3).

Brood. As in incubation, the foraging dives frequency was the most important during daylight (181 ± 85), following by the dawn (15 ± 6) and then both dusk (10 ± 7) and night (10 ± 13 , Kruskal-Wallis $X^2=314.84$, $df=3, p<0.001$). The number of deep dives per day did not differ between birds ($F_{18,139} = 0.636$, $p=0.87$). However, theaximal foraging depth, foraging dive duration, bottom duration, and diving efficiency differed significantly between birds ($F_{18,27983} = 150.1$, $p<0.0001$; $X^2=362.7$, $p<0.0001$; $X^2=196.8$, $p<0.0001$; $X^2=126.0$, $p<0.0001$, respectively).

Bout. Penguins performed 7.8 ± 4.7 bouts per day (range: 1-22) composed of 88.6 ± 76.7 dives (range: 3-324). Eighty five% of dives were included in a bout. Isolated dives were significantly shallower than in dives in bout (isolated: 21.7 ± 18.7 m; dives in bout: 51.3 ± 20.5 m, Mann-Whitney $p<0.0001$) and presented a lower diving efficiency ($0.08 \pm .07$ vs 0.35 ± 0.15 , Mann-Whitney $p<0.0001$). A positive relationship was found between the number of dives performed in a bout and the mean diving efficiency. The more the bouts were long, the more the average diving efficiency was high.

Body mass variations

From the start of November (5th - 10th November, 3987 ± 375) to the end of their in first trip ($n=6$, 12th - 7th December, 4550 ± 323 , Mann Whitney, $p<0.0001$), males increased their body mass by 12%. Their body mass decreased up to the beginning of brood by 19% (3678 ± 363 g, 15-17th December, $n=15$ Mann Whitney $p<0.0001$). Body mass of the end of brood stage (2015 season) were

not significantly different from the beginning (2012 season, 3600 ± 270 g, $n=6$, 26th December - 2nd January 2015, Mann Whitney $p=0.73$).

Females decreased considerably their body mass (26%) from the laying of first egg (5th - 10th November, 3889 ± 257 , $n=19$) to the relieve of incubating duties by males (2971 ± 386 g, 1st - 7th December, $n=7$, Mann - Whitney $p<0.01$). During their first foraging trip after laying females restored their body condition up to the value recorded at the laying period (3749 ± 322 g, $n=23$). During the brood stage, body mass decreased by 4% (Pearson correlation test: $R^2= -0.20$, $p=0.05$) and females reached 3615 ± 256 g at the end of December ($n=9$, 30 - 31st December).

Diet.

Crustaceans constituted almost all the diet by number (99% of 21370 found items, $n=23$ stomach samples). The main species were *Euphausia vallentini*, *Thysanoessa* sp. and *Themisto gaudichaudii* (43.7% %, 28.2%, 27.,0% respectively, $n= 21151$ items). By reconstituted biomass, *E. vallentini* was the most component of the diet bulk (45.45%), followed by *T.gaudichaudii* (30.59%), *Krefflichthys anderssoni* (15.75%) and then *Thysanoessa* sp. (8.21%).

An important shift in diet composition occurred throughout the breeding cycle, *i.e.* between the period ranging from the 27/11/2011 to 24/12/2011 (T1) between the 25/12/2011 to 01/01/2012)(T2). *E. vallentini* decreased considerably from T1 to T2(68.48% vs 23.75%, respectively) while both the importance of *T.gaudichaudii* and *K.anderssoni* increased (*T.gaudichaudii*: T1: 22.05% vs T2 38.65%;*K.andersoni*:T1: 5.88% , T2:25.05%, Table 7).

Discussion

This work presents the first detailed study on the macaroni penguin foraging strategies on Kerguelen islands over an entire breeding cycle. By using tracking and diving data, we provided quantitative information e on the oceanic environment and water column depth used during the summer. Coupled with the analysis of the contemporaneous

oceanographic data, we brought new information on the environmental parameters driving the foraging habitat by Macaroni penguins during incubation and chick rearing. By incorporating changes in diet composition and body mass over the breeding cycle, we investigated how Macaroni penguins adjust their foraging behavior in relation to the energetic constraints of the breeding cycle. After a first part of discussion on foraging strategies of Macaroni penguins in Kerguelen islands, we will compare the Kerguelen situation with the foraging strategy of the Crozet population Crozet islands, facing to but very distinct oceanic environment.

Foraging strategies of Macaroni from Kerguelen islands.

Incubation. In the incubation stage, males performed long, extended trips directed eastward ranging at least up 500km. The males travelled pelagic waters encompassing oceanographic conditions which vary considerably during the trips (figure 3, paper A3). Indeed, on the longitudinal gradient we observed that both time spent per cell and NPP increased in the same area (between 72 and 74°). In parallel, the SSH and SLA firstly decreased before increased. The variation of sea level anomaly suggests the presence of a eddy structure associated there with higher productivity, favorable to the penguins. Farther east, the SSH considerably increased as well as EKE (from 77°E). The variation of these two variables are typical of the border of a main frontal structure characterized by mesoscale and sub-mesoscale structures (eddies, filaments) aggregating patches of resources for top predators (Kostianoy et al. 2003, Pakhomov & McQuaid 1994, Riandey et al. 2005, Landry et al. 2008).

The Kerguelen large submarine plateau (one of the largest of the Southern Ocean constitute a natural barrier to the eastward Antarctic Circumpolar current flow. This relatively shallow (<2000m) plateau, is located in the northern part of the Antarctic Zone and strongly affect the pathway of the main surrounding oceanographic fronts such as the Polar Front, the Subantarctic front and Southern ACC front (Orsi et al. 1995). In consequence, the continuous iron enrichment from the islands and

the plateau, combined with a favorable light-mixing regime (decrease of winds pressure in summer combined with an ascent of the mixed layer) allow each summer the growth of an important phytoplankton bloom (Blain et al. 2001, Park, Fuda, et al. 2008, Park, Roquet, et al. 2008, Mongin et al. 2008). Indeed, the Kerguelen plateau is considered as one of the most productive area of the Southern Ocean, attractive for many top marine predators (*e.g.* Guinet et al. 2001, Lea et al. 2006, Bost et al. 2011, O'Toole et al. 2014). Several studies have demonstrated that marine predators from Kerguelen islands target and used the cold waters of the Polar Front during the breeding season which flow east ward the archipelago (Lea et al. 2006, 2008, Bost et al. 2011, Hindell et al. 2011). The response of macaroni penguins to the surrounding oceanographic variables is complex since the bird body condition has an high random effect in the relationship of time spent per cell with oceanographic variables (26%). This indicates that each bird responded differently to the oceanographic features. Although the productive area located close to the colony seems to be harvested, all birds have travelled further to the east. Bearings of trips varied also a lot between birds but the border of the Polar Front follows a relative southward direction on the east of the colony (Figure 2). It is probable that penguins targeted turbulent waters associated with this branch of the Polar Front, on a relative north-east/south-east gradient. During their first incubation trip, males have to restore their body condition from their arrival to the colony and prepare the second one (brood stage). During incubation, foraging macaroni penguins mainly rely on euphausiids (primarily *Euphausia valentini* and *Thysanoessa sp.*), amphipods (*Themisto gaudichaudii*) and in smaller proportion, myctophid fish (*Krefftichthys anderssoni*). These resources are found in high concentrations within the SAF and the PFZ (Pakhomov & McQuaid 1996, Pakhomov & Froneman 1999, Koubbi et al. 2011).

Brood

During the brood period, females foraged on areas located north-north east, first on the shelf before going farther, up to pelagic waters

(>1500m), without exceed 150km from the colony. During the course of the brooding period (December), they also increased their foraging time in waters associated with a more important productivity. In comparison to incubation, females have to regularly feed the chicks to ensure his survival and are thus highly timely constrained in to find favorable resources. Brooding birds still mainly feed on macro-zooplankton (*E.vallentini* and *T.gaudichaudii*) with however, higher proportions of myctophids fish (26% *K. anderssoni*) than in incubation (6%). Thus, females seem to respond to the energetic requirement of the chicks by hunting more calorific preys (myctophids, Croxall et al. 1984, Cherel & Ridoux 1992). This allows both to ensure the energy requirement of the chick and maintain a body condition on a basal level (Green et al. 2007, 2009). Indeed, the loss of body mass during the brooding season at Kerguelen islands was relatively low (4%) as in Kerguelen islands, in comparison with South Georgia (12%), although the trip duration was short. This confirms that the area close to the colony are productive at this season.

Looking at finer scale on the bloom repartition, a plume of surface chlorophyll-*a* extending northeast of the islands is observed, overlapping the foraging location of brooding females (Figure 6). Associated with mesoscale eddies of Subantarctic waters, this bloom is observed from the beginning of November to late January (Mongin et al. 2008) with a peak in mid december, when the brood period starts. This temporal matching could be a part of the Cushing hypothesis (1969, 1990, see Durant et al. 2007). He assumes that recruitment in a population (*i.e.* of predator) will be high if the most energetically part of the breeding season occurs at the same time as the peak availability of the lower trophic level (*i.e.* preys). Thus, a such temporal matching between the bloom growth and brooding period could have been selected through natural selection process, where partners breeding in the good timing could have a better breeding success.

The mechanisms improving the marine productivity close to the islands are complex but relatively well studied. Indeed, three contrasted

zones were identified influencing phytoplankton growth in a different way: over the shelf up to the slope (zone 1), on a fine zone along the shelf (zone 2) both used by brooding females, and offshore waters east of the islands used by females in crèche (zone 3, Figure 6). On coastal waters (zone 1), high concentrations of dissolved iron are found due to lithogenic input from the islands combined with inputs from the sediment of the shelf and plateau. However, the biomass of large phytoplankton cells (>10 μ m) is low (nearly half of the value found in offshore waters). The main hypothesis of this situation is that grazing pressure by abundant copepods in these waters is extremely important (Blain et al. 2001). Thus, although the net primary productivity is low, it does not indicate that the biomass of crustaceans is low.

During the brooding season, the species *D.pectinatus* is the most dominant species of copepods on coastal waters (Blain et al. 2001) and have an important power of energetic transformation. Indeed, these copepods transform the low energy of phytoplankton into high energy wax esters by lipid accumulation process. *D.pectinatus* is an important component of the diet of fish larvae and amphipods as *T.gaudichaudii* diet (Mayzaud et al. 2011). In consequence, *T. gaudichaudii*, followed by *Euphausia vallentini*, are abundant species of macrozooplankton found on coastal waters of Kerguelen and during summer months (Bost et al. 1994, Bocher et al. 2001, Koubbi et al. 2001, 2011). In the Southern Ocean *T. gaudichaudii* is the most abundant pelagic amphipod, occurring in large numbers in epipelagic waters of the Subantarctic waters. The shelf seem thus to be highly profitable to females during the brooding season for main other birds which feed on th *T.gaudichaudii* and *E. vallentini* (Rockhopper penguins, common diving petrels, Gentoo penguins (Bocher et al. 2000, 2001).

Females not only forage on the shelf but increased their foraging range on the shelf break (zone 2, figure 6). In this area, there is a northward intrusion of cold Antarctic surface waters along the coast of the Kerguelen Plateau, well observable on the figure 3. Although the iron concentrations are important, the mixed layer is very deep (~200m)

suggesting that the light-mixing regime of the area limit the phytoplankton growth rate, leading to decrease the zooplankton stocks (Blain et al. 2001). It contrasts with the foraging behaviour of females are attracted by this location. However, females also feed on myctophids during this period which are known to more live in deep waters (Perissinotto & McQuaid 1992). The shelf is a biogeographic barrier to the distribution of fishes (Duhamel 2009) and important concentrations of myctophids have been found along the slope (Guinet et al. 2001). This repartition may thus drive the foraging behaviour of females on the shelf break (Cherel & Ridoux 1992). Indeed, the higher part of fish in the diet seem to be an adjustment of females on the increase of the energetic requirement of the chicks during the brooding season, by hunting more calorific preys (myctophids, Croxall et al. 1984, Cherel & Ridoux 1992) in order to both ensure the energy requirement of the chick and maintain a body condition on a basal level.

In incubation and brood stage, females exhibit diet vertical depth, reaching on average 50m during daylight and do not dive deeper than 10m at night. This diel behaviour is typic of krill-eater penguins, since their preys, as *E.vallentini*, exhibith nycthemeral migrations (Perissinotto & McQuaid 1992, Pakhomov et al. 1994a). Although brooding period is more constraining for females, the diving rate is higher for females in incubation, suggesting *a priori* a more important foraging effort. However, none other parameter has differed. The only explanation would be that the foraging area where brooding birds forage is more profitable than in incubation. Over the plateau, the bloom starts to growth on the beginning of November and reaches a peak mid- December (Mongin et al. 2008). In our study, no variation of primary productivity on the foraging area used by brooding birds was found between the incubation and brood, in contrast with Crozet islands (Bon et al. submitted). No year effect and logger was detected to explain a such behaviour. Further analysis are needed to explore other variables, for example the distribution at depth of krill schools during the two periods.

In crèche, both females and males foraged in the zone 3 located in offshore waters (Figure 6). Females increased gradually their range from the colony going further east between 160 and 220km. Crèche is a period of high energy expenditure for Macaroni penguins (Green et al. 2009). Females continue to intensively feed on chicks which have more important energetic requirement in reason to his growth. They also more invest themselves in chick feeding since females deliver more meals (59%) than males (41%, Barlow & Croxall 2002b). In contrast, all males equipped before the 10th January have been immediately farther (~400km) before performing shorter trips in late January. No data were available on their body mass. However, the gain of mass when crèche starts seem to be characteristic of the species since birds have to restore their fat reserves (Croxall et al. 1984, Green et al. 2009). We do not have data on their diet in crèche. However, it has been observed that in the Southern Indian Ocean, the fish part of the diet may considerably increase in crèche in detriment of euphausiids part (e.g. 20% to > 90%, Heard Islands, Klages et al. 1989, Ridoux 1994, Green et al. 1998). This shift is not observed in South Georgia where Macaroni penguins mainly feed on an absent species of Indian waters, the Antarctic krill *E.superba*, which can composed 90% of the diet by mass of Macaroni penguins (Croxall et al. 1997). The variation in diet composition seem to be a strategy of Macaroni from Southern Indian islands to face with the higher energetic requirements of the period.

The Kerguelen plateau is very attractive for many myctophid eating predators as Antarctic Fur Seals *Arctocephalus gazella* (Cherel et al. 1997, Green et al. 1997), Macaroni penguins from Heard islands (Green et al. 1998, Hindell et al. 2011), King penguins (Bost et al. 2002, Charrassin et al. 2002). Moreover, *K.anderssoni* live in the the upper offshore water layers (0–200 m) during the day, at depths reachable to Macaroni penguins (Duhamel et al. 2000). We noticed in our study that crèching Macaroni penguins follow a very similar path than King penguins, foraging to the southeast up to 300 km from their colony, mainly along the eastern edge of the shelf (Charrassin et al. 2002). On this area, the phytoplankton biomass is higher than in

the two other zones (1, 2, Figure 6) and a persistent phytoplanktonic bloom is observed during November and December. It has been demonstrated that a cold tongue at 100m flow north-westward along the shelf break originating from the south (Park et al. 1998). The tidal current–bottom topography interaction could improve the high primary productivity in this sector supplying iron-enriched waters into upper layers of the ocean through vertical mixing (Charrassin et al. 2002, 2004). Moreover, the shallow mixed layer (~100m) may provide favourable light-mixing regime to the phytoplankton growth and be attractive to upper trophic levels, as cool fishes (Blain et al. 2001, Duhamel et al. 2000, Hulley 1981).

Inter-population comparison

In incubation, all studied males from Crozet islands are highly dependent of the turbulent and productive waters of the Subantarctic Front located ~ 400km north of the colony (Bon et al. 2015). During their trips, transit periods are followed by an increase of the foraging activity within the south border of the SAF where both productivity and turbulence increased. Each year, a phytoplanktonic bloom growth north of Crozet in a closed area formed by the deviation of the SAF north the Crozet plateau (Venables et al. 2007). However, this bloom spreads southwardly from November to December involving an important increase of productivity close to the islands (Bon et al. submitted, Venables et al. 2007). In incubation, we observed that foraging range of females are well adjusted to the bloom movements, foraging up to its southern border (~200km, Bon et al. submitted). In Kerguelen, males seem to be less constraint to find favorable areas by taking advantage of the biogeography of their environment. The characteristics of the Kerguelen plateau are favorable to a bloom development each year, increasing the stock of marine resources for upper trophic predators over the Kerguelen Plateau. Moreover, in contrast with Crozet, males exhibited an important inter-individual variability in trips bearings suggesting the favourable foraging area is wider.

Concerning the brood and crèche phase, females travelled farther with more distance realized per day than in Crozet and travel speed was similar between the two localities. These horizontal movements have an impact on the vertical behaviour since females from Kerguelen exhibited a lower foraging dives rate per hour (~12 to 15) than in Crozet (~20). During these short trips, the Crozet females forage however harder in terms of diving effort but birds from Kerguelen dove deeper or at the same depth and always spend higher time at the bottom phase. For a same depth, this suggests that diving behaviour of females from Crozet is less optimal than in Kerguelen (Houston & Carbone 1992). The number of wiggles is more important in Kerguelen suggesting a better foraging success. Thus, the less optimal behaviour could be related to a more dispersive behaviour of prey schools in Crozet waters forcing birds to forage in another patch (Watanabe et al. 2014). The study of prey behaviour and dives profiles could be helpful to understand if the prey behaviour differ between the two localities (Pichegru et al. 2011, Watanabe & Takahashi 2013).

Moreover, we found that the primary productivity close to Crozet islands was at the maximum in the brood phase (Bon et al. submitted) whereas no variation was detected close to Kerguelen islands in this study. The cost of travelling are lower for females of Crozet which thus can invest more energy in the diving effort. These results strongly suggest that preys distribution in Kerguelen waters must be more patchily distributed over the Plateau. In consequence, females from Kerguelen have to allocate more time per day in travelling behaviour to locate preys patches suggesting that their environment is less favorable.

Otherwise, birds from Kerguelen waters strongly use the resources on the shelf before going further (>100km), probably due to a depletion of resources close of the colony (Ashmole 1963). At Crozet, depletion process is less clear since females go and back foraging close to the islands (30km) during the brood stage indicating that resources could be still available in sustainable levels.

The situation differs for crèching males. Individuals from Crozet islands exhibited two opposite strategies. Some individuals targeted the SAF as in incubation whereas the other targeted the Polar Front located 400km south of the colony. In crèche, males have to build up their body reserves after a long fasting period. In parallel, we know that Macaroni penguins shift to a more oil-fish diet which are more nutritive than crustaceans (Ridoux 1994). In crèche, females still intensively feed on the chick. Males have time to target structures where preys are found in more profitable and available concentrations than close to the colony, as frontal structures where myctophids are found in high concentrations (Lubimova et al. 1987, Pakhomov et al. 1994b). In Kerguelen, males display the same strategies than in incubation with long foraging trips southeastward following the shelf break. The lower latitude of Kerguelen islands and the intrusion of cold tongue along the shelf break favour the presence of cool fishes groups, as myctophids, on the Kerguelen plateau (Hulley 1981) improving the accessibility of resources for males. The closer availability of resources allows to think that this place is *a priori* more favourable for males.

Comparing to other studied localities, the mass of the Crozet birds was quite low at the onset of laying. This may suggest a decrease in the body condition of breeders at their return from their migration grounds. A decrease of body condition of rockhopper penguins have been recently pointed out at Marion Island (Crawford et al. 2008). In parallel, long term studies have shown a decrease in population effectiveness while it has been demonstrated that body condition at the beginning of breeding season strongly influences the breeding success (Chastel et al. 1995, Tveraa et al. 1997, Robinson et al. 2005). The low weight of females at the return of their winter season needs to be investigated, notably by studying in more details the mass of birds when going back from wintering grounds in mid-october. This result highlights the needs to estimate the quality of wintering areas foraged by Crozet and Kerguelen islands which are well segregated (Thiebot, Cherel, et al. 2011b).

The variation of body mass informs us that males from Crozet islands are thinner at the laying time and they seem to gain less mass during their first trip than in Kerguelen (Figure 5). More data are needed to confirm it, but it strongly suggests that males are more constrained to find food in incubation than in Kerguelen. Concerning females, the body mass is perfectly overlapped and supports the fact that although the foraging movements differ, the energetic gain seems to be relatively similar between the two localities. Otherwise, in the two localities, the females adjusted their diet in relation to the greater energetic needs of chick rearing by increasing the consumption of highly caloric myctophid fish. The trend in body mass change was the same for brooding females provisioning chicks whatever the locality. This strongly suggests that body mass change was an adaptive response to the energetic constraint faced by provisioning females at this critical stage (Salamolard & Weimerskirch 1993, Cresswell et al. 2007).

The strong inter-variability of males' strategies in Crozet locality and the important associated gain of mass suggests that Crozet environment is particularly favorable for Macaroni penguins during crèche. Two main factors, the predictable development of phytoplankton bloom and the equidistance of the locality from two main frontal zones, seem to advantage the species during the breeding season. However, estimating which environment is not easy and needs to take account of other parameters as a better estimation of foraging success and information on the breeding success of the two populations.

Conclusion

On Kerguelen island, Macaroni penguins' foraging strategies are highly dependent to the productivity occurring on the plateau originating from complex currents - bathymetric interactions. The birds target areas depending on their breeding requirements with important shifts in their diets as in other localities. Macaroni penguin foraging provides a fruitful study case model of temporal relation between time of primary resources production and the breeding phenology of a top marine predator. Otherwise, the high difference of

foraging strategies displayed by the two populations, notably in crèche stage, suggest that Macaroni penguins can exhibit an important degree of phenotypic plasticity through the Southern Ocean. The study of contrasted populations is essential to better define which responses species will have face to global changes. Concerning Macaroni penguins, the knowledge is now sufficient to study in more details the plasticity degree of the species in the main populations of the Southern Ocean.

Bibliography

- Bailleul F, Cotté C, Guinet C (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Mar Ecol Prog Ser* 408:251–264
- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- Barlow KE, Croxall JP (2002) Provisioning behaviour of Macaroni Penguins *Eudyptes chrysolophus*. *Ibis* 144:248–258
- Blain S, Tréguer P, Belviso S, Bucciarelli E, Denis M, Desabre S, Fiala M, Martin Jézéquel V, Le Fèvre J, Mayzaud P, others (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep Sea Res Part Oceanogr Res Pap* 48:163–187
- Bocher P, Cherel Y, Hobson KA (2000) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar Ecol Prog Ser* 208:249–264
- Bocher P, Cherel Y, Labat J-P, Mayzaud P, Razouls S, Jouventin P, others (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser* 223:251–260
- Bon C, Della Penna A, Ovidio F d', Y.P. Arnould J, Poupart T, Bost C-A (2015) Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. *Mov Ecol* 3:32
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33
- Bost C-A, Goarant A, Scheffer A, Koubbi P, Duhamel G, Charrassin J-B, others (2011) Foraging habitat and performances of King penguins *Aptenodytes patagonicus*, Miller, 1778 at Kerguelen islands in relation to climatic variability. *Kerguelen Plateau Mar Ecosyst Fish Paris Société Fr D'Ichtyologie*:199–202
- Bost CA, Koubbi P, Genevois F, Ruchon L, Ridoux V (1994) Gentoo penguin *Pygoscelis papua* diet as an indicator of planktonic availability in the Kerguelen Islands. *Polar Biol* 14:147–153
- Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. *Mar Ecol Prog Ser* 227:51–61
- Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Camprasse E, Passerault M, Lacombe T, Bost CA. Some aspects of the breeding biology of the Macaroni penguins, *Eudyptes chrysolophus*, at Kerguelen islands, South Indian Ocean. *In prep*
- Charrassin J-B, Park Y-H, Le Maho Y, Bost C-A (2004) Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep Sea Res Part Oceanogr Res Pap* 51:2091–2103
- Charrassin J-B, Park Y-H, Maho YL, Bost C-A (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecol Lett* 5:317–319
- Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246
- Cherel Y, Guinet C, Tremblay Y (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croz, Kerguelen. *Polar Biol* 17:87–90
- CHEREL Y, RIDOUX V (1992) Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–127
- Costa DP (1991) Reproductive and Foraging Energetics of High Latitude Penguins, Albatrosses and Pinnipeds: Implications for Life History Patterns. *Am Zool* 31:111–130
- Cotté C, Park Y-H, Guinet C, Bost C-A (2007) Movements of foraging king penguins through marine

- mesoscale eddies. *Proc R Soc B Biol Sci* 274:2385–2391
- Crawford RJM, Makhado AB, Upfold L, Dyer BM (2008) Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. *Afr J Mar Sci* 30:185–188
- Cresswell K, Tarling GA, Trathan P (2007) Weight loss during breeding is adaptive for female macaroni penguins, *Eudyptes chrysolophus*. *Evol Ecol Res* 9:1053–1076
- Crossin G, Trathan PN, Crawford RJM (2013) Macaroni Penguin (*Eudyptes chrysolophus*) and Royal Penguin (*Eudyptes schlegeli*). In: *Penguins: Natural History and Conservation*, P. G. Borboroglu and P. D. Boersma (eds). P. G. Borboroglu and P. D. Boersma (eds), University of Washington Press, Seattle, p 185–208
- Croxall JP, Prince PA, Reid K (1997) Dietary segregation of krill-eating South Georgia seabirds. *J Zool* 242:531–556
- Croxall JP, Ricketts C, Prince PA (1984) Impact of Seabirds on Marine Resources, Especially Krill, of South Georgia Waters. In: Whittow GC, Rahn H (eds) *Seabird Energetics*. Springer US, p 285–317
- Cushing DH (1969) The regularity of the spawning season of some fishes. *J Cons* 33:81–92
- Cushing D (1990) Plankton Production and Year-Class Strength in Fish Populations - an Update of the Match Mismatch Hypothesis. *Adv Mar Biol* 26:249–293
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biol* 23:106–112
- Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res CR* 33:271–283
- Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783
- Gales R p. (1987) Validation of the stomach-flushing technique for obtaining stomach contents of Penguins. *Ibis* 129:335–343
- Green JA (2005) Do seasonal changes in metabolic rate facilitate changes in diving behaviour? *J Exp Biol* 208:2581–2593
- Green J, Boyd I, Woakes A, Green C, Butler P (2007) Feeding, fasting and foraging success during chick rearing in macaroni penguins. *Mar Ecol Prog Ser* 346:299–312
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538
- Green K, Williams R, Burton HR (1997) Foraging ecology of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. *Mar Mammal Res South Hemisphere* 1:105–113
- Green K, Williams R, Green MG (1998) Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. *Mar Ornithol* 26:27–34
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonadonna F, Donnay JP (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Halsey LG, Bost C-A, Handrich Y (2007) A thorough and quantified method for classifying seabird diving behaviour. *Polar Biol* 30:991–1004
- Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Mar Ecol Prog Ser* 224:283–290
- Hindell MA, Lea M-A, Bost C-A, Charrassin J-B, Gales N, Goldsworthy S, Page B, Robertson G, Wienecke B, O'Toole M, others (2011) Foraging habitats of top predators, and areas of ecological significance, on the Kerguelen Plateau. *Kerguelen Plateau Mar Ecosyst Fish Société Fr D'Ichtyologie Paris*:203–215
- Houston AI, Carbone C (1992) The optimal allocation of time during the diving cycle. *Behav Ecol* 3:255–265
- Hulley PA (1981) Results of the research cruises of FRV Walther Herwig to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). *Arch FischWiss* 31:1–300
- Hunt GL, Schneider DC (1987) Scale-dependent processes in the physical and biological environment of marine birds. *Seab Feed Ecol Role Mar Ecosyst*:7–41
- Jouventin P, Stahl JC, Weimerskirch H, Mouglin JL (1984) The seabirds of the French subantarctic islands and Adélie Land, their status and conservation. *Status Conserv Worlds Seab Camb UK Int Counc Bird Preserv Techn Publ* 2:609–625

- Klages NTW, Gales RP, Pemberton D (1989) Dietary segregation of macaroni and rockhopper penguins at Heard Island. *Wildl Res* 16:599–604
- Koubbi P, Duhamel G, Hebert C (2001) Seasonal relative abundance of fish larvae inshore at Iles Kerguelen, Southern Ocean. *Antarct Sci* 13:385–392
- Koubbi P, Moteki M, Duhamel G, Goarant A, Hulley P-A, O'Driscoll R, Ishimaru T, Pruvost P, Tavernier E, Hosie G (2011) Ecoregionalization of the myctophid fish in the Indian sector of the Southern Ocean: Results from generalized dissimilarity models. *Deep Sea Res Part II Top Stud Oceanogr* 58:170–180
- Kuhn CE, Johnson DS, Ream RR, Gelatt TS (2009) Advances in the tracking of marine species: using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar Ecol Prog Ser* 393:97–109
- Landry MR, Decima M, Simmons MP, Hannides CC, Daniels E (2008) Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep Sea Res Part II Top Stud Oceanogr* 55:1378–1388
- Lea M-A, Guinet C, Cherel Y, Duhamel G, Dubroca L, Pruvost P, Hindell M, others (2006) Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. *Mar Ecol Prog Ser* 310:77–94
- Lea M, Guinet C, Cherel Y, Hindell M, Dubroca L, Thalmann S (2008) Colony-based foraging segregation by Antarctic fur seals at the Kerguelen Archipelago. *Mar Ecol Prog Ser* 358:273–287
- Lescroël A, Bost C-A (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Mar Ecol Prog Ser* 302:245–261
- Lubimova TG, Shust KV, Popkov VV (1987) Specific features in the ecology of Southern Ocean mesopelagic fish of the family Myctophidae. *Biol Resour Arct Antarct Nauka Press Mosc*:320–337
- Mayzaud P, Cherel Y, Koubbi P (2011) Interannual biomass changes and life strategies of Subantarctic zooplankton in the Kerguelen ecosystem: an overview of the consequences in energy transfer to higher trophic levels. *Kerguelen Plateau Mar Ecosyst Fish Paris Société Fr D'Ichtyologie*:69–78
- Mongin M, Molina E, Trull TW (2008) Seasonality and scale of the Kerguelen plateau phytoplankton bloom: A remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* 55:880–892
- Orsi AH, Whitworth III T, Nowlin Jr. WD (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res Part Oceanogr Res Pap* 42:641–673
- Orians G., Pearson N (1979) On the theory of central place foraging. In: *Analysis of Ecological System*. D.J. Horn, G.R. Stairs and R.D. Mitchell, Ohio State University Press, Colombu, p 155–177
- O'Toole M, Hindell M, Charrassin J, Guinet C (2014) Foraging behaviour of southern elephant seals over the Kerguelen Plateau. *Mar Ecol Prog Ser* 502:281–294
- Paiva VH, Geraldès P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010) Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. *Mar Biol* 157:1385–1399
- Pakhomov EA, Froneman PW (1999) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Mar Biol* 134:501–515
- Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol* 16:271–286
- Pakhomov EA, Perissinotto R, McQuaid CD (1994a) Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar Ecol Prog Ser Oldendorf* 111:155–169
- Pakhomov EA, Perissinotto R, McQuaid CD (1994b) Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar Ecol Prog Ser Oldendorf* 111:155–169
- Park Y-H, Charriaud E, Fieux M (1998) Thermohaline structure of the Antarctic surface water/winter water in the Indian sector of the Southern Ocean. *J Mar Syst* 17:5–23
- Park Y-H, Fuda J-L, Durand I, Garabato ACN (2008) Internal tides and vertical mixing over the Kerguelen Plateau. *Deep-Sea Res Part II-Top Stud Oceanogr* 55:582–593
- Park Y-H, Gamberoni L, Charriaud E (1993) Frontal structure, water masses, and circulation in the Crozet Basin. *J Geophys Res Oceans* 1978–2012 98:12361–12385
- Park Y-H, Roquet F, Durand I, Fuda J-L (2008) Large-scale circulation over and around the Northern Kerguelen Plateau. *Deep-Sea Res Part II-Top Stud Oceanogr* 55:566–581

- Perissinotto R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Mar Ecol Prog Ser* 80:15–27
- Pichegru L, Ropert-Coudert Y, Kato A, Takahashi A, Dyer BM, Ryan PG (2011) Diving patterns of female macaroni penguins breeding on Marion Island, South Africa. *Polar Biol* 34:945–954
- Riandey V, Champalbert G, Carlotti F, Taupier-Letage I, Thibault-Botha D (2005) Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep Sea Res Part Oceanogr Res Pap* 52:2029–2048
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Mar Ornithol* 22:1–192
- Robinson S, Chiaradia A, Hindell MA (2005) The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis* 147:483–489
- Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Funct Ecol*:643–652
- Sato K (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J Exp Biol* 207:4057–4065
- Stahl J-C, Derenne P, Jouventin P, Mougin J-L, Teulieres L, Weimerskirch H (1985) Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le gorfou macaroni et *Eudyptes chrysocome*, le gorfou sauteur. *Oiseau Rev Francaise Ornithol* 55:27–43
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Thiebot J-B, Cherel Y, Crawford RJM, Makhado AB, Trathan PN, Pinaud D, Bost C-A (2013) A Space Oddity: Geographic and Specific Modulation of Migration in *Eudyptes* Penguins (EJ Woehler, Ed.). *PLoS ONE* 8:e71429
- Thiebot J, Cherel Y, Trathan P, Bost C (2011a) Inter-population segregation in the wintering areas of macaroni penguins. *Mar Ecol Prog Ser* 421:279–290
- Thiebot J, Cherel Y, Trathan P, Bost C (2011b) Inter-population segregation in the wintering areas of macaroni penguins. *Mar Ecol Prog Ser* 421:279–290
- Thiebot J-B, Lescroël A, Pinaud D, Trathan PN, Bost C-A (2011) Larger foraging range but similar habitat selection in non-breeding versus breeding sub-Antarctic penguins. *Antarct Sci* 23:117–126
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Prog Ser* 204:257–267
- Tveraa T, Lorensten S-H, Ikonen S, Saether B-E (1997) Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). *Behav Ecol* 8:465–469
- Venables HJ, Pollard RT, Popova EE (2007) Physical conditions controlling the development of a regular phytoplankton bloom north of the Crozet Plateau, Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* 54:1949–1965
- Watanabe Y, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. *Proc Natl Acad Sci* 110:2199–2204
- Watanuki Y, Mori Y, Naito Y (1994) *Euphausia superba* dominates in the diet of Adélie penguins feeding under fast sea-ice in the shelf areas of Enderby Land in summer. *Polar Biol* 14:429–432

Tables

Table 1 : Summary of tracking and diving data of Macaroni penguins and Kerguelen islands

	Tracking	Diving
Incubation	9♂	5♀
	9 trips	
Brood	8♀	24♀
	23 trips	
Crech	5♀ - 8♂	-
	22 trips	
Total id	13♀ - 17♂	29♀

Table 2: Trips characteristics of Macaroni penguins at Kerguelen

Stade	Sexe	Track	Range	Total distance	Duration	Travel Speed		Direction
						day	night	
			km	km	h	km.h ⁻¹		°
Incubation	9 ♂	<i>n</i> = 9	530 ± 121	713.6 ± 309.9	199.0 ± 99.3	3.69 ± 0.81	2.63 ± 0.95	94.2 ± 62.2
Brood	8 ♀	<i>n</i> = 23	81.8 ± 41.4	182.5 ± 52.0	49.8 ± 20.4	3.9 ± 0.9	2.9 ± 0.9	63.0 ± 30.0
Crèche	5 ♀	<i>n</i> = 11	178.2 ± 45.2	423.5 ± 67.8	142.7 ± 16.9	2.6 ± 0.8	2.7 ± 0.7	88.9 ± 71.3
	8 ♂	<i>n</i> = 11	319.0 ± 186.5	787.3 ± 443.0	414.0 ± 262.7	2.5 ± 0.5	2.8 ± 0.8	102.0 ± 10.2

Table 3: Results of mixed models of tracking parameters of Macaroni Penguins in Kerguelen islands. An autoregressive term (aut-ocorrelation) was put in the model M2. Random effects were selected on the trip scale.

M1 :	Brooding trip Range (km) ~ Date (day) - females			
	<i>Coeff ± SD</i>	<i>P</i>	<i>ΔAIC_{Null}</i>	<i>Random effect</i>
Intercept	30.9 ± 17.2	*	-9.3	58.47
Date	11.1 ± 2.6	***		
M2 :	Travel speed (km/h) ~ Day/Night - females			
	<i>Coeff ± SD</i>	<i>P</i>	<i>ΔAIC_{Null}</i>	<i>Random effect</i>
Intercept	4.3 ± 0.3	***	-17.2	NS
Night	-1.2 ± 0.3	***		
M3 :	Trip Range (km) ~ Brood / Crèche - females			
	<i>Coeff ± SD</i>	<i>P</i>	<i>ΔAIC_{Null}</i>	<i>Random effect</i>
Intercept	85.6 ± 11.3	***	-13.2	20.9
Crèch	93.6 ± 18.7	***		
M4 :	Trip Range (km) ~ Males/Females in Crèche			
	<i>Coeff ± SD</i>	<i>P</i>	<i>ΔAIC_{Null}</i>	<i>Random effect</i>
Intercept	178.2 ± 40.9	***	-3.71	NS
Males	140.9 ± 57.9	*		

Table 4: Results of mixed model of time spent per cell in relation with oceanographic parameters.

	Incubation ♂		Brood ♀	
	Coeff + SE	w	Coeff + SE	w
Fixed effects:				
Intercept	1.39 ± 0.10		2.8 ± 0.16	-
Distance from colony	0.11 ± 0.04	0.85	NI	
NPP	0.04 ± 0.03	0.56	0.12 ± 0.09	0.73
SLA	0.05 ± 0.03	0.70	NI	-
SSH	-0.09 ± 0.04	0.92	-0.16 ± 0.12	0.45
EKE	0.04 ± 0.03	0.53	NS	-
Bathymetry	NS	-	0.39 ± 0.10	0.99
Gradient of NPP	NS	-	NS	-
Gradient of bathymetry	NS	-	NS	-
Gradient of bathymetry ²	NS		0.09 ± 0.06	0.47
Random effects:				
Sd - residuel		0.42		0.88
Sd - year	NI		NI	
Sd - trip	0.25		0.50	

Table 5: Diving parameters of Macaroni penguins from Kerguelen islands during the breeding season.

Breeding stage	Shallow dives	Foraging Dives						
	Dives Rate	Dives Rate		Maximal depth	Dive duration	Bottom duration	DE	Wiggles
	per day	per day	per hour	m	s	s	-	-
Incubation n = 5	42 ± 68	262 ± 80	15 ± 7	51.1 ± 14.95	140.06 ± 22.2	66.82 ± 19.48	0.37 ± 0.12	7.61 ± 6.19
Brood n = 24	93 ± 89	204 ± 95	12 ± 7	50.78 ± 20.68	144.51 ± 30.5	62.18 ± 23.98	0.32 ± 0.15	5.52 ± 5.27

Table 6 : Results of significant mixed models of some diving parameters with day time and stage

Response variable	Log (Maximum depth)		Diving Efficiency		Dive Rate (per hour)		
Predictors	Coeff + SE	ΔAIC _{null}	Coeff + SE	ΔAIC _{null}		Coeff + SE	ΔAIC _{null}
Intercept	2.53 ± 0.05	-667.8	0.46 ± 0.02	-135.1	Intercept	10.60 ± 0.22	-22.44
Hour	0.24 ± 0.01	Random effect	-0.03 ± 0.00	Random effect	Incubation	3.10 ± 0.50	Random effect
Hour²	-0.01 ± 0.00	6.0%	0.001 ± 0.00	4.0%			1.4%

Table 7: Reconstituted stomach mass and relative mass of main species found in stomach sample of Macaroni penguins from Kerguelen islands. $n=23$

Main species	Reconstitutedstomach mass (g)	Relative part (%)
Total	1320.43	100
<i>Euphausiavallentini</i>	600.11	45.45
<i>Thysanoessasp</i>	108.35	8.21
<i>Themistogaudichaudii</i>	403.97	30.59
<i>Krefftichthysanderssoni</i>	208.00	15.75
Session 1	640.65	100
<i>Euphausiavallentini</i>	438.69	68.48
<i>Thysanoessasp</i>	23.00	3.59
<i>Themistogaudichaudii</i>	141.26	22.05
<i>Krefftichthysanderssoni</i>	37.70	5.88
Session 2	679.80	100
<i>Euphausiavallentini</i>	161.45	23.75
<i>Thysanoessasp</i>	85.34	12.55
<i>Themistogaudichaudii</i>	262.71	38.65
<i>Krefftichthysanderssoni</i>	170.30	25.05

Figures

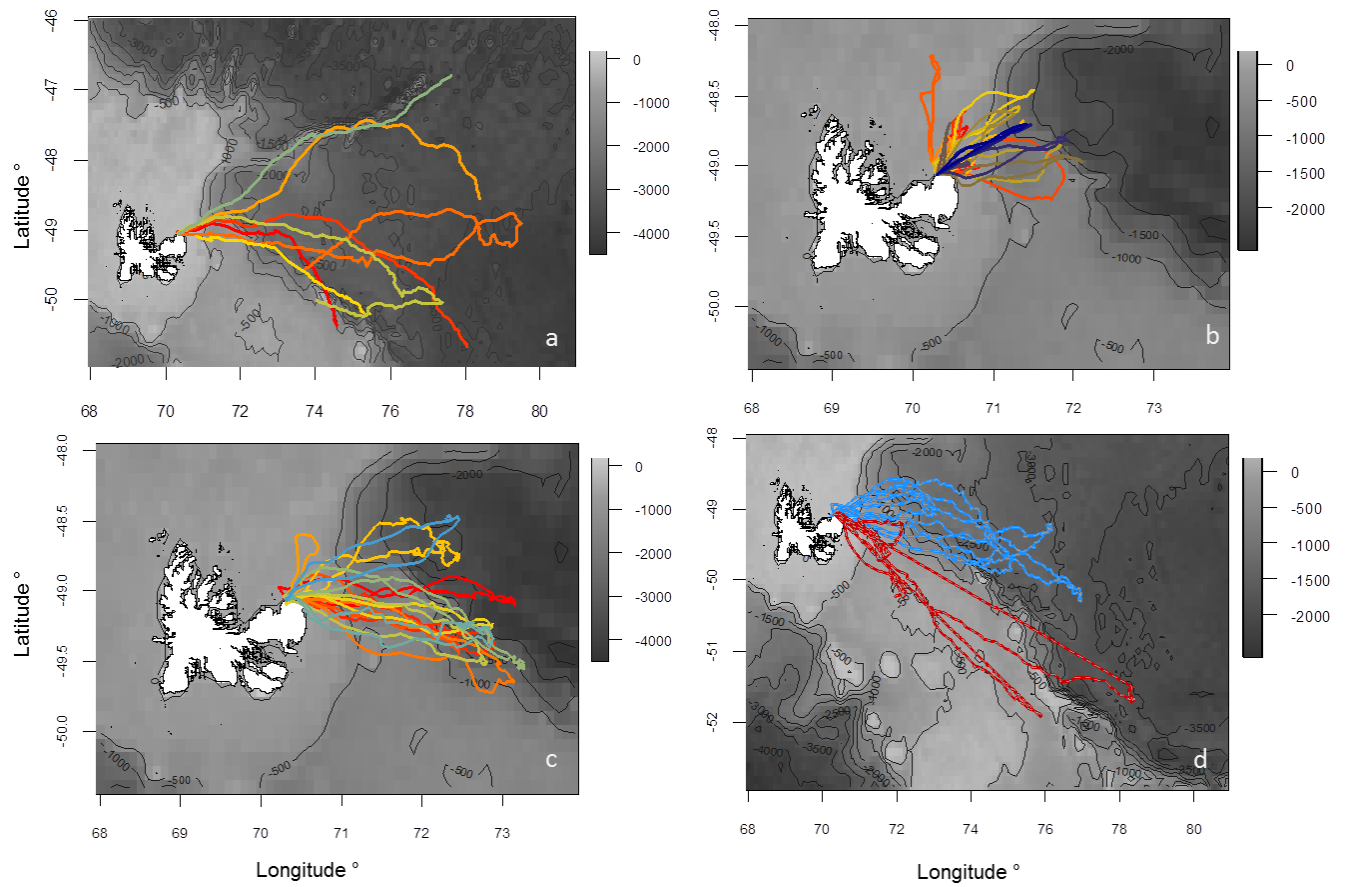


Figure 1: Foraging trips of Macaroni penguins at Kerguelen islands. a: Males in incubation stage (2011/2012) b: Brooding females (2011/2012) c: Crèche females (2014/2015) d: Crèche males (2012/2012:blue ; 2014/2015: red). Grey legend indicates the bathymetry (m).

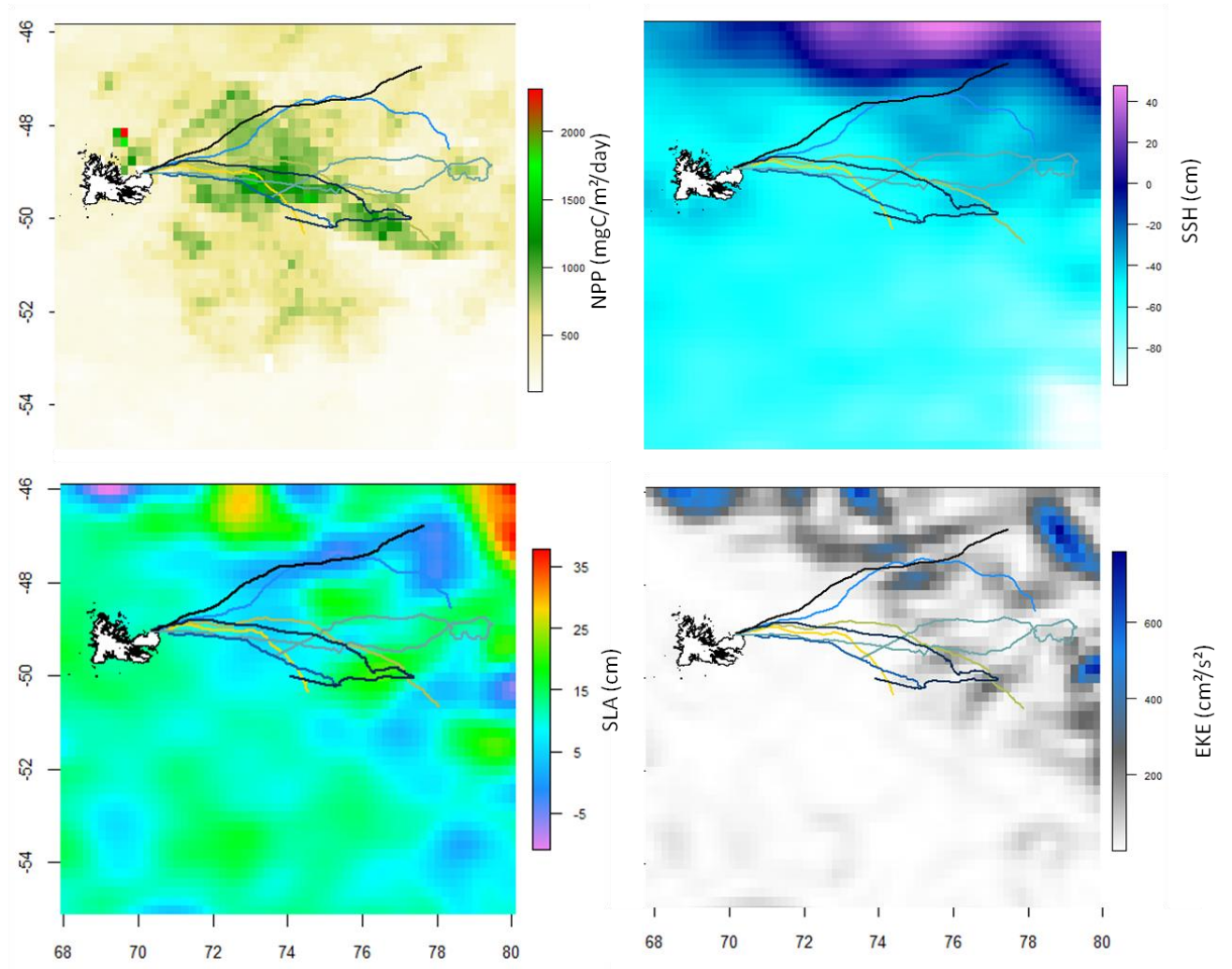


Figure 3: Tracks of males in incubation stage on maps of oceanographic features. NPP: Net Primary Productivity ; SSH: Sea Surface Height ; SLA: Sea Level Anomaly ; EKE: Eddy Kinetic Energy

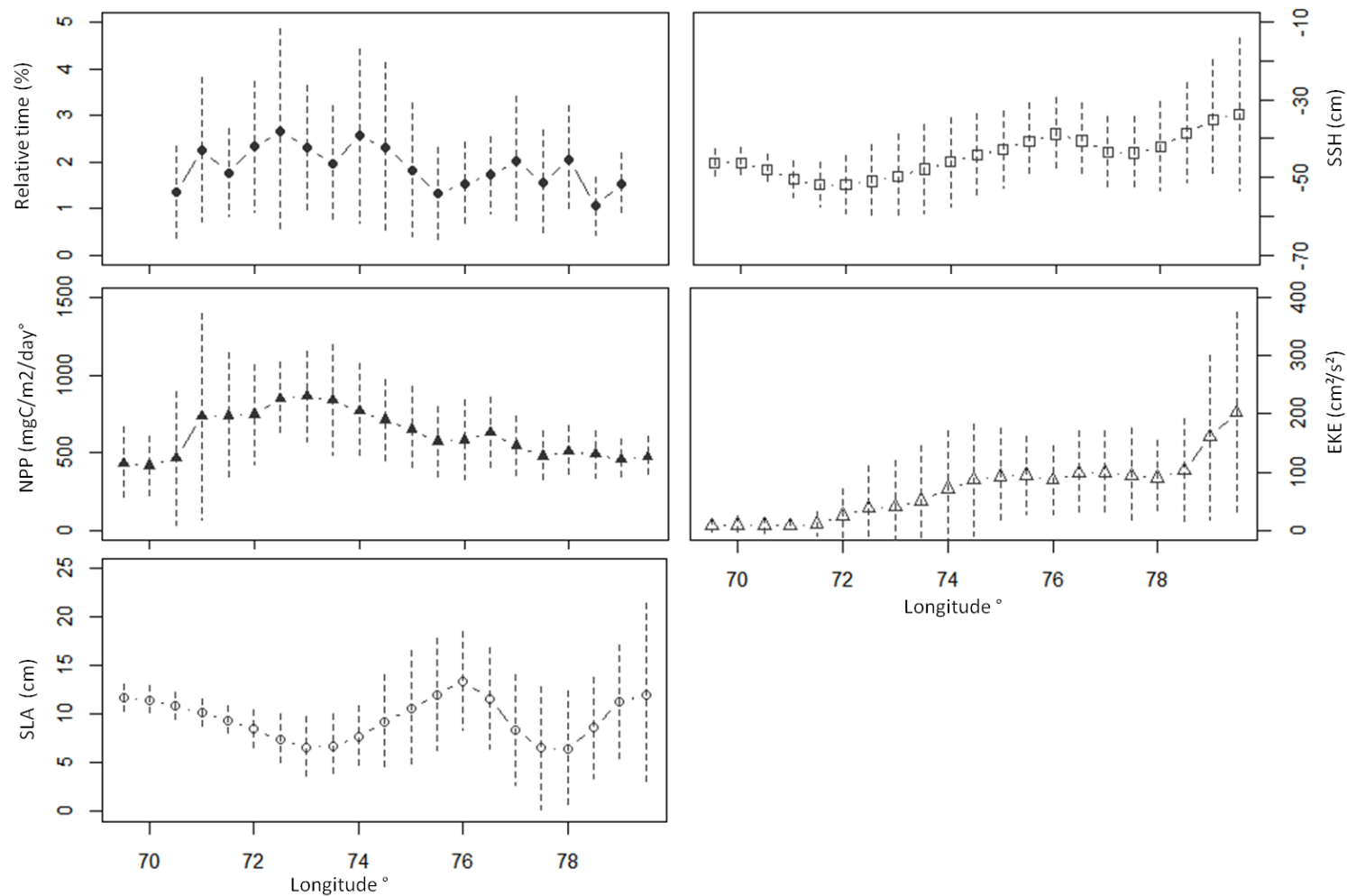


Figure 3: Longitudinal variation of time spent per cell of males and four oceanographic variables playing a significant role on the foraging time. Incubation stage. Values are averaged every 0.5° of longitude between -51° and -47° of latitude. NPP: Net primary productivity ; SSH: Sea surface height ; EKE: Energy kinetic energy; SLA: Sea level Anomaly

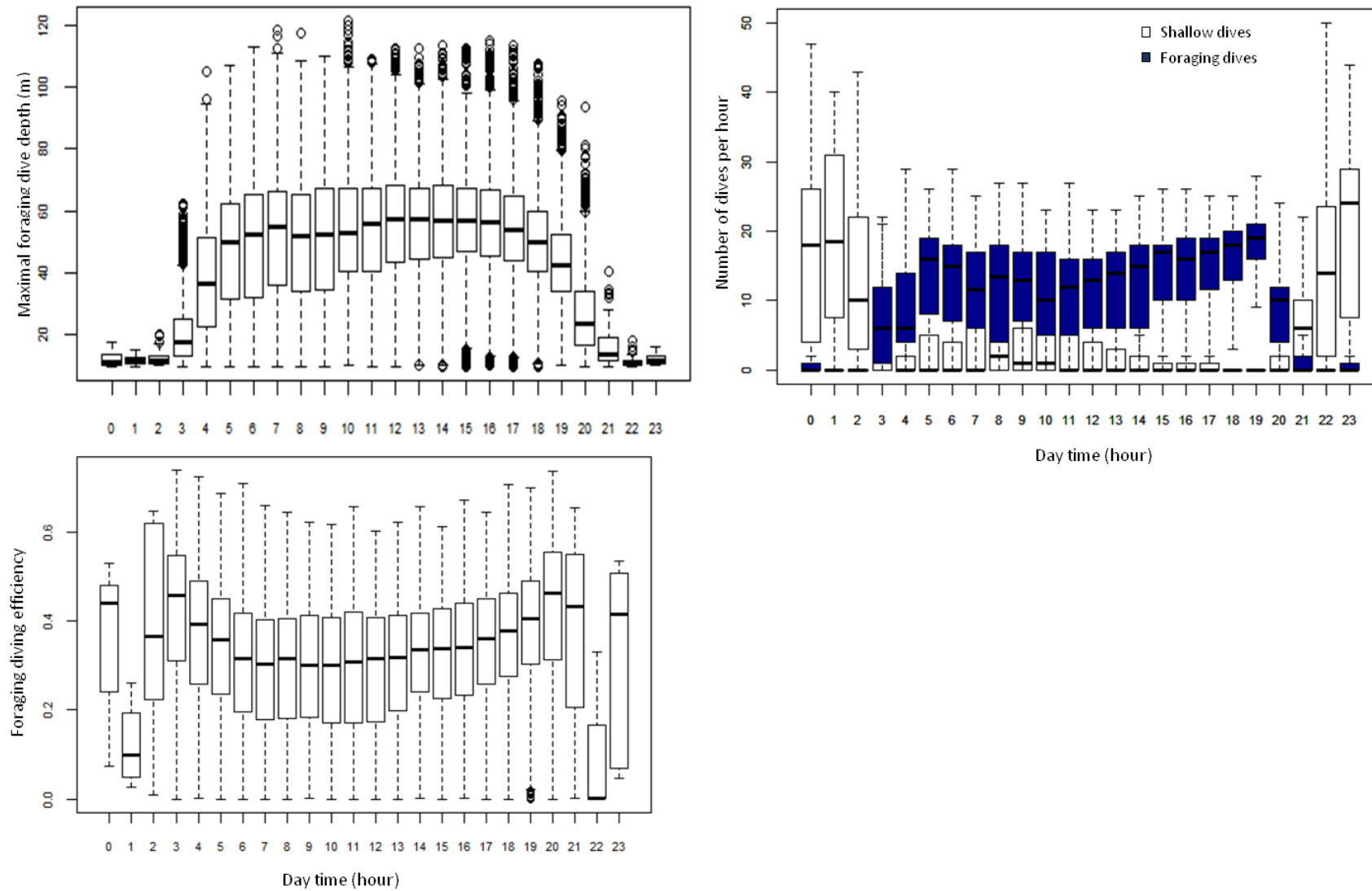


Figure 4 : Diving parameters in relation with day time from brooding females at Kerguelen Islands.

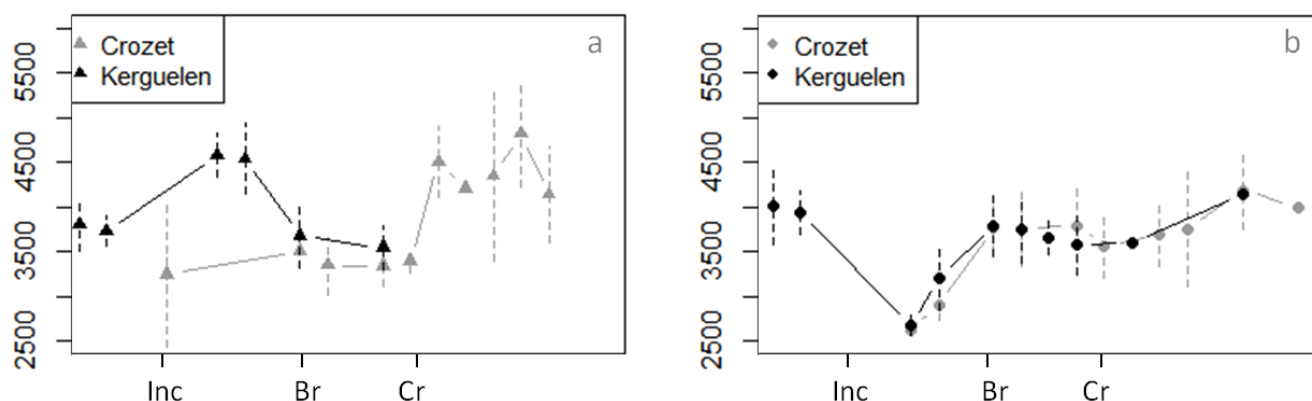


Figure 5: Variation of body mass of Macaroni penguins at Crozet and Kerguelen islands. a- Males; b- Females.

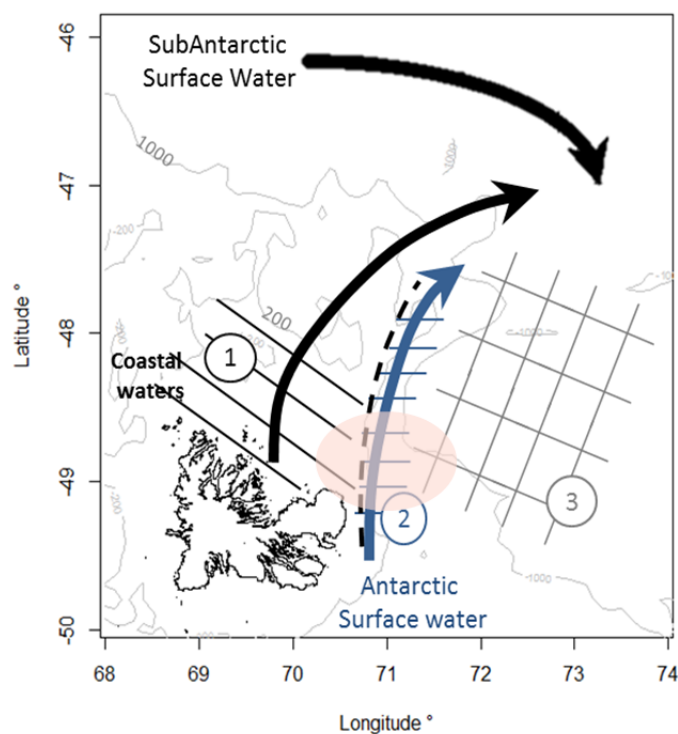
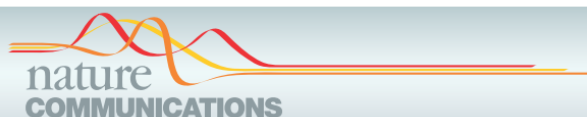


Figure 6: Schematic illustration of the circulation of the surface waters northeast of the islands, adapted from Blain *et al.* (2001). Pink area: foraging locations of brooding females. The dotted line is the estimated location of the shelf-break front. The hatched areas show the different biogeochemical systems: **Zone 1:** High-iron low-biomass case ; **Zone2:** unfavorable light mixing regime for phytoplankton growth. **Zone3:** High-iron high-biomass case. Grey lines indicate the 200 and 1000m isobaths.



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Large-scale climatic anomalies affect marine predator foraging behaviour and demography

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Determining the links between the behavioural and population responses of wild species to environmental variations is critical for understanding the impact of climate variability on ecosystems. Using long-term data sets, we show how large-scale climatic anomalies in the Southern Hemisphere affect the foraging behaviour and population dynamics of a key marine predator, the king penguin. When large-scale subtropical dipole events occur simultaneously in both subtropical Southern Indian and Atlantic Oceans, they generate tropical anomalies that shift the foraging zone southward. Consequently the distances that penguins foraged from the colony and their feeding depths increased and the population size decreased. This represents an example of a robust and fast impact of large-scale climatic anomalies affecting a marine predator through changes in its at-sea behaviour and demography, despite lack of information on prey availability. Our results highlight a possible behavioural mechanism through which climate variability may affect population processes.

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ARTICLE

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Long-term changes in population dynamics concurrent with climatic variability have been reported in an increasing number of wildlife species worldwide^{1–5}. However, the primary causes and underlying behavioural mechanisms generating such population changes are rarely identified unequivocally.

In marine ecosystems, climatic anomalies such as the El Niño Southern Oscillation (ENSO) may drastically alter food webs⁶. Understanding how the organisms respond to such climatic variability is essential to assess the potential impact of global warming on the future of marine ecosystems. Long-term data sets on the dynamics of food webs are thus of key importance but few are available because of logistic difficulties and high costs.

The climate variability at subtropical and subantarctic latitudes in the South Indian and Atlantic Oceans is mainly controlled by subtropical dipole events⁷ partly linked to both ENSO and the Southern Annular Mode (SAM)^{8,9}. These events are characterized by a tilted sea surface temperature (SST) anomaly dipole pattern oriented in the northeast–southwest direction in each basin, and are the leading mode of SST variability in both the southern subtropical Indian and Atlantic Oceans. How these subtropical large-scale climatic anomalies affect the ecosystems of the remote Southern Ocean is not known. In particular, the Southern Ocean holds considerable biomass of marine organisms including myctophid, one of the most important mesopelagic fish stocks in the world, which is yet poorly understood¹⁰. Several top predators rely on these mesopelagic fishes, especially in the Antarctic polar front (PF)¹¹, a major boundary corresponding to the northern limit of Antarctic waters¹². At the PF, the intense physical/biological interactions induce phytoplankton growth with subsequent increases in zooplankton biomass and concentrations of resources such as myctophid fish¹³.

Here we show how large-scale climatic anomalies in the Southern Hemisphere affect the foraging behaviour and population dynamics of a key predator of the Southern Ocean food webs, the king penguin (*Aptenodytes patagonicus*). First, we found that the occurrence of strong dipole events in the subtropical South Atlantic and Indian Oceans drives, at a very large scale, the temperature anomalies further south in the Southern Indian Ocean up to the polar frontal zone, which is the penguins' preferred foraging area¹¹. Secondly, we studied the inter-year changes in penguins distribution and foraging activities in relation to the PF position by analysing a unique satellite tracking and diving database from tagged king penguins (1992–2010, 16 years of data). By linking these changes in penguins' at-sea activities together with related demographic data sets we show how this large-scale climatic variability immediately impacts the foraging activity and ultimately the demography of these predators.

Results

At-sea foraging activities of penguins. The at-sea movements during the summer (from mid-December to mid-March) of foraging king penguins that breed on the Crozet archipelago, Southern Indian Ocean (Fig. 1a), were monitored annually from 1992 to 2010. The Crozet archipelago hosts the largest king penguins population (612×10^3 – 736×10^3 pairs) of the Southern Ocean¹⁴ (37%) (Supplementary Fig. 1) which have an estimated myctophid consumption of 8×10^5 tons/year¹⁵. When leaving the colony to forage, nearly all breeding individuals (93% of tracks) head south to forage (Fig. 1b). Foraging trips exhibits two distinct phases: a long distance commuting trips (300–500 km) to reach the northern boundary of the PF (Fig. 1b) and the time spent foraging at the PF¹¹. To accurately quantify the penguins foraging success (number of prey catching attempts), we instrumented individuals with miniaturized data loggers allowing detection of feeding events ($n = 4$ birds, Table 1)

or predicting foraging success from diving behaviour ($n = 7$ birds, Tables 2 and 3). Foraging success per day increased when the birds reached the PF. The catching success per foraging dive was variable but twice as high during the time spent at the PF than during the time spent commuting (see Methods, Tables 1 and 3, $P < 0.01$).

Consequences of the polar front variability. Between 1992 and 2010, SST anomalies affected the latitudinal position of the PF (Fig. 1). During the same period, penguin foraging ranges and the PF position exhibited extensive and concurrent variability (Fig. 1b, Fig. 2a; linear model, $F_{1,13} = 38.3$, $r^2 = 0.76$, $n = 14$, $P < 0.001$). Warm anomalies considerably increased the distance covered by penguins to reach the PF (Fig. 2a). According to the link between SST anomalies and the PF location, an increase of 1°C shifted its location southward by 130 km and the king penguin foraging range was similarly extended (data from the 1992–2010 period of penguins tracking). The travelling time from the colony to the PF was positively related to the PF location (linear model, $r^2 = 0.67$, $n = 110$, $P < 0.01$). Penguins were more affected in terms of foraging distance when attending small chicks during late summer (linear model, $r^2 = 0.56$, $n = 52$, $P < 0.05$) compared with the incubation period occurring earlier in the summer period (linear model, $r^2 = 0.30$, $n = 58$, $P < 0.05$). The time to reach the PF according to its location (linear model, $F_{1,80} = 30.6$, $P < 0.01$, Supplementary Fig. 2a,b) was not affected either by breeding stages or sexes ($P > 0.05$). On the other hand, the time spent foraging at the PF according to its location ($F_{1,80} = 23.2$, $P < 0.01$, Supplementary Fig. 2c,d) differed between breeding stages ($t = -5.61$, $P < 0.01$) but not between sexes ($P > 0.05$, Supplementary Fig. 2c,d).

In warmer years, the penguins not only went further but also they dived deeper (Fig. 2b). The SST changes in the oceanic area used by penguins induced concurrent changes in the depth of the thermocline (that is, the maximum of the vertical temperature gradient linked to the stratification of the water column¹²). The thermocline depth and topography are known to play a major role in fish aggregation^{16–17}. Thermocline changes affected king penguin diving behaviour, which usually targets the depth of the thermocline¹⁸. Thus penguins dived deeper with increasing depth of the thermocline for a given year (Fig. 2b; linear model, $r^2 = 0.58$, $n = 7$ years, $P < 0.05$).

Relationships with large-scale climatic anomalies. During the study, the PF position was linked to large-scale SST fluctuations in the subtropical South Indian and Atlantic Oceans, as illustrated by the concurrent variability of the PF position and the leading mode of the principal component analysis (PCA) of the SST fields during austral summer (Fig. 1c). The maxima of this leading PCA mode indicate the occurrence of 'positive' Subtropical Atlantic and Indian Oceans dipole (SAIOD) events (Fig. 1b) with positive SST anomalies in the southwest of the two basins (see Fig. 3). The latitudinal location of the PF was significantly associated with the occurrence of these positive SAIOD events during the summer (Fig. 1c; $r^2 = 0.63$, $n = 26$, $P < 0.001$).

Effects of the 1997 extra-tropical warm anomaly. An extreme positive SAIOD event occurred in 1997 with an abnormal large-scale warming of the southwest Indian Ocean, centred in the Crozet basin (Figs 1c,3). As a direct consequence, an unprecedented southward shift of the PF occurred during the same year (Figs 1c,2a).

During the very strong positive SAIOD event of 1997, the mean foraging distances performed by the penguins rearing a chick (596 ± 159 km) during summer (February–March) were the

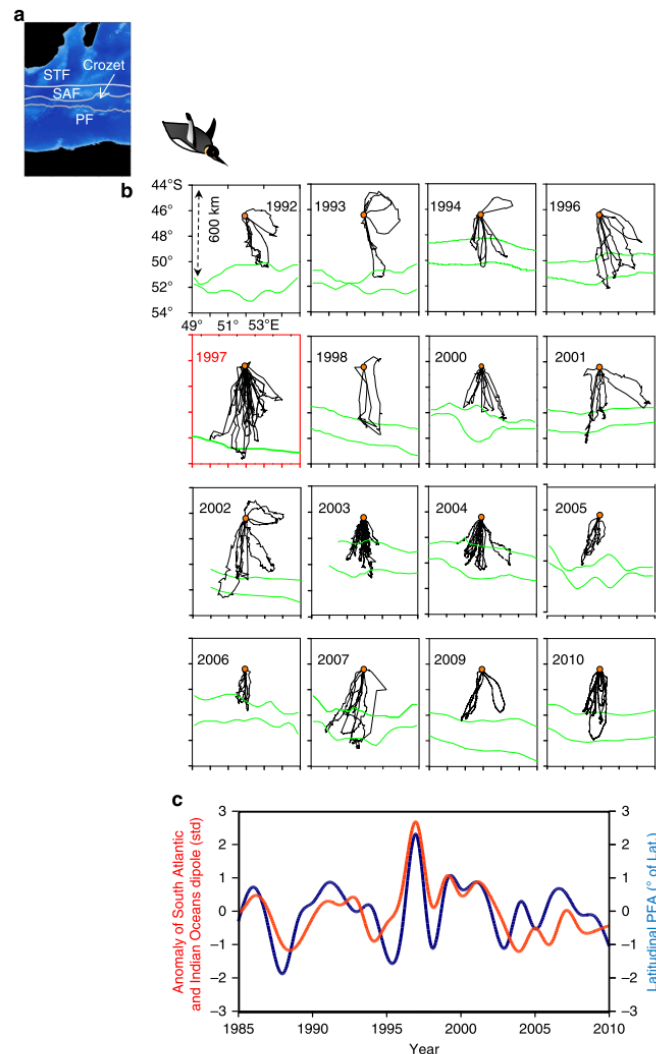


Figure 1 | Foraging distribution of penguins and their relationship with large-scale climatic anomalies. (a) Map of the Crozet sector, South Indian ocean. The white lines show the main frontal structures. (b) Satellite-tracks of at-sea king penguins from the Crozet Islands monitored over a 16-year period (1992–2010). The tracks are shown with the corresponding locations of the Antarctic PF (green lines; upper line: 5 °C sea surface isotherm; bottom: 4 °C sea surface isotherm). The orange dots show the position of the study colony (Baie du Marin, Possession Island, Crozet). The red box displays the exceptional situation during the summer 1997 with the extension of the penguins' foraging ranges in relation to the southward shift of the PF. (c) Time series of latitudinal PF location anomaly and of the leading mode from the PCA of SST anomalies over a combined South Atlantic-Indian domain (10°–50°S, 50°W–150°E). See Fig. 3 for the associated SST spatial pattern. This leading PCA mode (standardized time series, red curve) of February–March SST anomalies described 27% of the SST variability over the combined domain during the 1979–2011 period and will be referred to as the South Atlantic and Indian Oceans dipole (SAIOD) time series. The anomaly of the PF zonal position (PFA, positive = south, negative = north, in degree, blue curve) concerns the latitude estimated for the sector between 50/54°E. SAF: Sub-Antarctic front; STF: subtropical front; PF: polar front.

greatest reported over the whole study period, being doubled compared with the usual years (Fig. 1b). As the maximal foraging range corresponds to a high feeding activity of penguins¹¹, the favourable foraging areas considerably shifted southwards as

indicated by the tracking data. Diving behaviour was also affected in relation to such abnormal warming of the southwest Indian Ocean. During the same period *in situ* measurements from instrumented penguins travelling towards the PF indeed indicated

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NATURE COMMUNICATIONS | DOI: 10.1038/ncomms9220

Table 1 | Feeding success of king penguins instrumented with a feeding recorder during foraging trips to polar front from Crozet Islands during early chick rearing period (1996/97 season).

Bird	Feeding activity recorded (days)	Diving depth range (m)	Mean <i>N</i> prey ingested/day			Mean <i>N</i> prey/dive			Total number of feeding events
			polar front	Transit	<i>P</i>	polar front	Transit	<i>P</i>	
B	6.3	56–199	392.0 ± 186.6	86.6 ± 68	<0.001	5.4 ± 3.1	3.6 ± 2.6	<0.0001	1,407
C	7.5	50–306	735.0 ± 2.8	132.1 ± 99.2	<0.001	5.3 ± 3.6	1.8 ± 2.1	<0.0001	2,342
G	6.1	56–199	169.5 ± 50.2	25.5 ± 19.7	<0.001	4.8 ± 2.9	2.7 ± 1.9	<0.0001	580
I	9.0	51–243	207.0 ± 7.1	18.6 ± 8.6	<0.001	4.7 ± 2.6	1.8 ± 1.2	<0.0001	544

P significance derived from Wilcoxon rank sum tests.**Table 2 | Results of model averaging based on the best predictive models of prey capture established from diving parameters (at diving bout scales) of foraging penguins (early chick rearing period *n* = 7, 2009/10).**

Final models—bout scale	<i>w</i>	Coef ± s.e.m	<i>P</i> -value
Intercept	1	3.13 ± 0.09	0.00
Log (number of dives)	1	1.45 ± 0.18	0.00
Log (Number of dives ²)	0.92	− 0.25 ± 0.12	0.04
Maximal depth	0.50	− 0.12 ± 0.15	0.42
Number of wiggles	0.97	0.32 ± 0.11	0.01
Ascent rate	0.20	− 0.03 ± 0.11	0.76
Descent rate	1	0.47 ± 0.12	0.00
Number of step	0.45	− 0.11 ± 0.15	0.49
Surface duration	0.87	− 0.25 ± 0.15	0.09
C-index for fitted data	0.938	Excellent	
C-index for cross-correlation	0.923	Excellent	

The birds were instrumented with time-depth recorders and Argos transmitters. Coefficients (mean ± adjusted s.e.m.) from the final generalized linear model selected after a cross-correlation procedure. *w*: probability for the variable to be present in the selected model. The values of the concordance index (C-index) are shown for model averaged on fitting data sets and after final cross-validation. Explanatory variables correspond to mean values except the number of dives. The best predictive variables are in bold. The number of diving bouts used to fit the model and to validate it were 36 and 38, respectively.

Table 3 | Predicted feeding success of king penguins (*n* = 7) both tagged with a time-depth-temperature recorder (sampling rate: 1s) and an Argos transmitter during foraging trips to the polar front during the early chick rearing period (2009/10).

Bird	Sex	Feeding activity recorded (days)	Mean number of prey ingested/day			Mean number of prey/dive			Total number of predicted feeding events
			polar front	Transit	<i>P</i>	polar front	Transit	<i>P</i>	
B3	F	10	325 ± 310 (6)	111 ± 127 (4)	NS	3.1 ± 2.0 (774)	1.6 ± 1.2 (267)	<0.0001	2,404
W	F	9	161 ± 51 (5)	65 ± 41 (4)	<0.05	1.8 ± 0.5 (490)	1.5 ± 0.9 (168)	<0.05	1,308
N	M	13	366 ± 318 (7)	134 ± 128 (6)	NS	2.8 ± 1.9 (1,038)	1.8 ± 1.6 (498)	<0.0001	2,296
A5	M	21	24 ± 190 (13)	131 ± 145 (8)	NS	1.9 ± 0.9 (1,496)	1.9 ± 1.4 (611)	<0.0001	10,236
A7	M	22	318 ± 236 (9)	139 ± 94 (13)	NS	2.9 ± 1.0 (996)	3.3 ± 2.3 (889)	NS	7,550
A8	F	23	139 ± 93 (13)	68 ± 73 (10)	<0.05	1.8 ± 0.8 (979)	1.4 ± 0.7 (546)	<0.0001	7,905
O7	F	11	248 ± 251c (4)	25 ± 27(7)	<0.05	3.9 ± 1.8 (276)	0.7 ± 0.4 (179)	<0.0001	3,307

P-values derived from Mann and Whitney tests. Numbers in brackets are statistical effectives (days and dives) used for the tests.

a thermocline depth of ≈ 170 m (Fig. 2b), that is, 30 m deeper than during normal years¹⁸. As a consequence, the mean diving depth used by the penguins in the polar frontal zone was increased by 30.7% (Fig. 2b). Synchronously with these very unfavourable environmental conditions, the penguin breeding population experienced a 34% decline (Fig. 4) and recovered to their pre-event abundance only in 2002. This time period also corresponded to relatively low annual probabilities of adult survival¹⁹. Results from stochastic Gompertz population models (see Methods) indicate evidence of density dependence in the population, and suggest negative effects of SST anomalies, distance to the PF and SAIOD occurrences on breeding population size (Table 4). The decrease for the observed counts between 1993 and 1995 (and the increase between 1992 and 1993)

partly reflects counting error which was probably higher in these years. The decrease between 2005 and 2007 can be explained by the low population size (and thus low chick productivity) in 5–6 years earlier (2000–2002) corresponding to the average age at first breeding of king penguins.

There was also a negative effect of warm sea surface temperature anomalies (SSTA) on breeding success (Table 5), although the relationship was nonlinear, suggesting optimal SSTA in the main foraging area (Fig. 5). In particular the breeding success observed in 1997 was the lowest recorded over the whole study period. This strongly suggests that the increased foraging effort due to a southward shift of the PF has negatively affected some demographic parameters (recruitment and adult survival) of this long-lived species¹⁹, and therefore the population size.

Thus, both physical and biological compartments of the southwest Indian Ocean responded immediately to this climate forcing.

Discussion

Our results show that distinct large-scale climatic anomalies in the subtropical Indian and Atlantic Oceans had an immediate and major effect on the foraging habitat, diving behaviour, breeding success and population dynamics of a major top-

predator of the Southern Ocean, probably through decreases in prey availability at lower trophic levels²⁰. We provide evidence that the occurrence of strong dipole events in the subtropical South Atlantic and Indian Oceans drives, at a very large scale, the temperature anomalies further south in the polar frontal zone. These anomalies in turn affect king penguins in terms of at-sea distribution, foraging behaviour, breeding success and ultimately population dynamics.

Subtropical dipole events are the most important mode of SST variability in both the southern subtropical Indian and Atlantic Oceans, accounting 27% of the SST variability in these areas. Such modes of SST variability are controlled by the pulsations and shifts of the subtropical anticyclones and play even an active role at a global scale since they provide a remote control over ENSO variability in the equatorial Pacific^{9,21}. SAIOD occurrence during the summer was significantly associated with the location of the PF. Importantly, these anomalous SST patterns are strongly phase-locked to the austral summer season, which is the breeding period where top predators are most dependent on the PF¹¹. During this period, seabirds have to regularly return to the colonies to alternate with their incubating partner or for provisioning of the chick. Non-flying, swimming predators such as penguins are highly sensitive to environmental changes especially during the breeding period because of their low travelling speed, particularly during the breeding period characterized by limited foraging ranges^{22–23}.

Climatic anomalies in the Southern Ocean were found to impact top-predator populations^{7,19,23–27} which potentially integrate environmental changes at various temporal scales being close to the apex of food webs²⁶. In the northern hemisphere, several correlative studies have also reported impacts of large scale climatic anomalies on foraging success or demography of marine predators in diverse productive ecosystems. In northern Norway, movements of different water masses influence the water temperature which controls plankton abundance which in turns drives the growth of puffins' main prey, that is, first-year herring²⁸. Long-term time series of productivity for several seabird species breeding in the California Current System indicate that the perturbation in the availability of food may have a complex origin. Thus ENSO has an important effect but other global atmosphere–ocean phenomena can also affect the local food webs just as dramatically²⁹. However none of these studies showed a link between large-scale climatic events, foraging behaviour of a marine predator and its consequences on breeding success and population dynamics. Our study documents how extra-tropical climate anomalies may immediately affect a marine predator far in the Southern Indian Ocean by driving, at a very large scale, the temperature anomalies in the main feeding zone. It also established a link between large-scale climate changes, at-sea

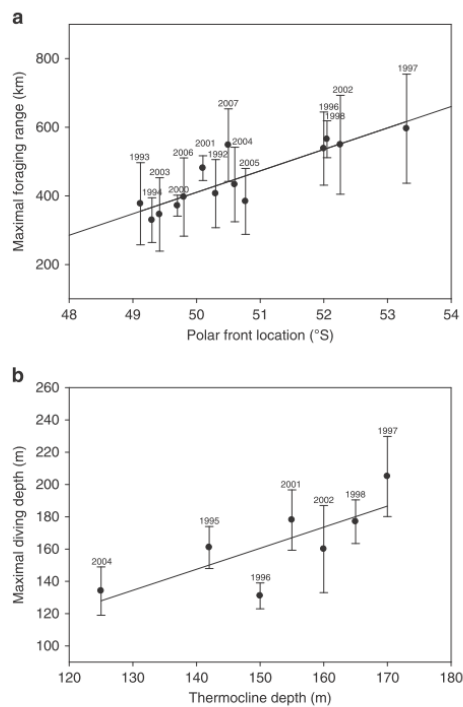


Figure 2 | Relationships between penguins foraging behaviour and conditions at the Polar Front in summer, South Indian Ocean (Crozet sector). Error bars are s.e.m. and the solid black line are regression slopes based on the data. **(a)** Mean maximal foraging range of penguins as a function of inter-annual variations in the PF location (1992–2007, $n = 14$ years). **(b)** Mean maximal foraging depth as a function of inter-annual variations in the thermocline depth in the polar frontal zone (1995–2004, $n = 7$ years).

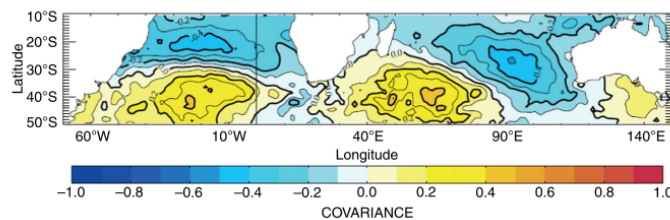


Figure 3 | Spatial pattern associated with the Subtropical Atlantic and Indian Oceans dipole (SAIOD) time series (that is, the leading mode of the principal component analysis (PCA) of February–March SST anomaly fields over the combined South Atlantic–Indian domain).

ARTICLE

NATURE COMMUNICATIONS | DOI: 10.1038/ncomms9220

foraging behaviour, breeding success and population dynamics over a long-term scale, although direct data on the prey availability are lacking

Future climatic scenarios indicate a warming of the surface waters that should lead to a progressive southward shift of the PF^{30–31} and to a deepening of the thermocline³², thus impacting myctophid distribution and potentially representing a serious threat for penguins and other diving predators of the Southern Ocean. This highlights the value of retrospective analyses on top-predator life histories combining foraging and demographic parameters through different climatic/habitat scenarios²⁰ and their potential to make robust predictions of the effect of climate change on ecosystems.

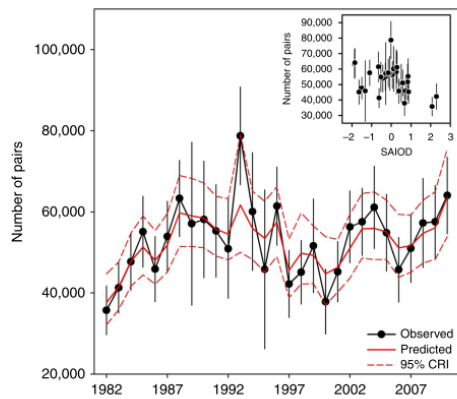


Figure 4 | Observed and modelled changes in the king penguin breeding population at Possession Island (Crozet) from 1982 to 2010. The modelled changes were obtained from a stochastic Gompertz model with density dependence and an effect of the Subtropical Atlantic and Indian Oceans dipole (SAIOD) time series. The inset shows the observed breeding population size as a function of SAIOD. Error bars are s.e.m.

Methods

Penguin satellite tracking. Between 1992 and 2010, 6–15 breeding penguins from the king penguin colony of the Baie du Marin (20,000 pairs³³), Possession Island, were fitted with Argos PTT Satellite Transmitters each austral summer, totalling 124 useable tracks. Such sample size was adequate with respect to the purpose of the tracking study according to the previous studies performed at the same colony^{11,18}. The capture, release and handling procedures received the approval of the ethics committee of the French Polar Institute (IPEV) and of the French Environment Ministry. The birds were gently handled and the devices fixed to the feathers of the back with a cyanolycrate adhesive securely fastened with cables-ties. The equipment procedure took 15 min. We instrumented randomly selected any penguin observed relieved on their egg or small chick by its partner of breeding duties within the ten first ranks of breeders in the colony where birds can be accessed without disturbance. Almost the same number of females and males were instrumented each year. The penguins were sexed when relieved by their partner by using the inter sexes differences in mates call. Logistic reasons restrained tracking to only incubating birds in 1992, 1993, 1996, 2000 and 2001. The transmission interval ranged between 45 and 60 s. The front of all transmitters was hydrodynamically shaped and a flexible antenna, spring mounted, was used to limit the drag effect^{34–35}. The transmitters weighted 1.8% of the mean adult weight. A track corresponds to the at-sea movements of a penguin during one foraging trip off the colony. Only birds having successfully foraged (no colony desertion) were kept for the analysis as failed breeders greatly increase their foraging range and the duration of their travels. No significant differences in breeding failure were reported among control and instrumented birds (respectively, 0.36 and 0.15%, $n = 34$ and 23 , $\chi^2_1 = 3.45$, $P = 0.06$). To compare the penguin foraging range to the PF location over the whole time series, we randomly selected the same number of incubating and brooding birds (early chick rearing period).

Penguin feeding activities. To obtain detailed insights into the feeding activity of penguins, we used two kinds of information: (i) data from fast-response temperature sensors surgically implanted in the oesophagus together with time-depth recorders (1996/97, $n = 4$ penguins, Table 1); and (ii) results from a predictive model of feeding success during penguins dives obtained from another instrumented group (2009/10, $n = 7$ penguins, early chick rearing) (Table 2). This was realized by combining different diving behaviours in a statistical procedure from the data sets obtained on the penguins instrumented in (i).

Concerning (i) we attached the oesophagus sensors together with a time–depth–temperature recorder on seven penguins at their departure to the sea. Oesophagus temperature loggers were attached to birds through surgical implantation³⁶. A total of four birds provided extensive feeding records ranging from 6 to 9 days at sea (Table 1). Oesophageal temperature and depth were recorded with a resolution of 0.01 °C and 0.1 m, respectively. The pressure sampling rate was 2 s in the depth range 0–200 m and 4 s in the range 200–400 m. Experiments on captive individuals showed that fast-response temperature sensors were sensitive enough to detect prey similar to the smallest fish (1.8 g) caught by the free-ranging penguins. Temperature drops were characterized as feeding or non-feeding events with regard to amplitude and duration of the change in temperature³⁶. Drops were characterized as feeding events for a 0.06 °C s^{−1} rate of temperature decrease³⁶.

Table 4 | Stochastic Gompertz population models testing for the effects of density dependence, sea surface temperature anomalies, distance to the polar front and South Atlantic–Indian Oceans Dipole on the breeding population size of king penguins on Possession Island, 1982–2011.

Model	<i>r</i>	<i>b</i>	<i>c</i>	<i>Pr(c) < 0</i>	σ	τ
DD + SSTA	0.101 (0.062; 0.141)	0.008 (0.002; 0.0133)	−0.020 (−0.078; 0.044)	0.758	0.114 (0.013; 0.185)	0.112 (0.000; 0.206)
DD + Dist	0.100 (0.060; 0.139)	0.008 (0.002; 0.013)	−0.038 (−0.107; 0.029)	0.870	0.106 (0.007; 0.177)	0.120 (0.024; 0.220)
DD + SAIOD	0.101 (0.063; 0.140)	0.008 (0.003; 0.014)	−0.067 (−0.133; 0.005)	0.971	0.113 (0.030; 0.187)	0.099 (0.008; 0.192)

DD, density dependence; Dist, distance from the colony to the polar front; SAIOD, the south Atlantic–Indian Oceans dipole; SSTA, sea surface temperature anomalies. Values in parentheses indicate 95% highest probability density intervals for *r*, *b*, *c*, σ and τ . *Pr(c) < 0* indicates the probability that the slope coefficient between population size and the covariate was negative.

Table 5 | GAM results for the breeding success of king penguins from Possession Island as a function of SSTA, distance to the PF and SAIOD.

Covariate	F-test	P-value	Adjusted R ²
SSTA	4.572	0.023	0.417
Dist	1.711	0.217	0.124
SAIOD	2.730	0.102	0.187

Dist, distance from the colony to the polar front; GAM, generalized additive models; PF, polar front; SAIOD, the south Atlantic–Indian Oceans dipole; SSTA, sea surface temperature anomalies.

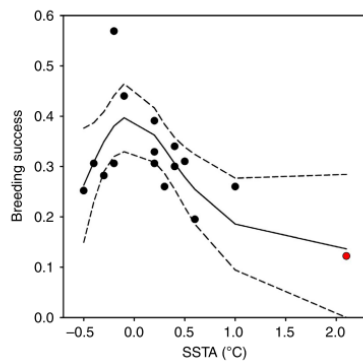


Figure 5 | Fitted GAM results showing the relationship between the king penguin breeding success data and sea surface temperature anomalies (SSTA) in their main foraging area at the PF for the period 1987–2010. Dotted lines indicate 95% confidence intervals. The red dot indicate the year 1997.

Data were analysed using Jensen System Software programs (Laboe, Germany) and custom-made Matlab programs.

Concerning (ii), a generalized linear model was built to relate the feeding events (response variable) provided by four birds instrumented during early chick rearing period as indicated in (i) to different diving variables (explanatory variables): maximal depth, number of wiggles (quick variations of depth in three successive points during which the vertical speed passes below 0 m s^{-1}), number of steps (periods within a dive during which vertical speed decreases to 0.35 m s^{-1} , vertical ascent and descent rates and time spent at the surface previously a dive. Wiggles have been identified as reliable indicators of the feeding success^{37–40}.

The penguins' vertical swimming speed (1.3 m s^{-1} during the ascent and descent phase of the dive) prevents any underestimation of wiggles and steps occurrence³⁷. The analysis was conducted on the R statistical environment⁴¹. The overdispersion was tested (function *dispersiontest* package 'AER') and a negative binomial family was chosen (function *odTest*, $P < 0.0001$, package 'pscl'). Models were thus built using the *glm.nb* function (package 'MASS'). The explanatory variables were centred and scaled to facilitate the convergence of models and to compare the weight of different variables between them⁴². All possible combinations of variables were performed and classified according to the Akaike Information Criterion⁴³. The QAIC was preferred in order to deal with the overdispersion of response variable. The n first models with the summed QAIC weight w (probability of a model to be the best 'true' model) inferior of 0.95 were submitted to a model averaging procedure (function *model.avg* package 'MuMIn'). The full model-averaged coefficients (with shrinkage) and their adjusted s.e.m. are presented in Table 2. Complete models were built (two scales: dive; and diving bout: sequence of foraging dives, brooding stage). The identity of birds was not included as random effect as their number was too low. Thus, a model per individual was built in order to ensure that relation between the response and explanatory variables were similar to the complete models. Once models fitted, their predictive performance was estimated using a cross-validation procedure. The quality of the predictive power was given by the C-index which measures the probability of concordance between predicted and observed data (C-index, package 'hmisc'⁴⁴) (Table 2). At the diving bout scale, the strongest predictors of feeding events were wiggles (Table 2). The concordance index between observed data and predicted prey captures during diving bouts was 'excellent' (C-index 0.90).

This predictive models was used to predict prey captures during diving bouts of an another penguin study group ($n = 7$, early chick rearing period, 2009/10) during their foraging trip to the PF (Table 3). These penguins were instrumented both with an Argos transmitter and a time-depth-temperature recorder before going to sea. The birds were recaptured after 9–23 days spent at sea and the instruments recovered.

Depth-temperature profiles recorded from penguins. We used temperature data from Mk5 and Mk9 data loggers (Wildlife Computers, Redmond, USA) attached to penguins foraging at the PFZ. The birds were caught in the same colony than the other studied groups. The loggers weighted 0.3–0.6% of the mean adult weight, respectively. The number of birds equipped was 8, 2, 3, 5, 6, 8 and 4 for the years 1995, 1996, 1997, 1999, 2001, 2002 and 2004, respectively ($n = 36$, 20 males, 16 females). When animals were at sea, depth was sampled every 2 or 5 s and temperature was sampled every 5, 10 or 20 s depending on the sensors used. Depth was recorded with a 2 m resolution. The resolution of the different temperature

sensors varied from 0.1 to 0.3°C . The time constants (time required for the sensor to register 66.3% of the change in temperature) were found to be 6 s for Mk5 (refs. 45) and 1 s for Mk9 data loggers used. For Mk5 and Mk9, 95% of the total temperature change was attained in less than 20 s. Thermocline depth corresponded to the modal depth reached by king penguins during foraging dives from spring to summer¹⁸. The time spent at the bottom of the dive (from 1.0 to 1.3 min) allowed accurate estimations of the thermocline profile calculated⁴⁵.

Population parameters. The breeding population at Possession Island was inferred from the counts of breeding pairs of the four largest colonies on the island. These four colonies represented ≈ 80 –90% of the total population breeding on the island and the abundance of breeding pairs varied in parallel at all four colonies³³. The average distance between colonies was $10.3 \pm 5.9 \text{ km}$ (min: 1.8 km, max: 15.0 km). Breeding pairs were counted using oblique photographs taken from promontories overlooking colonies in January (corresponding to the peak of laying period), when incubating birds are clearly distinct because they exhibit regular spacings between individuals³³. Counts were not made every year at all colonies due to logistical reasons. The total number of counts included 65 colony.years (that is, there were 43.9% missing data). To obtain a complete time series of the number of breeding pairs from 1982 to 2011, we first combined the time series with missing observations from the four colonies, and performed a log-linear regression model with Poisson error terms using the program TRIM⁴⁶. Missing counts were predicted from a model estimated on observed counts where year was entered as a discrete explanatory variable, taking into account overdispersion and serial correlation. We then used the stochastic Gompertz population model to analyse the effect of covariates on breeding population size while taking into account density dependence, since density dependence in this king penguin population was suggested by a previous study³³, which suggested density dependence in adult fecundity and possibly on survival. By log transforming the population abundance in year t (N_t) and putting $x_t = \ln(N_t)$, this model was defined through:

$$x_{t+1} = r + (1 - b)x_t + cz_t + e_t$$

where $1 - b$ is the lag 1 autocorrelation of the log transformed population abundance, r is the growth rate for $N = 1$, b is a measure of the strength of density dependence, z_t is the value of a covariate in year t , and e_t is normally distributed process error with mean zero and s.e.m. τ (refs 47,48). When $b = 0$ the process is density independent. The parameter c captures the effect of the covariate. When $c > 0$ or $c < 0$ the covariate has a positive or negative effect on population size, respectively.

Uncertainty in population abundance estimates was modelled with a log normal distribution so that the log transformed population abundance estimate in year t was given by $y_t = x_t + \eta_t$, where η_t is sampling error with mean zero and s.e.m. σ . Following⁴⁶ models were fitted using a Bayesian approach implemented in R via JAGS⁴⁸. We chose weakly informative normal priors for parameters b and c , and weakly informative uniform priors on the interval 0–3 for parameters σ and τ . As recommended by Lebreton and Gimenez⁴⁹, we used an informative prior for r based on the demographic invariant approach⁵⁰. This prior was a normal distribution with mean 0.10 and standard deviation 0.02. Inferences were drawn for posterior distributions based on 50,000 Markov Chain Monte Carlo simulations with two chains after a burn-in set of 10,000 updates. We assessed the convergence of the model fits by visually checking the trace of the posterior parameter estimates and computed Gelman and Rubin's R-hat convergence statistics.

In addition to population abundance we used annual breeding success data from earlier studies performed on the Baie du Marin colony of Possession Island^{51–55}, and unpublished data. Breeding success was obtained for 1987–1989, 1993, 1997–2004, 2006–2010 and estimated as the proportion of eggs laid by breeding pairs that fledged a chick. We investigated the relationships between breeding success and environmental covariates using non-parametric smoothing regression techniques⁵⁶ (Table 4). Generalized additive models (GAM) were specified with a Gaussian family, used a penalized cubic regression spline, and the optimal amount of smoothing was estimated using cross-validation. The adjusted R-squared for the model was defined as the proportion of variance explained, where original variance and residual variance were both estimated using unbiased estimators. This quantity could be negative if the fitted model was worse than a one parameter constant model⁵⁶.

To investigate the effects of environmental covariates on breeding success we performed generalized additive models.

Environmental data. The time period considered for the climate analysis was 1979–2011. For the SST climatic analyses we use monthly mean data from the Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST1.1) data set⁵⁷. PCA was used to extract the principal modes of variability of the SST fields⁵⁸.

SST is a major variable determining king penguin foraging habitat⁵¹ and is highly correlated with other physical variables such as air temperature and sea ice extent. Surface isotherms are accurate indicators of the location of the PF, which is originally defined by the northern limit of Antarctic water. This subsurface water mass is measured by the northernmost extension of the 2°C isotherm that corresponds to the 4–5 $^\circ\text{C}$ surface isotherms during summer¹². We consider here the summer northern limit of the PF as the 5°C surface isotherm¹². Environmental covariates entered in the population model defined above were: (1) sea surface

ARTICLE

NATURE COMMUNICATIONS | DOI: 10.1038/ncomms9220

temperature anomalies (SSTA) south of Crozet in the polar frontal zone frequented by king penguins during summer (January–February)¹⁸; (2) distance to PF (Dist), calculated as the distance separating Possession Island to the 5 °C isotherm south of the island; (3) the southern Atlantic–Indian Oceans dipole (SAIOD) time series, which is defined as the first principal component of the PCA of SST anomaly fields over a combined South Atlantic–Indian domain (10°–50°S, 50°W–150°E) during February–March. The SSTA data were derived from satellite measurements AVHRR/MODIS E-W. The SSTA were estimated during February–March over the tracking period in a box south of Crozet corresponding to the area prospected by penguins over the whole period, i.e., between 47° and 53°S in latitude and between 49° and 55°E in longitude east and west of Crozet. Because SSTA, Dist and SAIOD were correlated, only one covariate at a time was entered in the stochastic Gompertz population model.

References

- Hughes, L. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61 (2000).
- Parnesian, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669 (2006).
- Walther, G. R. et al. Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
- Hunt, G. L. Jr et al. Climate impacts on eastern Bering Sea food webs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. *ICES J. Mar. Sci.* **68**, 1230–1243 (2011).
- Baier, C. T. & Napp, J. M. Climate-induced variability in *Calanus marshallae* populations. *J. Plankton Res.* **25**, 771–782 (2003).
- Barber, R. T. & Chavez, F. P. Biological consequences of El Niño. *Science* **222**, 1203–1210 (1983).
- Forcada, J. & Trathan, P. N. Penguin responses to climate change in the Southern Ocean. *Global Change Biol.* **15**, 1618–1630 (2009).
- Hermes, J. C. & Reason, C. J. C. Ocean model diagnosis of interannual coevolving SST variability in the South Indian and South Atlantic Oceans. *J. Climate* **18**, 2864–2882 (2005).
- Terray, P. Southern Hemisphere extra-tropical forcing: a new paradigm for El Niño–Southern Oscillation. *Clim. Dyn.* **36**, 2171–2199 (2011).
- Collins, M. A. et al. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biol.* **31**, 837–851 (2008).
- Bost, C. A. et al. Importance of Southern Ocean fronts for seabird and marine mammals. *J. Mar. Syst.* **78**, 363–376 (2009).
- Park, Y.-H., Gambèroni, L. & Charriaud, E. Frontal structure, water masses, and circulation in the Crozet Basin. *J. Geophys. Res.* **98**, 12361–12685 (1993).
- Pakhomov, E. A., Perissinotto, R. & McQuaid, C. D. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Progr. Ser.* **134**, 1–14 (1996).
- Bost, C. A. et al. in *Penguin Book* (eds Dee Boersma, P. & Borboroglu, P. G.) 7–21 (University of Washington Press, 2013).
- Guinet, C., Cherel, Y., Ridoux, V. & Jouventin, P. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarc. Sci.* **8**, 23–30 (1996).
- Ballance, L. T., Ainley, D. G. & Hunt, G. L. Jr. in *Encyclopedia of Ocean Sciences* 5 (eds Steele, J. H., Thorpe, S. A. & Turekian, K. K.) 2636–2644 (Academic Press, 2001).
- Hulley, P. A. in *Fishes of the Southern Ocean* (eds Gon, O. & Heemstra, P. C.) 146–178 (J.L.B. Smith Institute of Ichthyology, 1990).
- Charrassin, J. B. & Bost, C. A. Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar. Ecol. Progr. Ser.* **221**, 285–297 (2001).
- Le Bohec, C. et al. King penguin population threatened by Southern Ocean warming. *Proc. Natl. Acad. Sci. USA* **105**, 2493–2497 (2008).
- Trathan, P. N., Forcada, J. & Murphy, E. M. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Phil. Trans. R. Soc. B* **362**, 2351–2365 (2007).
- Boschat, G., Terray, P. & Masson, S. Extratropical forcing of ENSO. *Geophys. Res. Lett.* **40**, 1605–1611 (2013).
- Weimerskirch, H. Are seabirds foraging for unpredictable resources? *Deep Sea Res.* **54**, 211–223 (2007).
- Ainley, D. G. *The Adélie Penguin, Bellwether of Climate Change* (Columbia University Press, 2002).
- Forcada, J., Trathan, P. N., Reid, K. & Murphy, E. J. The effects of global climate variability in pup production of Antarctic fur seals. *Ecology* **86**, 2408–2417 (2005).
- Barbraud, C. & Weimerskirch, H. Emperor penguins and climate change. *Nature* **411**, 183–186 (2001).
- Croxall, J. P., Trathan, P. N. & Murphy, E. J. Environmental change and Antarctic seabird populations. *Science* **297**, 1510–1514 (2002).
- Lyver, P. O. et al. 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 (2014).
- Durant, J. M., Anker-Nilssen, T. & Stenseth, N. C. Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc. R. Soc. Lond. B Biol. Sci.* **270**, 1461–1466 (2003).
- Ainley, D. G., Sydeman, W. I. & Norton, J. Upper trophic level predators indicate interannual negative and positive anomalies in the California current food web. *Mar. Ecol. Progr. Ser.* **118**, 69–79 (1995).
- Aoki, S., Yoritaka, M. & Masuyama, A. Multidecadal warming of subsurface temperature in the Indian sector of the Southern Ocean. *J. Geophys. Res.* **108**, 8081 (2003).
- Péron, C., Weimerskirch, H. & Bost, C. A. Projected poleward shift of king penguins (*Aptenodytes patagonicus*) foraging range in response to future global warming. *Proc. Biol. Sci.* **279**, 2515–2523 (2012).
- Sallée, J. B., Speer, K. G. & Rintoul, S. R. Zonally asymmetric response of the Southern Ocean mixed-layer depth to the Southern Annular Mode. *Nat. Geosci.* **3**, 273–279 (2010).
- Delord, K., Barbraud, C. & Weimerskirch, H. Long-term trends in the population size of king penguins at Crozet archipelago: environmental variability and density dependence? *Pol. Biol.* **27**, 793–800 (2004).
- Wilson, R. P., Kreye, J. M., Lucke, K. & Urquhart, H. Antennae on transmitters on penguins: balancing energy budgets on the high wire. *J. Exp. Biol.* **207**, 2649–2662 (2004).
- Cotté, C., Park, Y. H., Guinet, C. & Bost, C. A. Movements of foraging king penguins through marine mesoscale eddies. *Proc. Biol. Sci.* **274**, 2385–2391 (2007).
- Charrassin, J. B. et al. Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proc. Biol. Sci.* **268**, 151–157 (2001).
- Halsey, L. G., Bost, C. A. & Handrich, Y. A thorough and quantified method for classifying seabird diving behaviour. *Pol. Biol.* **30**, 991–1004 (2007).
- Bost, C. A. et al. Change in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep-Sea Res.* **54**, 248–255 (2007).
- Hanuisse, N. et al. Measuring feeding activity in a deep diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as foraging proxies. *J. Exp. Biol.* **213**, 3874–3880 (2010).
- Simeone, A. & Wilson, R. P. In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Mar. Biol.* **143**, 825–831 (2003).
- The R Foundation for Statistical Computing [www.cran.r-project.org/web] (2013).
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extension in Ecology with R* (Springer, 2009).
- Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach* 2nd edn (Springer, 2002).
- Harrell, F. E. *Regression modelling strategies: with applications to linear models, logistic regression, and survival analysis* (Springer, 2001).
- Charrassin, J. B., Park, Y. H., Le Maho, Y. & Bost, C. A. Fine resolution 3-D temperature fields off Kerguelen from instrumented penguins. *Deep Sea Res.* **51**, 2091–2103 (2004).
- Pannekoek, J. & Van Strien, A. J. M. *Trends & Indices for Monitoring Data*. Research Paper N° 634, Statistics Netherlands, Voorburg (1996).
- Jacobson, A. R., Provenzale, A., Von Hardenberg, A., Bassano, B. & Festa-Bianchet, M. Climate forcing and density-dependence in a mountain ungulate population. *Ecology* **85**, 1598–1610 (2004).
- Plummer, M. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. (eds Steele, J. H., Thorpe, S. A. & Turekian, K. K.) DSC 2003, 20–22 March (Vienna, Austria, 2003).
- Lebreton, J.-D. & Gimenez, O. Detecting and estimating density-dependence in wildlife populations. *J. Wildl. Manag.* **77**, 12–23 (2013).
- Niel, C. & Lebreton, J.-D. Using demographic invariants to detect overharvested bird populations from incomplete data. *Conserv. Biol.* **19**, 826–835 (2005).
- Weimerskirch, H., Stahl, J. C. & Jouventin, P. The breeding biology and population dynamics of King Penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis* **134**, 107–117 (1992).
- Descamps, S., Gauthier-Clerc, M., Gendner, J.-P. & Le Maho, Y. The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). *Avian Sci.* **2**, 1–12 (2002).
- Gauthier-Clerc, M. et al. Long-term effects of flipper bands on penguins. *Proc. Biol. Sci.* **271**, S423–S426 (2004).
- Le Bohec, C. et al. Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded king penguins. *J. Anim. Ecol.* **76**, 1149–1160 (2007).
- Saraux, C. et al. Reliability of flipper-banded penguins as indicators of climate change. *Nature* **469**, 203–208 (2011).
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extensions in Ecology with R* (Springer, 2009).
- Rayner, N. A. et al. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* **108**, 4407 (2003).
- Bretherton, C., Smith, C. & Wallace, J. An intercomparison of methods for finding coupled patterns in climate data. *J. Clim.* **5**, 541–560 (1992).

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Author contributions

C.A.B., C.C., Ch.B., Y.H., C.G. and H.W. designed the experiments; C.A.B., C.B., K.D., Y.N., Y.H. and H.W. supervised the experiments on the field; C.A.B., C.C., C.B., Ch.B., Y.H. and O.G. performed the analysis of biological data. P.T. performed the analysis of environmental data. C.A.B., Ch.B., C.B., P.T. and C.C. wrote the paper.

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Diving behaviour in Eastern rockhopper penguins *Eudyptes chrysocome filholi* during incubation.

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Abstract

In the marine environment, the heterogeneous distribution of resources in three dimensions constrains the diving predators in their foraging. According to the optimal foraging theory, they have to optimize their foraging effort to maximize the gain /cost ratio, in order to get the best energy benefit. Penguins, as central place foragers and divers unable to fly, are strongly constrained by the distance to reach the feeding areas and physiological limitations because of diving. For the first time, this study describes the diving foraging strategies of the eastern rockhopper penguin *Eudyptes chrysocome filholi* during the incubation. The diving behavior has been studied throughout the dives, the dive bouts, 24 h cycle and the entire journey at sea. Our results show that i) the penguins prefer exploring between 40 - 60m where the feeding patches seem more profitable, ii) the depth tends to increase during the middle phase of the journey. iii) Finally, the penguins show differences in depth and efficiency of dives between genders, in accordance with their sexual dimorphism. This study raises the relevance of studying foraging strategies throughout the cycle and help to a better understanding of factors of population decline.

Introduction

Penguins are key avian consumers of the southern food webs (Brooke, 2004). Compared to flying seabird, penguins are constrained because of their obligatory swimming or diving at-sea movements. They are thus spatially limited into the space vertically and horizontally. Indeed diving birds are much more affected by the distance than flying birds because they are forced to forage closer to the colony and are thus limited in possibility to food patch (Hunt and Schneider, 1987; Weimerskirch, 2007). On the one hand because of their diving behavior they are also limited by their time in apnea, pressure, reached depth and recovery time. They have to come back regularly to the surface in order to renew their oxygen stores (Carbone and Houston, 1994; Kooyman and Ponganis, 1998). Southern Penguins are also endothermic animals living in extreme environment where the cold sea water increases the heat loss. Therefore they have

to cope with strong energetic expenditures (Butler, 2001).

These constraints are harder for small size divers predators such as the genus *Eudyptes* (Williams, 1995). Indeed, the duration, depth and diving efficiency increase with the size and the weight according to an allometric relation (Butler and Jones, 1997; Charrassin, 1999; Schreer and Kovacs, 1997). In this way the waited optimal strategy for this kind of organisms would be a repetition of several little dives (Costa, 2007) with a maximization of the bottom time what allows an access to better food patch with a minimum time needed to reach the favourable depths.

In this work we studied the diving behavior of the Rockhopper Penguin *Eudyptes chrysocome filholi* during the incubation at the Kerguelen Islands, south Indian Ocean, an important breeding locality for the species (more than 85 500 pairs) (Weimerskirch et al., 1989). During the incubation,

at-sea constraints and benefits are very different from those generally studied at other phase of the cycle e.g. guard or crèche phase (Ricklefs, 1990, 2000). During incubation, males and females switch to feed at sea and do not have to come back daily at the colony. Thus their foraging activity can be extended during many days (Borboroglu and Boersma, 2013). They have time to go further and exploit potentially more efficient resources (Wilson, 1995) in better quantity and quality. This allows them to better recover their body condition previously diminished by fasting incubation and make store before come back for the crèche period.

This work aims to study their diving behavior during incubation in attempting to answer several questions: 1) How Rockhopper Penguins optimize their diving behavior?

2) Do they adjust their diving parameters according the food success at the scale of i) the dive, ii) bout, iii) the diel migration of their prey (nycthemeral migration) and iv) the trip. 3) Finally this species being strongly dimorphic (males are bigger than females, (Williams, 1995)), is there any difference of dives parameters according gender?

First we predicted that Rockhopper Penguins optimize their strategies with a maximization of the bottom time and minimizing their transit time. After identification of an optimal foraging depth, penguins would have advantages to return at the same depth the fastest they can in order to not lose any possibilities of capture (Hanuise et al., 2013). Dive bouts would be composed of many dives corresponding to an efficient foraging time (Mori et al., 2002) with break times that decrease until a threshold demonstrating their physiological constraints (Hanuise et al., 2013).

Our second prediction expected that Rockhopper Penguins do not have the same way to dive according to the time of the day. It is known that some macro-zooplankton organism doing nycthemeral migration (e.g. Euphausiacea) can be found at great depth during the day and at the surface at night (Perissinotto and McQuaid, 1992; Smetacek et al., 1990).

Finally we predicted that males and females differed in their diving behavior because of different energetic constraints (Cook et al., 2007; Groscolas et al., 2010). Indeed even if both gender take part in incubation, males firstly at-sea forage (Borboroglu and Boersma, 2013; Warham, 1963; Williams, 1995) and will not undergo the same fasting duration. Females fast longer than males (circa 15 days) before go again at sea but for a shorter time. Thus they have less energy for foraging and would have to be more efficient. Concerning males, they stay on land more than 20 days after their feed trip to assume the next guard phase (Tremblay et al., 2000). Therefore they have to acquire important stores during the trip at sea to i) restore their body reserve and ii) prepare this second period of fasting. That could have consequences on a greater effort in terms of dive depth, bottom time or number of dives during a bout (Cook et al., 2007).

Material and Methods

Study site and deployments

Fieldwork was conducted during December 2000 and January 2001 (Tremblay et al., 2000) at Mayes Island (49°28' S, 69°57' E), Golfe du Morbihan, Kerguelen Archipelago, during the incubation. During this fieldwork 14 Eastern Rockhopper penguins individuals (7 males and 7 females) were fitted with Time Depth Recorder ("TDR" Mark V, Wildlife Computers, Redmond, Washington, USA). The procedures received the approval of the ethics committee of the French Polar Institute (IPEV) and of the French Ministry of the Environment.

The tag were 9.5 cm long, 3.7 cm wide, 1.5 cm high, and weighed 70g, *i.e.* corresponding to about 3% of the bird's body cross-sectional area and <3% of its body mass, respectively (Tremblay et al., 2000). The tags were hydrodynamically shaped to reduce the drag effect (Bannasch et al., 1994). The devices continuously recorded each 2 second depth (resolution ± 1 m) and light data as well as temperature data every 30 seconds. In our study, the foraging trip was considered as starting at the first recorded dive and finishing at the last recorded one. TDR were removed when penguins

came back from the sea and returned to the nest at the colony after their foraging trip – between 10 and 20 days in average.

Diving analysis

In this study the data of 12 individuals (7 males and 5 females) were analysed as data of the two other birds were either not collected or unreliable. In order to estimate the logger-effect, the partners of the 14 individuals together with 43 others non-equipped couples were followed to constitute a control group with a repertory of the phenology and the dates of departure and arrival.

Recorded diving data were analysed thanks the software Multi Trace-Dive (©Jensen Software Systems). Diving behavior can be studied at different scales (Halsey et al., 2007): dive scale and bout scale (discrete series of dives) (Halsey et al., 2007; Watanabe et al., 2014). Therefore the following analyse parameters were used: because of the 1m resolution of the logger, the depth threshold value was 3m to detect dive events. The depth data were manually zero offset corrected to define the sea-surface. Two types of dive are distinguished: dive with a depth smaller than 5m as travelling and deeper than 5m as foraging (Tremblay et al., 2003).

Bottom phase was estimated as starting at 75% of the maximal depth and have to last more than 15% of the total dive duration (Halsey et al., 2007). Wiggles were detected when the amplitude of depth variation is equal or bigger than 2m and with a maximal duration of 80 seconds. All analyzed dives (n=75301) were pelagic and not benthic according to Tremblay and Cherel (Tremblay et al., 2000).

Concerning the bout analysis, only bouts with at least 3 following dives were considered (Halsey et al., 2007). Thus bouts are detected when their duration lasts minimum 270 seconds, *i.e.* the mean duration of three dives, what allows avoiding the isolated dives. In order to distinguish well the different bout without to omit none dive, the minimal bout interval is set as 150 seconds *i.e.* more than the mean dive duration (93.5 ± 35 seconds). In this study, most of the dive belongs to well defined bouts.

This study described also the diving behavior in Intra Depth Zone (IDZ) which is defined as following dives at the similar maximal depth at $\pm 10\%$ (Tremblay et al., 2000). This index allows to estimate if the penguins come back at the same foraging patch or not and thus to assess the foraging success of bout according depth (Tremblay et al., 2000). Day-phases were defined according the characteristics of nautical ephemerid *i.e.* 6 degrees above the horizon (United States Naval Observatory). The diving effort during the trip at sea was assessed through the daily dive rate which is defined as the mean vertical distance during a dive per day, that to say twice the depth per number of trip day (Boyd et al., 1994).

$$\text{dive rate} = \frac{\sum \text{maximale depth} \times 2}{\text{total number of travel day}}$$

The energetic profit of dives was evaluated on the all journey at sea through the index bottom time. The dive benefit was estimated thanks an index of foraging success defined as the bottom time relative to the total time at sea (Pütz and Cherel, 2005; Ydenberg and Clark, 1989).

$$\text{Index Gain dive per day} = \frac{\text{Total bottom time}}{\text{total time at sea}}$$

Daily mass gain of the sea journey could be calculated by comparing mass at departure and return of the same equipped birds.

Statistics analysis

Statistic analysis were carried out thanks the software R (version i386 3.1.0 and 2.13.0) (R Development Core Team, 2008). Homoscedasticity and normality of the variable were tested respectively with Bartlett test and Shapiro-Wilk test. In the case of a distribution of homogeneous and normal variables, parametric tests such as Anova with the Tukey HSD function and correlation test such Pearson were used. In the opposite case, non-parametric test of Kruskal-Wallis with the function `kruskalmc` (package `pgrimes`) and the correlation test of Spearman were applied. The significance threshold was set to $\alpha \leq 5\%$.

Generalized linear mixed models (GLMMs) were carried out according to the maximum likelihood method described by Burnham and Anderson (Anderson, 2008; Burnham and Anderson, 2002). In the case of normal distribution, lme models were built. In the opposite case glmer or glmmPQL were made according to the need of the possible autocorrelation term addition. The model selection was made according the Akaike index criteria (AIC), the weight of the variable, the residuals' homogeneity and p-values.

Models glmPQL testing relation between number of wiggles and maximal dive depth as well as number of wiggles and bottom duration according evolution of trip have been carried out on a smaller number of statistic individual because of the limited computational capabilities: 10,000 dives randomly selected in the dataset (on 75,301 dives). For such models, packages MASS (Venables and Ripley, 2002), car (Fox and Weisberg, 2010), nlme (Pinheiro et al., 2007) and lme4 (Bates et al., 2014) were requisite.

A linear mixed model lme was built in order to explain the bottom time (response variable) in function of the maximal depth and sex (explicative variables).

The evolution of wiggles during bottom time was used to obtain an proxy of hunting success (Bost et al., 2007) through a generalized linear mixed models glmPQL. This model was established to explain the relation between the wiggles' number at the bottom (response variable), depth and sex (explicative variables). A Poisson family was specified according to the response variable's distribution. An autocorrelation term was added to take into account the dives' autocorrelation.

At the bout scale, linear mixed models lme were built to explain bouts' number and duration together with the dives' percentage in "IDZ" (response variables) in function of sex and the trip's progress (explicative variables). An autocorrelation term was added to take into account the bouts' autocorrelation.

In all models, interactions were tested and the inter-individual variability was considered by an addition of random term. The explicative variables

have been reduced centred in order to make easier the convergence models and to compare the weight of different variables together.

Results

Potential impact of TDRs' deployment on the penguin's body condition

The logger effect was tested on the one hand comparing the trip duration between fitted animals and non-fitted animals (control group) and on the other hand comparing the body mass of the fitted birds at their departure and at their return.

The fitted animals stayed longer at sea than the control-birds with an extension of the trip's time around 13% for males and 18% for female (Kruskal-Wallis chi-squared = 7.18, df = 1, $P = 0.007$).

The body mass of logged birds increased nevertheless between departure and return at the colony (Anova, $F=58.12$, $Pr(>F) = 7.37e-09$): thus birds showed a mass gain of 39.81% in average being 43.76 % for females (Anova, $F=58.44$, $Pr(>F) = 1.75e-05$) and 36.99% for males (Anova, $F = 82.15$, $Pr(>F) = 3.11e-07$). Body mass between sex were different at the departure (Anova, $F = 29.48$, $Pr(>F) = 0.000153$) and at the return (Anova, $F = 20.27$, $Pr(>F) = 0.000724$).

Behavior at sea

Dive scale

Males dived deeper (Kruskal-Wallis chi-squared = 1822.82, df = 1, $P < 2.2e-16$) and longer than female (Kruskal-Wallis chi-squared = 4499.85, $P < 2.2e-16$) (Table 1). A linear mixed model was used to determine factors explaining the bottom time being the foraging time et showed the influence of depth (lme, Value = 2.73, Std.Error = 0.09, $DF = 70879$, $T = 28.02$, $P = 0$) with a quadratic aspect (lme, Value= -4.39, Std.Error= 0.05, $DF = 70879$, $T = -82.93$, $P = 0$). A breaking point is noticeable around 40 meters deep suggesting an optimal level of depth at 40 meters (Fig.1) . The interaction between sex and depth appeared to influence the bottom time (lme, Value= -4.48, Std.Error= 0.05, $DF=70879$, $T = -38.11$, $P = 0$) suggesting that males

and females could behave differently at particular dive depth (Fig.1) even though the variable sex didn't seem to play a role. Indeed females present longer bottom duration than males around 80m.

Neither depth (glmPQL, Value= -0.014, Std.Error= 0.008, $DF=9985$, $T = -1.66$, $P = 0.0962$), nor sex (glmPQL, Value= 0.052, Std.Error= 0.064, $DF=10$, $T = 0.82$, $P = 0.433$) have an influence on the number of wiggles at the bottom.

Concerning the recovery time after a dive at the surface the post-dive duration increased linearly with depth (lm, Estimate Std=0.41, Std. Error=0.008, $T = 49.146$, $Pr(>|t|) < 2e-16$, $R\text{-squared} = 0.16$) (Fig.2).

Males stayed generally longer at the surface after a dive than females (lm, Estimate Std=1.27, Std. Error=0.35, $T = 3.586$, $Pr(>|t|) = 0.000336$).

Between 45 and 75 meters deep, the females' post-dive duration tended to be longer than males' but the interaction between depth and sex didn't appear significant (lm, Estimate Std=0.0016, Std. Error=0.0093, $T = 0.174$, $P(>|t|) = 0.86$) (Fig.2).

Bout scale

During dive bouts, penguins tended to return at the same depth when the dives' number into the bout increases. Indeed the analysis of dives reaching the same depth level showed that the percentage of dives in Intra Depth Zone (IDZ) increased in a quadratic way with the number of dives in the bout (lme, Value= -3.66, Std.Error = 0.41, $DF = 983$, $T = -8.86$, $P = 0$). No direct sex difference appeared (lme, Value= 4.76, Std.Error = 3.04, $DF=10$, $T = 1.56$, $P = 0.1486$) but the interaction between sex and dives' number seemed significant (lme, Value=-3.65, Std.Error = 1.47, $DF = 983$, $T = -2.34$, $P = 0.019$) suggesting that males and females do not return at the same depth of precedent dive according the number of dives.

Thus the percentage of dives in IDZ grow linearly with the mean maximal bout depth (lme, Value=18.69, Std.Error = 0.67, $DF=984$, $T = 28.20$, $P = 0$). Sex didn't have any influence on this relation (Fig.3).

Circadian cycle scale

Eastern Rockhopper Penguins didn't dive with the same intensity and at the same depth according to the timing of the day. Thus the dive's number differed according to the circadian cycle: dawn, day, dusk, and night (Kruskal-Wallis chi-squared = 35.88, $df = 3$, $P = 7.94e-08$). Most of the dives (86.93%) were performed during day phase. No difference between the sexes was observed. The birds dived at different depth during the circadian cycle and specially deeper during the day (Kruskal-Wallis chi-squared = 10250.4, $df = 3$, $P < 2.2e-16$) with a mean depth during dawn of 22.87 ± 15.25 m, 40.50 ± 19.19 m at day, 13 ± 10.24 m at dusk and 10.74 ± 12.17 m at night. A tendency to increase in depth in the middle of the journey was noteworthy, although it was not significant (Fig 4).

Some inter-sex differences occurred. Males dived deeper during dawn (Kruskal-Wallis chi-squared = 209.17, $df = 1$, $P < 2.2e-16$) and day (Kruskal-Wallis chi-squared = 1969.48, $df = 1$, $P < 2.2e-16$) while females reached deeper depths at night (Kruskal-Wallis chi-squared = 379.42, $df = 1$, $P < 2.2e-16$).

During dive bouts, the number of following dives reaching the same depth (Intra-Depth-Zone – IDZ) appears significantly different concerning phases (Kruskal-Wallis chi-squared = 1111.551, $df = 3$, $P < 2.2e-16$). Hence most of dive belonging to an IDZ occurred during dawn and day (respectively 59% and 57% versus 47% at dusk and 44% at night).

Trip scale

Males dived deeper than females during the whole trip (lme, Value= 7.16, Std.Error= 2.05, $DF = 10$, $T = 3.49$, $P = 0.0057$). The bottom time didn't change neither during the trip (lme, Value = -0.03, Std.Error = 0.34, $DF = 1986$, $T = -0.09$, $P = 0.93$) nor according sex (lme, Value = -0.31, Std.Error = 2.15, $DF = 10$, $T = -0.14$, $P = 0.89$). Similarly no difference in wiggles during bottom phase was occurred either during the trip (lme, Value = 0.01, Std.Error = 0.01, $DF = 1985$, $T = 0.57$, $P = 0.56$) or between males and females (lme, Value = 0.05, Std.Error = 0.06, $DF = 10$, $T = 0.81$, $P = 0.43$).

The percentage of dives reaching the same "floor" (Intra-Depth-Zone - IDZ) increased quadratically

with the trip progress (lme, Value = -10.71, Std.Error = 1.41, $DF = 983$, $T = -7.59$, $P = 0$). The highest percentages of IDZ dives were in the middle of the journey and the lowest at the beginning and end of trip.

On the other hand, the dive intensity differs during the journey characterised by quadratically changes of bouts number with the trip evolution: few bouts in the middle of the trip but relatively high values at the beginning and end (lme, Value = 0.47, Std.Error = 0.09, $DF = 88$, $T = 5.21$, $P = 0$). However no inter-sex difference is obvious (Fig 5). Regarding the bout duration, a trend to increase in depth in the middle with a quadratic aspect is distinguishable (lme, Value = -1.05, Std.Error = 0.18, $DF = 89$, $T = -5.75$, $P = 0$) (Fig 5?).

Proxies of foraging effort/benefit:

Males had a higher daily dive effort than females (mean dive rate: 31.70 m/day versus 24.93 m/day (Anova, $DF = 1$, Sum Sq= 82464492, Mean Sq= 82464492, $F = 6.41$, $Pr(>F) = 0.003$).

Females had a daily mass gain more important than males (Anova, $DF = 1$, Sum Sq = 3.51, Mean Sq=3.51, $F = 12.19$, $Pr(>F) = 0.004$). In average females won 4.70% of their mass per day of sea trip while males won only 3.10%.

Discussion

This study is the first to describe the diving behavior of Rockhopper Penguins *Eudyptes chrysocome filholi* during incubation. Overall, it allowed to confirm the diving strategies of this species highlighted in other localities (Hull, 2000; Tremblay and Cherel, 1999) and pointed out several behavioral adjustments in both genders faced to the need to restore the body reserves after long incubation fasting. Differences of foraging strategy occurred in temporal way and between genders at different scales.

Diving performances at the dive scale

Maximal dive depth appears to be the principal constraint driving the dive characteristics of Eastern Rockhopper Penguins. Thus Rockhopper Penguins during incubation dived in average deeper and longer than during the guarding stage

(36.5 ± 18.3 m vs 27 m and 93sec vs 89sec, respectively) (Tremblay et al., 2000). However average maximal depths reached were rather modest compared to the depth reached by other species of penguins (Borboroglu and Boersma, 2013; Charrassin et al., 2002; Cherel et al., 1999; Deagle et al., 2008; Rey et al., 2007; Rodary et al., 2000; Tremblay et al., 1997, 2003; Watanuki and Burger, 1999; Williams, 1995). Differences with other species can be explained by the differences in body size which determine physiological abilities to dive, as the heaviest animals are physiologically able to dive deeper (Halsey et al., 2006; Kooyman and Kooyman, 1995). Penguins diving capacity is particularly limited by the air volume storage into the circulatory system which depends on body size and metabolism diving (Butler, 2001; Costa, 2007; Ponganis and Kooyman, 2000). Indeed anaerobic capacity of the swimming muscles determine the maximal dive depth (Costa, 2007) which are lower than Adelie's or Gentoo's who are bigger and dive deeper. However, other environmental variables may also affect the diving performances of diving predators as hydrological features (Charrassin and Bost, 2001), bathymetry (Cook et al., 2013), prey availability (Bost et al., 2002; Wilson, 1995) or the patch's quality (Mori et al., 2002).

Among penguins, males usually dive deeper than female. This variation between genders can be explained by the sexual dimorphism of Rockhopper Penguins especially concerning their body size (Kooyman, 1989). The heavier weight of males would allow them to access deeper resources during this stage of the annual cycle at which the planktonic bloom still does not seem to happen (Razouls et al., 1997). The females foraging trips coincide at a more advanced stage (15 days) and this difference in the timing of foraging trips could allow them to access different prey patches in density and quality.

Concerning the dive duration, our study showed that males dived also longer than female during the incubation. The time spent in apnea is a variable influenced by the depth (Carbone and Houston, 1994; Tremblay et al., 2000) and other variables that are related to it such as pressure which increases with it (Carbone and Houston, 1994) or yet the regulation of deep oxygen supply

(Watanabe et al., 2014). Thus the duration and depth being linked, it makes sense that males dive longer than females.

Diving depth also impacted the durations of the different phases of the dive. In most divers species the bottom time usually increases until a threshold value (Charrassin, 1999). However in small divers like penguins it seems to represent a compromise between maximizing the acquisition of resource and their associated cost (Boyd, 1997). In the case of the Rockhopper penguin, individuals seem to privilege the exploration of 40-60 m depth as indicated by the highest bottom time value. As the bottom time corresponds to the theoretical effective feeding period (Charrassin et al., 2002; Mori et al., 2002), these depths seem as the most profitable depth levels for prey supply. These depth levels coincides with the known distribution of macro-zooplankton shoals (Euphausiids) in summer in Kerguelen (Razouls et al., 1997) and Southern Ocean (Perissinotto and McQuaid, 1992). Macrozooplankton is the main food of these predators (Cherel et al., 2007; Tremblay and Cherel, 1999) and so their availability at-depths determine the diving behavior of rockhopper penguins. However, no recent data is available to test this hypothesis.

Another time variable influenced by the depth is the post-dive duration for the recovery time (Carbone and Houston, 1994). This one increases linearly with depth during incubation. In addition, our study showed gender differences. Males stay longer on the surface after a dive than females. This is still logical because if males dive longer and deeper than females, they undergo greater pressure and need more time to recover.

Bout scale

Besides, our study showed that rockhoppers penguins frequently carry out repetitive dives in discrete bouts (33 minutes on average). The occurrence of diving bouts varies during the trip. Indeed penguins tend to perform more bouts at the beginning and end of the trip at sea. However, the length of these bouts tends to increase in the middle of the trip. Bouts duration corresponding to the exploitation time of a good quality patch

(Watanabe et al., 2014), the middle of the trip appears to be the most efficient foraging moment. We do not have geographic information of this stage of the journey, but it is possible that the time of trip before allow them to access to better patch away of shore. Another explanation could be that they do not go far but with the time of trip, they improve their foraging strategies and become more efficient. Once satiated, they dive back to the colony and allow more energy to travel than to hunting but enjoy opportunistic preys.

Moreover this work points out that the dive number in "Intra Depth Zone" (IDZ) increases also linearly with depth after 40 m deep whereas the maximum bottom duration is reached at 40m and the post dive duration increase faster after 40m depth. This suggests that penguins keep on feeding actively beyond the depth threshold even if the metabolic costs potentially increase according the oxygen dive cost and their Aerobic Dive Limit (Kooyman and Ponganis, 1998). Diving bouts in IDZ are more profitable as shown by the most important meals brought to chicks (Tremblay and Cherel, 1999). It can be deduced that the area's profitability takes precedence over the optimum depth in terms of energy costs. This can be explained by the ability of diving predators to anticipate and regulate the dive transit duration and post dive duration according to the fishing success of the previous dive (Hanuise et al., 2013). At the trip scale, our findings indicate that the percentage of dives in IDZ increase in a quadratic way during the trip so as the duration of bout and their mean maximal dive depth. This implies strongly that food patches are better in the middle of the trip.

Day scale

At the day scale, dive's number differs according to the nyctemeral phases with 86.93% of dives performed during day phases and most of dive belonging to an IDZ occurred during dawn and day. This circadian preference can be explained by the visual prey detection in penguins (Wilson, 1995) and the spatial and temporal distribution of their main prey. Thus during the day, this preys are localized deeply but are gathered in dense shoal. So penguins may have interest to dive deeply to

access such profitable patches. Besides few dives during the darkest phases were performed suggesting an another resource or other fishing technics. The most plausible explanation would be capture of others prey that Euphausiids, emitting bioluminescence during nyctemeral migration and so would be shallower and apparent to penguins (Pakhomov et al., 1996) .

Trip Scale

Finally, at the trip scale the highest percentages of IDZ dives were in the middle of the journey and the lowest at the beginning and end of trip following the mean maximal bout depth trend. The bottom time didn't change during the trip but the bouts number varies quadratically with few bouts in the middle of the trip but relatively high values at the beginning and end. At the opposite the bouts duration follow a quadratic trend with maximal bout duration at the middle trip. These results suggest that rockhopper penguins perform many short bouts at shallow depth during the start and the end of the trip. Whereas they perform longer and deeper bouts and so less numerous during the middle of the trip. These middle trip bouts follow the precedent dive depth and attest of a exploration of a good patch. Our study suggests that foraging strategies of rockhopper penguins seem to be the most efficient during the middle of the trip. Actually penguins incubating make longer trips than rearing period. This gives them time to go far to find dense patches. In this case the middle of the trip could represent the greatest distance to the colony during the trip. In this work, rockhopper penguins colony is located on Mayes Island in the Morbihan Gulf. This available time until the middle of the trip would allow penguins to go outside of the Gulf and so to forage in deep sea. This would offer more patch opportunities in term of density, diversity and occurrence.

Differences in benefits and costs of trips between genders

The diving behavior of rockhopper penguins during incubation seems to vary according gender. Indeed males still dived deeper and made a significant higher daily dive effort than female during the all

trip. This variation of dive characteristic can be explained by the difference of morphology and weight. Males being bigger, they can physiologically reach easier deeper depth than females (Butler, 2001; Groscolas et al., 2010; Kooyman and Ponganis, 1998). However daily mass-gain is more important for females than males. In average females won 4.70% of their mass per day of sea trip while males won only 3.10%. This intersex difference can be relate with the difference of stage of trip in the cycle and the food availability during each stage (Cook et al., 2013; Razouls et al., 1997). It is known that resources can be limited through local depletion during the breeding season (Cook et al., 2013). Resource distribution could be one explanation for the difference in diving behavior and weight between genders.

Conclusion

To sum up, rockhopper penguins appear to adopt different dive behaviors according the moment of the journey: one type at the beginning and end of the trip and another one during the middle of the trip. The first type behavior can be characterized by travelling dives while prospecting in order to maximize their swimming effort by occasional prey capture. The second one would be illustrated by dives coming one after another quickly and intensively related to a high fishing success.

In addition our study shows that foraging strategies vary between genders including depth, dive duration and recover time. A sexual segregation within habitats or specialization on different types of prey would be possible (Newton, 1998 in Bearhop et al., 2006). But this segregation can also be temporal according the shift of foraging trip in the cycle between males and females. This difference of foraging strategies in term of characteristic and timing would allow them to face up the energetic constraints and to have access to different resources, while minimizing the overlap of trophic niche during the breeding season (Cook et al., 2013) and also avoid possible food competition (Ratcliffe et al., 2013).

Besides diving abilities of rockhopper penguins are limited by its size. Therefore they dive less deep than the larger twin species macaroni penguins *Eudyptes chrysolophus* during incubation with a maximum dive depth reaching 97m against 158m in Heard Island (Green et al., 1998) but 99.2 m in Kerguelen, well the mean dive depth is equivalent (Sato et al., 2004). However, others factors come into account to explain this difference between these species. For example the availability of prey could be different because the macaronis' cycle and rockhopper penguins' cycle and are shifted 3 weeks. Another reason could be the foraging area. Macaroni penguins could forage in other area, and prefer other patch at other distance of the colony.

Thus, a complete study of foraging and its associated energy cost during the annual cycle would be quite relevant. These data could be collected during the incubation but also during the winter and pre-moulting periods which are key period to better identify and better understand the costs and the associated benefits. This present study suggests that the succeeding dive in Intra Depth Zone would allow penguins to use the same patch diving at the same depth until end of stock. Diving birds could anticipate the dive depth according the previous fishing success. This hypothesis could be check equipping birds with embedded micro probes (an external data logger and both oesophageal temperature and Hall sensors) measuring food intake (Hanuise et al., 2010). Besides, the lack of geographical location of foraging journeys did not allow us to characterize the areas visited by males and females, whereas spatial differences exist in other species of penguins as macaroni penguin at this stage (Barlow and Croxall, 2002). Through to the laying of GPS we could know the supply areas of rockhopper penguins during the incubation and whether a spatial segregation between the sexes and species. It would be also interesting to take into account in the same individuals the energy expenditure of dives and the energetic strategy of both sexe thanks to heart recorder with also the monitoring of the diving behavior during the all trip associated with the mesure of the overall dynamic body acceleration (OBDA) (Wilson et al., 2006).

References

- Anderson, D.R. (2008). Model based inference in the life sciences: a primer on evidence (Springer).
- Bannasch, R., Wilson, R.P., and Culik, B. (1994). Hydrodynamic Aspects of Design and Attachment of a Back-Mounted Device in Penguins. *J. Exp. Biol.* 194, 83–96.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *ArXiv14065823 Stat.*
- Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A., Croxall, J.P., and others (2006). Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar. Ecol. Prog. Ser.* 311, 157–164.
- Borboroglu, P.G., and Boersma, P.D. (2013). Penguins: Natural History and Conservation (University of Washington Press).
- Bost, C.A., Zorn, T., Le Maho, Y., and Duhamel, G. (2002). Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. *Mar. Ecol. Prog. Ser.* 227, 51–61.
- Bost, C.A., Handrich, Y., Butler, P.J., Fahlman, A., Halsey, L.G., Woakes, A.J., and Ropert-Coudert, Y. (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, I.L. (1997). The behavioural and physiological ecology of diving. *Trends Ecol. Evol.* 12, 213–217.
- Boyd, I.L., Arnould, J.P.Y., Barton, T., and Croxall, J.P. (1994). Foraging Behaviour of Antarctic Fur Seals During Periods of Contrasting Prey Abundance. *J. Anim. Ecol.* 63, 703–713.
- Brooke, M. de L. (2004). The food consumption of the world's seabirds. *Proc. R. Soc. Lond. B Biol. Sci.* 271, S246–S248.
- Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (Springer Science & Business Media).
- Butler, P.J. (2001). Diving Beyond the Limits. *Physiology* 16, 222–227.

- Butler, P.J., and Jones, D.R. (1997). Physiology of diving of birds and mammals. *Physiol. Rev.* 77, 837–899.
- Carbone, C., and Houston, A.I. (1994). Patterns in the diving behaviour of the pochard, *Aythya ferina*: a test of an optimality model. *Anim. Behav.* 48, 457–465.
- Charrassin, J.B. (1999). *Stratégies de recherche alimentaire du manchot royal (aptenodytes patagonicus) au cours de son cycle annuel.* Université Louis Pasteur, Strasbourg.
- Charrassin, J.-B., and Bost, C.-A. (2001). Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar. Ecol. Prog. Ser.* 221, 285–298.
- Charrassin, J.-B., Maho, Y.L., and Bost, C.-A. (2002). Seasonal changes in the diving parameters of king penguins (*Aptenodytes patagonicus*). *Mar. Biol.* 141, 581–589.
- Cherel, Y., Tremblay, Y., Guinard, E., and Georges, J.Y. (1999). Diving behaviour of female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, during the brooding period at Amsterdam Island (Southern Indian Ocean). *Mar. Biol.* 134, 375–385.
- Cherel, Y., Hobson, K.A., Guinet, C., and Vanpe, C. (2007). Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J. Anim. Ecol.* 76, 826–836.
- Cook, T.R., Cherel, Y., Bost, C.-A., and Tremblay, Y. (2007). Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. *Antarct. Sci.* 19, 55–63.
- Cook, T.R., Lescroël, A., Cherel, Y., Kato, A., and Bost, C.-A. (2013). Can foraging ecology drive the evolution of body size in a diving endotherm? *PLoS One* 8, e56297.
- Costa, D.P. (2007). *Diving Physiology of Marine Vertebrates.* eLS.
- Deagle, B., Gales, N., and Hindell, M. (2008). Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. *Mar. Ecol. Prog. Ser.* 359, 295–309.
- Fox, J., and Weisberg, H.S. (2010). *An R companion to applied regression* (Sage Publications).
- Groscolas, R., Viera, V., Guerin, N., Handrich, Y., and Côté, S.D. (2010). Heart rate as a predictor of energy expenditure in undisturbed fasting and incubating penguins. *J. Exp. Biol.* 213, 153–160.
- Halsey, L.G., Blackburn, T.M., and Butler, P.J. (2006). A comparative analysis of the diving behaviour of birds and mammals. *Funct. Ecol.* 20, 889–899.
- Halsey, L.G., Bost, C.-A., and Handrich, Y. (2007). A thorough and quantified method for classifying seabird diving behaviour. *Polar Biol.* 30, 991–1004.
- Hanuise, N., Bost, C.-A., and Handrich, Y. (2013). Optimization of transit strategies while diving in foraging king penguins. *J. Zool.* 290, 181–191.
- Hull, C.L. (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. *Can. J. Zool.* 78, 333–345.
- Hunt, J.G.L., and Schneider, D.C. (1987). Scale-dependent processes in the physical and biological environment of marine birds. *Seab. Feed. Ecol. Role Mar. Ecosyst.* 7–41.
- Kooyman, G.L. (1989). Diverse divers.
- Kooyman, G.L., and Kooyman, T.G. (1995). Diving Behavior of Emperor Penguins Nurturing Chicks at Coulman Island, Antarctica. *The Condor* 97, 536–549.
- Kooyman, G.L., and Ponganis, P.J. (1998). THE PHYSIOLOGICAL BASIS OF DIVING TO DEPTH: Birds and Mammals. *Annu. Rev. Physiol.* 60, 19–32.
- Mori, Y., Takahashi, A., Mehlum, F., and Watanuki, Y. (2002). An application of optimal diving models to diving behaviour of Brünnich's guillemots. *Anim. Behav.* 64, 739–745.
- Newton, I. (1998). *Population Limitation in Birds* (Academic Press).
- Pakhomov, E.A., Perissinotto, R., and McQuaid, C.D. (1996). Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser. Oldendorf* 134, 1–14.
- Perissinotto, R., and McQuaid, C.D. (1992). Land-based predator impact on vertically migrating zooplankton and micronekton advected to a

Southern Ocean Archipelago. *Mar. Ecol. Prog. Ser.* Oldendorf 80, 15–27.

Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D. (2007). Linear and nonlinear mixed effects models. R Package Version 3, 57.

Ponganis, P.J., and Kooyman, G.L. (2000). Diving physiology of birds: a history of studies on polar species. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 126, 143–151.

Pütz, K., and 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.

Ratcliffe, N., Takahashi, A., O'Sullivan, C., Adlard, S., Trathan, P.N., Harris, M.P., and Wanless, S. (2013). The Roles of Sex, Mass and Individual Specialisation in Partitioning Foraging-Depth Niches of a Pursuit-Diving Predator. *PLoS ONE* 8, e79107.

Razouls, S., De Bovée, F., Delille, D., Fiala, M., and Mayzaud, P. (1997). 13 Temporal variability of bacteria, phytoplankton and zooplankton assemblages of the sub-Antarctic Morbihan Bay (Kerguelen Archipelago). *Antarct. Communities Species Struct. Surviv.* 86.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (ISBN 3-900051-07-0, URL <http://www.R-project.org>).

Rey, A.R., Trathan, P., Pütz, K., and Schiavini, A. (2007). Effect of oceanographic conditions on the winter movements of rockhopper penguins *Eudyptes chrysocome chrysocome* from Staten Island, Argentina. *Mar. Ecol. Prog. Ser.* 330, 285–295.

Ricklefs, R.E. (1990). Seabird Life Histories and the Marine Environment: Some Speculations. *Colon. Waterbirds* 13, 1–6.

Ricklefs, R.E. (2000). Density dependence, evolutionary optimization, and the diversification of avian life histories. *The Condor* 102, 9–22.

Rodary, D., Wienecke, B.C., and Bost, C.A. (2000). Diving behaviour of Adélie penguins (*Pygoscelis adeliae*) at Dumont D'Urville, Antarctica: nocturnal

patterns of diving and rapid adaptations to changes in sea-ice condition. *Polar Biol.* 23, 113–120.

Sato, K., Charrassin, J.-B., Bost, C.-A., and 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.

Schreer, J.F., and Kovacs, K.M. (1997). Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* 75, 339–358.

Smetacek, V., Scharek, R., and Nöthig, E.-M. (1990). Seasonal and Regional Variation in the Pelagic and its Relationship to the Life History Cycle of Krill. In *Antarctic Ecosystems*, D.K.R. Kerry, and P.D.G. Hempel, eds. (Springer Berlin Heidelberg), pp. 103–114.

Tremblay, Y., and Cherel, Y. (1999). Synchronous Underwater Foraging Behavior in Penguins. *The Condor* 101, 179–185.

Tremblay, Y., Guinard, E., and Cherel, Y. (1997). Maximum diving depths of northern rockhopper penguins (*Eudyptes chrysocome moseleyi*) at Amsterdam Island. *Polar Biol.* 17, 119–122.

Tremblay, Y., Cherel, Y., and others (2000). Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar. Ecol. Prog. Ser.* 204, 257–267.

Tremblay, Y., Cherel, Y., and others (2003). Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Mar. Ecol. Prog. Ser.* 251, 279–297.

Venables, W.N., and Ripley, B.D. (2002). Modern applied statistics with S (Springer).

Warham, J. (1963). The Rockhopper Penguin, *Eudyptes chrysocome*, at Macquarie Island. *Auk* 229–256.

Watanabe, Y.Y., Ito, M., and Takahashi, A. (2014). Testing optimal foraging theory in a penguin-krill system. *Proc. R. Soc. B Biol. Sci.* 281, 20132376–20132376.

Watanuki, Y., and Burger, A.E. (1999). Body mass and dive duration in alcids and penguins. *Can. J. Zool.* 77, 1838–1842.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? Deep Sea Res. Part II Top. Stud. Oceanogr. 54, 211–223.

Weimerskirch, H., Zotier, R., and Jouventin, P. (1989). The Avifauna of the Kerguelen Islands. Emu 89, 15–29.

Williams, T.D. (1995). The Penguins: Spheniscidae (Oxford; New York: Oxford University Press).

Wilson, R.P. (1995). Foraging ecology. Penguins Oxf. Univ. Press Oxf. 81–106.

Ydenberg, R.C., and Clark, C.W. (1989). Aerobiosis and anaerobiosis during diving by western grebes: An optimal foraging approach. J. Theor. Biol. 139, 437–447.

Table

Table 1: Summary table of diving parameters of Rockhopper Penguins from Mayes Island, Kerguelen archipelago, fitted with TDRs during incubation in 2000/2001. Mean $\pm$ standard deviation, in brackets minimal and maximal values calculated based on 70 893 foraging dives' observations.

Individual	Trip duration (days)	Number of dives	Number of bouts	Percentage of dives in IDZ (%)	Maximum depth (m)	Dive duration (sec)	Bottom duration (min)	Number of dives in one bout	Number of wiggles in one dive	Post-dive duration (sec)
Females	11.2	4482	76.2	55.2	32.4 ±15.2 (5.4 -89)	85.9±20.3 (11.2 - 144)	33.5 ± 15.0 (0 - 88)	172.3 ± 91.9 (3 - 356.4)	0.8± 1.4 (0 - 9.2)	32.6 ± 35.5 (6.8-1155.2)
Female_TDR03_nid17	11	4804	115	50.15	29.8 ± 14 (5.3-65)	81.3±17.1 (14 - 126)	30.7 ± 13.2 (0 - 70)	150.5 ± 85.7 (3 - 285)	0.6± 1.2 (0 - 8)	26.2 ± 26.4 (0 - 564)
Female_TDR09_nid47	12	5541	58	54.8	30.1 ± 16.6 (5.38 - 69.6)	80.5 ± 23.5 (10 - 144)	31.9± 14.7 (0 - 82)	217.8 ± 120.8 (3 - 482)	1.0± 1.7 (0 - 11)	27.6 ±2 1.0 (0-396)
Female_TDR10_nid16	14	5336	119	53.2	31.7 ± 14.7 (5.1 - 72)	83.6 ± 22.2 (14 - 148)	32.8 ± 16.4 (0 - 88)	174.5± 92.3 (3 - 356)	0.5 ± 1.1 (0 - 10)	37.2 ± 65.1 (0-2730)
Female_TDR13_nid34	15	1589	24	62.8	30.7 ± 13.2 (5.4 - 58.4)	85.1 ± 18.9 (8 - 134)	33.2 ± 13.4 (0 - 74)	135.84± 55.8 (3 - 199)	0.5 ± 1.1 (0 - 6)	34.0 ± 29.5 (0 - 818)
Female_TDR15_nid22	14	5140	65	55.2	37.0 ± 17.4 (5.9 - 89)	99.0± 19.8 (10 - 152)	39.0 ± 17.2 (0 - 78)	182.9 ± 105.0 (3 - 460)	1.53 ± 2.1 (0 - 11)	38.2 ± 35.4 (0 - 1268)
Males	17.40	6926	98.6	54.9	39.73± 20.6 (5.3 - 97.7)	98.9± 45.4 (12.6 – 196)	33.0± 16.2 (0 - 96)	215.3 ± 135.8 (3 - 507.6)	0.9± 1.6 (0 - 15.6)	35.3± 63.8 (0 - 900.7)
Male_TDR02_nid35	17	7445	118	49.1	35.6 ± 21.8 (5 - 93.4)	94.8± 28.7 (4 - 184)	30.9± 20.8 (0 - 86)	182.1± 152 (3 - 626)	0.9 ± 1.8 (0 - 27)	35.4 ± 82.5 (0 - 790)
Male_TDR06_nid3	19	7724	95	50.9	35.2 ± 19.8 (5.6 - 93.7)	99.3 ± 25.1 (4 - 168)	36.1 ± 15.8 (0 - 90)	234.6 ± 141.7 (3 - 576)	1.1 ± 1.7 (0 - 12)	33.2 ± 56.2 (0 - 1141)
Male_TDR08_nid49	17	6887	116	57.4	41.3 ± 22.5 (5.2 - 95.4)	91.7 ± 22.2 (10 - 186)	25.9 ± 12.7 (0 - 92)	195.9 ± 119.6 (3 - 461)	0.4 ± 1.0 (0 - 7)	38.5 ± 35.3 (0 - 750)
Male_TDR12_nid19	13	5351	74	61.6	48.3 ± 21.4 (5.7 - 97.7)	102.4 ± 18.6 (24 ± 146)	30.9 ± 15 (0 - 80)	242.1 ± 139.3 (3 - 499)	0.9 ± 1.6 (0 - 10)	36.1 ± 32.6 (0 - 1262)
Male_TDR14_nid50	20	8009	86	53.2	38.2 ± 22.3 (5 - 94.9)	93.7 ± 24.2 (10 - 160)	31.1 ± 14.1 (0 - 90)	244.4 ± 146.9 (3 - 513)	0.8 ± 1.5 (0 - 10)	31.9 ± 25.3 (0 - 416)
Male_TDR16_nid52	20	6855	101	56.09	37.6 ± 18.4 (5.4- 89.6)	104 ± 178.3 (16 - 166)	38.7 ± 17.2 (0 - 88)	186.7 ± 109 (3 - 416)	1.1± 1.7 (0 - 10)	35.2 ± 185 (0 - 1236)
Male_TDR18_nid12	16	6211	100	56.2	41.9 ± 17.8 (5.9 - 84.9)	106.5± 20.7 (20 - 196)	37.4± 17.7 (0 - 96)	221.4 ± 141.9 (3 - 462)	1.2 ± 2.0 (0 - 13)	37.0 ± 29.5 (4 - 710)
Mean	15.5	5878.6	89.0	55.1	36.5± 18.3 (5.4- 97.7)	93.5 ± 35 (4 - 196)	33.2 ± 15.7 (0 - 96)	197.4± 117.5 (3 - 626)	0.9 ± 1.6 (0 - 27)	34.2± 52.0 (0 -2730)

*IDZ= Intra Depth Zone

Figures

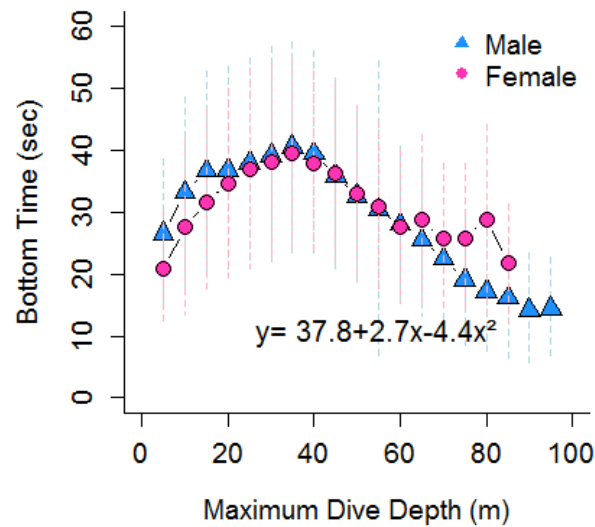


Figure 1. Relation between bottom time during a dive and the maximum dive depth. Time in seconds and maximum dive depth in meters. The smooth curves with pink circles represent the mean bottom time of female, with of either side the respective standard deviation in vertical dotted lines. The other one with the blue triangles represents those of males. The equation of the model is indicated in black. The top of the curve is the breaking point which suggest an optimal depth around 40m

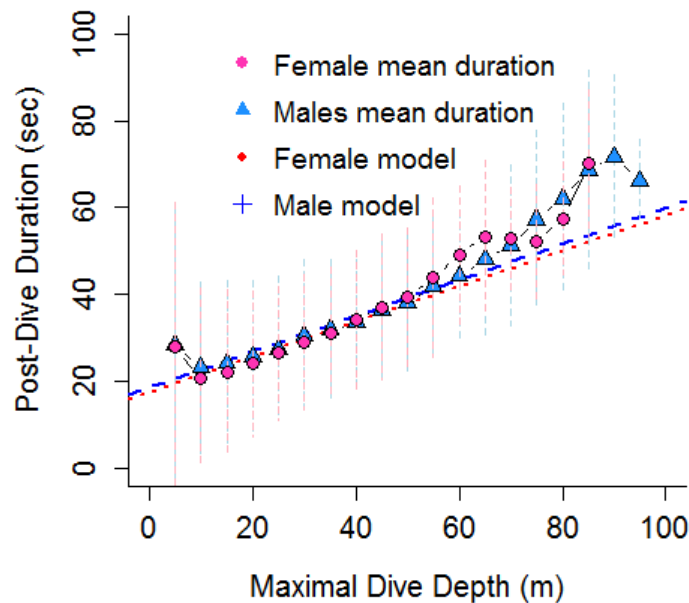


Figure 2. Relation between post-dive duration and the maximum dive depth. Duration in seconds and maximum dive depth in meters. The smooth curves with pink circles represent the mean post-dive duration of female, with of either side the respective standard deviation in vertical dotted lines. The other one with the blue triangles represents those of males. The straight line represents the linear model, in thin dotted red for females and thick dotted blue for males, which shows that post-dive duration increase linearly with depth.

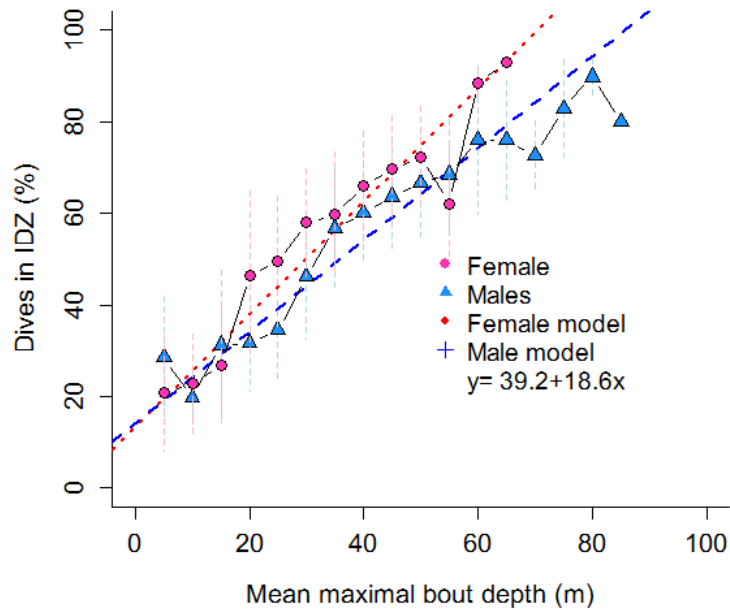


Figure 3. Relation between percentage of dive in "IDZ" (Intra Depth Zone) and the mean maximum dive depth. Mean maximum dive depth in meters. The smooth curve with pink circles represents the mean percentage of dives in IDZ of female, with of either side the respective standard deviation in vertical dotted lines. The other one with the blue triangles represents those of males. The straight line represents the linear model, in thin dotted red for females and thick dotted blue for males, which shows that percentage of dive in IDZ increase with depth. The equation of the model is indicated in black.

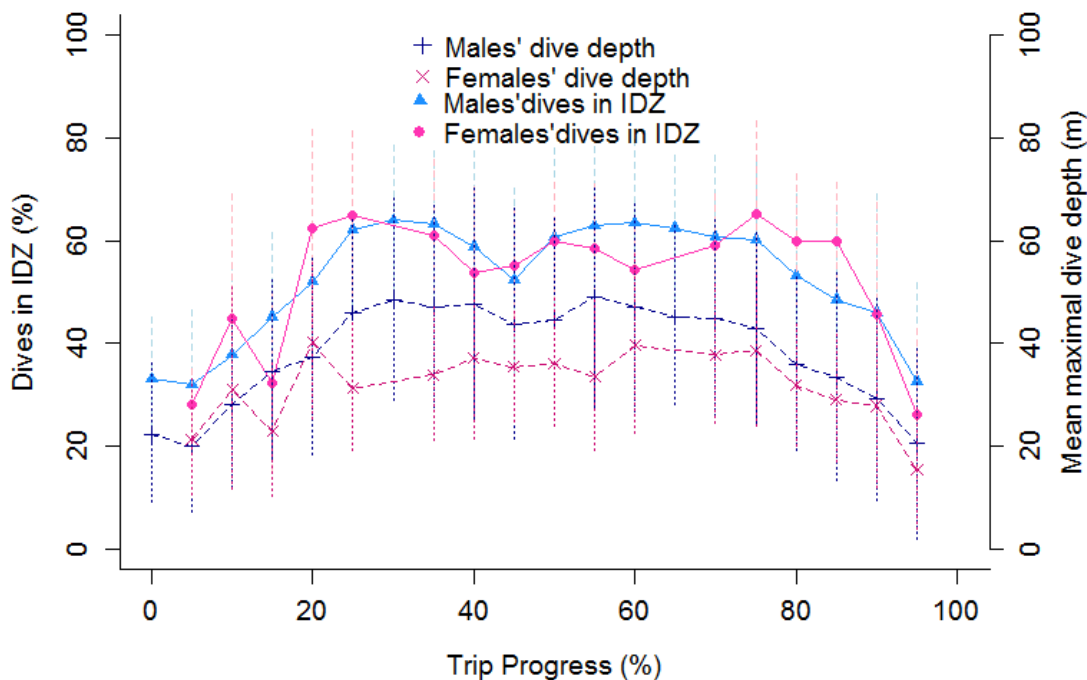


Figure 4. Evolution of percentage of dive in "IDZ" (Intra Depth Zone) and mean maximum dive depth during the trip. Mean maximum dive depth in meters and trip progress in percent. The smooth curve with pink circles represents the mean percentage of dives in IDZ of female, with of either side the respective standard deviation in vertical dotted lines. The other one with the blue triangles represents those of males. The dotted smooth curve represents the maximal dive depth in dark pink with "X" for females and dark blue cross for males, with of either side the respective standard deviation in vertical dotted lines.

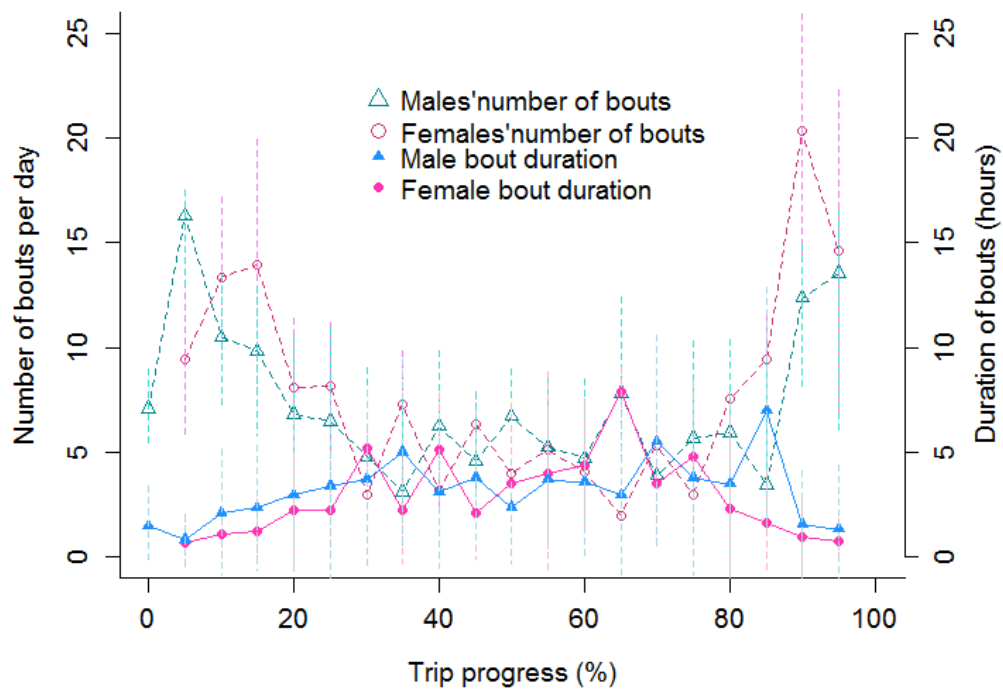


Figure 5. Evolution of number of bouts per day and duration of bouts during the trip. Duration of bouts in hours and trip progress in percent. The smooth curve with pink full circles represent the bout duration of female, with of either side the respective standard deviation in vertical dotted lines. The other one with the full blue triangles represents those of males. The dotted smooth curve with empty pink circle represents the number of bouts per day, with of either side the respective standard deviation in vertical dotted lines. The other one with the empty blue triangles represents those of males.

Résumé

L'océan Austral abrite encore des populations exceptionnelles de prédateurs marins (manchots, albatros, phoques...). Bien qu'activement étudiés, l'approche fonctionnelle des relations proies-prédateurs souffre encore d'un manque de connaissances chez les prédateurs marins. Etudier comment ces animaux utilisent les habitats est essentiel pour mieux comprendre leur écologie. Par ailleurs, dans une période où les écosystèmes sont soumis à d'importantes pressions d'origine anthropique (surpêche, pollutions, changement climatique), la connaissance de l'écologie d'une espèce est primordiale pour bien caractériser les aires à protéger.

Le gorfou macaroni *Eudyptes chrysophlopus* est un oiseau marin pélagique et constitue l'espèce de manchot la plus abondante dans l'océan Austral (> 6 millions de couples). Au cours des 30 dernières années, les effectifs des populations de Géorgie du Sud et de l'île Marion ont fait face à une diminution drastique (> 30%). Actuellement, les populations de gorfou macaroni des Terres Australes et Antarctiques Françaises (archipel des îles Crozet et îles Kerguelen) abritent encore plus de 50% des effectifs mondiaux. Cependant, les comportements de recherche alimentaire de ces deux populations étaient jusqu'à présent encore mal connus.

Au cours de cette thèse, nous avons étudié les stratégies de recherche alimentaire du gorfou macaroni, au cours de l'intégralité de son cycle de reproduction (incubation, élevage et crèche) de Kerguelen et Crozet, îles caractérisées par des environnements océanographiques contrastés. Les ajustements du comportement alimentaire face aux contraintes énergétiques liées à la reproduction et aux variations de la production biologique de leurs environnements ont été examinés en détail.

Grace à des mesures biologiques d'origine télémétrique et/ou d'appareil embarqué (trajectoires, comportement de plongées) couplées à des données satellitaires (données environnementales), nous avons pu mettre en évidence l'existence :

- 1) d'un comportement de recherche alimentaire spécifique et de genre :

Sur les 2 sites étudiés, un ajustement similaire des déplacements, de l'effort d'approvisionnement, du régime alimentaire a été observé en réponse aux contraintes énergétiques imposées par la reproduction. En incubation, les deux sexes ciblent principalement les fronts océanographiques, les tourbillons et les zones filamentaires situées en eaux pélagiques au cours de longs trajets. En période d'élevage, les femelles s'approvisionnent plus près des côtes, majoritairement sur le plateau et au bord des talus afin de pouvoir alimenter régulièrement la progéniture. En crèche, les mâles ciblent à nouveau les structures frontales tandis que les femelles vont plus loin qu'en élevage tout en restant inféodées aux talus. A l'aide de la littérature, nous avons pu observer que cette stratégie semble opérer à l'échelle de l'aire de répartition de l'espèce.

- 2) d'une plasticité phénotypique inattendue :

L'approche comparative entre les îles Kerguelen et Crozet a permis d'étudier les points communs et les différences des stratégies d'approvisionnement entre les deux localités, liées aux conditions environnementales locales. Les deux populations semblent toutes deux très dépendantes des pics saisonniers de productivité primaire. En revanche, des variations d'éloignements à la colonie inter-site et intra-sexe plus importantes qu'attendues ont été observées mettant en évidence une flexibilité phénotypique insoupçonnée pour un prédateur marin pélagique.

Cette étude est l'une des rares ayant couvert l'ensemble d'un cycle de reproduction chez les manchots. L'importante variabilité comportementale démontrée réitère le besoin impératif de prendre en compte l'intégralité d'un cycle pour mieux comprendre et définir les stratégies d'approvisionnement d'une espèce.

Mots clés : écologie comportementale – stratégies d'approvisionnement – habitats – cycle de reproduction – manchots – océan austral

Summary

The Austral Ocean still hosts a great population of marine predators (i.e. penguins, albatross, and seals). Despite well studied, the functional approach investigating the relationship between prey and predators in the marine ecosystem is still poorly known. Knowledge on habitat selection and use of marine species is essential to better understand their ecology and behaviour. The knowledge about the ecology of key species is essential to characterise and identify the areas to protect and to predict the future of populations that may be affected by global changes. This is particularly true in an area where the natural ecosystems are more and more perturbed by anthropogenic activities (i.e. over-fishing, pollution, and climate change).

The Macaroni penguin is the most abundant penguin species in the Austral Ocean (> 6 millions pairs). It is also the biggest consumer of secondary resources, in terms of biomass, in the world. Over the past 30 years the Macaroni penguin populations situated in South Georgia and Marion Island suffered of 30% population decline. At the moment, Kerguelen and Crozet Islands (French Southern Territories) still host more than 50% of their global population, however the foraging behaviour of this species is still poorly known.

The objective of this research is to study the different foraging behaviour strategies of a pelagic seabird: the Macaroni penguin *Eudyptes chrysophyllus* during its whole breeding cycle (incubation, brood, crèche). The populations' object of study breed in different oceanographic conditions: the Kerguelen and Crozet archipelagos.

The variation in foraging behaviour driven by energetic constraints, which is associated to the reproduction and to the biological production, has been studied in details.

Telemetry data (i.e. trajectories and diving behaviour) combined with environmental data obtained by remote sensing allowed determining that:

1) Foraging strategies of Macaroni penguin breeding in two different locations differ in terms of movement, foraging effort and foraging niche during their breeding cycle in response to reproduction constraints. In incubation, both sexes carried out long journeys and targeted large oceanographic structures such as fronts, eddy and transport fronts. During the brooding phase, the females foraged closer to the colony adjusting their foraging behaviour based on their offspring needs, targeting the shelf and the slope. When crèche started, males targeted large scale structures whereas females still foraged on the slope. At this time, a shift in the diet composition was observed.

2) The comparative approach between Kerguelen and Crozet allowed to highlighting differences in foraging strategies, in response to local environmental conditions. However, greater than expected variations in foraging areas were observed inter-site and inter-sex. These results have pointed out an unexpected phenotypic flexibility for a pelagic marine predator..

This research investigated the entire breeding cycle of a penguin, a fact still rare in ecology. The observed degree of behavioural variability reiterates the imperative to take into account an entire cycle to better understand and define the foraging strategies of a species.

Key words: ecology – foraging strategies – oceanographic features – breeding cycle – penguins – southern ocean