At-sea ecology of the Emperor penguin (Aptenodytes forsteri) : Foraging strategies and evaluation of methodological and conservation tools

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Département de Biologie Polaire (LIA 647 'BioSensib')

Centre Scientifique de Monaco &

CNRS-IPHC, Département Ecologie, Physiologie et Ethologie (UMR 7178)

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Discipline/ Spécialité : Ecologie – Ethologie

Ecologie en mer du manchot Empereur (*Aptenodytes forsteri*)

Stratégies spatio-temporelles de prospection et de recherche alimentaire, et évaluation des outils méthodologiques et de conservation

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Résumé en français

Contexte général

L'océan Austral est l'un des écosystèmes les plus productifs de notre planète et héberge les plus importantes communautés d'oiseaux marins. Néanmoins, les écosystèmes polaires montrent une vulnérabilité aux changements globaux bien plus intense que les autres écosystèmes. Le besoin de protection de l'océan Austral est plus que jamais d'actualité compte tenu de l'évolution attendue des changements globaux en l'absence de mise en œuvre d'une politique environnementale ambitieuse.

Résultant des bouleversements environnementaux tels que l'altération des courants marins et de la circulation atmosphérique, la dégradation de la glace de mer, l'acidification des eaux ou la hausse de leur température, les répercussions attendues sur l'écologie des espèces sont multiples et variées (abondance, distribution, compétition pour l'accès à la nourriture et à l'habitat). Parallèlement, bien que régulés par la Commission pour la conservation de la faune et la flore marines de l'Antarctique (CCAMLR), le développement des activités de pêche et la possibilité d'accéder à de nouveaux espaces libérés par le retrait de la banquise sont des menaces additionnelles bien réelles.

Dans un tel contexte, il est urgent de collecter un maximum d'informations, démographiques, écologiques ou comportementales, sur les espèces constitutives de ces écosystèmes afin de disposer d'un état initial de connaissances avant que notre capacité à désentrelacer les causes des conséquences ne soit altérée.

Puisque toutes les espèces ne peuvent être étudiées, une stratégie pertinente consiste à utiliser des espèces dites « sentinelles » tels que les oiseaux de mer ou les mammifères marins. Ces prédateurs supérieurs sont affectés par la cascade de changements intégrés le long du réseau trophique. L'étude à long terme des variations affectant leurs populations (démographie, distribution, comportements) est ainsi révélatrice des changements plus globaux sous-jacents subis par le système. Néanmoins, à l'heure actuelle, le manque de données sur la dynamique spatiale et temporelle des écosystèmes et l'hétérogénéité des changements, même à des échelles spatiales relativement petites, ajoute une incertitude considérable sur les projections concernant les systèmes biologiques. L'accumulation de connaissances approfondies est donc fondamentale, et est un prérequis nécessaire à la mise en place de mesures de conservation pertinentes et efficaces, comme l'implémentation d'aires marines protégées (AMP) sur des zones identifiées comme des points chauds de biodiversité.

Les prédateurs marins sont difficilement observables en mer. Leur suivi et l'acquisition de données multiples, telles que leur localisation et leur profondeur de plongée à un instant donné, nécessitent l'utilisation d'enregistreurs de données (*biologgers*) déployés sur les animaux. Ces dispositifs, utilisés dans le cadre de cette thèse, peuvent stocker l'information et requièrent une récupération ou bien une transmission des données à distance par satellite. Chaque technique présente des avantages et des inconvénients, mais les informations recueillies permettent, une fois analysées, d'examiner la distribution et les activités en mer des individus équipés. Il est ainsi possible d'affiner notre compréhension des interactions existant entre une espèce et les différentes composantes (biotiques et abiotiques) de son environnement dans un souci notamment de gestion, de conservation ou d'estimation des potentialités d'adaptation future aux changements globaux.

Ces différentes problématiques, e.g. *biologging*, distribution et compréhension des activités en mer, enjeux de conservation, sont abordées au cours de cette thèse avec, pour espèce modèle, le manchot empereur (*Aptenodytes forsteri*).

Cette espèce emblématique de l'Antarctique occupe une position élevée au sein du réseau trophique marin antarctique et se situe à l'avant-garde des impacts du réchauffement climatique. En effet, les projections démographiques récentes estiment que 80% de colonies pourraient avoir disparu d'ici la fin du siècle si les émissions de gaz à effet de serre sont maintenues à leur niveau actuel.

A ce jour, 61 colonies, à la répartition circum-continentale, ont été localisées par satellite, mais peu ont été effectivement visitées et encore moins étudiées. Moins d'une dizaine de colonies ont fait l'objet de suivi en mer d'individus adultes, et seulement quatre pour des juvéniles. La connaissance effective de la distribution en mer de cette espèce est de ce fait extrêmement parcellaire et n'est connue que sur le quart du pourtour continental. Or, les colonies se répartissent sur un gradient latitudinal de 1400 km. Les individus de colonies éloignées sont donc vraisemblablement soumis à des contextes écologiques et des problématiques différents.

Unique prédateur à place centrale se reproduisant au cœur de l'hiver austral, le manchot empereur adulte alterne les allers-retours entre sites de nourrissage en mer et sa colonie tout au long de la période de reproduction et de l'élevage de son unique poussin annuel. L'espèce se caractérise également par une phylopatrie importante, i.e. les individus présentent une fidélité forte à leur site de reproduction et reviennent généralement, année après année, se reproduire au sein de la même colonie. Ces caractéristiques sont idéales pour le déploiement de *biologgers* puisqu'elles permettent leur récupération si besoin et la mise en place d'un suivi à long terme des individus équipés. Le déploiement d'enregistreurs de données sur ces oiseaux plongeurs permet également la collecte de données environnementales *in-situ* (température ou conductivité de la colonne d'eau par exemple) dans des zones inaccessibles la majeure partie de l'année (sous la banquise), offrant des informations uniques sur les écosystèmes polaires bien que le défi logistique et technique soit complexe à relever.

L'ensemble de ces critères fait du manchot empereur un modèle biologique de choix pour illustrer l'importance de la collecte de données dans l'océan Austral à des fins de conservation et de suivi à long terme de l'environnement tout en améliorant notre connaissance sur l'espèce et son rôle au sein des réseaux trophiques.

Le manchot empereur est régulièrement utilisé pour sensibiliser le public de par son statut d'espèce endémique et charismatique de l'Antarctique et d'espèce parapluie, i.e. sa vaste aire de répartition entrainerait la protection d'un grand nombre d'espèces si elle était protégée, notamment de ses proies (krill, calandre antarctique et calmar) et des réseaux trophiques inférieurs. Prédateur supérieur jouant un rôle pivot au sein des écosystèmes antarctiques, il reste cependant beaucoup à apprendre sur la répartition et les activités en mer de cette espèce. Pour combler ce manque de connaissances, j'ai co-initié et co-supervisé la mise en place d'un programme de recherche sur la colonie de manchots empereurs de la Baie d'Atka à proximité de la Station de recherche allemande Neumayer III, en bordure de la mer ouest de Weddell. La mer de Weddell abrite le tiers de la population de manchots empereurs, mais leur comportement en mer n'y avait encore jamais été étudié. Signalons que dans ce cadre, cette thèse a initié et contribué à la mise en place depuis 2017 du second observatoire à long terme de l'espèce afin d'évaluer la vulnérabilité des écosystèmes de l'Antarctique. Jusqu'à présent, la quasi-totalité des données démographiques était en effet issue d'une seule colonie répondant à un environnement particulier.

Chapitre 1- Evaluation des outils méthodologiques et nouveaux développements

Guidés par le principe de raffinement du cadre des trois R (*Remplacer, Réduire, Raffiner*) qui préconise de tester et d'évaluer en permanence les protocoles de recherche afin de minimiser les perturbations de la faune, dans ce premier chapitre nous décrivons et évaluons nos protocoles pour la fixation des *biologgers*, la capture des animaux et la récupération des dispositifs après le déploiement.

Au cours de deux sessions de terrain de quatre mois (été austraux 2017-2018 et 2018-2019), nous avons capturés/recapturés 70 adultes et 8 juvéniles afin de réaliser le déploiement et la récupération de *biologgers* (plateformes GPS ou ARGOS, et Time-Depth Recorder (TDR)). Afin de garantir que les données recueillies soient d'une qualité exemplaire d'un point de vue scientifique et éthique, les effets délétères potentiels des procédures de déploiement doivent être évalués et atténués.

Bien que les manchots empereurs soient l'objet d'équipements depuis près de 30 ans, nous avons revus et recapturés, pour la première fois, des manchots empereurs équipés un an auparavant juste après leur mue annuelle. Ces informations nous permettent de démontrer que la technique utilisée en routine pour des déploiements à long terme, qui consiste à coller le *biologger* directement sur les plumes du dos des manchots, est préjudiciable aux oiseaux. Elle provoque la perte des plumes porteuses et en conséquence des dispositifs déployés. Par conséquent, nous avons mis au point et proposons une méthode alternative d'attache sur le dos qui a conduit à des déploiements réussis. Les *biologgers* sont restés en place durant plus d'un an, entre les deux périodes de mue des individus équipés. Nous avons également réalisé, pour la première fois chez cette espèce, le déploiement de *biologger* (TDR) à la patte, au moyen d'un montage en bracelet de notre conception. Ces dispositifs ont parfaitement fonctionné jusqu'à leur récupération après 10 mois de déploiement, et comme chez les autres espèces de manchots pour lesquelles des systèmes analogues sont utilisés, aucun impact majeur de perturbation pour l'animal n'a été mis en évidence. Enfin, nous fournissons des méthodes de capture et de manipulation des manchots empereurs qui induisent un minimum de perturbation et confère un maximum de sécurité et d'efficacité. En particulier, l'utilisation d'un corral permet la capture simultanée de plusieurs individus sur le site même de la colonie. Toutes les procédures ont été documentées et partagées sous forme de vidéos et diaporamas.

Cette étude est la première à fournir des procédures aussi détaillées et éprouvées pour capturer/recapturer et déployer des dispositifs externes de télémétrie sur les manchots empereurs. Elle est ainsi destinée à servir de ressource de base pour faciliter les futures recherches sur cette espèce sensible. Elle souligne également l'importance de surveiller les impacts potentiels, à court et long terme, des déploiements de *biologgers* sur les animaux dans leur milieu naturel, et la nécessité de rester critique vis-à-vis des protocoles établis.

Chapitre 2- Evaluation des outils de conservation

Après l'évaluation des outils méthodologiques employés au cours de mes recherches, l'étude de la distribution spatiale de manchots empereurs juvéniles lors de leur première année en mer, est combinée à celle de la littérature existante afin d'estimer si les outils de conservation mis en place à l'échelle de l'océan Austral sont adaptés et pertinents pour garantir la protection des manchots empereurs.

En janvier 2019, nous avons équipé huit oiseaux de 6 mois à leur départ de leur colonie de naissance, en Baie d'Atka, avec des balises ARGOS qui nous transmettaient leur localisation plusieurs fois par jour par satellite. Nous avons enregistré leur voyage au cours de cette première année en mer dans le secteur atlantique de l'océan Austral. Ces informations sont cruciales puisque la colonie de la Baie d'Atka n'est que la cinquième colonie sur les 61 recensées où des juvéniles ont été suivis. Les quatre autres colonies sont situées à plusieurs milliers de kilomètres, et ne couvrent qu'un quart du continent (mer de Ross et Antarctique de l'Est).

L’analyse des données révèle une dispersion des juvéniles sur une étendue bien plus vaste qu’enregistrée dans les autres secteurs étudiés. Leur habitat s'étend jusqu’à 48,5° de latitude Sud, soit plus de 600 km au nord que ce qui avait été observé jusqu’alors. Nous mettons ainsi en évidence que les juvéniles de manchot empereur et de manchot royal (*A. patagonicus*), deux espèces sœurs d’un point de vue phylogénétique, cohabitent spatialement et temporellement, alors que les adultes de chaque espèce utilisent des niches écologiques bien distinctes, une découverte d’intérêt majeur pour les chercheurs en écologie évolutive.

La méta-analyse des données de suivi en mer des manchots empereurs juvéniles suggère que, au départ de leur colonie de naissance, tous les juvéniles migrent vers le nord jusqu’à atteindre le courant antarctique circumpolaire. Ils y restent au maximum deux mois avant de repartir vers le sud et de passer le reste de leur première année dans le *pack* (banquise dérivante). Cette vaste amplitude de dispersion les entraine aux limites de l’océan Austral et de la juridiction de la CCAMLR. Un développement des pêcheries est, à terme, fortement envisagé dans ces zones où elles seraient alors en compétition directe pour la ressource avec les manchots empereurs juvéniles, c’est-à-dire un des stades les plus critiques de leur existence en termes de survie. Enfin, nous mettons en lumière que les juvéniles passent la grande majorité de leur première année (89,5% dans notre étude) en dehors des limites des AMP existantes ou en discussion depuis des années à la CCAMLR.

L’adjonction des données issues de la littérature aux données que nous avons collectées offre une vision d’ensemble qui révèle que les efforts de conservation existants et prévus dans l'océan Austral n'assurent pas une protection efficace des manchots empereurs. Nous soulignons également la nécessité de collecter des données de référence pour l'espèce, en particulier en Antarctique occidental, autour de la Péninsule et dans les colonies situées au plus profond de la mer de Weddell, afin d'optimiser et d'évaluer la mise en œuvre de futures mesures de conservation.

Chapitre 3- Stratégies spatio-temporelles de prospection et de recherche alimentaire

Dans cette optique d’acquisition de données de référence, et dans le cadre des négociations concernant la mise en place d’une AMP en mer de Weddell, nous avons également équipé des manchots empereurs adultes sur la colonie de la Baie d’Atka. Au cours de deux étés, 36 individus ont été équipés de GPS-TDR en fin de période de nourrissage du poussin. Ces déploiements d’une durée de 16±6 jours ont permis un enregistrement de 1 à 3 trajets en mer selon les individus. Nous avons aussi déployé 8 balises ARGOS après la mue annuelle des adultes en janvier 2018. Elles ont fonctionné plusieurs mois (150±30 jours) jusqu’au début de l’hiver austral. Ces 8 individus portaient également chacun un TDR à la patte, dont quatre ont été récupérés après un an.

En associant les positions des individus à leur profondeur de plongées, nous sommes ainsi capables d'interpréter *a posteriori* leur comportement au cours de la période de déploiement afin de déterminer leurs stratégies spatio-temporelles de prospection et de recherche alimentaire. Parallèlement, les conditions environnementales rencontrées par les individus ont été extraites des bases de données satellitaires accessibles en ligne. Nous avons alors examiné l'influence des conditions environnementales et de l'habitat (concentration en glace, distance au bord de la banquise, distance aux différents fronts, bathymétrie et pente des fonds marins) sur la distribution spatiale dans le temps des individus et sur leur comportement de plongée. Nous avons, de plus, combiné ces informations à celles d'une étude similaire réalisée au début des années 2000 sur la colonie de Pointe Géologie en Terre-Adélie[1].

Quel que soit le site d'étude, la distribution en mer des individus au fil d'une année dépend du sexe, de la concentration en glace, de la saison et de la distance à la colonie. Au cours de la période d'élevage du poussin, les adultes reproducteurs sont contraints de rester dans un rayon de 104±74 km autour de la colonie occupant un domaine vital de 26728 km². Une fois la reproduction terminée, les adultes exploitent de nouvelles zones triplant la taille de leur zone de prospection (92990 km²) alors que la zone exploitée par les juvéniles couvre 2,6 millions de km².

Les analyses préliminaires comparatives des comportements de plongée révèlent cependant des différences entre sites à des périodes spécifiques de l'année. Nous montrons que la répartition journalière des plongées est différente entre les deux sites au cours de l'été austral (novembre et décembre). Les individus équipés en Baie d'Atka présentent deux pics de plongées au cours de la journée. L'un se produit en milieu de « nuit » (bien que ce soit le jour polaire à ces latitudes) et le second à la mi-journée. Ils sont entrecoupés de périodes de moindre activité. *A contrario*, les plongées des individus équipés à Pointe Géologie présentent une distribution en cloche avec un maxima en milieu de journée et une faible activité de nuit. Les individus équipés de balises ARGOS en Baie d'Atka présentent cette répartition tout au long de l'année jusqu'au début de l'été austral. Un changement du comportement de plongée est alors observé et devient similaire à celui des individus équipés de GPS-TDR présentant deux pics d'activité journaliers.

Bien que préliminaires, ces analyses suggèrent un changement d'alimentation au cours de l'été austral pour les individus se reproduisant en Baie d'Atka. Les changements environnementaux (diminution de

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[1] En plus d'avoir déjà pris part à des études sur la colonie de manchots empereurs de Pointe Géologie (étude présentée en annexe de cette thèse), j'ai réalisé une période de terrain en début de thèse sur ce site afin d'initier un programme de suivi en mer similaire sur des manchots Adélie (*Pygoscelis adeliae*), et dont les résultats préliminaires sont présentés en annexe. Cette période de terrain impliquait la supervision quotidienne de deux Volontaires de Service Civique.

l'épaisseur et retrait de la banquise, allongement de la durée du jour) induisent potentiellement un changement dans l'abondance, la distribution nycthémérale et le type de proies disponibles dans ce secteur, entrainant un changement dans les stratégies d'approvisionnement des manchots.

Conclusion

Une connaissance plus approfondie de la niche écologique du manchot empereur est essentielle pour estimer les changements induits par les bouleversements environnementaux attendus au cours du siècle. La collecte de ces informations en mer nécessite l'équipement de quelques individus répartis sur différentes colonies afin de couvrir l'ensemble des conditions environnementales susceptibles d'être rencontrées par l'espèce à l'échelle de la population globale. Afin d'obtenir les données les plus représentatives possibles du comportement de la population, il est cependant nécessaire de disposer d'outils et de techniques les moins perturbants pour les animaux équipés. La mise en place et le partage de nouvelles méthodologies de capture et d'équipement au cours de cette thèse, afin de servir de ressource de base pour faciliter les futures recherches sur cette espèce sensible, répond à ce besoin.

Ces précieuses informations élémentaires sont indispensables pour la mise en place de mesures adéquates de conservation comme nous l'illustrons pour les juvéniles. L'application d'une vision d'ensemble a permis de mettre en évidence la non-adéquation entre leur utilisation de l'océan et les systèmes de protection (AMP notamment) existants ou prévus. Elle a également confirmé l'hypothèse de l'importance des structures océaniques particulières (fronts et courant circumpolaire) pour cette classe d'âge à l'échelle du continent bien que les raisons n'en soient pas encore déterminées. Enfin, nous apportons de nouvelles connaissances sur la répartition spatio-temporelle en mer des manchots empereurs et leur comportement de recherche alimentaire. Ces données sont de premières importances afin d'éviter ou limiter la compétition spatio-temporelle avec les pêcheries si celles-ci continuaient à se développer dans l'océan Austral.

En définitive, nous soulignons la nécessité de conduire des études similaires sur d'autres colonies afin de disposer d'une vision la plus holistique qu'il soit de la niche écologique de l'espèce à l'échelle de l'océan Austral. Ces informations sont d'ailleurs un prérequis pour appuyer la révision du statut de l'espèce sur la Liste Rouge de l'Union Internationale pour la Conservation de la Nature (UICN) à un niveau plus adapté aux menaces multiples qui pèsent sur cette espèce.

Scientific communications

Manuscript chapters

Houstin, A., D. P. Zitterbart, A. Winterl, S. Richter, V. Planas-Bielsa, A. Ancel, J. Fournier, D. Chevallier, B. Fabry and C. Le Bohec (submitted) - « *Biologging of emperor penguins - attachment techniques and associated deployment performance* ».

Houstin, A., D. P. Zitterbart, K. Heerah, O. Eisen, V. Planas-Bielsa, B. Fabry and C. Le Bohec (submitted) - « *Juvenile emperor penguin range calls for extended conservation measures in the Southern Ocean* ».

Houstin, A., D. P. Zitterbart, K. Heerah, O. Eisen, A. Winterl, S. Richter, A. Ancel, V. Planas-Bielsa, B. Vallas, D. Chevallier, B. Fabry and C. Le Bohec (in prep) - « *Foraging tactics of emperor penguins differ between sites and seasons* ».

Annexes

Richter, S., R. Gerum, A. Winterl, **A. Houstin**, M. Seifert, J. Peschel, B. Fabry, C. Le Bohec, and D. P. Zitterbart (2018) - « *Phase Transitions in Huddling Emperor Penguins* » - Journal of Physics D: Applied Physics 51 (21) - DOI: 10.1088/1361-6463/aabb8e.

Winterl, A., S. Richter, **A. Houstin**, B. Fabry, C. Le Bohec, D. P. Zitterbart (2020) - « *micrObs - a customizable and robust time lapse camera* » - HardwareX - DOI: 10.1016/j.ohx.2020.e00134.

Vibert, L., **A. Houstin**, V. Planas-Bielsa, P. Blanchard, D. Ménard, D.Couet, E. Schloësing, Y. Le Maho, T. Blasco, J. Fort, C. Le Bohec (in prep) - « *Effects of individual characteristics and environmental conditions on foraging tactics of Adélie penguins* ».

Eckbo, N., C. Le Bohec, N.A. Warner, V. Planas-Bielsa, C. Cornec, D. Herzke, **A. Houstin**, Q. Schull, S. Zahn, N. Carrasco, Y. Le Maho, J.M. Durant, G. Wing Gabrielsen, K. Borgå (in prep) - « *Foraging tactics and breeding constraints predict contaminant accumulation in fasting Adélie penguins* ».

Work in progress

Winterl, A., S. Richter, **A. Houstin**, B. Fabry, C. Le Bohec, D. P. Zitterbart (in prep) « *Path selection in Adélie penguins* ».

Posters

Houstin, A., V. Planas-Bielsa, N. Chatelain, J. Courtecuisse, Y. Le Maho, S. Richter, D. P. Zitterbart and C. Le Bohec (2017) - « *Insight into an Adélie penguin colony* » - XIIth SCAR Biology Symposium, Louvain, Belgium.

Planas-Bielsa, V., **A. Houstin**, N. Chatelain, J. Courtecuisse, Y. Le Maho, C. Le Bohec (2017) - « *The breeding foraging dilemma in Adélie penguins* » - XIIth SCAR Biology Symposium, Louvain, Belgium.

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Chapter I. Introduction

I.1 Conservation biology

In the current context of global change (IPCC 2014, 2019) and mass extinction (Barnosky et al. 2011, Ceballos et al. 2015), conservation biology stands at the forefront. Conservation biology was formally conceptualised over the 1980s as a new field focused on understanding (description, explanation, and appreciation), protecting, and perpetuating biological diversity at all scales and all levels of biological organisation (Soulé 1985, Meffe and Carroll 1997).

This multidisciplinary science (Fig. 1), which applies the principles of ecology, biogeography, population genetics, anthropology, economics, sociology, to the maintenance of biological diversity throughout the planet (Barbault 2008), can be represented as a pyramidal structure (Fig. 2). The base consists of documenting the extent of biodiversity, i.e. accumulate information (baseline data, for instance). Above the base is the "knowledge" level, which is the understanding of the nature, causes, and consequences of processes and dependencies between individuals, species, and ecosystems. In other words, through the first two blocks of the pyramid, abiotic and biotic influences, including human impacts, on the functioning of the different ecosystems are assessed. Finally, at the top of the pyramid is the policy level. All the information and the knowledge gathered are compiled to develop practical methods to prevent species extinctions, and to allow for persistence of ecosystem processes and/or services (Hunter and Gibbs 2006, Van Dyke 2008).

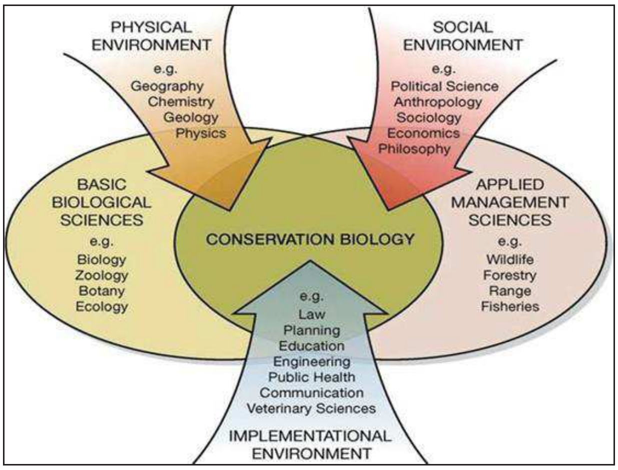

Fig. 1. Illustration of the multidisciplinary of conservation biology. Adapted from Jacobson (1990).

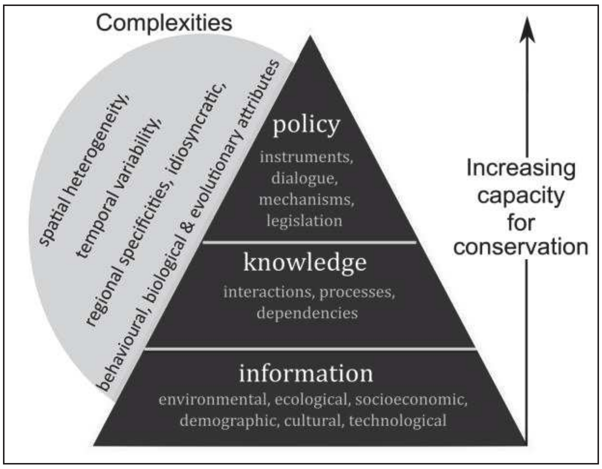

Fig. 2. Schematic view of the hierarchical organisation of conservation biology. Adapted from Mazaris (2017).

This framework has been formalised at the international level with the signature of the Convention on Biological Diversity (CBD, CBD (2010)) at Rio in 1992 by 195 states and the European Union with the objective to develop national strategies for the conservation and sustainable use of biological diversity. This strategic plan was subdivided in 2010 in 20 objectives called the Aichi Biodiversity Targets (CBD 2010) establishing a biodiversity policy framework. In particular, the Target 11 states: "*By 2020, at* *least 17% of terrestrial and inland water, and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes*". In 2018, only 15% of the land surface and inland waters and 7% of the ocean were protected, but only 1% of the Areas Beyond National Jurisdiction (UNEP-WCMC et al. 2018). However, doubts subsist on the real implementation and enforcement of the protection for many of them (Rife et al. 2013, Pieraccini et al. 2017, Smith and Jabour 2018, Riggio et al. 2019), jeopardising the planet's life support systems (CBD 2018).

In this context and more than ever before, our ability to understand how living organisms, amongst which top predators, will be coping with these environmental changes depends on the development of appropriate ecosystem and biodiversity management measures (Caro 1998).

My PhD project falls within the framework of conservation biology, from the bottom (high-quality baseline data acquisition) to the top of the pyramid (evaluation of existing and planned conservation measures) through the middle part (understanding foraging strategies in relation to environmental drivers) at the scale of the polar and subpolar ecosystems.

I.2 The Southern Ocean

I.2.1. Oceanography and geography

The Southern Ocean (SO) is the vast water mass encircling the Antarctic continent. Debates still occur on its extent and delineation. The most commonly accepted definition, not recognised by all countries, fixes its northern limit at 60°S (International Hydrographic Organisation (IHO 2002), but its functional definition is usually extended at least to the Antarctic Polar Front, around 55°S (Moore et al. 1999, Gersonde et al. 2005). Other limits have also been considered like the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) boundaries (Brooks et al. 2020a) or south of the 40°S (Hindell et al. 2020).

One of the main oceanographic features in the Southern Ocean is the Antarctic Circumpolar Current (ACC), the largest ocean current, flowing clockwise (from west to east) far offshore (between 40°S and 65°S), and connecting the Atlantic, Indian and Pacific Oceans (Fig. 3; Orsi et al. 1995). The Southern Ocean consists of vast masses of water with different physical and chemical properties (e.g. temperature, salinity, density). The areas where different masses meet are called “fronts”. They are narrow areas having a sharp horizontal gradient of water properties (e.g. salinity, temperature; see Orsi et al. 1995, Sokolov and Rintoul 2009, Talley et al. 2011, Kim and Orsi 2014). The fronts are used as boundaries to divide the Southern Ocean in ‘zones’. The fronts and zones they delineate as well as the typical meridional (north-south) circulation and water masses are summarized schematically in Fig. 4 from Talley et al. (2011).

The Northern limit of the Antarctic Circumpolar Current is the non-circumpolar Subtropical Front. The ACC counts three major fronts (Fig. 3). The Sub-Antarctic Front sets the northern boundary of the circumpolar Southern Ocean. Then, comes the Polar Front (PF) characterised by an isothermal temperature of 2°C at a depth of 200 metres. Finally, the most southerly front is the Southern Antarctic Circumpolar Current Front (Fig. 3; Orsi et al. 1995, Talley et al. 2011). A fourth feature, the Southern Boundary of the Antarctic Circumpolar Current (SBACC), which marks the southern limit of the circumpolar flow (Orsi et al. 1995, Sokolov and Rintoul 2009), is defined as the southern edge of the low oxygen layer of the Upper Circumpolar Deep Water. The SBACC is not a dynamical front and is sometimes merged with the Southern Antarctic Circumpolar Current Front (Orsi et al. 1995, Talley et al. 2011). The Southern Boundary separates the Antarctic Circumpolar Current from the subpolar region (Fig. 4).

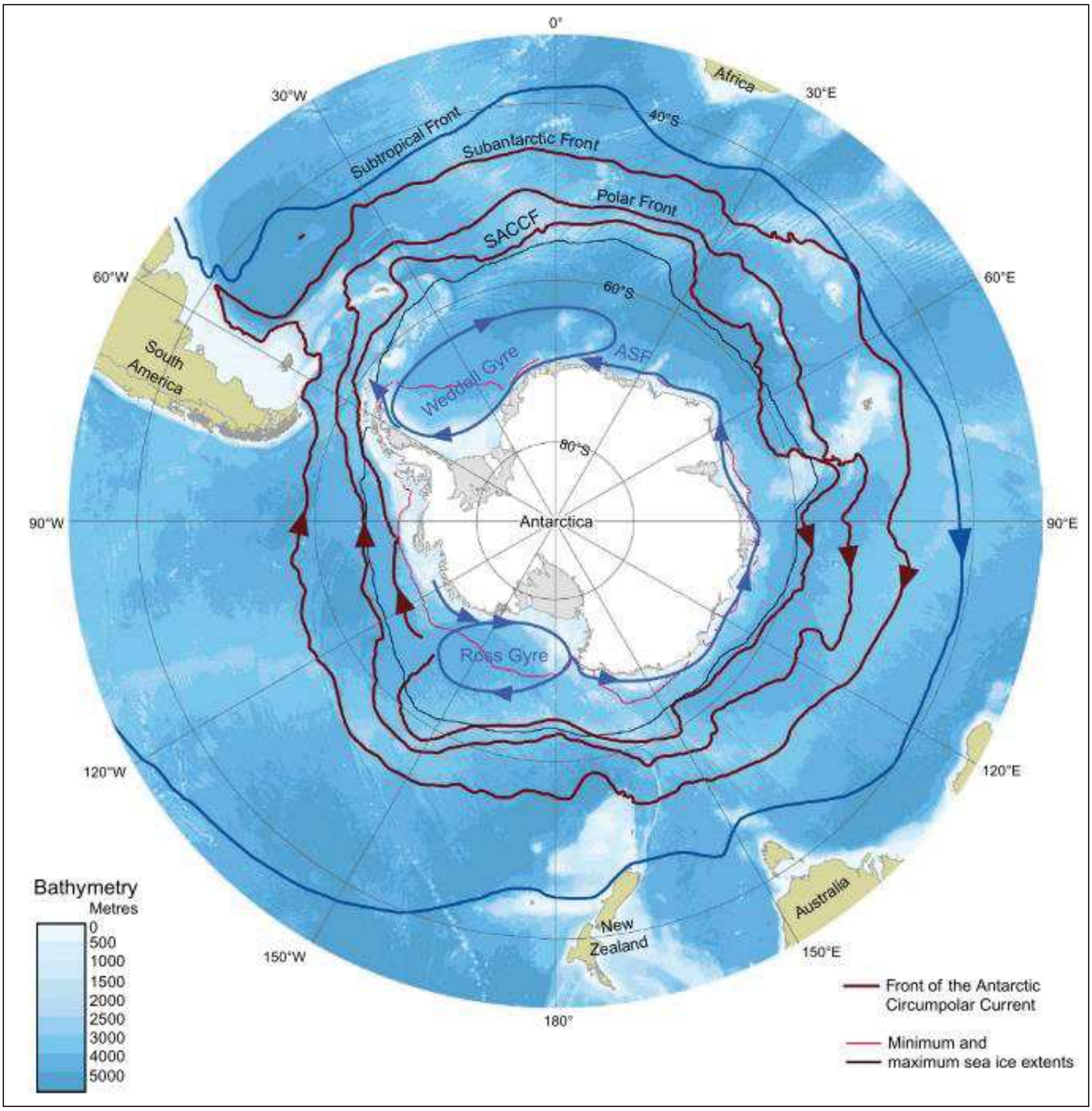

Fig. 3. Major physical features of the Southern Ocean: bathymetry, major fronts, currents, and subpolar gyres. SACCF is Southern Antarctic Circumpolar Front and ASF is Antarctic Slope Front. Arrows indicate direction of current flow. Adapted from Stark et al. (2019).

The fronts are important areas of nutrient mixing and act as latitudinal ecological boundaries for numerous marine species distribution (Sokolov and Rintoul 2007). South of the ACC and close to the Antarctic continent, the inshore Antarctic Coastal Current or Antarctic Slope Front (ASF) circulates from east to west and separates very dense cold and fresh shelf water from warmer and saltier water offshore (Talley et al. 2011, Stark et al. 2019). Both currents (i.e. ACC and ASF), influenced by the wind-driven Ekman transport, form the Ross and Weddell Sea gyres (Nicol 2006), two productive areas due to the upwelling of cold, nutrient-rich water in their centre (Stark et al. 2019).

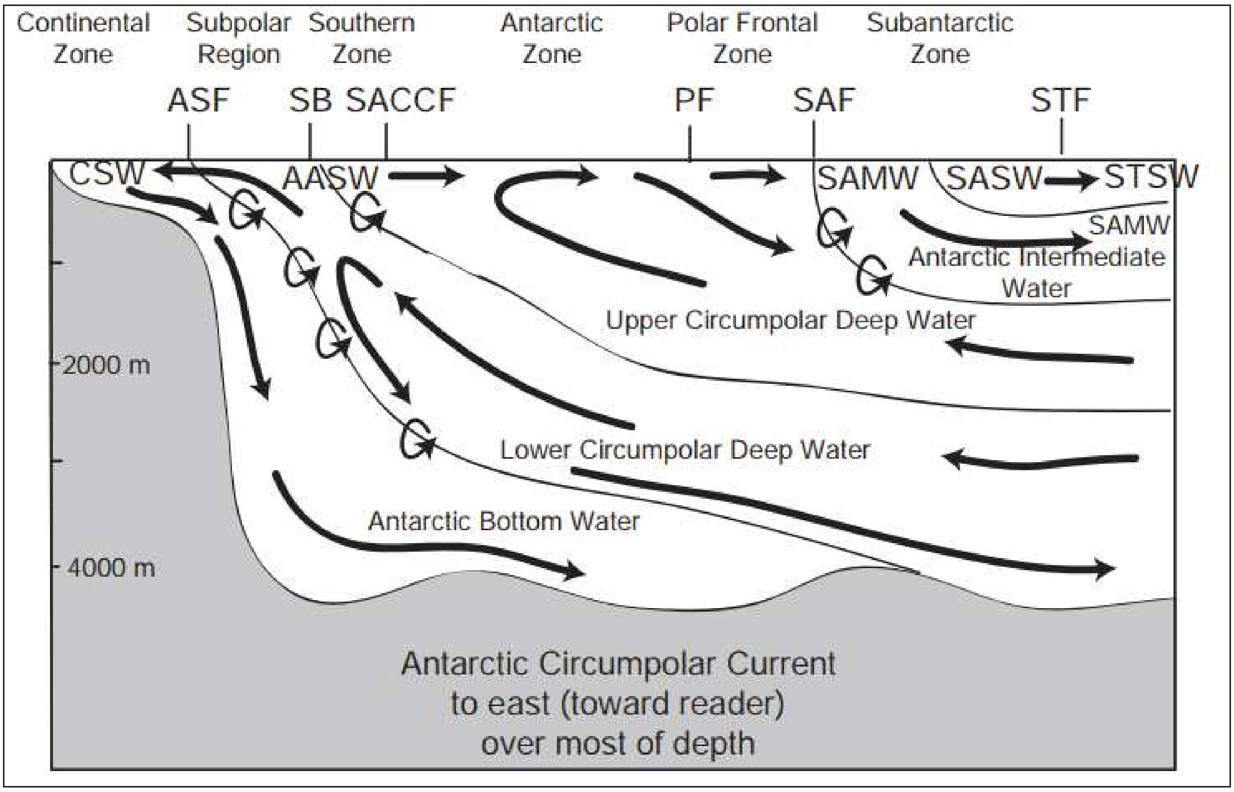

Fig. 4. Schematic meridional section in the Southern Ocean showing the water masses, meridional circulation, fronts, and most zones. CSW = Continental Shelf Water, AASW = Antarctic Surface Water, SAMW = Sub-Antarctic Mode Water, SASW = Sub-Antarctic Surface Water, STSW = Subtropical Surface Water, ASF = Antarctic Slope Front, SB = Southern Boundary, SACCF = Southern ACC Front, PF = Polar Front, SAF = Sub-Antarctic Front, STF=Subtropical Front. Adapted from Talley et al. (2011).

The Southern Ocean is also one of the major thermal exchange points between the oceans, the atmosphere and the cryosphere, and a central contributor in the thermohaline circulation (Stark et al. 2019). As the Antarctic circumpolar surface waters cool, they become denser and plunge beneath warmer, saltier sub-Antarctic waters forming the Antarctic Bottom Waters (Deacon 1937, Freeman and Lovenduski 2016) that spread northwards into the abyss of the three ocean basins. Hence, at the Polar Front, the warm and deep saline waters flowing southward from other oceans upwell and are transported around Antarctica by the ACC (Schmitz 1995, Stark et al. 2019) making the PF a very productive area, concentrating up to 20% of the world’s marine productivity (Laubscher et al. 1993, Bathmann et al. 1997, Carr et al. 2006).

I.2.2. Sea ice

I.2.2.1. Sea ice physical characteristics

Sea ice is a substrate, which, after initial freezing of seawater, is profoundly modified by interactions between physical, biological, and chemical processes (Dieckmann and Hellmer 2010). Sea ice undergoes a significant yearly cycling in surface extent around Antarctica, being maximal in September and minimal in February (Fig. 3; Parkinson 2014). Sea ice is broadly classified as marginal ice zone (MIZ), pack ice, or fast ice. Fast ice is a stationary and consolidated substrate that forms in sheltered and coastal locations where it is anchored to the coastline, icebergs, glaciers and shelves and remains several years (Massom et al. 2009, Stark et al. 2019). Pack ice is mobile, in the form of ice floes usually up to 2 m thick that are transported by wind and currents (Stark et al. 2019). It forms offshore and melts every year. MIZ is the area in between the pack ice and the open water, corresponding basically to loose pack ice floes (Massom and Stammerjohn 2010, Stroeve et al. 2016).

Through its extent, structure and seasonality, sea ice plays a critical and highly dynamic role in the global climate system (e.g. albedo effect, physical barrier to gases, heat fluxes) as well as on the ecology of the Southern Ocean ecosystem (Massom and Stammerjohn 2010).

I.2.2.2. Sea ice community

Sea ice is a major component of the biogeochemical cycles of the Southern Ocean and of the structure and dynamics of Antarctic marine ecosystems (Massom and Stammerjohn 2010). It provides food, in forms of nutrients trapped when the water froze, and habitat for various groups of organisms including bacteria, algae, fungi, and invertebrates. Sea ice retreat and melting in summer releases all the trapped nutrients and induce considerable phytoplankton blooms (Massom and Stammerjohn 2010, Arrigo et al. 2014, Stark et al. 2019). Additionally, during winter, the sea ice and the bottom of the sea ice is colonised by algae where they can be up to three times more abundant than in the water column (Smith et al. 2007). These algae, as the phytoplankton bloom induced in summer, is an important source of nutrition for diverse crustaceans and in particular euphausiids (e.g. Antarctic krill, (*Euphausia superba*)) and small fishes (Arrigo et al. 2014). In turn, these species represent a source of food for top predators and/or the prey they rely on (Fig. 5; Ainley et al. 2010).

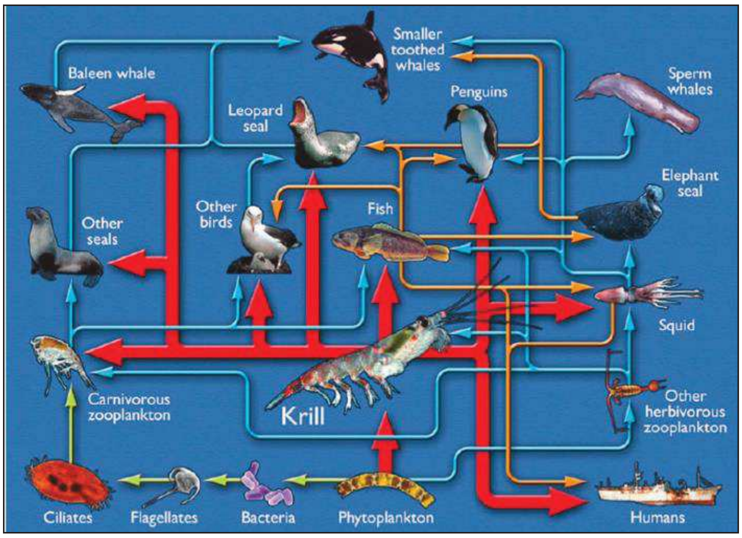

Fig. 5. Trophic network of the Southern Ocean. Adapted from the British Antarctic Survey.

Sea ice plays also a direct role for several top predators. The two Antarctic penguin species (emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguins) as well as seal species (Ross (*Ommatophoca rossii*), crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*) and Weddell (*Leptonychotes weddellii*) seals) are ice-obligate and associated with sea-ice year-round. Only emperor penguins and Weddell seals inhabits the fast-ice during the austral winter (Ainley et al. 2005).

I.2.3. Threats

Polar ecosystems are substantially more vulnerable than other ecosystems and expected to experience many climate change effects within this century including ocean acidification, changes to currents and winds as well as rising temperatures and sea ice degradation (Constable et al. 2014, Stark et al. 2019). These modifications are expected to lead to multispecies effects (top-down or bottom-up), including changes to prey abundance and availability, desynchronization of trophic levels, range shifts, and thus increased competition for food and habitat (Rintoul et al. 2018, Rogers et al. 2020). Measurable negative effects on wildlife have already been recorded as highlighted by the loss of an emperor penguin colony close to the West Antarctic Peninsula due to rise in local mean annual air temperature and coincident decline in seasonal sea ice duration around this colony (Trathan et al. 2011). Climate change is also expected to result in human access to new fishing areas (Rintoul et al. 2018, Rogers et al. 2020), where fisheries would compete for food and habitat with marine predators, not mentioning the possibility of top predators to be part of the by-catch (Anderson et al. 2011) or the risk of oil pollution (Culik et al. 1991, Trathan et al. 2015, Ropert-Coudert et al. 2019). Additional pressures are also likely to come into action. Tourism in Antarctica is increasing and is likely to disturb breeding animal populations (Fig. 20; see Tin et al. 2014, Schillat et al. 2016, Ropert-Coudert et al. 2019), while the spreading of new pathogens or diseases as well as of invasive species is an increasing concern (Gardner et al. 1997, Grimaldi et al. 2015, IPCC 2019, Ropert-Coudert et al. 2019, Hughes et al. 2020). The establishment of invasive species, both fauna and flora, on land and at sea, has even already been recorded (Olech and Chwedorzewska 2011, Potocka and Krzemińska 2018, Cárdenas et al. 2020). For example, in 2004, an outbreak of avian cholera that killed 2,500 to 3,000 chinstrap penguins (*Pygoscelis antarctica*) at Cooper Bay, South Georgia, was attributed to human visitation (Ropert-Coudert et al. 2019), while invasive mice are attacking adult and chick seabirds in sub-Antarctic islands causing population declines (Dilley 2018, Jones et al. 2019). Scientific activities and the establishment of scientific stations for geopolitical purposes have also greatly expanded over the last few decades. Such developments require and induce the transportation of more people and the development of facilities. For example, to increase its capacity, the Australian Antarctic Division is planning to build, near the Australian Davis research station, the first concrete airport in Antarctica[2]. Wilson's storm petrels (*Oceanites oceanicus*) that nest at the site will be displaced while native lichens, fungi and algae will be destroyed. Additionally, Weddell seals breed within 500 metres of the proposed runway site that also counts numerous adjacent lakes[3]. Finally, the accumulation of plastics/microplastics and other contaminants (e.g. heavy metal like mercury, pesticides, persistent organic pollutants) in Antarctic species and their potential long-term effects on individuals and populations has become a major concern (see Annex D[4] and Blévin et al. 2013, Ropert-Coudert et al. 2019).

This accumulation of anthropogenic pressures on top of global warming (Fig. 6) on the fragile ecosystems of the Southern Ocean is likely to adversely impact their resilience and ability to withstand climate change (Stark et al. 2019, Wauchope et al. 2019, Brooks et al. 2020a). In this context and despite its remoteness and pristine appearance, the urgency of the threats to the Southern Ocean and the need for protection is critical now more than ever before (Chown and Brooks 2019, Brooks et al. 2020a) and stands as a major challenge for the governing and management bodies of this ocean.

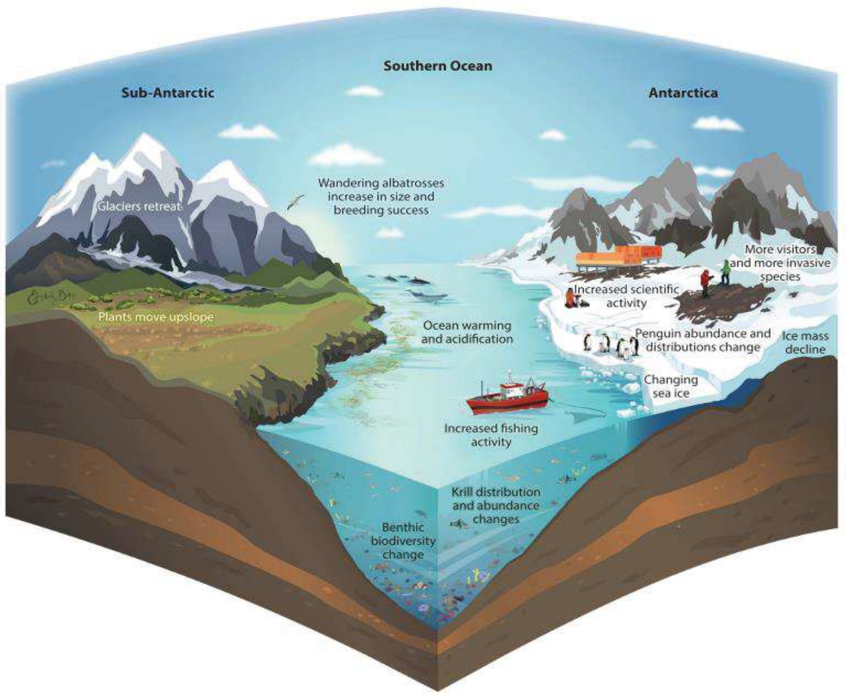

Fig. 6. Schematic of the changes facing the sub-Antarctic (left), Southern Ocean (centre) and Antarctic (right) environments. Adapted from Chown and Brooks (2019).

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[2] See https://www.antarctica.gov.au/antarctic-operations/travel-and-logistics/aviation/davis-aerodrome/

[3] See https://theconversation.com/australia-wants-to-build-a-huge-concrete-runway-in-antarctica-heres-why-thats-a-bad-idea-139596

[4] I have been involved during my PhD project, through fieldwork and preliminary analyses, in a study focusing on the contaminant accumulation on Adélie penguins from Pointe Géologie. The ready to submit version of the resulting manuscript is presented in Annex D.

I.2.4. Governing bodies and management regime

I.2.4.1. Antarctic Treaty System (ATS) – an international framework for protecting Polar Regions

The Antarctic region is regulated under a unique system of international governance: the Antarctic Treaty System (ATS; ATS 1959) constituted by the Antarctic Treaty adopted in 1959 and subsequent agreements (ATS 1959)[5]. ATS defined Antarctica as the land and ice shelves south of 60°S latitude, high seas being excluded. ATS was established to prevent Antarctica from being a military field and to promote scientific cooperation. In 1991, the Protocol on Environmental Protection to the Antarctic Treaty (ATS 1991), also known as the "Madrid protocol", completed the ATS and designated Antarctica as a "*natural reserve, devoted to peace and science*" while banning industrial operations until 2048 at least (Article 2, ATS 1991). Delegations from the Parties meet once a year at the Antarctic Treaty Consultative Meetings (ATCM), the international forum for the administration and management of the region. Before the Antarctic Treaty, seven countries had territorial claims over parts of Antarctica (Fig. 7), sometimes overlapping. They all signed the Treaty that maintained the *status quo* by putting all claims in abeyance (Article 4). To date, 54 countries have signed the Treaty. However, only 29 have had substantial research activities in Antarctica and have, thus, the right to participate in the decision-making regarding the regulation of the continent. They are called the Consultative Parties. The 25 Non-Consultative Parties can attend the Consultative Meetings, but they cannot participate in the decision-making[6].

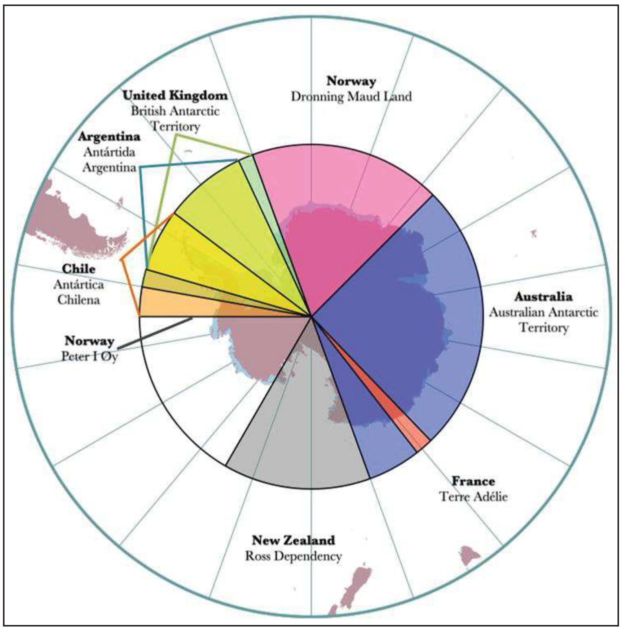

Fig. 7. Map of Antarctica showing territorial claims. Adapted from Natural Earth http://www.naturalearthdata.com.

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[5] https://www.ats.aq/e/key-documents.html

[6] https://www.ats.aq

I.2.4.2. Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) – an international framework in charge of the Southern Ocean management

The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) came into force in 1982 (CCAMLR 1980) in response to the growing large-scale exploitation of Antarctic krill in the Southern Ocean. Composed of 25 member states plus the European Union (see Fig. 8 to visualise all members and the 11 Acceding States[7]), the aims at conserving marine living resources and their rational use resorting with an ecosystem management approach based on scientific data integration (CCAMLR 1980).

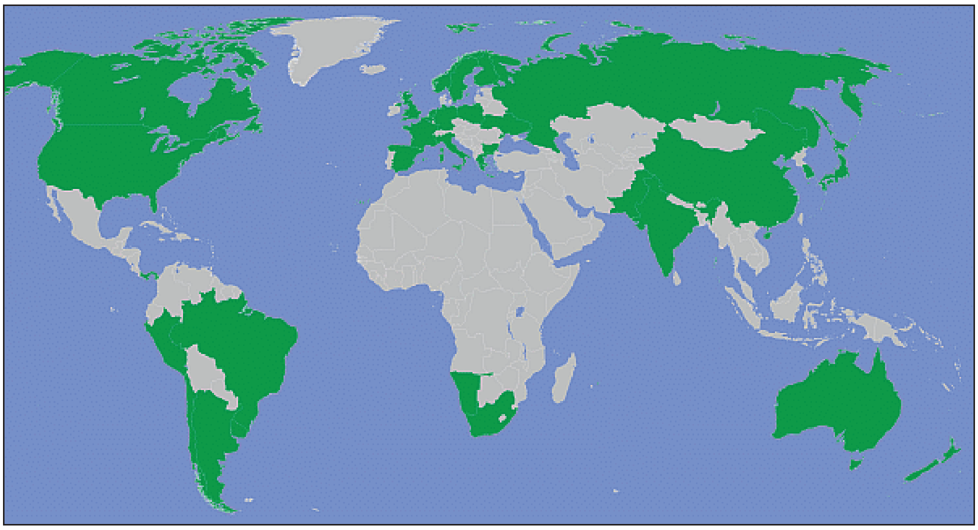

Fig. 8. Map showing CCAMLR members and Acceding States (in green). Adapted from http://www.geo-ref.net

CCAMLR's Article 2 states that any harvesting and associated activities shall not have long-term or irreversible adverse effects on either the harvested species or dependent and ecologically associated species and populations (Nicoll and Day 2017). The CCAMLR can then be considered as the ocean complement to the Treaty (Brooks 2013). In order to have a relevant ecosystem-based approach, the administrative boundaries of the CCAMLR aim to correspond to the ecological boundaries of the Southern Ocean: therefore, the CCAMLR jurisdiction limits are roughly aligned with the Polar Front (Fig. 10). The CCAMLR is in fact the ATS body responsible for the management of the fisheries, through quota allocations and gear limitations, and for the set up and implementation of conservation measures yearly reviewed and updated within its jurisdiction[8]. However, the adoption of any measure needs a consensus between members that have different economic and political aims, which can sometimes take years of negotiations (Sylvester and Brooks 2020).

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[7] An acceding State is a Contracting Party bound by the provisions of the CAMLR Convention but is not a CCAMLR Member. Acceding States do not contribute financially to the organisation, participate in decision-making and are not permitted to fish in the CCAMLR Area.

[8] See https://www.ccamlr.org/

Although the Statutes of the CCAMLR distinguish it from a simple Regional Fisheries Management Organisations (RFMO), CCAMLR's main focus is on fisheries management, and most of the conservation measures adopted by the CCAMLR are fisheries management related (Nicoll and Day 2017). Currently, four commercial fisheries occur within the CCAMLR boundaries: fisheries for Antarctic krill (*Euphausia superba*), mackerel icefish (*Champsocephalus gunnari*), Patagonian and Antarctic toothfish (*Dissostichus eleginoides* and *D. mawsoni)*. They are under the regulation of the CCAMLR and must comply with the regulatory framework enforced. Conservation measures can be divided in two mains parts: the compliance and fisheries regulation, and the protected areas.

(i) Compliance and fisheries regulation overview

The CCAMLR area is divided in domains and units management zones where quotas are allocated by units and species every year. The aim is to minimise the impact harvesting activities may have on the sustainability of target species. To avoid competition and mitigate by-catch of top predators, a spatiotemporal regulation is applied in accordance with top-predator species' biology to limit their disturbance during the breeding period. Additionally, to limit by-catch, for several species, by-catch Total Allowable Catches (TACs) are fixed. If this by-catch TAC is reached, then the fishery has to move in another area or to stop even though the TACs for fishable species have not been reached (Schiffman 2009). Other regulations apply to the type and size of gear to use (e.g. weighted lines, bird exclusion devices, night setting), notably to preserve the benthic ecosystem and to reduce mammal and seabird (mainly albatrosses and petrels; Kock et al. 2000) mortality and injury during longline and trawl fishing.

To fight against illegal, unreported and unregulated fishing (IUU fishing), estimated in the 90's to be six times more important than legal fishing inside the CCAMLR area[9] (Stark et al. 2019), and thus exceeding sustainable limits, the CCAMLR adopted a set of measures. The CCAMLR implements a Vessel Monitoring System (VMS), i.e. each vessel is equipped with an automatic location communicator (ALC) to transmit its position and must report fine-scale catch data. Vessels can be inspected at sea or at port. Additionally, the CCAMLR introduced in 2000 a Catch Documentation Scheme (CDS) for toothfish (the most valuable fishery, see Fig. 9). This document makes it possible to trace the origin and the trade cycle of catches in order to prohibit the trade of non-verified catch. As a result, IUU fishing has significantly reduced (Agnew et al. 2009, Chown and Brooks 2019) but still remains a concern (CCAMLR website) since the CCAMLR does not impose any legal obligations against non-party states (Bender 2008). However, the CCAMLR is more than a RFMO since its mandate goes beyond the simple management of fisheries and includes the notion of conservation and sustainable management of deep-sea species.

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[9] https://www.ccamlr.org/en/compliance/illegal-unreported-and-unregulated-iuu-fishing

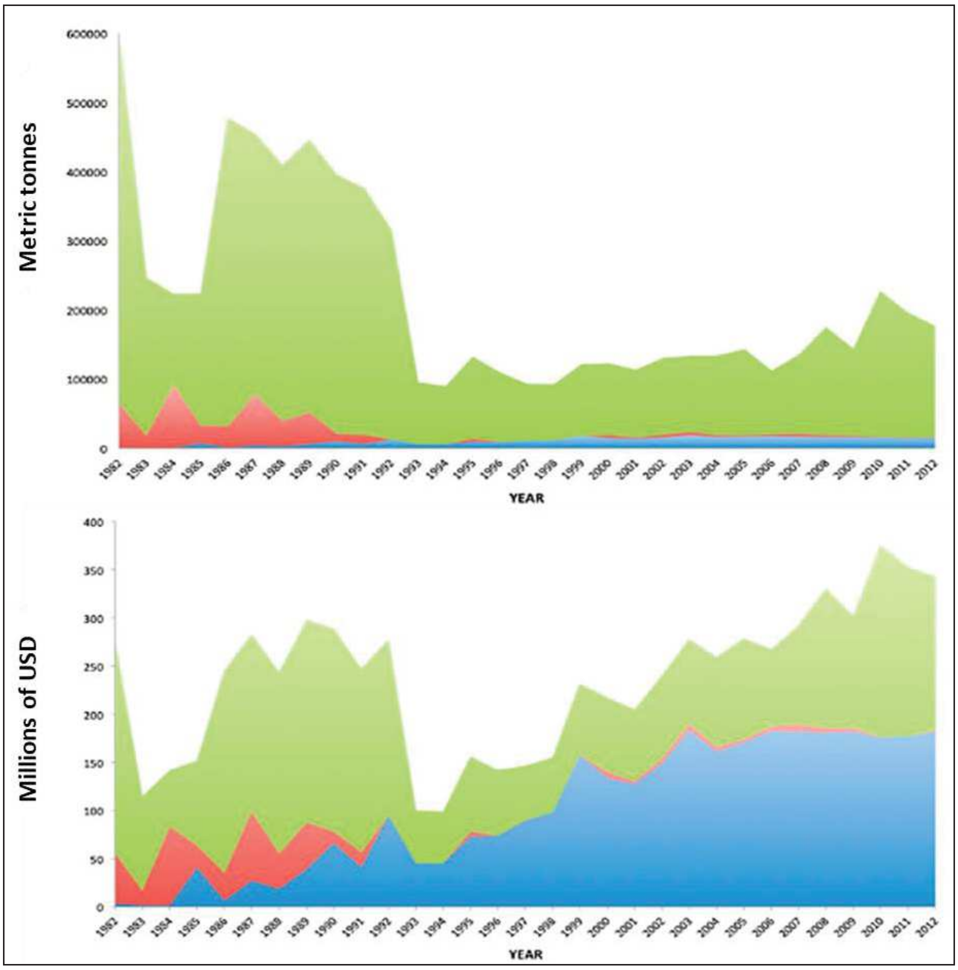

Fig. 9. Total catch composition (top) and commercial value (bottom) of landed toothfish (blue), icefish (red), and krill (green) in the CCAMLR area between 1982 and 2012 for all Member States combined. Adapted from Brooks (2013)**.**

(ii) Towards a representative system of marine protected areas in the Southern Ocean

The establishment of marine protected areas (MPAs) is another approach to efficiently safeguard the marine biodiversity (Sciberras et al. 2013, Speed et al. 2018, Laffoley et al. 2019). According to the International Union for Conservation of Nature (IUCN), a protected area is a "*clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values*" (WCPA/IUCN 2013). This description encompasses MPAs. They aim to conserve biodiversity by mitigating ocean threats, to preserve and to restore ecosystems, and to regulate fisheries in order to ensure sustainable use of the resources. Six different categories of MPAs exist depending on the management and governance type, from a strict "no-take" policy to a sustainable use of natural resources (WCPA/IUCN 2013). Herein, we consider MPAs in its broad meaning of being a marine area that provides protection for all or part of the natural resources it contains (CCAMLR website). Noteworthy, the definition of the CCAMLR is slightly different than from the IUCN and does not include the "long-term" notion (CCAMLR 1980). Thus, the CCAMLR area as a whole cannot be considered as a

MPA (Nicoll and Day 2017) according to IUCN criteria, despite what the CCAMLR states (CCAMLR 2011). The CCAMLR area is a management zone in which protected areas are nested.

Since 2002, the concept of a representative network of MPAs has emerged to be able to preserve marine biodiversity as whole and not only as small disconnected hot spots of biodiversity (UN 2002). A MPA network consists of a networked-system of individual MPAs designed to ensure interconnectivity and representativeness of ecosystems (WCPA/IUCN 2007), i.e. it represents all the habitats and species present in a region. Several studies (O'Leary et al. 2016, Dinerstein et al. 2019) suggest reaching a global level of protection of at least 30% of each marine habitat to ensure an effective protection of the high seas (IUCN 2014).

In this context, the CCAMLR has agreed to develop a representative system of MPAs based on the best scientific evidence available and an ecosystem-based management approach (Teschke et al. 2016a, Brooks et al. 2020a)[10]. As a result, in 2009, the South Orkney Islands Southern Shelf MPA became the first MPA established in the Southern Ocean, followed by the implementation of the Ross Sea region MPA in 2017 (Fig. 10). MPAs have also been established under national jurisdiction within the CCAMLR boundaries around several sub-Antarctic Islands (Kerguelen Island, Crozet Island, Prince Edward Islands, Heard Island and McDonald Islands, South Georgia and South Sandwich Islands) owned by states members of the CCAMLR (Australia, France, South Africa and the United Kingdom) (Table 1).

Table 1. List of current and proposed MPAs within the CCAMLR area.

MPA	Size (km²)	Status	Proposed by	Designated	Region
South Orkneys Islands	94 000	Designated	United Kingdom	2009	Antarctica
Ross Sea region	1 525 000	Designated	New Zealand, United States	2016	Antarctica
East Antarctica	969 000	Proposal	Australia, France, European Union	N/A	Antarctica
Weddell Sea	1 968 000	Proposal	Germany, European Union	N/A	Antarctica
Antarctic Peninsula	466 000	Proposal	Argentina, Chile	N/A	Antarctica
Heard Island and McDonald Island	71 000	Designated	Australia	2002	sub-Antarctic
Kerguelen	568 000	Designated	France	2006	sub-Antarctic
Crozet	410 000	Designated	France	2006	sub-Antarctic
South Georgia and South Sandwich Islands	1 241 000	Designated	United Kingdom	2012	sub-Antarctic
Prince Edward Islands	161 000	Designated	South Africa	2013	sub-Antarctic

Adapted from Brooks et al. (2020a).

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[10] See also https://www.ccamlr.org/en/science/marine-protected-areas-mpas

These areas are managed in compliance with the CCAMLR legislation (CCAMLR 1980). As a result, currently, 12% of the waters inside the CCAMLR boundaries are protected but they are not representative of the full range of ecosystems existing in the Southern Ocean (Fig. 10; Brooks et al. 2020a). In the coming years, three new MPAs adjacent to the continent might be established (Table 1). If the current proposals were adopted, then 22% of the CCAMLR waters would be under protection (Fig. 10; Brooks et al. 2020a).

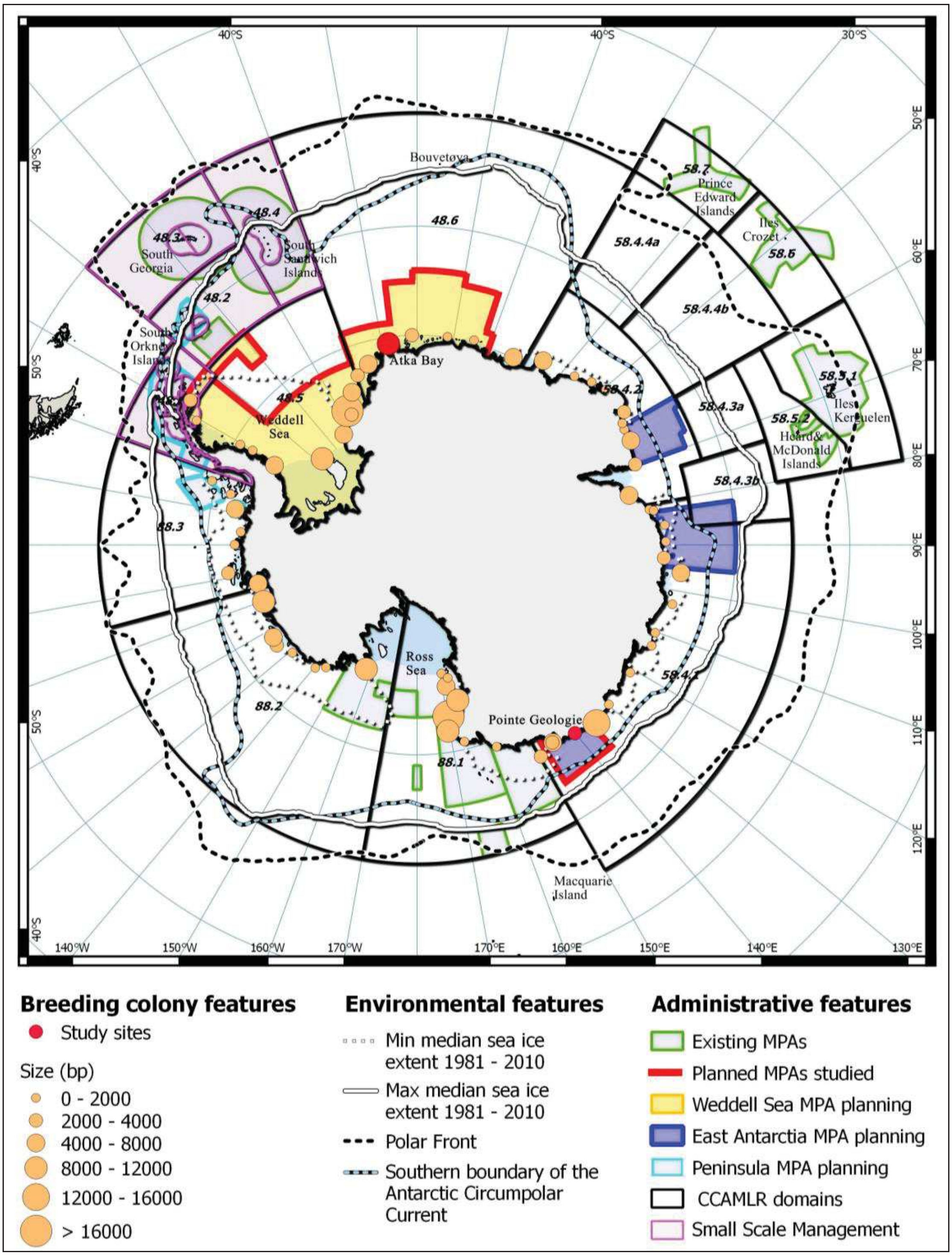

Fig. 10. Map of proposed and existing MPA within the CCAMLR area and distribution of emperor penguin breeding sites. Adapted from Trathan et al. (2020) and Brooks et al. (2020b).

I.3 Using the marine predator-biologging couple to monitor the Southern Ocean

I.3.1. Marine predators as sentinels of their environment and umbrella species

The marine environment, which covers 71% of the Earth surface, is highly dynamic and heterogeneous. As such, monitoring its change over time and 3-dimensional space represents a tremendous challenge. In order to overcome this challenge, a strategy is to use so-called "sentinel" species such as seabirds or marine mammals (Durant et al. 2009, Le Bohec et al. 2013, Hazen et al. 2019). Those species are often far ranging and stand near the top of the trophic networks (Burger 2006, Hazen et al. 2019), which are relatively short in the Southern Ocean (Smith et al. 1999). They are also easier to monitor than lower trophic level organisms and integrate information from the bottom to the top of the trophic networks (bottom-up control) over multiple spatiotemporal scales (Croxall et al. 2002, Frederiksen et al. 2007). In other words, they are subject to variations in the structure of trophic networks, which are themselves subject to environmental changes.

Most of the apex predators are long-lived species, thus long-term monitoring of the variations affecting their populations (e.g. demographic, distribution, behaviour) is indicative of the more global underlying changes in the system (Durant et al. 2009, Hazen et al. 2019). This characteristic makes them also suitable for studying whether the effects of climate change can be mitigated by phenotypic plasticity (e.g. morphological, physiological, behavioural traits) and microevolutionary changes (Le Bohec et al. 2013). These reasons explain why several species of penguins, such as the Emperor penguin or pinnipeds, such as the southern elephant seal (*Mirounga leonine)*, are therefore the focus of long-term monitoring programs.

As a result, marine predators have been recognised as a crucial component of spatial and ecosystem-based management, such as MPA design and systematic conservation planning (Maxwell et al. 2013). Their protection would encompass a wide range of habitats and would be beneficial to many ecological structures and species ("umbrella" species concept[11]; Roberge and Angelstam 2004).

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[11] An umbrella species is a species whose conservation is expected to confer protection to a large number of naturally co-occurring species.

Nevertheless, due to the remoteness and harsh environmental conditions of the Polar Regions, which imply technical and logistical constraints for data collection, their physical environment and ecosystems are still under-sampled (Fedak 2013). However, baseline data on species distribution, demography and ecology, as well as their environmental main drivers, are crucial to set up an efficient monitoring of climate change impacts on these ecosystems (Maxwell et al. 2013, Trathan et al. 2018), and a necessary prerequisite for the establishment of relevant and effective conservation measures in the Southern Ocean (Ropert-Coudert et al. 2020). The study of the distribution and demography of marine predators is thus of primary interest to fill part of these gaps (Hindell et al. 2020).

Marine top predators are long-lived species, iteroparous (i.e. breed several times during life), with a low fecundity per reproductive episode and a late sexual maturity, but they present a very high parental investment (Stearns 1976, 1992, Le Bohec et al. 2013). Therefore, from an evolutionary perspective, they correspond to the organisms that are expressing the K-selection strategy (MacArthur and Wilson 1967) of the so-called r-K gradient (Pianka 1970), and the survival of adults primes over the one of their offspring. Their life-history traits make them particularly sensitive to the rapidity of current environmental changes (Burrows et al. 2011, Mahlstein et al. 2013, Poloczanska et al. 2013). Indeed, their long generation time (e.g. 16 years for the emperor penguin (Jenouvrier et al. 2014) but see review for penguins in Forcada and Trathan (2009)) makes evolutionary adaptability unlikely (Forcada and Trathan 2009, Cristofari 2016). This mismatch between the time they would require to adapt and the velocity of the changes is seriously threatening their future (Trathan et al. 2007, Jenouvrier et al. 2019, Tulloch et al. 2019, Rogers et al. 2020) even though populations of the same species disseminated around Antarctica may not respond uniformly due to regional differences in changes to the physical environment (Constable et al. 2014, Jenouvrier et al. 2019).

I.3.2. General use of biologging

Marine predators are challenging to observe at sea (Hooker et al. 2007). As a result, electronic devices – called *biologgers* – are deployed on animals to measure a variety of parameters using sensors (Kays et al. 2015, Hays et al. 2016). This approach is referred as *Biologging*: the "*use of miniaturised animal-equipped tags for logging and/or relaying data about an animal's movements, behaviour, physiology and/or environment*" (Rutz and Hays 2009). Since its beginning in the 1940s (Scholander 1940), the collection of telemetry data has been steadily expanding (Fig. 11; McIntyre 2014, Forin-Wiart et al. 2019). This technique benefits from technological advances (e.g. miniaturisation, design optimisation, storage capacity, power consumption) that permit to collect an increasing amount of varied data at finer spatial and temporal scales (Ropert-Coudert et al. 2009b, Bograd et al. 2010, Wilmers et al. 2015).

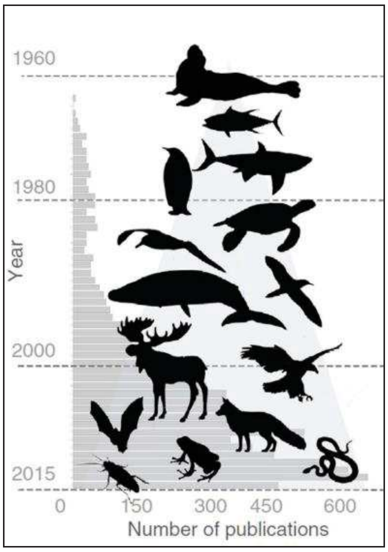


Fig. 11. Number of biologging studies.
Adapted from (Forin-Wiart et al. 2019).

Biologgers can record data related to physiological (e.g. heart rate, blood flow, stomach-pH) or behavioural (e.g. movement, speed, acceleration) parameters as well as environmental data (e.g. pressure, temperature, salinity, light, sound, imagery), (see references in Cooke et al. 2004, Ropert-Coudert et al. 2009a, Hussey et al. 2015, Börger et al. 2020). These data enable scientists to assess the relationships between marine organisms and their environment from a new perspective. For instance, in the marine environment, Time-Depth Recorders (TDRs) are used to track diving behaviour with the timeframe of a second, and to gain insight into foraging tactics of seabirds and pinnipeds (Bost et al. 2007, Pichegru et al. 2011, Vacquié-Garcia et al. 2015; see Chapter V). The combination of magnetometers and accelerometers recording data at frequencies of several tens of Hz makes it possible to reconstruct the movements of individuals underwater in 3-D (Wilson et al. 2007, Shiomi et al. 2008). More broadly, biologging provided new insights in a lot of domains: in the spatiotemporal distribution of species (Block et al. 2011, Hindell et al. 2020) and their habitat use (Widmann et al. 2015, Evans et al. 2019), in the allocation of time-budget (Watanabe et al. 2012, Jeanniard-du-Dot et al. 2017) and the construction of energy landscapes (Shepard et al. 2008, Wilson and Vandenabeele 2012), in the understanding of various physiological parameters (see review in Ponganis 2007) and the ontogeny of some behaviours, in the understanding of movement tactics and foraging strategies (Pütz et al. 1998, Heerah et al. 2014), and also in oceanography by sampling remote and inaccessible areas of the oceans (Boyd et al. 1999, Fedak 2013).

I.3.3. Biologging as a tool for conservation

In addition to providing critical fundamental information on the movements and behaviours of a variety of species over a long period of time, biologging data are a suitable tool for conservation

(Bograd et al. 2010, Heylen and Nachtsheim 2018, Hays et al. 2019). For instance, the utilisation distributions, i.e. the probability of space use (Fieberg and Kochanny 2005) derived from the tracks, permit to assess the spatiotemporal distribution of marine predators and, consequently, to highlight overlap with threats (Pichegru et al. 2009, Maxwell et al. 2013, Oppel et al. 2018). Alternatively, areas where predators concentrate are indicators of abundant presence of lower trophic level communities and thus are areas of high ecological importance, known as "hotspot of biodiversity" (Myers 1988, 1990). Identified hotspots of biodiversity of the Southern Ocean are presented in Fig. 12. Therefore, they are of major importance for conservation and require specific management attention in regards of the threats (rapid environmental changes, fishing, pollution, and many other anthropogenic disturbances) to these high priority areas.

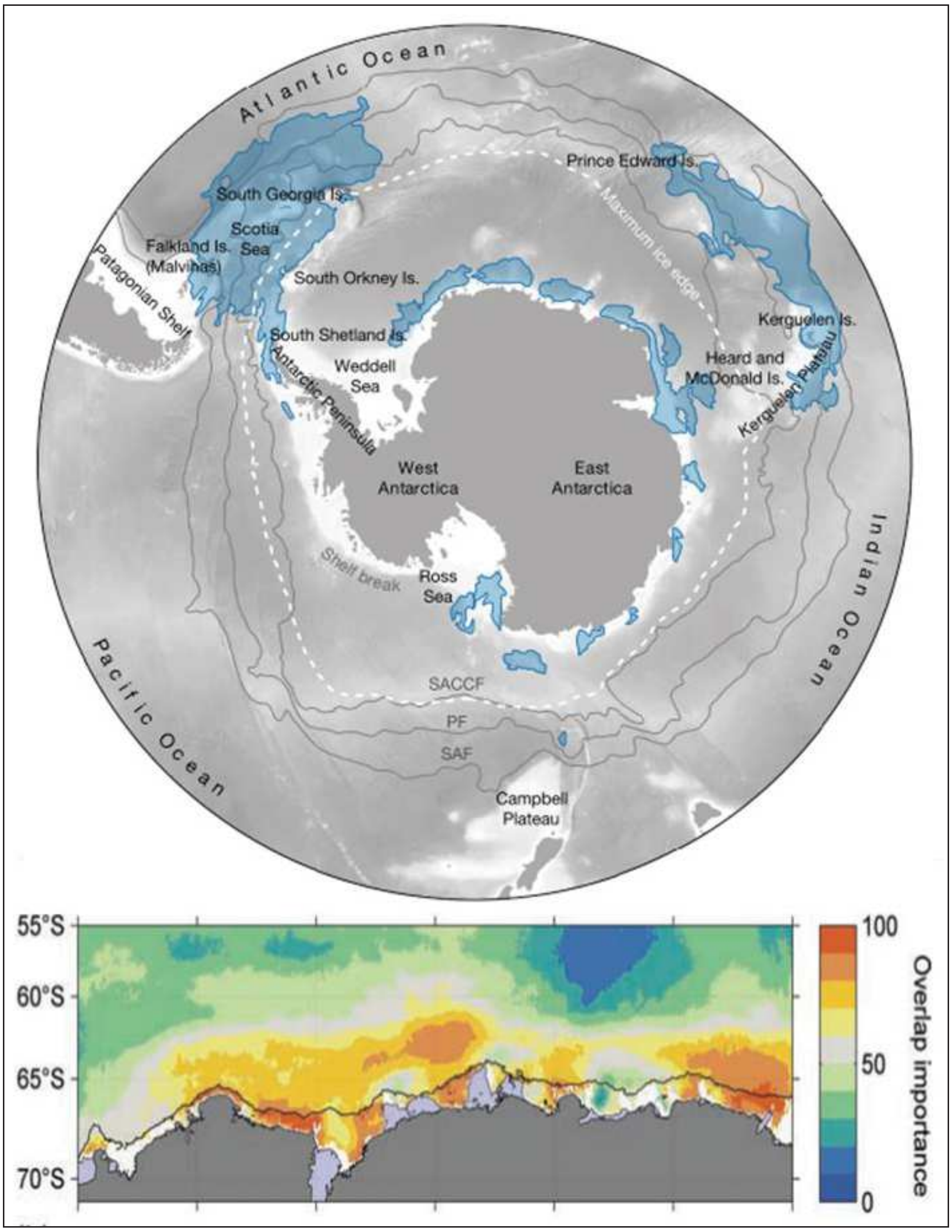


Fig. 12. Hotspots of biodiversity in the Southern Ocean. Adapted from Hindell et al. (2020) on top and Raymond et al. (2015) at the bottom.

However, many marine predators are far-ranging species, sometimes at the ocean basin scale (Weimerskirch et al. 2014, Reisinger et al. 2018), at least during some of their life stages (juvenile, immature or adult, breeder or non-breeders; see Carneiro et al. 2020). For instance, juvenile king penguins ((*Aptenodytes patagonicus*); see Orgeret et al. 2019) and juvenile or sabbatical wandering albatrosses ((*Diomedea exulans*); see Weimerskirch et al. 2014, Reisinger et al. 2018) have a much greater home range than breeding adults. As such, they are a challenge for spatial management (Hyrenbach et al. 2000, Game et al. 2009). Biologging is thus a valuable tool to identify migration routes and possibly determine where to establish corridors that link the breeding and foraging grounds of migratory species or habitats used at different stages of the life-history (Harrison et al. 2018, Dunn et al. 2019, Carneiro et al. 2020). It can also reveal important habitats for specific life-history stages and their potential overlap with threats (Dunn et al. 2019, Carneiro et al. 2020), especially for juveniles that remain outside of hotspot regions, since they often target less productive waters than adults (Riotte-Lambert and Weimerskirch 2013, Carneiro et al. 2020).

Recently, tracking data have also been used to track illegal fishing poaching in sub-Antarctic waters (Weimerskirch et al. 2020). Wandering albatrosses were equipped with specific devices made to track vessels, including the ones that switched off their compulsory transmitter and thus suspected of illegal fishing. If this is of great interest, we have to keep in mind that this could also expose “wildlife-spies”, and other seabirds in this case, to retaliation given the economic stakes. Several examples have been reported in the literature. In Africa, carcasses are being poisoned to eliminate vultures, whose overhead circling could reveal the poachers’ presence (Ogada et al. 2016) while around Crozet archipelago killer whales where being killed to prevent them from feeding on longlines (Tixier et al. 2017).

Long-term biologging observations are and continue to be used to understand the influence of climate variations and to predict the impacts of climate change on ecosystems (Costa et al. 2010a). Indeed, tracking data can be included in predictive models in which different scenarii can be anticipated due to the variation of parameters related to the animals, the environment or anthropogenic activities (Bestley et al. 2013, Stillman et al. 2015, Van der Vaart et al. 2016), giving cues for future management priorities. A last aspect not to neglect is the huge potential of tracking data in terms of outreach, public education, and communication (Hazen et al. 2012). They can be presented in a highly attractive way (e.g. animated maps, videos, Graphical Interchange Formats (GIFs), 3D visualisation or used in virtual reality; see Fig. 13) to raise awareness, to deliver a message to the governing bodies responsible for the decisions in conservation policy and management, and also to stakeholders (Heylen and Nachtsheim 2018).

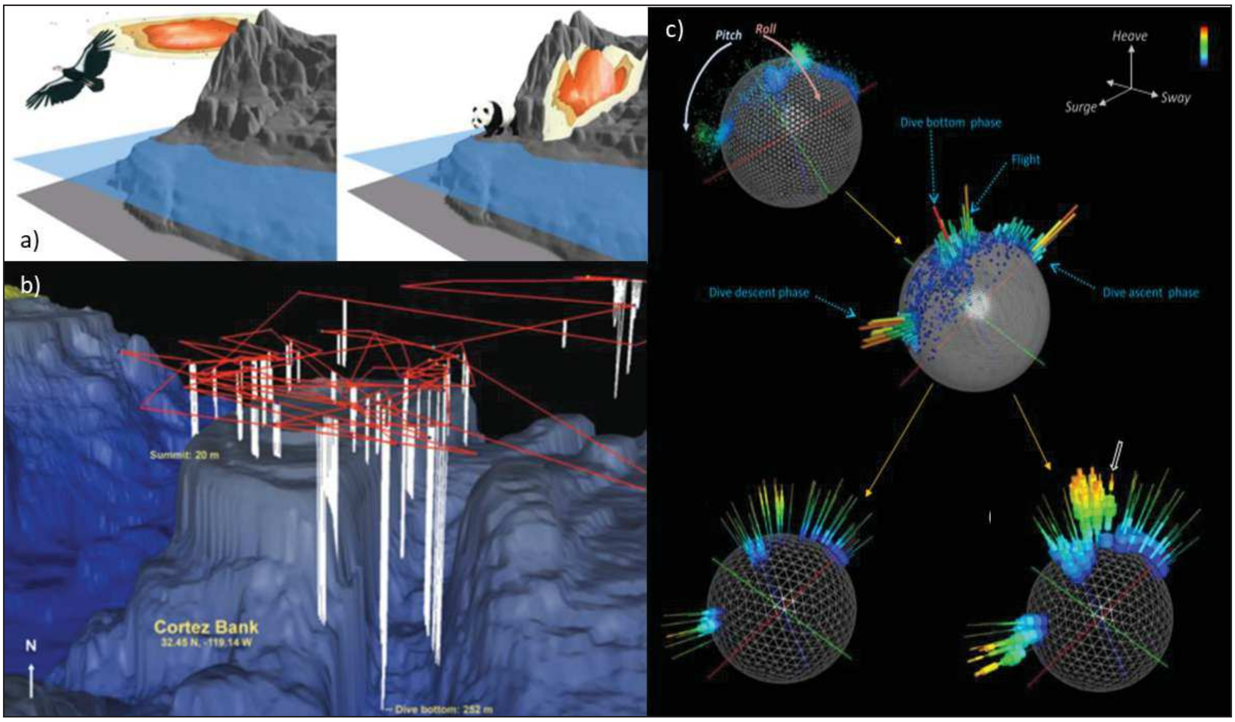


Fig. 13. Example of visualisation of various biologging data. a) Space use in 3D (Tracey et al. 2014), b) Benthic dive of a southern elephant seal on seamounts (Maxwell et al. 2012), c) Spherical plot of data from an accelerometer (Wilson et al. 2016).

I.3.4. Ethical consideration

Biologging data are of particular importance for conservation purposes. However, equipping animals with devices raises ethical questions since it involves adverse effects for the carrying individuals (Wilson and McMahon 2006, McMahon et al. 2012). This is not a trivial paradox. Capture is not always required to deploy a biologging device on a wild animal, e.g. for cetaceans (Mul et al. 2019). However, the act of deploying is in itself a disturbance (Wilson and McMahon 2006). Several studies have highlighted that biologgers cause discomfort to tagged animals and may even impede their movements or reduce their fitness (Culik and Wilson 1991, Ropert-Coudert et al. 2000, 2007, Wilson and McMahon 2006, Beaulieu et al. 2009, Vandenabeele et al. 2014). Such disruption can lead to biases in the behaviour of equipped animals, resulting in misinterpretation (Culik and Wilson 1991, Saraux et al. 2011a). To minimise the perturbation, protocols of capture, equipment and recapture, need to be optimised and continuously enhanced. Impacts of biologging studies can be reduced by applying the Three Rs principles (*Replacement, Reduction, Refinement*) defined in 1959 by Russel and Burch in the context of animal testing (Russel and Burch 1959) to biologging studies (Horning et al. 2019):

1) *Replacement* alternatives refer to methods that avoid or replace the use of animals. It is not always achievable. The use of old data with more advanced modelling techniques is a form of replacement as well as passive monitoring techniques (e.g. acoustic or video recordings) and genetic studies (e.g. biopsy on dead individuals, scat collection).

2) *Reduction* alternatives refer to the use of the lowest possible number of individuals to answer the research questions. The collection of higher resolution data, of multisensory logger, and the collaboration between projects are good practices to achieve this goal. Animal-borne devices can sample otherwise inaccessible areas and benefit to other disciplines. For instance, the Conductivity-Temperature-Depth-profiles collected by seals are also used by oceanographers (Boehlert et al. 2001, Fedak 2013).

3) *Refinement* alternatives are interpreted as the enhancement of experimental procedures to minimise negative effects on animals. Size, mass, shape, and positioning of biologgers were identified as the main parameters to work on to optimise tags (Hawkins 2004). Great advances have been made in terms of miniaturisation, design optimisation, storage capacity, and power consumption, and biologging continue to progress (Wilmers et al. 2015, Kay et al. 2019).

In the absence of other alternatives, biologging data are of such importance for the understanding of wildlife movements and behaviour, and in the establishment of conservation measures and protective policies, that the benefits outweigh the risks and justify its use (McMahon et al. 2012, Wilmers et al. 2015). However, it is still crucial to monitor and report potential impacts of biologger deployments on animals, and scientists need to remain critical towards established protocols as implied in the Three Rs framework.

I.4 Habitat concepts and foraging ecology of marine top predators

I.4.1. Habitat selection

In the simplest form, the habitat of an organism is the place where it lives (Odum 1971). Since then, a habitat has been more explicitly defined as being the sum of the resources and conditions leading to the occupancy of an area by a given organism to ensure its reproduction and survival (Block and Brennan 1993, Hall et al. 1997, Krausman 1999).

The notion of habitat is scale dependent, and several levels can be considered in time and space (Krausman 1999). Understanding the whole distribution of a species as well as the differential use of habitat is crucial to implement adequate conservation measures at the relevant location. Johnson (1980) was the first to establish a habitat selection scale, and he defined four natural ordering habitat selection processes. The first-order selection (macroscale) refers to the geographical or physical range of a species (distribution area). The second-order selection corresponds to the home range of an individual within the population range. The third-order selection identifies how the habitat components (i.e. physical and biological resources) are used within the home range to meet the life requisites such as foraging or nesting. This order corresponds to the classical definition of 'habitat use' given by Block and Brennan (1993). The fourth- and last order selection (microscale) refers to how the components of a habitat are used. For instance, if the third-order selection corresponds to a foraging area, then the fourth order would be the acquisition of food items from those available at that site (Johnson 1980, Krausman 1999).

In this context, the habitat selection by an individual is an active behavioural process that results from a compilation of innate and learned behaviours (Hutto 1985). This process allows an individual to distinguish among various components of its environment and leads to the disproportional use of environmental conditions to influence its fitness and survival (Block and Brennan 1993). According to the life-history theory, organisms tend to optimise their individual fitness, i.e. maximise their genetic contribution to future generations (Stearns 1992). However, throughout their lives, individuals are facing constraints that affect their survival and/or reproduction and to which they must adjust (McNamara and Houston 1996). Under the process of natural selection, behavioural and physiological traits have been selected and result in a set of behavioural strategies observable at different spatio-temporal scales (e.g. foraging at the seasonal or daily scale, habitat selection) for all activities of an individual (e.g. breeding, resting, foraging, migrating, dispersing). Among all the activities that an animal exhibits, foraging appears to be the most crucial since collecting sufficient food supply is a basic requirement of all other life-history traits (Stevick et al. 2002).

I.4.2. Foraging ecology

Resource acquisition is a central activity throughout the life of organisms and is the corner point for successful reproduction. Behaviours associated with food search and food intake are strongly subject to the mechanisms of natural selection and have a high selective value (Bell 1980). The optimal foraging theory predicts that, in a complex environment, animals should forage so as to maximise the "benefit/cost" ratio of feeding behaviours (i.e. energy gain; MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986; Fig. 14). However, the environmental characteristics of a habitat vary at different spatial and temporal scales that directly influence the distribution, abundance, and thus availability of resources (Hunt et al. 1999, Weimerskirch et al. 2005, Bost et al. 2009a). As such, resources are heterogeneously distributed and aggregated in "patches" of various sizes and densities (Fauchald et al. 2000, Fauchald and Tveraa 2006).

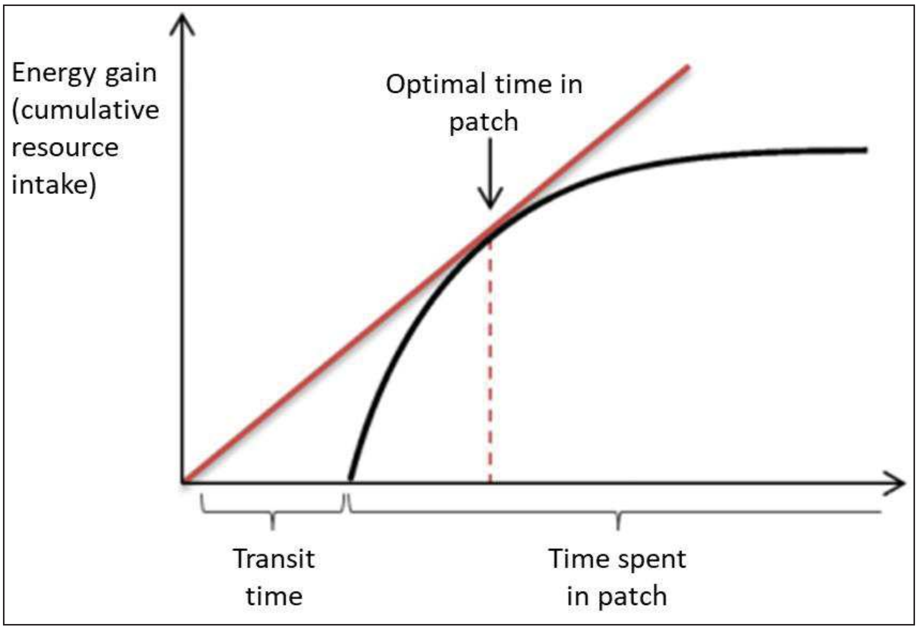


Fig. 14. Illustration of the Marginal Value Theorem from the Optimal Foraging Theory. Adapted from (Charnov 1976). The optimal time spent in a patch is given by the tangent to the cumulative food intake curve. The predator needs to spend enough time in the patch to cover the energy expenditure of moving from one patch to another but also to leave the patch before the resource is too depleted as resource intake within a patch diminishes with time.

Predators have to perpetually adapt their foraging behaviour according to the distribution and availability of prey (Charnov 1976, Fauchald et al. 2000). The predictability of prey patches at finer scales is lower than at coarser scales (Weimerskirch et al. 2005). At large scales, prey may be aggregated in predictable areas (e.g. seamount region, front), while at smaller scale they might congregate in refuges or in one dense and compact swarm difficult to locate (Fauchald and Tveraa 2006, Bost et al. 2009a). Yet, to maximise the resource acquisition, the optimal foraging theory suggests that predators will maximise the time spent in the vicinity of a successful prey patch by decreasing their displacement speed and increasing their turning frequency (Kareiva and Odell 1987, Fauchald and Tveraa 2003). As such, they minimise the travelling and associated energetic expenditure between patches (MacArthur and Pianka 1966). In other words, predators tend to maximise the time spent in a profitable area, and they concentrate their search activity in an area with a high density of prey. This behaviour is known as 'Area Restricted Search' (ARS) behaviour (Kareiva and Odell 1987; Fig. 15).

This behaviour has been observed in many taxa in the horizontal dimension, including seabirds (Scheffer et al. 2010, Sommerfeld et al. 2013, Widmann et al. 2015, Jouma'a et al. 2017). However, depending on the species and environmental conditions, the detection of foraging areas with this method is not always reliable (Robinson et al. 2007, Weimerskirch et al. 2007, Bastille-Rousseau et al. 2010). Noteworthy, results are particularly misleading for species diving in ice-covered areas (Bailleul et al. 2008) like, for instance, Weddell seals and emperor penguins. For such species, haul-out behaviour as well as resting or slow and meandering movements at the surface could lead to the inaccurate detection of ARS. However, for diving animals, resources are distributed heterogeneously in 3 dimensions, i.e. both in the horizontal and vertical dimensions. As such, marine predators adopt ARS behaviour not only along their track, but also at depth during their dive (Fig. 15; Zimmer et al. 2007, Bailleul et al. 2010). When diving, marine predators usually spend some time at particular depth and increase their vertical sinuosity by performing undulations called wiggles, making an identifiable ARS vertical behaviour (Fig. 15; Heerah et al. 2014). Thus, by studying simultaneously spatial locations of animals' as well as the depth ranges they move in, it is possible to determine favourable habitats for foraging marine predators.

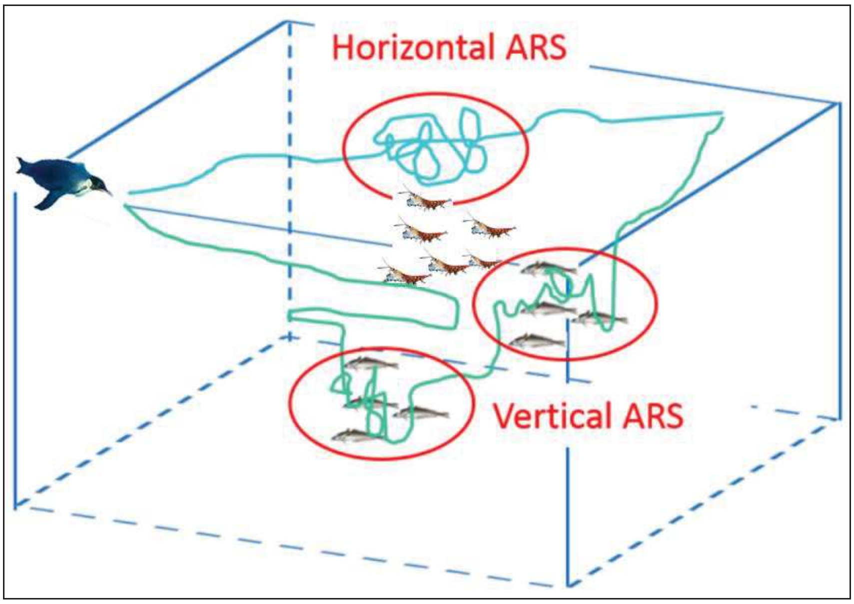


Fig. 15. Illustration of Area Restricted Search (ARS) behaviour in the horizontal and vertical dimensions. Adapted from Heerah (2014).

Studying foraging activities is fundamental in ecology since foraging controls the energy intakes and as such the fitness of individuals. Understanding the foraging strategies (where, how, and when) of marine top predators is a necessity to identify profitable areas, to set up an efficient monitoring of the effects of environmental changes (i.e. natural and anthropogenic) on individuals and population dynamics, and to implement conservation measures when relevant.

I.5 Structure and aim of the thesis

My PhD project is part of a global framework, which is the setting up of the second Life Observatory of emperor penguins worldwide. This Life Observatory that I co-initiated and co-supervised, will help to predict how this species copes with environmental changes. With my work, I specifically aim to contribute to a better understanding of the distribution and ecology at sea of the Emperor penguin with conservation purposes in mind.

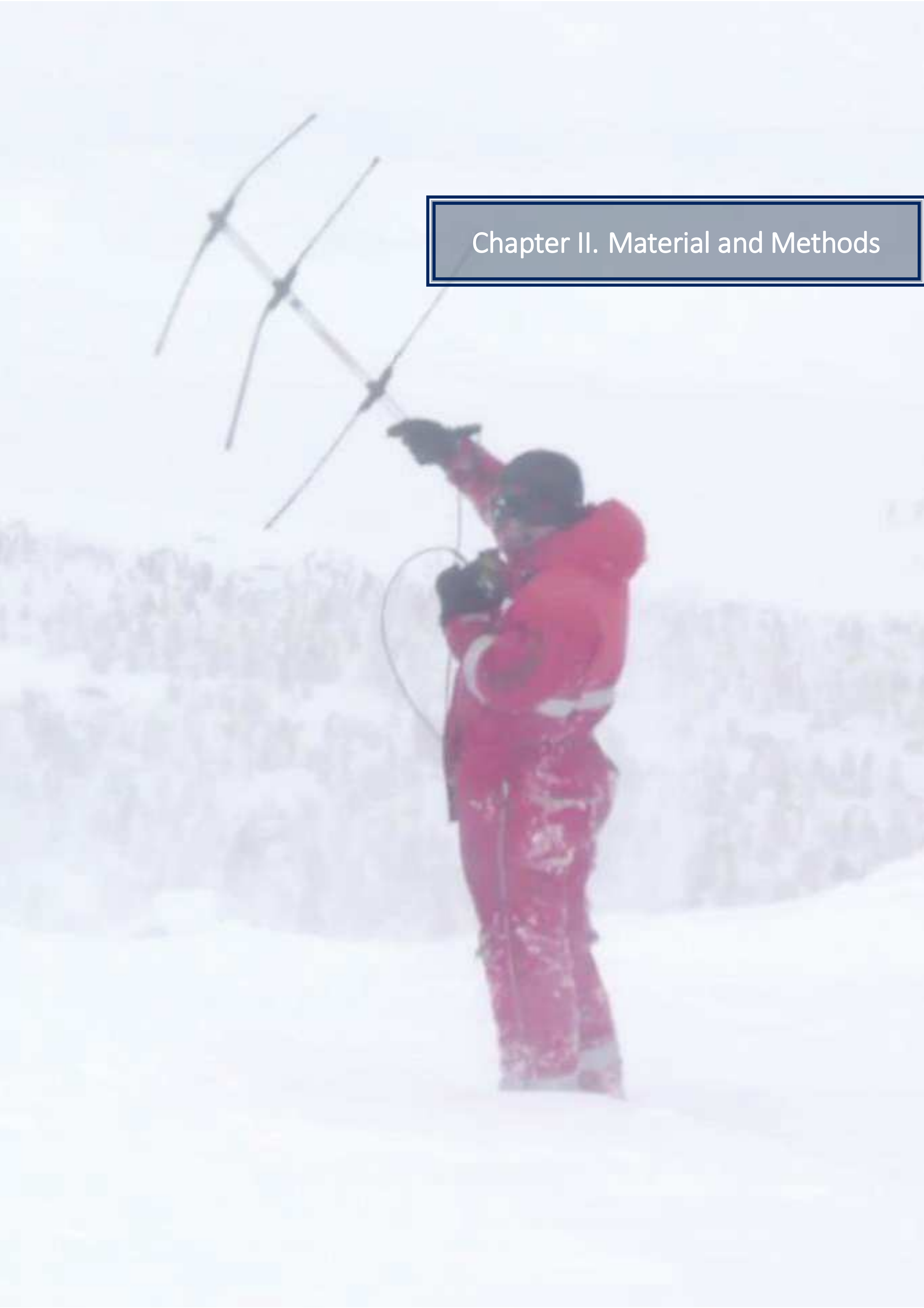
Chapter III aims to provide the description and assessment of the different techniques of capture, handling, and equipment we used on-site on emperor penguins. Indeed, there was no dedicated paper on this topic in the current literature. To fill this gap, we produced a publication with an exhaustive documentation to provide a standardised framework for future deployments on adults and juveniles of this species. Some of the techniques and conclusions are applicable to other penguin species.

Little is known about the early life at-sea of emperor penguins, even though this is a critical phase in their life and a crucial one for the viability of the global population. As such, in Chapter IV, we assessed the distribution of juvenile emperor penguins in the Weddell Sea region and the Atlantic sector of the Southern Ocean, home to a more than a third of the species' global population, but where the species distribution at sea had never been studied. Through a meta-analysis including our and previous and rare tracking data on juvenile emperor penguins available in the literature, we further investigated if they make use of the existing or proposed MPAs around Antarctica.

In Chapter V, we assessed the distribution in the Atlantic sector of the Southern Ocean of adult emperor penguins in various breeding phases and status. Together with the juveniles' information (Chapter IV), it exposes for the first time a global picture of the species at-sea distribution in this area. We additionally explored the environmental factors (e.g. sea ice, bathymetry) influencing their movements and habitat use and preference. Finally, we also investigated and compared the fine-scale vertical foraging behaviour of adults from two localities, birds from Atka Bay colony foraging in the Weddell Sea and Atlantic sector of the Southern Ocean, and Pointe Géologie colony and their use of the d'Urville Sea.

In addition, over the course of my PhD project, I was also involved in other research works on Antarctic (i.e. emperor and Adélie) penguin ecology. These studies, in which I appear as a co-author, can be found as Annexes of this thesis in the form of articles, either already published or in preparation. Annex A(published) and Annex B (published) relate to the use of remote-controlled and energetically self-sufficient observatories to investigate the spatio-temporal dynamics of penguin movements on land and colony structuring. Annex C (in preparation) is a study that I co-initiated and co-supervised, and that explores the foraging behaviour of Adélie penguins in the d'Urville Sea. Annex D (ready to submit) focuses on the contaminant accumulation on Adélie penguins.

Chapter II. Material and Methods



II.1 The species

II.1.1. General biology

The Emperor penguin (*Aptenodytes forsteri*) belongs to the order of the Sphenisciformes (family: Spheniscidae) and, together with the king penguin, to the genus Aptenodytes (etymology from ancient Greek: “A” for “without”, “pteno” for “wing” or “feather”, and “dytes” for “diver”). They are the tallest (ca. 80 cm - 120 cm when the neck is fully stretched) and heaviest (up to 45 kg) living penguins (Stonehouse 1953), and their lifespan remains still unknown but estimated to be around 35-40 years (Jenouvrier et al. 2014).

The population is currently estimated to count around ca. 270 000 breeding pairs (Fretwell et al. 2012, Trathan et al. 2020, Fretwell and Trathan 2020). The 61 known colonies have a circum-continental distribution along the shoreline of mainland Antarctica, at latitudes comprised between 64°S and 78°S (Fig. 16) and are in average 300 km apart (Ancel et al. 2017). A single colony counts few hundreds to 25 000 breeding pairs (Fretwell et al. 2012). Several new colonies have been discovered only recently (Wienecke 2011, Fretwell et al. 2012, Ancel et al. 2014, Fretwell and Trathan 2020), and some might still remain undiscovered until now (Ancel et al. 2017).

Intensive debates are currently taking place regarding the existence of a single panmictic population (Cristofari et al. 2016) or the existence of several (estimated to be at least four) metapopulations (Younger et al. 2017). Additionally, the Emperor penguin has long been considered as a highly philopatric species (Prévost 1961, Ancel et al. 2013a) and the location of the colonies stationary. Recent works (Fretwell et al. 2014, LaRue et al. 2015, Fretwell and Trathan 2019) suggest that this pattern might not be exclusive and that colony location appears more dynamics than previously thought (LaRue et al. 2015).

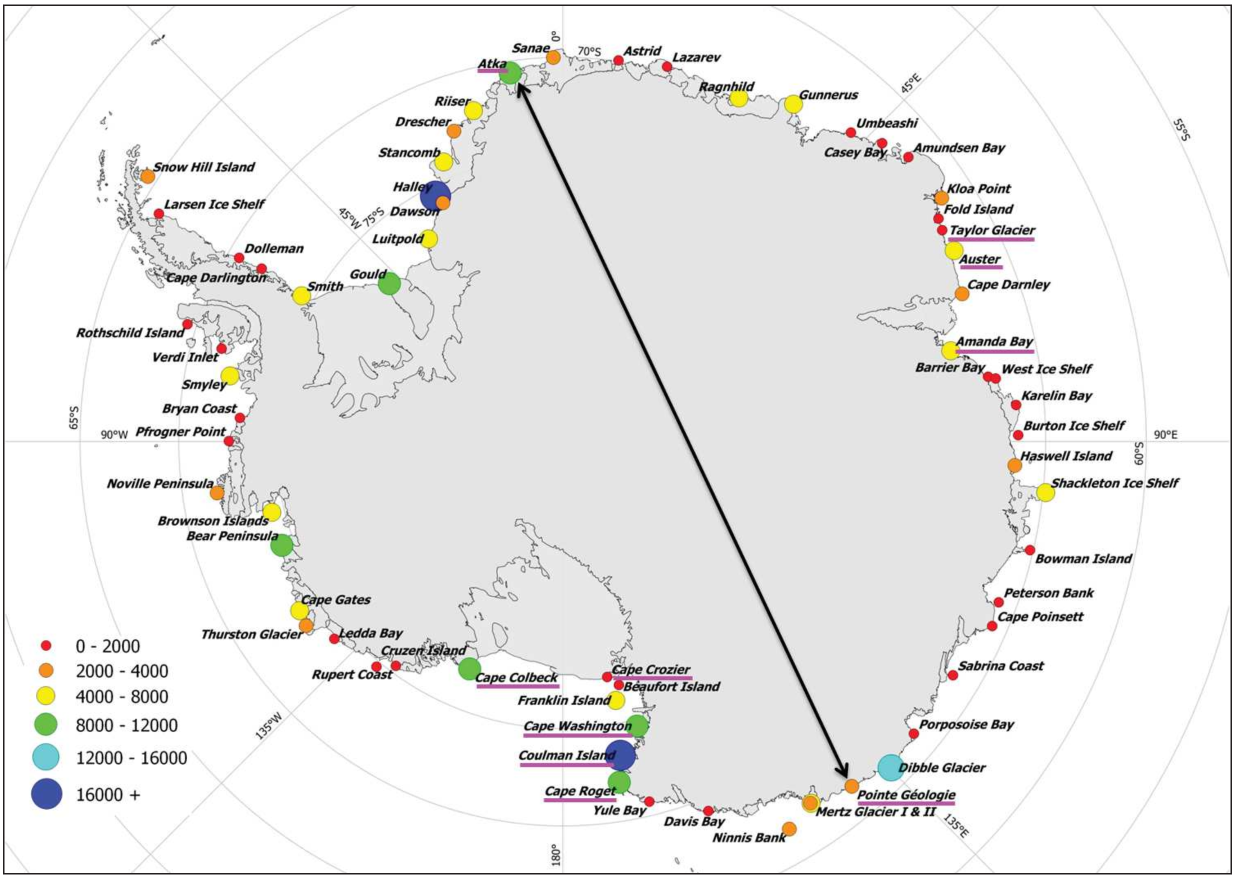


Fig. 16. Distribution and population size of emperor penguin colonies. Study sites are indicated by the black arrow. Adapted from Trathan et al. (2020) and counts from (Fretwell and Trathan 2020). Recent movement between Halley Bay and Dawson-Lambton colonies are not accounted for (Fretwell and Trathan 2019). Colonies where tracking occurred are underlined in violet.

II.1.2. Life-history and breeding traits

The Emperor penguin shares common life-history traits with other seabirds. They are long-lived species with a long generation time, a late sexual maturity; they breed in colony and produce few offsprings but invest (time and energy) in the quality of their one and only annual chick (Stonehouse 1953, Prévost 1961). Also similarly to other seabirds, the breeding cycle of the Emperor penguin can be divided into three main phases: breeding, moulting, and interbreeding period (Hamer et al. 2001). However, variations in phenotypic and life-history traits and strategies are expected and can be observed: for instance, the phenology can greatly differ due to the latitude of the colony (e.g. 2-4 weeks of delay in the arrival, laying, fledging dates between Atka Bay and Pointe Géologie; Houstin, Le Bohec, Zitterbart, unpublished observations). However, a classical annual breeding cycle can be described as follows (Fig. 17).

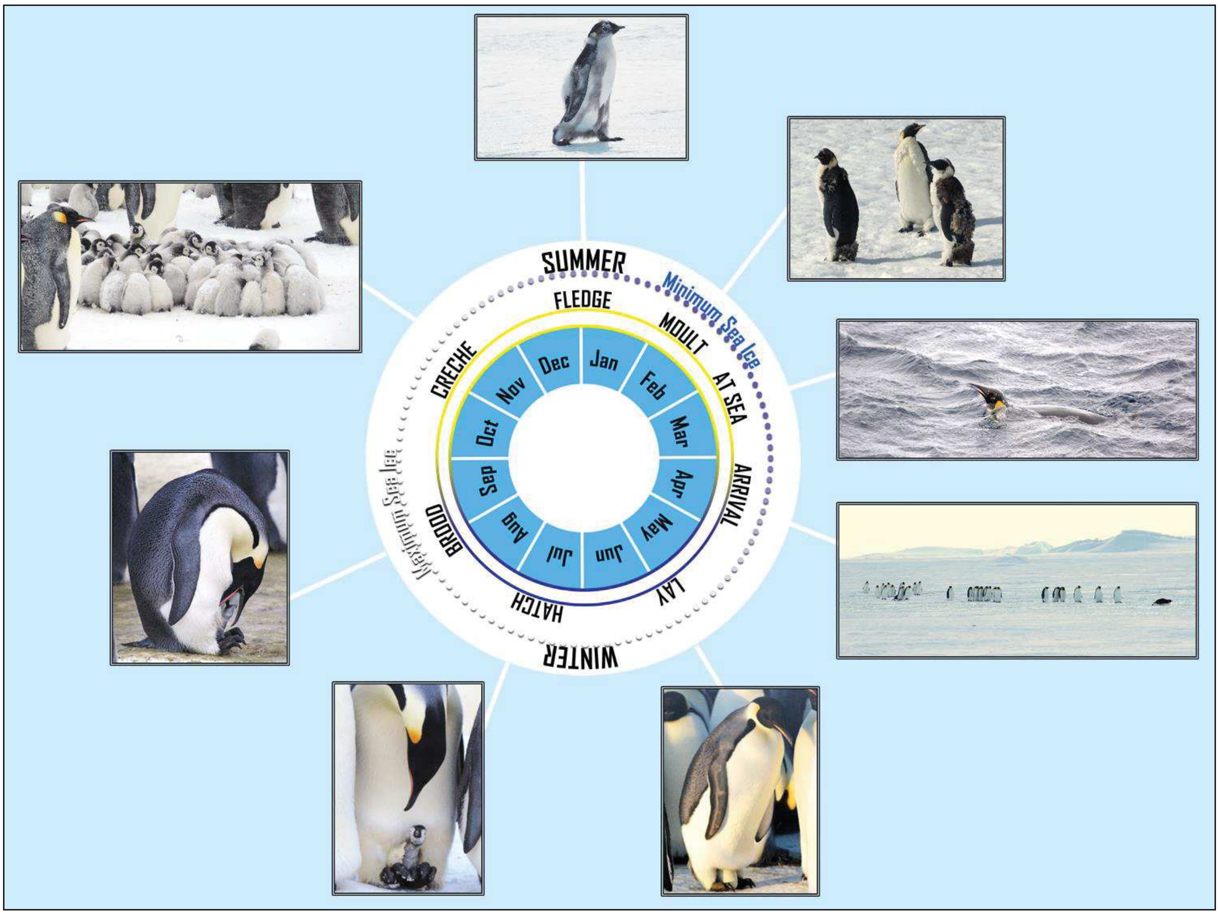


Fig. 17. Different phases of the annual breeding cycle of the Emperor penguin in relation to sea ice dynamic (dashed line). Note that phenology can vary by several weeks depending on the latitude of the colonies. Adapted from Trathan et al. (2020).

In late March beginning of April, males and females gather at their colony site, mostly located on stable fast-ice, but occasionally on lands or shelves (Fretwell et al. 2014). The colony site should provide a stable ground up to the end of the breeding season in December-January. After a period of courtship which can last up to 6 weeks (Prévost 1961, Isenmann 1971, Ancel et al. 2013b), pairs are forming and copulating, and a unique egg is laid at the beginning of the austral winter. Females then leave the colony to forage at sea, while males incubate the egg during 64 days in average (Stonehouse 1953, Prévost 1961), enduring a fast of ca. 4 months (Le Maho 1977). Chicks hatch in the middle of the winter (July-August). In the following 6-7 weeks, chicks are not thermally independent, hence one parent always accompanies their offspring, while the other is foraging in the pack-ice (Labrousse et al. 2019a). By November, chicks become thermally independent and are left on their own on the colony site, while both parents alternate independently between foraging at sea and return to feed their chick. These commuting trips occur until chicks fledge in December or January (Stonehouse 1953, Prévost 1961, Ancel et al. 2013a). In December or January, depending on the latitude of the colony, chicks moult and fledge. By the end of the austral summer, the adult emperor penguins also perform their annual moult. The moulting process lasts on average 30 days (Groscolas 1978) during which birds need to remain out of water on ice floes or coastal fast ice (Kooyman et al. 2004). After few weeks spent foraging at sea to replenish their body reserves (Kooyman et al. 2004), adults will mostly come back breeding, the proportion of adults skipping a breeding season being unknown (Goetz et al. 2018). Juveniles will not return to their colony of origin and spend their first years of life at sea. Female emperor penguins will start breeding at 3-6 years of age, while males between 4-8 years (Jenouvrier et al. 2005, 2014).

II.1.3. Foraging behaviour

II.1.3.1. Distribution at sea

Like all the seabirds and pinnipeds of the Southern ocean, the Emperor penguin is a central-place forager (Orians and Pearson 1979), i.e. these predators have to commute between their breeding colony to feed their offspring and their feeding areas. The species is even the only central-place predator breeding in the middle of the austral winter (Ainley et al. 2005). So far, all the emperor penguins tracked since the 80s were from colonies located in the Ross Sea (several colonies between 155°W and 170°E) and around Dumont d'Urville (66°40'S, 140°01'E) and Mawson (67°36'S, 62°52'E) research stations in East Antarctica, covering approximately a third of the continental perimeter (Fig. 16). The distribution at sea of the Emperor penguin around the rest of Antarctica remains unknown. However, all the tracking studies (Table 9) revealed similar distribution patterns between sites to date.

During the chick-rearing period, constrained by the highly-demanding chick provisioning, breeding adults are staying in the vicinity of the colony (within a ca. 150 km radius in average) foraging in cracks, flaw leads, ephemeral and persistent polynyas, i.e. areas of open water, or persistently loose sea ice (Ancel et al. 1992, Kirkwood and Robertson 1997, Wienecke and Robertson 1997, Rodary et al. 2000a, Zimmer et al. 2007b, Massom et al. 2009, Labrousse et al. 2019a). In the only study carried out on non-breeding adults, Goetz and colleagues (2018) revealed that, on the contrary, an unknown proportion of the non-breeding birds spend this time-period a thousand kilometres away from any colony in the pack ice. When breeding is over and the chick is left alone to fledge, adults range a bit further (~350 km) during their pre and/or post-moult period extending from December to March (Kooyman et al. 2004, Wienecke et al. 2004, Zimmer et al. 2007b).

During their first year at sea, juveniles appear to venture north of the 60th parallel, i.e. out of the classical Southern Ocean delineation, at the beginning of their journey, before spending the winter in the pack ice (Kooyman et al. 1996, Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al.

2013, Labrousse et al. 2019b). Nothing is known about their moulting area (Fretwell and Trathan 2009) and their following years at sea before their return for breeding.

Whether similar patterns exist for juvenile and adult emperor penguins in the Atlantic sector is nonetheless still an open question, while a better understanding of this species within the Weddell Sea is a priority (Teschke et al. 2016a, Labrousse et al. 2019b, Trathan et al. 2020).

II.1.3.2. Diving

The knowledge of the horizontal distribution at sea of the Emperor penguin is not sufficient to determine its feeding grounds. Their energetic supply requires both horizontal and vertical transit phases to access resources. The concomitant use of biologgers to record marine predator locations and their behaviour while foraging at sea, can give us insights about the spatio-temporal distributions of the food web (Wilson 1993, Ropert-Coudert et al. 2001, Pichegru et al. 2007, Elliott et al. 2008).

Emperor penguins are the deepest diving species of seabirds: they can dive as deep as 564 m (Wienecke et al. 2007) for as long as 32 minutes (Goetz et al. 2018). However, the vast majority of the dives occurs below 150 m and lasts less than 10 minutes with less than 2-min recovery between consecutive dives (Kirkwood and Robertson 1997, Wienecke et al. 2007, Zimmer et al. 2008, Goetz et al. 2018).

As other penguin species (Williams 1995, Halsey et al. 2007), most of the emperor penguin dives consist of three distinct phases: i) a constant descent phase, followed by ii) a bottom phase, with a horizontal trend that can still be slightly ascending, and iii) a steeper ascent phase. After a dive, there is a period of recovery, called post-dive duration, preceding the next dive (Fig. 18). According to the current literature, the majority of the feeding events occurs during the bottom phase (Chappell et al. 1993, Kirkwood and Robertson 1997, Zimmer et al. 2007b). These feeding events are indicated by undulations known as wiggles and common in all penguin species (Rodary et al. 2000b, Simeone and Wilson 2003, Ropert-Coudert et al. 2006, Halsey et al. 2007, Zimmer et al. 2007b).

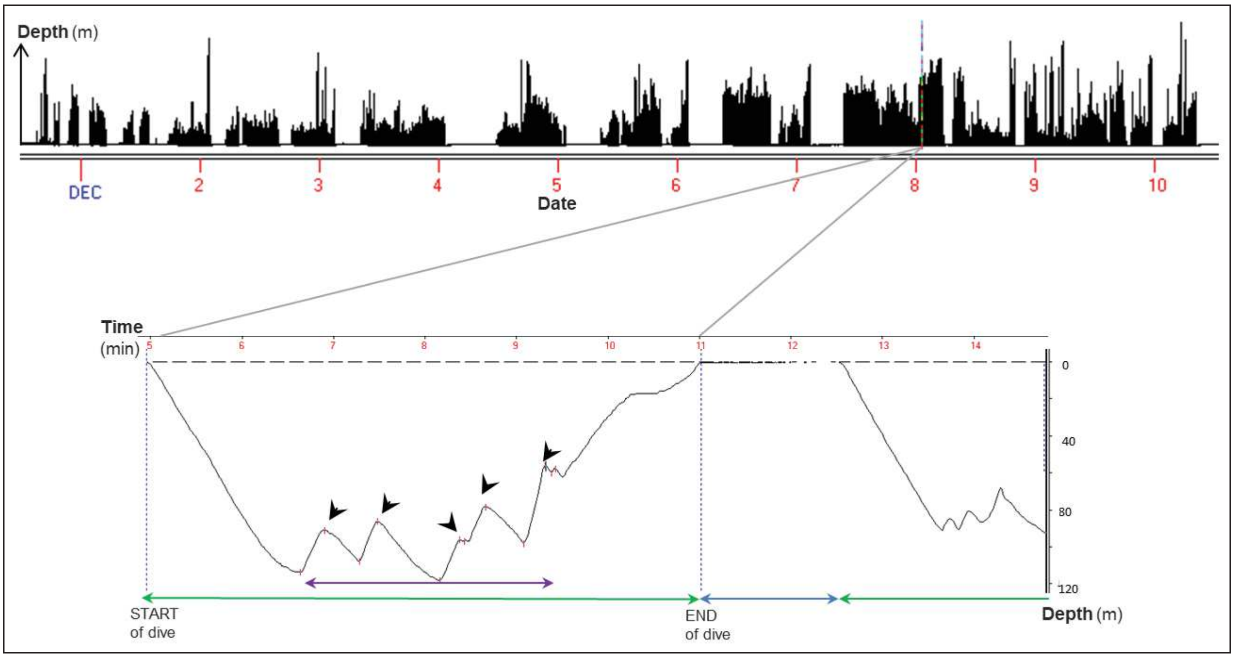


Fig. 18. Depth profile (on top) of an emperor penguin and zoom on a dive (bottom). The duration of the dive is indicated by the green arrow, the bottom phase by the purple arrow and the post-dive duration by the blue arrow. Wiggles are indicated only at their maximum by black triangles.

However, two main types of foraging behaviour of emperor penguins emerge in the literature. If most of the birds and dives are pelagic, i.e. occurring in the water column, emperor penguins have also been reported to perform benthic dives over the shelf area (Rodary et al. 2000a, Goetz et al. 2018). Benthos prey items have been found to be part of the diet of emperor penguins from Auster (Robertson et al. 1994, Kirkwood and Robertson 1997), revealing that adult emperor penguins are also able to feed on benthic prey where and when the sea-floor is accessible (sea ice presence can prevent access to areas). Sub-ice foraging has been documented on tape (Ponganis et al. 2000), however, the importance of this behaviour has not been quantified yet.

In definitive, such information indicates that emperor penguins hunt opportunistically for available prey throughout the water column (Kooyman and Kooyman 1995, Zimmer et al. 2007b, Wienecke et al. 2007).

II.1.3.3. Diet

The diet of the Emperor penguin has been investigated by different techniques: stomach flushing (Offredo and Ridoux 1986, Robertson 1991, Ainley et al. 1992, Piatkowski and Pütz 1994, Kirkwood and Robertson 1997, Zimmer et al. 2007a), scat analysis (Green 1986, Kooyman et al. 2004), stable isotopes (Zimmer et al. 2007b, Cherel 2008), and once by camera (Ponganis et al. 2000).

Their diet is composed of fish, mostly nototheniids and particularly Antarctic silverfish ((*Pleuragramma antarcticum*), see detailed description in Mintenbeck and Torres (2017) and Vacchi et al. (2017)), crustaceans (mainly Antarctic krill (*Euphausia superba*), see detailed description in Siegel (2016)), and squids (particularly the arrow squid (*Psychroteuthis glacialis*) and the Antarctic neosquid (*Alluroteuthis antarcticus*), see detailed description in Rodhouse et al. (2014); Fig. 19).

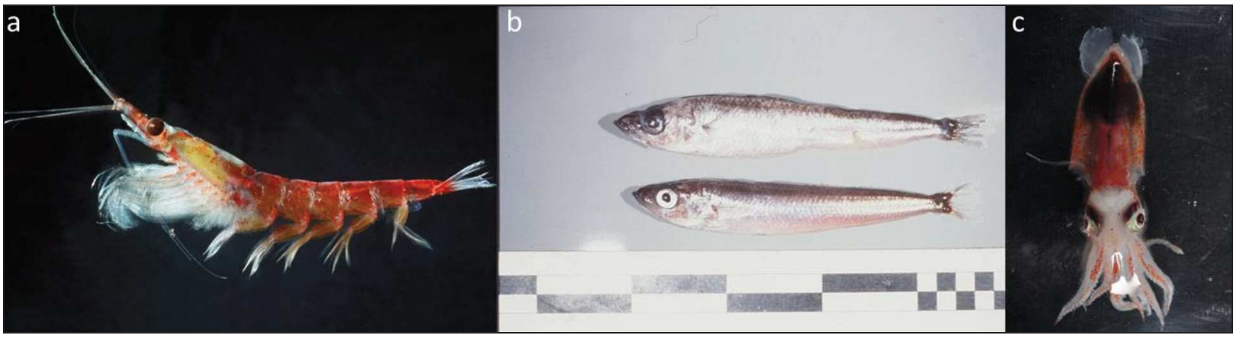


Fig. 19. Main prey of emperor penguins. a) Krill (*Euphausia superba*). b) Antarctic silverfish (*Pleuragramma antarcticum*). c) squid (unknow sp.). © Stephen Brookes, Antarctic Australian Division, Dale Maschette, respectively.

The diet composition and prey item proportions vary enormously among studies with time of year and location (Table 2; Ratcliffe and Trathan 2012).

For instance, emperor penguins from Pointe Géologie colony in Adélie Land (our second study site, see page 71) have been mostly described as ichthyophagous by two studies that occurred 20 years apart (Offredo and Ridoux 1986, Cherel 2008). In addition to Antarctic silverfish, they also consume squids (Zimmer et al. 2007a), and adults fed for themselves on the same prey as those given to their chicks (Cherel 2008), at least during the chick-rearing period. On the contrary, in the Weddell Sea, at Drescher inlet colony (~650 km south-west of Atka Bay, our first study site, see page 70), ice-associated Antarctic krill was the main prey item during the breeding season (Klages 1989) but was supplanted by the consumption of squids and fish in the post-moult diet (Piatkowski and Pütz 1994, Pütz 1995).

Noteworthy, for a same site in East Antarctica (at both Auster and Taylor colonies), diet composition greatly varied between years, switching from fish and squid in 1988 (Robertson et al. 1994) to krill in 1993 (Kirkwood and Robertson 1997). The presence of demersal and bentho-pelagic fish in the diet has also been reported at these colonies (Robertson et al. 1994, Kirkwood and Robertson 1997).

Table 2. Information on Emperor penguin diet obtained from stomach content collected at different locations and years/seasons. Adapted from Kooyman (2002).

Colony	Area	Diet (% mass)	Period	Year	Location	Reference
Drescher Inlet	Weddell Sea	52 K, 38 F, 10 S	Oct-Nov	1986	72.9°S, 19.4°W	Klages 1989
Drescher Inlet	Weddell Sea	25 K, 75 F, 0 S	Feb	1990 & 1992	72.9°S, 19.4°W	Pütz 1995
Taylor	East Antarctica	0 K, 31 F, 69 S	Nov	1988	67.5°S, 60.9°E	Robertson et al. 1994
Auster	East Antarctica	0 K, 55 F, 45 S	July-Nov	1988	67.4°S, 64.1°E	Robertson et al. 1994
Auster	East Antarctica	68 K, 26 F, 5 S	Aug	1993	67.4°S, 64.1°E	Kirkwood and Robertson 1997
Auster	East Antarctica	10 K, 20 F, 65 S	Nov	1993	67.4°S, 64.1°E	Kirkwood and Robertson 1997
Cape Washington	Ross Sea	8 K, 92 F, 0 S	Nov	1992	74.7°S, 165.4°E	Cherel and Kooyman 1998
Coulman Island	Ross Sea	0.5 K, 96 F, 3 S	Nov	1993	73.3°S, 169.6°E	Cherel and Kooyman 1998
Pointe Géologie	d'Urville Sea	2 K, 95 F, 3 S	Oct-Nov	1982	66.67°S, 140.01°E	Offredo et al. 1986
Pointe Géologie	d'Urville Sea	by far dominated by fish*	Oct-Nov	2002	66.67°S, 140.01°E	Cherel et al. 2008

K = krill, F = Fish, S = squid. * stable isotope analysis, no mass available.

II.1.4. Threats and conservation status

The Emperor penguin is a sea ice obligate species, i.e. birds are found year-round in association with sea ice (Ainley et al. 2010b, 2016, Trathan et al. 2011). They depend on sea ice as breeding ground (fast ice) for the vast majority of the colonies (Fretwell et al. 2012), for feeding (Trathan et al. 2011, Labrousse et al. 2019a), for moulting (Kooyman et al. 2004) as well as for resting and as a shelter from predators (leopard seals and killer whales (*Orcinus orca*) when foraging at sea (Ainley et al. 2016)). Specific environmental conditions at each emperor penguin colony (e.g. distance to oceanic fronts, persistence of sea ice in time and space, seaward extent of Antarctic continental shelf, presence of specific oceanic currents like gyres) may be affected differently by the ongoing and future impacts of climate change. However, most climate models agree that future global climate change will lead to reduction in sea ice area of ca. 30 to 40% over the 21st century, depending on the emission scenario under consideration (Bracegirdle et al. 2015, Palerme et al. 2017). Late formation and early retreat are also expected to occur, while emperor penguins need a stable sea ice during nine months for the completion of their breeding cycle. The most recent projections under different climate change scenarios have concluded that the species faces the risk to be nearly extinct (80% of colonies lost and a population decline of 81%) within the next 100 years (Jenouvrier et al. 2019) in the absence of an ambitious policy to limit greenhouse gas emissions. These projections considered only the demographic parameters of adult emperor penguins due to the lack of long-term demographic data on juvenile and immature populations. It is likely that the integration of such data would make forecasts of survival even more pessimistic (Trathan et al. 2020).

In addition to sea ice degradation (in extent and persistence) through changes to currents and winds, rising temperatures and ocean acidification, climate change is expected to lead to multispecies effects, including changes to prey abundance and availability, range shifts and competition with other Antarctic predators (IPCC 2019, Rogers et al. 2020).

Currently, the fisheries are not considered as being a direct threat for emperor penguins since the Antarctic krill fisheries operate relatively far from emperor breeding sites (Trathan et al. 2020). However, the sea ice retreat will soon give access to new fishing areas and may change the spatio-temporal repartition of krill stocks (Rintoul et al. 2018, Rogers et al. 2020). If these new ice-free areas were to be exploited, the competition with fisheries for accessing the resources together with the risk of potential by-catch events would be additional threats for the species. Nevertheless, it is important to keep in mind that we still know very little about the distribution of juveniles (4 studies) and non-breeding birds (1 study) which, unlike breeding birds, venture thousands of kilometres ashore (Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b). A better understanding of these life-history stage is notwithstanding critical since their ignorance when assessing overlap with threats is likely to bias estimates of the risks, as shown by Carneiro and colleagues (2020) on 22 species of albatrosses and petrels.

Direct anthropogenic threats at breeding sites might also occur and must continue to be regulated and rules enforced by the Antarctic Treaty System to ensure that colonies are not affected by future developments such as tourism (Fig. 20), new aircraft runways, and new or enhanced research facilities.

Fig. 20. Tourism pressures at Atka Bay colony. a) A tourist plane flying over the colony. b) Tourists around the colony.

Currently, due to the uncertainty (in time and intensity) of the threats linked to climate change and the relative paucity of data available on the distribution and activity at sea of the species, the Emperor penguin is listed as Near Threatened (NT) on the International Union for Conservation of Nature (IUCN) Red List of threatened species (Birdlife International 2018). The IUCN Red List classifies species under different categories (Fig. 21) that indicate an estimated risk of extinction. Classified as 'NT', means that the species is considered close to being at high risk of extinction in the near future. Noteworthy, several researchers, specialists of the Emperor penguin, consider that the species require an IUCN designation of, at least, Vulnerable (VU) to properly reflect the species' status (Trathan et al. 2020). Such a classification would provide an opportunity to increase the protection level of the species through the ATS and ensure that regional management actions decided by the CCAMLR would take into consideration any activity that might affect emperor penguins (Trathan et al. 2020). For instance, any breeding colonies would be protected according to the same set of rules (e.g. approach distances, number of people, vehicles allowed close by and distances), not only the few existing rules that are currently specifically designated as Antarctic Specially Protected Area (ASPA) through the ATS.

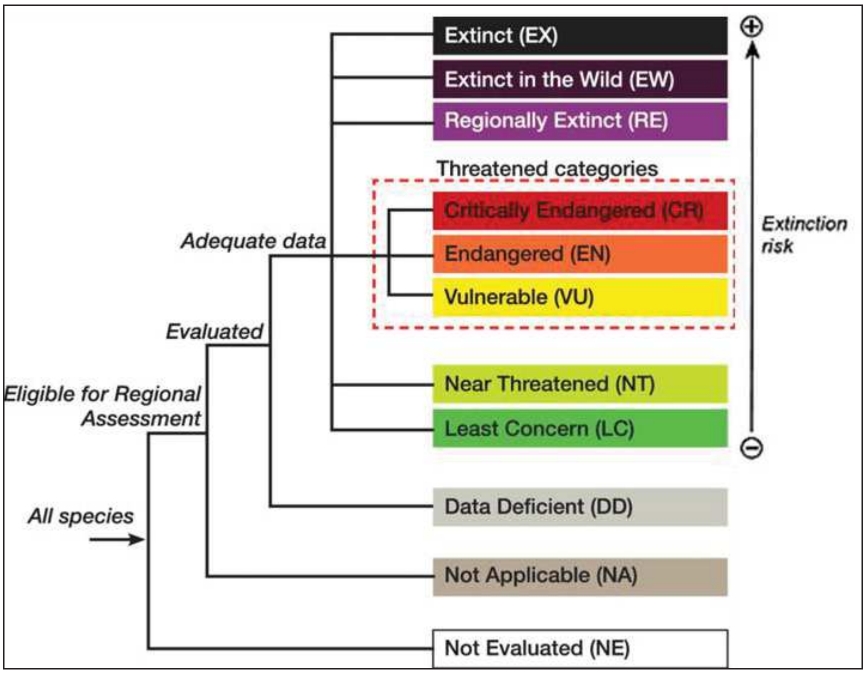


Fig. 21. IUCN categories. Adapted from www.iucnredlist.org.

II.2 Data collection

II.2.1. The study sites

II.2.1.1. Atka Bay colony and Neumayer-Station III

Fieldwork performed during this PhD was conducted, from November 2017 to January 2018 and November 2018 to January 2019, at the Atka Bay emperor penguin colony (70°37'S, 08°09'W), ca. 8 km northeast of the German Antarctic research station of Neumayer III, on the Ekström shelf ice in the Dronning Maud Land (Fig. 16 and Fig. 22).

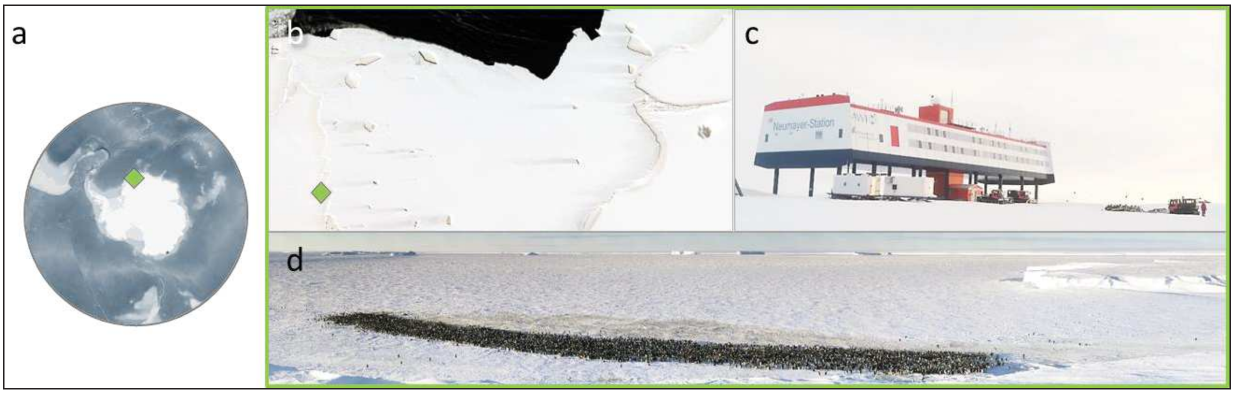


Fig. 22. Atka Bay study site. a) Location of Atka Bay in Antarctica. b) Satellite image of Atka Bay with the classical location (in green) of the emperor penguin colony. c) Research station of Neumayer III. d) Panorama of Atka Bay emperor penguin colony.

Atka Bay (AB) emperor penguin colony is located deep inside the west side of the Atka Bay along the ice-shelf. The ice is very stable during the year and the bay is only ice free in January-February (König-Langlo et al. 1998) providing a safe ground for the emperor penguins colony over their breeding season. The colony (or subgroups) can and do climb on the ice-shelf through natural snow ridges during the year (Zitterbart et al. 2014). The on-land behaviour of the colony is being investigated since the summer season 2012/2013 (Richter et al. 2018a), and in 2017, we set-up the 2nd Life Observatory of the species. The colony is estimated to host currently 13 to 14 000 breeding pairs (Le Bohec & Zitterbart pers. com.). AB is situated in the Atlantic sector of the Southern Ocean, at the Eastern boundary of the Weddell Sea. In this region, the shelf is relatively narrow (~20 km), and the continental slope consists of a complex pattern of troughs, flat ridges, steep slopes, seamounts, outcrops, and narrow ridges (Fig. 23; Jerosch et al. 2016) that stretch over a hundred kilometre wide. AB is situated in waters where the main oceanographic feature is the cyclonic (clockwise rotating) Weddell Sea Gyre that drives the currents from west to east (Vernet et al. 2019).

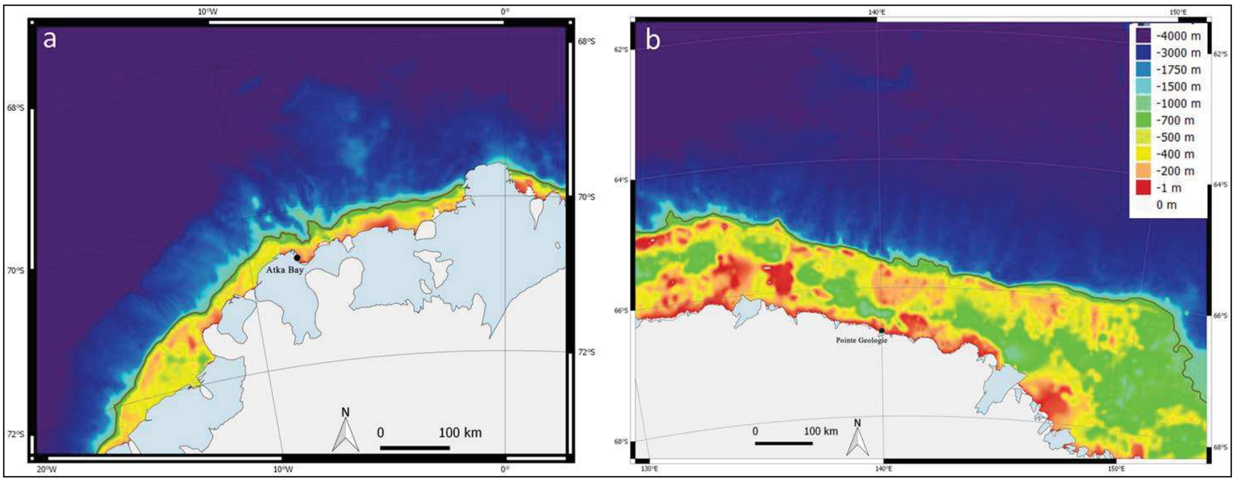


Fig. 23. Study sites bathymetry. a) Bathymetry around the Atka Bay and Ekström shelf ice. b) Bathymetry around the Pointe Géologie archipelago.

II.2.1.2. Pointe Géologie colony and Dumont d'Urville Station

In addition, existing data were used in this PhD from past equipment of emperor penguins (1998, 2001, 2005) at the Pointe Géologie colony (66.67°S, 40.01°E), ca. 1 km of the French research station of Dumont d'Urville, on Pétrels' Island in Pointe Géologie archipelago in Adélie Land (Fig. 16 and Fig. 24)[12].

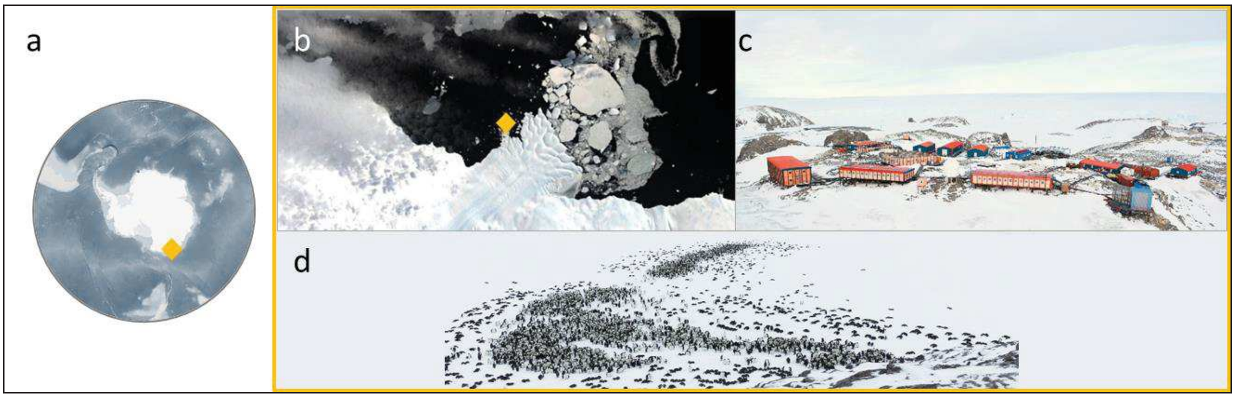


Fig. 24. Pointe Géologie study site. a) Location of Pointe Géologie archipelago in Antarctica. b) Satellite image of Pointe Géologie archipelago with the classical location (in yellow) of the emperor penguin colony. c) Research station of Dumont d'Urville. d) Panorama of Pointe Géologie emperor penguin colony.

The Pointe Géologie (PG) archipelago is made of several islands located aside the Antarctic continent and the Astrolabe glacier. The sea ice is very stable and may remain several years, providing a perfect ground for the emperor penguin colony. Given the proximity of the research station, PG has been monitored continuously since 1956 (Prévost 1961, Barbraud and Weimerskirch 2001). The breeding

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[12] Since my overwinter in Dumont d'Urville, from November 2013 to March 2015, I'm involved in numerous studies on the emperor but also Adélie penguins breeding at PG. Resulting publications and preliminary results from these studies are presented in Annexes of the thesis (see page 236).

behaviour of the species is mostly known through observations made on this colony (Jouventin 1971, Ancel et al. 2009, Jenouvrier et al. 2009a, 2012, 2017), which is the 1st Life Observatory of the species. The colony counts currently around 4000 breeding pairs (Barbraud et al. 2020). PG is located at the eastern edge of East Antarctica in the Indian sector of the Southern Ocean. The Antarctic continental shelf is about 100 km wide and marked by two plateau 100-300 m deep (Adélie and Mertz banks) separated by two big depressions (Adélie Depression and d'Urville Trough) and canyons up to 1000 m depth (Fig. 23; Beaman et al. 2011). The bathymetric features play a crucial role on the hydrological circulation over the Antarctic shelf in the region (Williams et al. 2010).

II.2.2. Biological data collection

II.2.2.1. Fieldwork at Atka Bay

During two 4-months field sessions that occurred in the austral summers 2017-2018 and 2018-2019[13] at the Atka Bay emperor penguin colony (Fig. 16), we captured/recaptured 70 adults and 8 juveniles in order to carry out the deployment and recovery of biologgers. We deployed tracking devices (ARGOS platforms, GPS devices), TDR, and accelerometers.

(i) Choosing the tracking devices

Two different types of tracking devices with specific capacities can be used to track marine wildlife with accuracy and during the polar day[14]:

- The Advanced Research and Global Observation Satellite (ARGOS) technology:

ARGOS is a system for locating and collecting georeferenced data by satellite. A specific beacon (referred as ARGOS platform or Platform Transmitters Terminals, PTT) sends messages to compatible satellites (ARGOS class). The location of the ARGOS platform can be estimated by comparing the time difference between the transmission of the signals by the ARGOS platform and their reception by the satellite (Doppler Effect). Each location is accompanied by an estimate of precision (error classes or ellipses), depending in particular on the number of messages that have reached the satellite before it

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[13] I also carried out a first field work session during the austral summer 2016-2017 in Adélie Land to initiate a similar monitoring program at sea on Adélie penguins (*Pygoscelis adeliae*). The preliminary results of this project are presented in Annex C of the thesis.

[14] The two latest requirements are not met by Global Locating System (GLS; Phillips et al. (2004).

passes. This precision varies from a hundred metres to several tens of kilometres (Lopez et al. 2014, CLS 2016). With this system, the data are transmitted to the user who does not need to retrieve the beacon.

- The Global Positioning System (GPS):

Contrary to ARGOS, GPS devices do not emit any signal, but satellites are sending messages received by a beacon. By triangulating signals received from different satellites, the GPS device can calculate its position with a very high spatial accuracy, most of the time less than 100 m (Costa et al. 2010b). With this system, the data are not transmitted, the GPS device needs to be recovered to get access to the data.

In other words, ARGOS platforms are less accurate but do not need to be recovered, while GPS devices are more accurate but need to be recovered to access the data.

Our choice has been mainly determined by 1) our research questions and the degree of precision required to address them (e.g. Where and how far do chick-rearing adult emperor penguins from the Atlantic sector of the SO travel to forage? What are the foraging grounds of the adults during the winter?), 2) the constraints linked to the biology of the Emperor penguin (e.g. annual moult in January), but also 3) some logistical constraints to perform our study, as we were having access to the penguin colony only from November to January. During late chick-rearing period, just before their annual moult, adult emperor penguins alternate trips at sea and return at the colony for feeding their chick. These recurring returns of the adult to feed its chick, approximately once per week, make this period ideal for captures, deployments, and recaptures for data logger retrieval. As such, we chose to use GPS devices with a high frequency sampling for this period (November-December). On the contrary, after their annual moult, the majority of the juveniles will not come back at the colony for at least two years (Mougin and Van Beveren 1979), and studies suggest that most of the adults moult in the pack ice (Kooyman et al. 2000, 2004, Wienecke et al. 2004, 2010). There is also no certainty that adults moulting at a colony are actual breeders from that particular colony, and that they will return for the next season. Therefore, successfully retrieving the devices is unlikely and the use of transmitting devices (ARGOS platform) is by far the most prevalent technique after the moult to ensure data recovery over the winter.

(ii) Time-Depth Recorders (TDR)

TDR are archival data loggers that measure and store pressure and temperature as a function of time. Obtaining at high frequency (usually 1 Hz) the depth reached per unit of time of a diving predator allows to efficiently reconstruct the animal's diving behaviour during its foraging trips at sea (e.g.

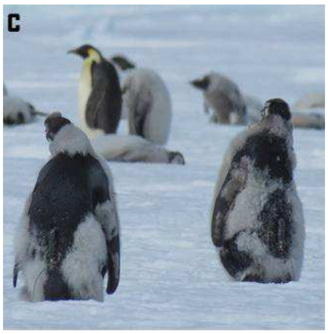
Charrassin et al. 2002, Dragon et al. 2012). The use of these devices does not provide indications on geographical movements, but only information in the water column. However, by combining the positions of individuals recorded by the tracking devices with the diving depth simultaneously recorded by the TDR, we are able to interpret *a posteriori* birds' behaviour during the deployment period and determine the spatio-temporal prospecting and foraging strategies. These devices provide valuable information on the feeding behaviour, exploration effort and hunting success of the diving predators (e.g. Wienecke and Robertson 2002, Scheffer et al. 2010, Zimmer et al. 2010a, Evans et al. 2013, Viviant et al. 2014, Heerah et al. 2015, Carter et al. 2016).

(iii) Deployments

In total, we performed 3 types of deployments (Table 3), by equipping:

- breeding adults for short-term period (few weeks) to monitor their foraging activities during the late-chick-rearing period with GPS devices and an extra TDR,
- adult birds at the end of their annual moult to monitor their distribution and diving behaviour over a full year (long-term period) with ARGOS platform and an extra TDR,
- 5-months old fledged chicks to track them during their first year at sea (long-term period) with ARGOS platform only, because of their multi-year dispersal behaviour (Mougin and Van Beveren 1979) that would prevent device retrieval the next field season.

Table 3. Summary of deployments performed at Atka Bay.

Deployment duration	Short-term	Long-term	Long-term
Life-history stage	ADULT	ADULT	JUVENILE
Number of individuals	36 *(16 in 2017/18,* *20 in 2018/19)*	8	8
Logger type	GPS-VHF-acc*+ TDR	ARGOS + TDR + acc*	ARGOS
Period of equipment	Late chick-rearing	Post-moult	Post-moult chick at fledging
Monitored period	1 to 3 weeks between Nov-Dec	Year	Year
Illustration of the instrumentation performed			

Adults were also equipped with accelerometers (acc), as an extra device for long-term deployment, or included in the Axy-Trek logger for short-term deployment. Note that the analysis of these data will not be presented in this thesis. **a.** An adult emperor penguin equipped with TDR in the middle of the back and a GPS underneath. **b.** An adult emperor penguin equipped with an accelerometer in the middle of the back, an ARGOS platform underneath, and a leg-banded TDR on its right ankle. **c.** Two juvenile emperor penguins both equipped with an ARGOS platform.

Over the two summer seasons, we deployed 36 GPS Axy-Trek from TechnoSmArt (Table 4) on late-chick-rearing adults (short-term deployments). To remotely monitor the presence/absence of the birds in the colony and to facilitate the device recovery, GPS devices were combined with VHF beacon that could last 6 months. To ensure a one month functioning of the GPS battery, one location was collected every 15 minutes. In 2017-2018, locations were collected every three minutes. However, the water switch unit did no function correctly and the GPS kept trying to get a signal under water. Consequently, the battery power diminished faster than expected and the tracking duration lasted only around a week. To prevent such issue, in 2018-2019, we changed the sampling frequency and collected one location every 15 minutes. As a result, the batteries lasted around a month.

Right after their moult, 8 juveniles and 8 adults were equipped with SPOT-367 ARGOS platforms from Wildlife Computers (Table 4, long-term deployments). The platforms were programmed to transmit their locations every day at 4, 6, 10, 16, 19 and 21:00 GMT, to be synchronized with the best ARGOS satellite coverage. With such a programming, the batteries were expected to last around 15 months.

We also used two different TDR devices according to their memory size and thus the amount of data they could store. 'Cefas g5+' were used for short-term deployments and 'Lotek Lat 1800' for long-term deployments (Table 4). They were both programmed to record depth and temperature at 1 Hz frequency with a 30 cm resolution and 1% accuracy.

Table 4. General information on the loggers deployed including the logger type, name, dimensions, and weight, as well as the manufacturer names and location.

Logger type	ARGOS	Accelerometer	TDR	GPS - Acc	VHF	TDR
Logger name	Spot 367	WACU	Lat 1800	Axy-Trek	RI-2B 6 months	g5+
Manufacturer	Wildlife Computers, Redmond WA, USA	MIBE, CNRS DEPE IPHC, Strasbourg, France	Lotek Wireless Inc, St. John's, Canada	TechnoSmArt Europe S.r.l, Roma, Italy	Holohil Systems Ltd, Ontario, Canada	CEFAS Technology Ltd, Lowestoft, UK
Dimensions (mm)	107 x 18 x 21	21 x 13 x 4 raw 70 x 16 x 16 mounted	36 x 13 x 10	105 x 38 x 18 *		35.5 x 12
Weight in air (g)	45	10	9	60 *		6.5
Device picture						

*Loggers combined together by TechnoSm*Art*.

Birds' capture and handling procedures, logger deployment techniques, birds' release and ethical matters in biologging studies are reported in details in Chapter III of this thesis.

II.2.2.2. Data previously collected at Pointe Géologie

We used tracking data from 33 individuals equipped with ARGOS platforms at the Pointe Géologie colony in Adélie Land (see page 71) between 1998 and 2005 (see Table 5 for details). Tracking data from 2005 were previously published in Zimmer and colleagues (2007b).

Table 5. Summary of deployments performed at Pointe Géologie.

Year	Period of equipment	Monitored period	Number of birds	Logger type, Manufacturer	Device dimensions (mm) and weight in air(g)
2005	Late chick-rearing	Nov-Jan	18	Splash & SPOT-5, Wildlife computers	78*50*23 ; 105 71*34*26 ; 78
2005	Incubation	May-Sep	3	ST-10, Sirtrack*	130*50*30 ; 230
2001	Incubation	May-Jul	3	ST-10, Sirtrack*	130*50*30 ; 230
1998	Brooding	Jul-Oct	9	ST-10, Sirtrack*	130*50*30 ; 230

*Sirtrack, Havelock North, New Zealand; NB: it is now Lotek NZ.

In 1998 and 2001, locations were collected every 100 minutes except between 9h - 13h local time. In 2005, the loggers were duty cycled to be 6h on and 6h off. Amongst the birds monitored in November 2005, 4 birds were equipped with Splash ARGOS platforms, which also recorded the diving depth every 2 seconds with a 0.5 m resolution. The dive data were already published in Zimmer and colleagues (2008, 2010).

II.2.3. Conservation management policy and environmental variables

The distribution at sea of our tracked emperor penguins was investigated in relation to the geographical coverage of planned and existing conservation efforts in the Southern Ocean (see Fig. 36). We also aimed to evaluate the influence of environmental variables on the distribution at sea and the foraging activities of our equipped birds.

II.2.3.1. Main conservation and management bodies

The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) is the main policy-maker of the Southern Ocean (CCAMLR 1980). The boundaries of the CCAMLR jurisdiction are therefore the main limits defining the potential implementation of conservation efforts in this circumpolar area. In addition to the CCAMLR limits, we also considered the existing and proposed Marine Protected Areas (MPAs) around the Antarctic continent and around sub-Antarctic islands (Brooks et al. 2020a). Moreover, given the role of primary importance played by the International

Union for Conservation of Nature (IUCN) in raising awareness and as a political and financial lobby for conservation purposes, we included the range of the Emperor penguin species defined by the IUCN as a boundary delineating potential implementation of conservation efforts for the species.

All the boundaries were obtained online as shapefiles, except for the proposed Domain 1 MPA since no shapefile was available (Table 6).

Table 6. List of features related to conservation management in the Southern Ocean.

Feature	Data provider source	Official documents
CCAMLR boundaries	https://gis.ccamlr.org	CCAMLR, 2019
Existing Antarctic MPAs	https://gis.ccamlr.org	CCAMLR, 2019
Proposed Weddell Sea MPA	www.mpatlas.org	CCAMLR 37/29, 2018
Proposed East Antarctic MPA	www.mpatlas.org	CCAMLR 38/21, 2019
Proposed Domain 1 MPA	drawn from www.mpatlas.org	CCAMLR 37/31, 2018
South Georgia and South Sandwich Islands MPA	www.protectedplanet.net	www.gov.gs
Sub-Antarctic MPAs	www.protectedplanet.net	Governmental websites
IUCN range	www.iucnredlist.org	Birdlife 2018

II.2.3.2. Environmental variables

To characterise the marine environment used by the emperor penguins, we extracted and used remote-sensing datasets collected by satellites and available online.

(i) Sea ice

The Emperor penguin is a sea ice obligate species (Ainley et al. 2005). Sea ice information is therefore a major feature to consider. Sea ice concentration values (ranging from 0 to 100%) were obtained from Advanced Microwave Scanning Radiometer (AMSR-2) satellite estimates of daily sea ice concentration at 3.125 km resolution from the University of Bremen (https://seaice.uni-bremen.de/data/amsr2/ ; Spreen et al. 2008). This sea ice concentration (SIC) product has been widely used in recent studies (SCAR 2014, Shi and Su 2018, Labrousse et al. 2019b, Herr et al. 2019).

ASMR-2 estimates were not available before 2006. Consequently, for Pointe Géologie data analysis, we used daily sea ice concentration at 12.5 km resolution from the Institut Français de la Recherche pour l'Exploitation de la Mer (IFREMER, ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/ ; Ezraty et al. 2007), also used in previous studies (Widmann et al. 2015, Ropert-Coudert et al. 2018).

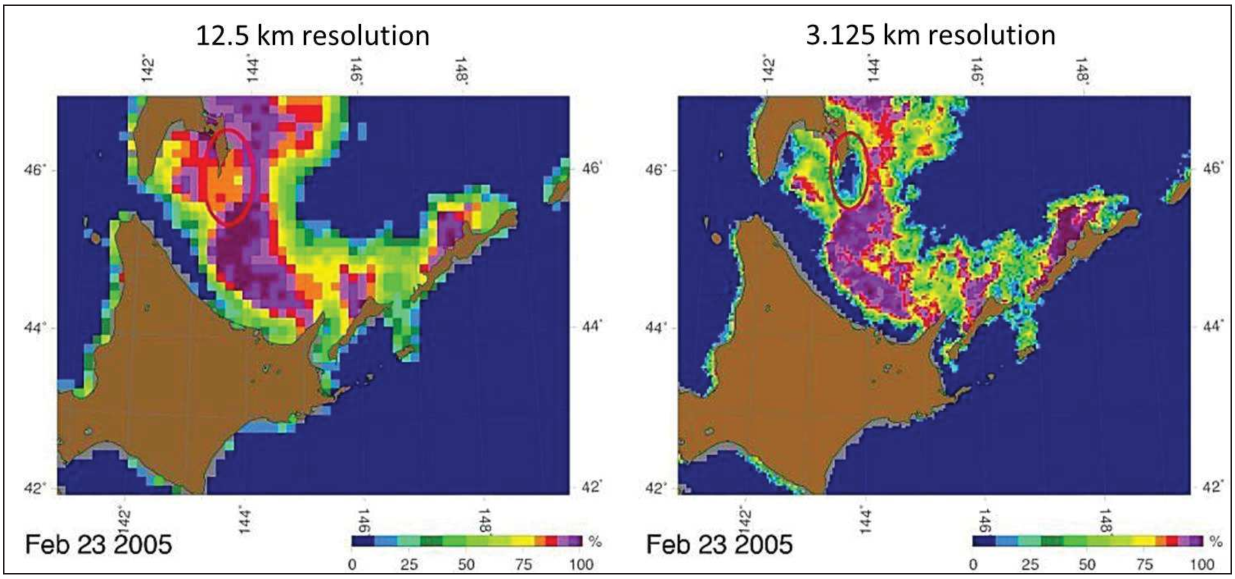


Fig. 25. Comparison of sea ice concentration depending on the resolution used. The colour code gives the ice concentration between 0 and 100%. Missing data is marked grey, and land is shown in brown. The red ellipse marks a region of open water visible at high resolution (3.125 km) but not visible at the 12.5km resolution. Adapted from Spreen et al. (2008).

The maximum and minimum median sea ice extent 1981-2010 used for visualisation purposes on Fig. 36 and Fig. 39 were obtained from the National Snow and the Ice Data Center NSDIC (Fetterer et al. 2016). The sea ice edge defined by the 15% sea ice concentration isocline (Cavalieri 1991, Stammerjohn and Smith 1997) was extracted daily. Contours corresponding to outlying floes or polynyas were removed from the datasets to prevent bias in the sea ice edge distance computation with QGIS '*r.contour.step*' tool.

To account for spatial variability of sea ice, at each location, we additionally computed the sea ice concentration over an area bounded by a radius corresponding to the kernel smoothing factor. We also computed the percentage of sea ice > 90% over the bounded area to take into account the absence of cracks and daily polynyas that emperor penguins use to dive and forage.

(ii) Oceanographic features

The Southern Ocean fronts and the Southern Boundary of the Antarctic Circumpolar Current (Orsi et al. 1995) were downloaded from https://gis.ccamlr.org.

The bathymetry covariate at one-minute horizontal spatial resolution was obtained from the ETOPO1 Global Relief Model provided by the NOAA National Geophysical Data Center (Amante and Eakins 2009). The bathymetry indicates whether the birds are located in neritic or oceanic waters, and if they perform benthic dives (Rodary et al. 2000a).

The bathymetric grid was used to compute a gradient of bathymetry (or slope) grid with the '*terrain*' function from the R package '*raster*' (Hijmans and van Etten 2020). The slope value of each cell in degree was computed from the bathymetric value of eight neighbouring cells.

(iii) Habitat features

We divided the Southern Ocean in 3 habitat types to take into account the effect of bathymetry and water movements: 1) The continental shelf break was considered as the area along the continent below the 1000 m isobaths (Knox 2007, Nicholls et al. 2009). We then used the classification of Douglass and colleagues (2014) to segregate 2) the Antarctic continental slope area (roughly areas around the continent with ranging between 1000 and 4000 m) from 3) the deep ocean (abyssal plain) characterised by a low bathymetry slope and depth > 4000 m.

II.3 Data analysis

Analyses were performed using the software R v. 3.5.0 (R Core Team 2018) and QGIS v. 2.18.18 (QGIS Development Team 2017) with the data package '*Quantarctica3*' (Matsuoka et al. 2018).

II.3.1. Spatial analysis

Spatial datasets always contain some aberrant points. Moreover, due to the difference in sampling frequencies and of accuracy between GPS and ARGOS locations, our datasets needed to be standardised to make comparisons feasible and meaningful. Once the location datasets are cleaned and standardised, the distribution at sea and the habitat used by the birds can therefore be estimated.

In this thesis, data were divided into 5 study groups according to the study site and the period of deployment (Table 7). Each group was processed with the same routine, but with some particularities (e.g. presence of several foraging trips for some birds, different sampling frequencies between devices).

Table 7. Summary of the study groups according to the study site and the period of deployment.

Study group	Life-history stage	Colony	Tracking period	Tracking device	Number of individuals	Multiple foraging trips
juvABy	Juvenile	Atka Bay	year	ARGOS	8	n
adABf	Adult	Atka Bay	fall	ARGOS	8	y
adABs	Adult	Atka Bay	summer	GPS	22	y
adPGs	Adult	Pointe Géologie	summer	ARGOS	18	y
adPGw	Adult	Pointe Géologie	winter	ARGOS	15	n

II.3.1.1. Location cleaning and filtering

Erroneous locations were filtered out using a speed filter from the R package '*argos filter*' (Freitas et al. 2008) with the maximum travel speed fixed at 15 km.h^{-1} following previous studies on emperor penguins (Wienecke and Robertson 1997, Labrousse et al. 2019b). As such, all locations requiring unrealistic swimming speed were removed.

Tracking datasets for each individual were divided into foraging trips when relevant (Table 7). Locations within 5 km from the deployment site were considered as the bird having returned to the colony and subsequent locations distant to more than 5 km from the colony were considered as a separate foraging trip. The risk of pseudo-replication, by the use of trips from the same individuals as independent samples, was investigated by comparing within- and between-individual variances as described in Lascelles and colleagues (2016). Since the variance between individuals from each study group was not greater than within individuals, each single trip per individual was considered as independent.

II.3.1.2. Interpolation of locations at a regular time step

To correct the different sampling frequencies within and between study groups (from several minutes to several hours), we chose to interpolate locations at every hour (Lascelles et al. 2016, Heerah et al. 2019). To do so, we used a state-space modelling approach (Johnson et al. 2008) in order to estimate hourly locations with respect to the uncertainty of transmitted locations. Concretely, a *'Kalman filter'*, which accounted for location errors, was applied using the R package '*crawl*' (Johnson 2014), and the Continuous-time Correlated Random Walk (CRW) models were used to predict locations at a regular hourly time step interval (Johnson et al. 2008, Heerah et al. 2019; see Fig. 29 to visualise an example of interpolations).

II.3.1.3. Estimation of distribution at sea

Following the procedures developed by Lascelles et al. (2016), we computed the kernel utilisation distributions, i.e. a measure of probability of occurrence (Worton 1989), for each group. In this method, each location is assigned a probability density function. The spatial sum of these probability density functions gives the Utilisation Distribution (UD; Fig. 26), which is the relative frequency of use for a given spatial unit.

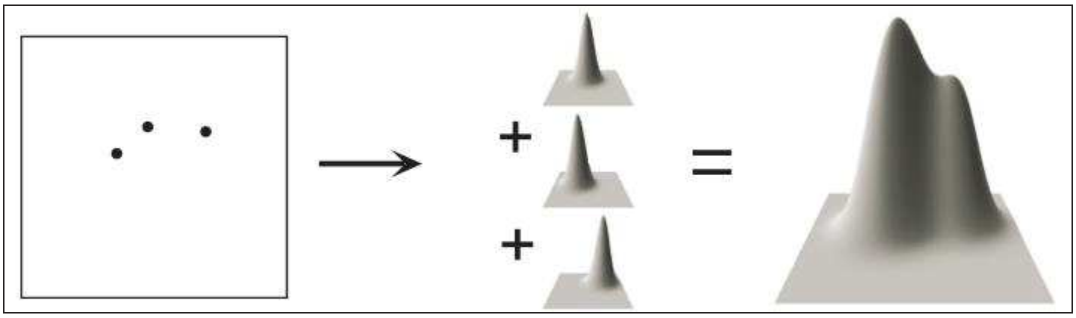


Fig. 26. Principle of the smoothing of a group of points by the kernel method. The probability density function of the presence of an event is calculated from the sum of the kernel functions placed above each observed location. Adapted from Calenge (2005).

It is then possible to draw contours of differential intensity of space use by the animals. The area of interest is then defined as the area included by the contour of the UD so that the volume below the distribution and within the contour represents a certain percentage of the total volume (Worton 1989, Calenge 2005): the 90% contour reflects the general distribution of the group or 'home range', while the 50% contour delineates the more intensively used territory and is referred as 'core area' (Börger et al. 2006).

In order to define the smoothing factor, i.e. the width of the kernel function, we used a first passage time (FPT) analysis (Fauchald and Tveraa 2003, Scheffer et al. 2010, Widmann et al. 2015, Vacquie-Garcia et al. 2017). FPT is defined as the time taken by an individual to cross the area of a circle with a given radius. FPT is computed over each location and for an increasing range of radii (from 2 to 150 km and incremented by 2 km in our study). The maximum peak in relative variances across the range of radii values indicates the optimal scale of interaction of the birds of each group with the environment (Bailleul et al. 2008) and corresponds to the smoothing factor of the kernel analysis (Lascelles et al. 2016, Heerah et al. 2019). Kernels (Fig. 39) were computed with the R package '*adehabitatHR*' (Calenge and Royer 2020).

Additionally, in order to compare our data with previous results from the literature, we used a traditional technique to delineate the extensive distribution of the birds from each study site. We drew with GIS software polygons encompassing the whole tracks of the birds from each study site (see Fig. 27 to visualise an example of a resulting polygon, referred as 'Distribution area' and page 126 for the details of the method). The size of each kernel and polygon was calculated with the R package '*raster'* (Hijmans and van Etten 2020) for comparisons.

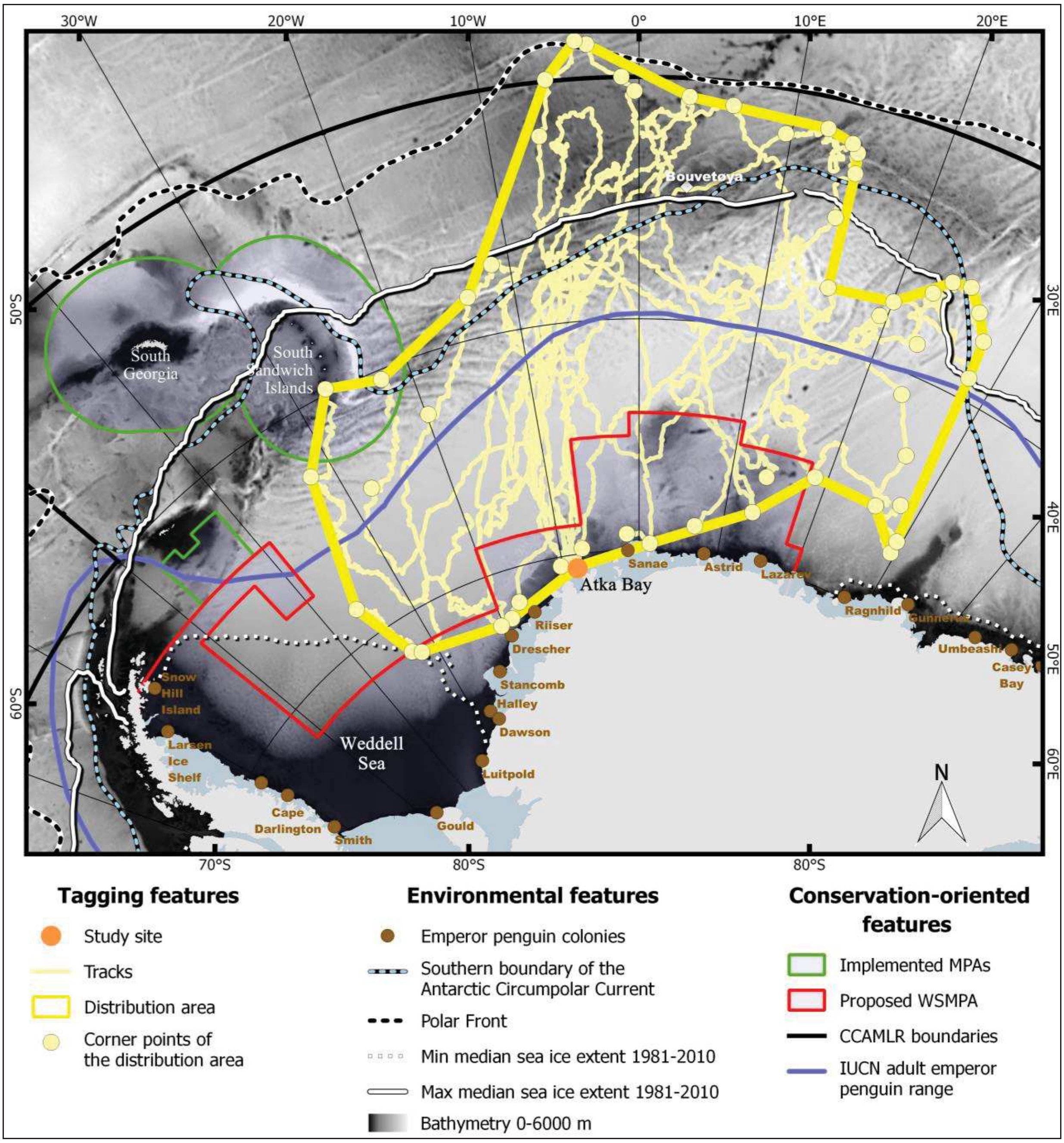


Fig. 27. Distribution over the first year at sea of the 8 juvenile emperor penguins tagged at Atka Bay in 2019. Main environmental, conservation and management features of this sector of the Southern Ocean are specified in the legend. MPAs: Marine Protected Areas; CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources; IUCN: International Union for Conservation of Nature; WSMPA: Weddell Sea Marine Protected Area.

Since locations were interpolated on a regular time step, the values of FPT at each location are a measure of occupancy. For several species like elephant seals or king and Adélie penguins, FPT can be used as a proxy to identify foraging areas (Scheffer et al. 2010, Widmann et al. 2015, Vacquie-Garcia et al. 2017) through the concept of Area Restricted Search (ARS; Kareiva and Odell 1987, Fauchald and Tveraa 2003). Marine predators are supposed to maximise their research behaviour of prey. Areas with high FPT values are therefore considered as foraging areas, and areas with lower FPT values as transiting zones between foraging areas. However, the differentiation is not so binary for emperor penguins. Indeed, when out at sea, adult and juvenile emperor penguins do not spent all their time diving. They also rest on sea ice especially during the wintertime (see Fig. 28 from our study, but also Zimmer et al. 2008, Watanabe et al. 2012, Goetz et al. 2018, Labrousse et al. 2019a). Consequently, the FPT values from our tracked birds rather segregate areas of residence (resting and foraging) characterised by high FPT values, from areas or periods of travel characterised by low FPT values.

The environmental drivers of FPT values were investigated (see page 147) with Generalized Additive Mixed (GAMMs) given their flexibility to identify nonlinear functional relationships between species distribution and environmental conditions (Zuur 2009).

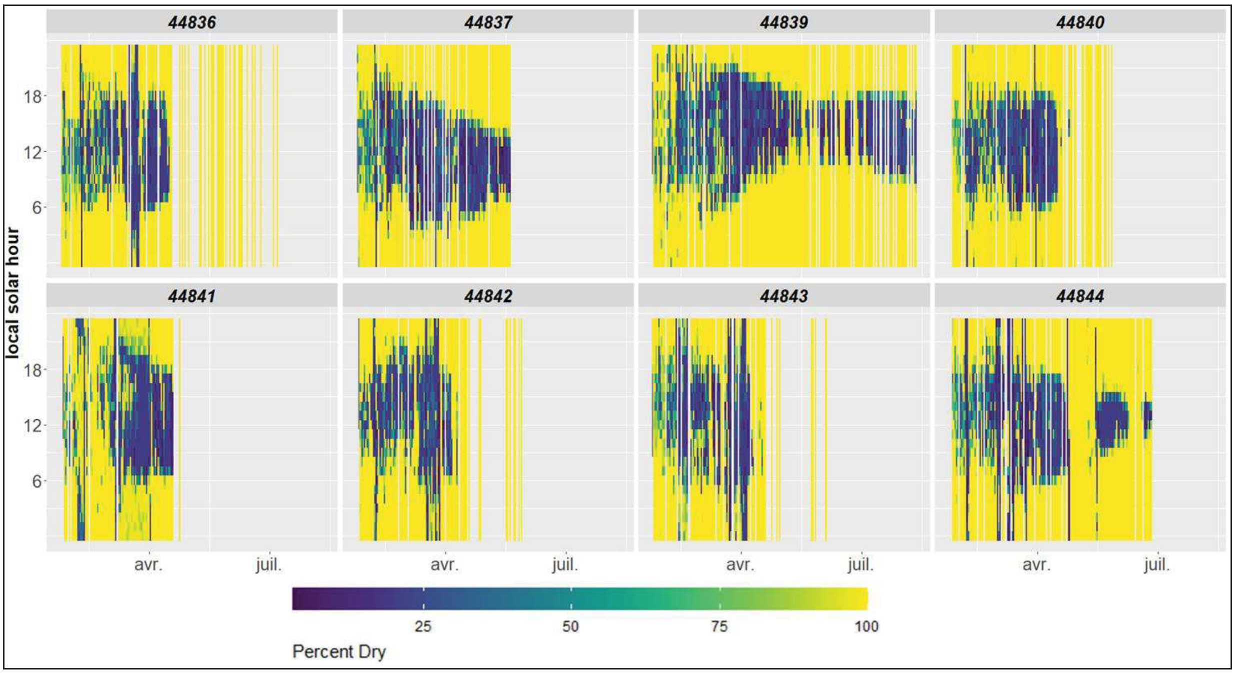


Fig. 28. Raw hourly proportion of immersion collected by the ARGOS platforms deployed on the 8 adult emperor penguins at Atka Bay in January 2018. Each panel corresponds to one bird; the x-axis represents the date and the y-axis the daily hours. Period of diving are in blue and period out of water are in yellow.

II.3.1.4. Environmental variables at the exact locations

To account for location error when extracting environmental variables, we used the fitted CRW model to create a dataset of 100 simulations of each location and individual bird (Johnson 2008). The 100 values for the bathymetry, the gradient of bathymetry and sea ice concentration covariates, and the distance covariates associated with each possible location, were first extracted and then averaged, giving a mean value and its standard deviation for each location along the mean track (Fig. 29 and also Heerah et al. 2016).

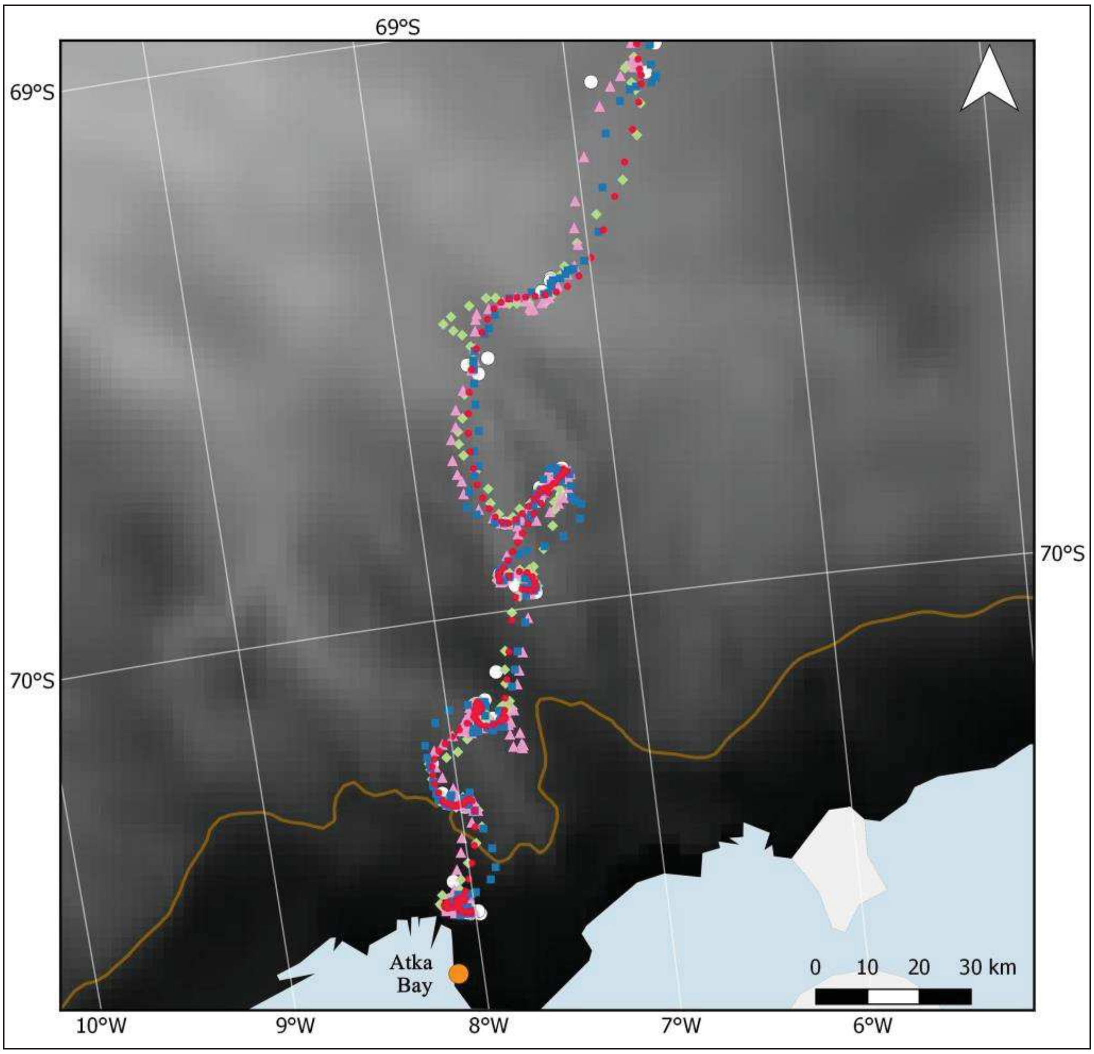


Fig. 29. Interpolation and simulation of locations. White dots are true ARGOS location of the bird (a juvenile leaving Atka Bay colony). Red dots are the hourly interpolated locations. Blue, green and pink features represent 3 different crawl simulations. Dark to grey gradient in the background represents the bathymetry with the 1000 m isobaths in brown, and the Antarctic continent in light blue. Atka Bay colony location is indicated with an orange dot.

II.3.1.5. Estimation of distances

The distance from the locations of the birds to the sea ice edge, to the colony location or to the oceanic fronts was computed with the R package '*geosphere*' (Hijmans et al. 2019).

II.3.1.6. Residence time in management bodies and environmental features

To assess the intensity of use of features related to conservation management in the Southern Ocean by the tracked birds, we averaged the proportion of time they spent monthly inside each feature, referred hereafter as 'residence time'. We also computed the residence time per individual over the total tracking duration of each bird. Additionally, for each study site and each management feature, we computed the proportion of the distribution area falling inside the boundaries of a particular feature with the R package '*raster*' (Hijmans and van Etten 2020).

We tested the statistical effect of the individuals and of the months on these proportions using Kruskal-Wallis rank sum tests. When a significant difference was measured among individuals or months, the Tukey's 'Honest Significant Difference' multiple comparison of means test was used to identify which individual(s) or month(s) differed from others (Thiebot et al. 2013, 2019).

II.3.2. Dive analysis

Dive extraction was carried out with the MT-Dive software (Multi Trace-Dive, Jensen Software Systems, Laboe, Germany). The software split the pressure recordings into dives by looking at the inflexion points near the surface and allows for Zero Offset correction between dives to correct for drifting recordings while extracting various metrics (see below). Start and end of dives were considered from the last record at the surface, and dive duration as the time between dive start and end. The data processing is not perfect and some artefacts need to be corrected after extraction. For instance, some dives might be duplicated, other might not be correctly split resulting in too long dives. This analysis considers for the moment only the dives deeper than 5 m.

Wiggles were defined as deviation of the depth at 3 points on which the vertical speed drops below 0 m/s (inflexion points) and with a change of depth above a threshold depending on the resolution of the TDR used (Fig. 30; Simeone and Wilson 2003). The definition of the bottom phase is less homogenous in the literature. In most studies on emperor penguins, the bottom phase is defined as the part of the dive deeper than 85% of the maximum depth (Kirkwood and Robertson 1997, Zimmer et al. 2007b, 2008, 2010, Wienecke et al. 2007), which was the default set up of the software from Wildlife Computers (Wienecke et al. 2007). Other values have also been used in other species (90% (Charrassin et al. 2002, Bost et al. 2007) or 75% (Enstipp et al. 2019) in king penguins, for instance). Halsey and colleagues Halsey et al. (2007) and Hanuise et al. (2013) defined the bottom phase as starting with the first wiggle that occurs deeper than a particular threshold and ending with the last wiggle that finishes deeper than this threshold. Others used various speed threshold (Rodary et al. 2000b, Ropert-Coudert et al. 2007, Preston et al. 2008). The start and end of bottom phases were defined as the first and last time the rate of change of depth became <0.5 m/s during a dive associated with a slimness parameter fixed at 0.1. The choice of these values was confirmed with visual inspection of thousands of dives. Such parameters allow maximising the detection of wiggles occurring during the part of the dive slightly ascending. The definition of the bottom phase we used is thus flexible to changes in the depths of the dives during which the majority of feeding events may occur.

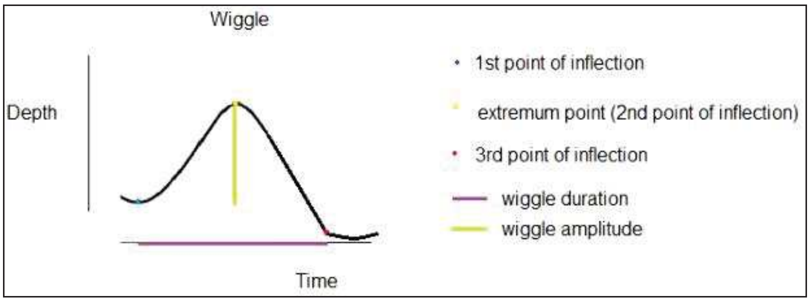


Fig. 30. Wiggle definition. Adapted from Mt-Dive manual.

Additionally to the dive detection, the software allow us to extract several metrics to describe each dive, e.g. the maximal and mean dive depths, the dive, bottom time and post-dive durations, the speed of ascent and descent. We considered the dive depths, the bottom time duration, the number of wiggles, the dive efficiency (DE; Ydenberg and Clark 1989, Zimmer et al. 2010), which is the ratio of the bottom duration by the sum of the dive time and the post-dive surface interval time and the Attempts of Catch Per Unit Effort (ACPUE), which is the ratio of the number of wiggles by the bottom time, as reliable indicators of foraging effort (Zimmer et al. 2010, Le Guen et al. 2018). By computing the prospection effort per unit of time (i.e. number of dives made per hour), we also estimated at what time of the day the birds intensified their diving effort in order to compare their diving performance according to the breeding site, the breeding status, and the seasonality.

Chapter III. Biologging of emperor penguins - attachment techniques and associated deployment performance

Biologging of emperor penguins - attachment techniques and associated deployment performance

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III.1 Abstract

An increasing number of marine animals are equipped with biologgers, to study their physiology, behaviour and ecology, often for conservation purposes. The Refinement principle from the Three Rs framework (*Replacement, Reduction, Refinement*) urges to continuously test and evaluate new and updated biologging protocols to minimise wildlife disturbance.

The Emperor Penguin (*Aptenodytes forsteri*) is regularly used to raise awareness, and, as key top predator and umbrella species, plays a central role in the Antarctic ecosystem but much remains to be learned about the distribution and activities at sea of the species. To fill parts of this gap, we equipped adults for short-term (GPS, Time-Depth Recorder (TDR)) and long-term (i.e. planned for one year) deployments (ARGOS platforms, TDR), as well as juveniles for long-term deployments (ARGOS platforms) in the Weddell Sea region and in the Atlantic sector of the Southern Ocean where they had not been studied yet.

In this report, we describe and evaluate our protocols for the attachment of biologgers on-site, the capture of the animals and the recovery of the devices after deployment. Our unprecedented recaptures of long-term equipped emperor penguins demonstrated that the traditional technique gluing the biologgers directly to the back feathers is detrimental to the birds. It causes excessive feather breakage and the loss of the devices. We propose an alternative method of attachment for back-mounted devices that led to successful year-round deployments on juveniles and evaluate the first deployments of leg-bracelet mounted TDRs on emperor penguins.

Our findings highlight the importance of monitoring potential impacts of biologger deployments on the animals and the need to remain critical towards established protocols. We propose alternative techniques and a standardised study design for emperor penguins capture and on-site logger deployment that help mitigate the potential negative impacts of logger deployment on these birds.

III.2 Introduction

Over the last decades, biologging technology - the "use of miniaturised animal-equipped tags for logging and/or relaying data about an animal's movements, behaviour, physiology and/or environment" (Rutz and Hays 2009) - has rapidly progressed and led to fundamental advances in ecology of e.g. terrestrial (Fortin et al. 2005, Marker et al. 2008, Kays et al. 2015) and marine predators (Ropert-Coudert et al. 2009a, Bograd et al. 2010, McIntyre 2014) including seabirds (Ancel et al. 1992, Clarke et al. 1998, Sato et al. 2002, Wilson et al. 2002, Zimmer et al. 2008, Massom et al. 2009, Bost et al. 2009b, Weimerskirch et al. 2014, Pistorius et al. 2017, Chimienti et al. 2017). This technical evolution that included miniaturisation, design optimisation, storage capacity and power consumption, was supported by the development of new analytical techniques and processing software (Hussey et al. 2015, Carter et al. 2016).

Biologgers can cause discomfort to the tagged animals and may even impede their movements, especially in the case of diving seabirds like penguins where the increased water drag can increase the energy expenditure (Culik and Wilson 1991, Ropert-Coudert et al. 2000, 2007, Beaulieu et al. 2009, Vandenabeele et al. 2011). However, by collecting high-resolution data on a small number of animals, biologging can comply with the *Reduction* principle of the Three Rs framework (*Replacement, Reduction, Refinement*; Russel and Burch 1959). The miniaturisation of devices (Wilmers et al. 2015), the establishment of guidelines (Kenward 2001, CCAMLR 2014) and the activities of study review boards that oversee the ethical treatment of animals in scientific studies (Wilson and McMahon 2006, Casper 2009, Ratcliffe et al. 2014, Williams et al. 2019) also help to mitigate adverse impacts.

Yet, especially in the case of penguin tracking studies, the inability to observe the animals carrying the devices at sea bears the risk that deleterious effects may not be obvious (Vandenabeele et al. 2011) or may even remain unnoticed if birds are not resighted. For instance, after decades of flipper banding of thousands of penguins (Wanless and Oatley (2000) and see references in Jackson et al. 2002), it was only in the 2000's that studies (Gauthier–Clerc et al. 2004, Dugger et al. 2006, Saraux et al. 2011a, Le Maho et al. 2011) assessed its long-term effect, and showed that flipper bands dramatically decreased the survival and breeding success of their carrier. This finding raised important questions about ethics and bias in scientific studies; an issue already highlighted by Wilson et al. (1986). Flipper banding of penguins is a prime example why it is necessary to study potential impacts of device deployments on animals, as well as to remain critical towards - and keep testing - new methods to minimise wildlife disturbance. It has to be noted that of the five studies (Wienecke et al. 2010, Thiebot et al. 2013, Kooyman et al. 2015, Goetz et al. 2018, Labrousse et al. 2019b) where emperor penguins (*Aptenodytes* *forsteri*) have been tagged with external biologgers for a year-round deployment duration, none has reported the recovery of the device or a sighting of an equipped bird after deployment. The causes of signal loss remained unclear (Kooyman and Ponganis 2004, Kooyman et al. 2015) and the fate of the device-carrying birds uncertain.

Nonetheless, data obtained from biologgers are often of such importance for conservation biology that the benefits may outweigh the risk for the animals. For example, tracking studies that determine the home range and movement corridors of species are often a prerequisite for conservation management policies (Block 2005, Small and Taylor 2006, Cooke 2008, Costa et al. 2012) as demonstrated by the establishment of the Ross Sea Marine Protected Area (MPA) in 2017. This first MPA adjacent to Antarctica was partly justified by the range of Adélie penguins (*Pygoscelis adeliae*) during their energy-intensive premoult period (CCAMLR 2009, Hays et al. 2016).

Emperor penguins have not yet been tracked in the Weddell Sea and in the Atlantic sector of the Southern Ocean, thus not much is known about their distribution in the area. To improve the scientific knowledge about this species and to provide data in support of the development of a MPA in the Weddell Sea area, we have equipped several adult and juvenile emperor penguins. Data logger types were chosen according to our research questions and subject to seasonal constraints. We document for the first time the resighting and recapture of long-term equipped emperor penguins as well as device recovery. Indeed, while back-mounted loggers have already been successfully used for long-term deployments on emperor penguins (Goetz et al. 2018, Labrousse et al. 2019b), their physical impact has never been assessed presumably due to the logistical difficulties in resighting the birds before the annual moult.

Furthermore, we present the first leg-band biologger attachment and deployment on emperor penguins. Several leg-band devices had been successfully tested and deployed on other penguin species (Adélie and macaroni (*Eudyptes chrysolophus*) penguins, see Bost et al. 2009a, Ratcliffe et al. 2014, Thiebot et al. 2019) and it was shown that the leg-band devices minimised drag, induced little behavioural disturbance and did not jeopardize birds' survival. To date, no such deployment had been documented on emperor penguins. Additionally, we describe and discuss methods for catching, handling or retrieving (resight and recapture) emperor penguins. These necessary procedures lack standardisation across studies. Some use a rugby-like catch method (Robertson 1991, Zimmer 2007), others would use a crook (Cockrem et al. 2008, Kooyman et al. 2015)) or a fixed enclosure (Kooyman et al. 1992b, Williams et al. 2011) and the impacts of these procedures on the targeted bird are rarely reported.

Summarising, in this manuscript, we describe and review protocols for on-site capture, handling and release of emperor penguins, biologger attachment and recovery techniques that minimise the impacts on the birds' welfare. These protocols could be used to standardise and facilitate further studies on emperor penguin movement ecology of highest ethical standards.

III.3 Material and Methods

III.3.1. Study site, species, and deployments

This study was conducted at the Atka Bay emperor penguin colony (70°37'S, 08°09'W) in close vicinity (~ 10 km) of the German research base Neumayer Station III (70°39'S, 08°15'W) during two consecutive summer campaigns (November to January) in 2017/2018 and 2018/2019. During these campaigns, we deployed biologgers for short- and long-term deployments. Monitoring periods of weeks to months in summer (Ponganis et al. 2000, Zimmer et al. 2007b, 2010, Watanabe et al. 2012) are referred to as "short-term", while year-round planned monitoring that include austral winter are referred to as "long-term" (Kirkwood and Robertson 1997, Rodary et al. 2000a, Zimmer et al. 2007b).

The deployment protocols to use on emperor penguins largely depend of the species' phenology (and of logistic constraints). The Emperor penguin is the only bird species breeding during the austral winter (Prévost 1961), almost exclusively on sea ice (Fretwell et al. 2012) all around Antarctica (Ancel et al. 2017). After a courtship period in March and April, depending on the colony's latitude, and an incubation period of around 64 days, the chicks hatch in the middle of the austral winter. As central place foragers (Orians and Pearson 1979), male and female do alternate trips at sea to find food for their sole offspring. By October, the chick becomes thermally independent and is left on its own while both parents go foraging at sea and return to feed their chick independently (Stonehouse 1953, Prévost 1961). These recurring returns of each adult to feed its chick, approximately once per week, allow for the deployment and retrieval of short-term data loggers. In December or January, chicks moult and fledge. By the end of the austral summer, the adult emperor penguins moult. For both moulted chicks (i.e. juveniles) and adults, a reliable attachment of long-term logging devices on their backs is only possible after moulting is largely completed. The majority of the juvenile penguins will not return to the colony for at least two years (Mougin and Van Beveren 1979) and previous studies suggest that most of the adults moult on the pack ice (Kooyman et al. 2000, 2004, Wienecke et al. 2004, Zimmer et al. 2007b). There is also no certainty that adults moulting at the colony are actual breeders from that particular colony and that they will return for the next season. Therefore, successfully retrieving the devices is unlikely and the use of transmitting devices is by far the most prevalent technique to ensure data collection.

In this study, we used two methods of capture (corral or crook, see the capture protocols section for details) to catch three categories of birds (a pair of an adult with its chick in November/December, juveniles and moulted adults in January) in order to deploy and/or recover six different types of loggers (Table 4). Depending on the duration (short- or long-term) of planned equipment, biologgers were attached by one of four techniques (back-attachment-tape/-cyanoacrylate-glue/-tape-epoxy and leg-band). The four deployment protocols are briefly presented below and summarised in Table 8. Additionally, all birds, i.e. adults and chicks, were marked with subcutaneous passive integrated transponder (PIT of 3.85 × 32 mm and 0.8 g, Texas Instruments Remote Identification System, TIRIS, Texas, USA) implanted between the tail and left leg (Additional file 2) allowing remote identification of individuals with automatic reading systems. All protocols adhered to current best-practise standards to reduce the risk of physical harm and stress to individuals and the colony.

Table 8. General information on deployments and captures.

Category of attachment	Back-taped	Leg-banded & back glued	Back-taped-epoxied
Deployment duration	Short-term	Long-term	Long-term
Life-history stage	ADULT	ADULT	JUVENILE
Logger type	GPS - VHF - TDR	TDR - ARGOS	ARGOS
Monitored period	summer	winter	winter
Number of individuals equipped	36	8	8
Capture setup	with its chick at the colony edge	alone at the edge of groups	groups on their way to the sea
Capture technique	corral + crook	crook or corral	corral
Minimum of persons required	3	2 to 3	3
Recapture technique	crook	crook	not possible, not returning to breeding site
Minimum of persons required	2	2	

III.3.1.1. Short-term deployment: back-taped loggers

We equipped 16 adults in 2017/2018 and 20 adults in 2018/2019 with a GPS-Acc-VHF logger (a combination of a Global Positioning System (GPS), a 3-axis Accelerometer (Acc) and a Very High Frequency (VHF) locator beacon) and a separate Time-Depth Recorder (TDR, see Table 4 for technical details on the loggers). Both are archival devices and, therefore, need to be retrieved to access the data. The VHF locator beacon sends a device-specific signal that allows us to locate the equipped birds in the colony and facilitate device recovery. To minimise deleterious effects such as extra drag on diving animals (Culik and Wilson 1991, Bannasch et al. 1994), we followed the recommendations of previous studies. The hydrodynamically-shaped devices represented less than 1% of the penguin's cross-sectional area, weighed less than 3% of the bird's mass (Kenward 2001) and were attached on the lower back of the birds with adhesive tape.

III.3.1.2. Long-term deployment: back-glued loggers

In January 2018 we equipped 8 adults that had completed their moult with an Advanced Research and Global Observation Satellite (ARGOS) platform and a separate accelerometer. ARGOS platforms sent the locations of the birds through the Collecte Localisation Satellites (CLS) ARGOS service (Toulouse, France). The streamlined devices were attached by direct contact between cyanoacrylate glue and the feathers in the middle of the lower back of birds (Wilson et al. 1997b, Casper 2009).

III.3.1.3. Long-term deployment: back-taped-epoxied loggers

In January 2019, we equipped 8 juveniles with ARGOS platforms. The devices were attached to the lower back of birds with adhesive tape that was secured with epoxy glue. Importantly, the epoxy glue did not come in contact with the back feathers.

III.3.1.4. Long-term deployment: leg-banded loggers

In January 2018, the same 8 birds equipped with ARGOS loggers (see section III.3.1.2 above) were also equipped with an additional TDR sensor that was attached with a leg-bracelet. Similar leg-bracelets had been successfully deployed on other penguin species (Bost et al. 2009a, Thiebot et al. 2011b, 2019, Ratcliffe et al. 2014 and Houstin, Fournier, Le Bohec, unpublished observations on Adélie penguins).

III.3.2. Capture protocols

A very limited number of scientists have ever handled a non-anaesthetised adult emperor penguin. Handling such an animal can be difficult as they are strong but fragile birds (especially the flippers) with a body mass ranging from 15 (this study) to ca. 40 kg depending on age, sex, season and location (Prévost 1961, Le Maho et al. 1976). While it is always better to transfer such skills directly in the field, this may not always be possible due to the limited number of qualified and experienced persons able to train others. Therefore, our study and the associated protocols aim to fill part of this gap.

The techniques developed in this study to approach, capture and handle an adult emperor penguin require only (in our experience this is a minimum) two qualified and empowered field staff (referred to hereafter as specialists). While at least one of the specialists should have prior field experience with emperor penguins, it is sufficient for the other specialist to have experience in handling other wildlife species and a thorough understanding of the protocols and guidelines. In addition to the two specialists, at least one, but better two, assistants with general fieldwork experience are required to support the capture and handling of the penguins.

III.3.2.1. Adult-Chick capture protocol

Here, we present a technique to capture an adult emperor penguin with its thermally independent chick during the late chick-rearing period. Catching a duo can be of interest for research questions concerning demography, kinship, evolutionary ecology or ecophysiology. To avoid larger disturbances it is ideal to capture birds at the outer rim. Therefore, the first step is to observe the outermost 3-4 rows of animals from a distance, to locate adults that are feeding the same chick several times and that are either stationary or moving towards the outer edge of the colony. Note that allofeeding behaviour is quite common in emperor penguins (Jouventin et al. 1995) but allofeeders usually do not stay with the same chick at this time of the season (Houstin, Le Bohec, unpublished observations).

(i) Capture equipment

Three main tools are required:

- One 2 to 3 m long stick (e.g. lightweight bamboo sticks) used to direct targeted birds out of the colony (Fig. 31a).
- One 2.5 m long light crook made of stainless steel or aluminium, bent at 50 cm from one end by an angle of approximately 135 degrees (Fig. 31a), used to direct birds and catch them if necessary. Note that a crook is more efficient than a hook from which penguins manage to escape by twisting their neck.
- A corral made of three separate panels (Fig. 31a). Each panel consists of plastic pipes joined together to form a 3 m by 0.8 m frame. For every metre in length, a vertical plastic tube is added for stability. A polypropylene net (aviary net with a mesh size of 2 cm) is connected to the frame using cable ties. This construction results in lightweight (e.g. 4.5 kg), sturdy and field serviceable panels. When the panels are connected (Fig. 31b), the triangle formed can be closed with two large reusable cable ties at each of the three joints. We suggest covering one of the panels with a plain fabric, even if this makes the panel more difficult to handle when there is wind. The fabric reinforces the corral, provides shade to the birds and prevents them from attempting to go through the net. It also protects the fieldworkers from wind and allows them to hide behind the panel to calm the birds before release.

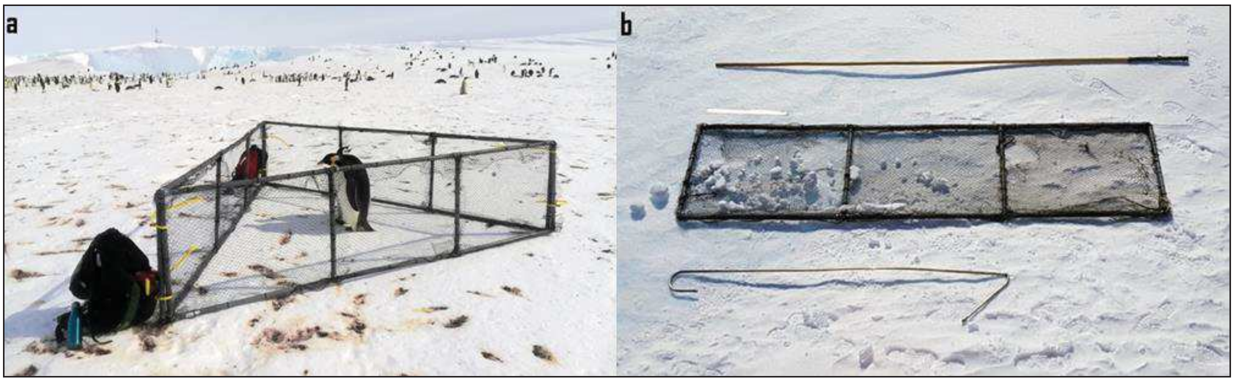

Fig. 31. Required tools to capture emperor penguins. a An adult-chick pair inside the corral. **b** A 3 m long bamboo stick at the top, one of the panels of the corral (a 50 cm ruler is placed just above it to facilitate scaling) in the middle, and the crook at the bottom.

(ii) Corral capture procedure

When the target adult-chick pair is located, the two specialists (one with the bamboo stick, and the other one with the crook) move towards the birds from two sides, starting approximately 40 m away from the colony. The first step for the specialists is to position themselves “behind” the pair, so that the birds are between them and the outer edge of the colony. The second step is to guide the pair slowly out of the colony by walking one-step at a time behind them. The specialists move very slowly to minimise the disturbance of the colony. The resulting disturbance is minimal (Additional file 3) especially if compared to a natural event like the intrusion of a Weddell seal (*Leptonychotes weddellii*) into the colony (Additional file 4). Meanwhile, the two assistants are positioned at a distance of approximately 100 m from the colony edge with the three corral panels and await instructions by radio communication at a minimal volume. Situational awareness is crucial to anticipate the location where the pair will exit the colony and to ensure a fast least-disturbing capture.

Once the pair is ~30-40 m outside the colony, one assistant hands one of the panels to the specialist with the bamboo stick, and returns to his/her own position. Once the panels have been placed equidistantly (~30 m) around the penguin pair, everybody moves closer to the pair and close the corral around it. It is to be noted that the last few metres (< 5 m) before the corral is fully closed, the team has to move in a smooth, swift and highly coordinated manner, so that no escape route is presented. If executed correctly, the penguins will remain stationary, looking for the best escape route, and find themselves in the closed corral before an escape is attempted. The specialist with the crook helps to close and secure the corral with reusable cable ties. If the adult attempts to escape, use the crook to catch the bird and prevent the escape (see section III.3.2.2 below). Four persons are the optimal number to carry out this capture protocol. If everybody is experienced, it can be executed comfortably, for the animals as well as for the scientists, with three people. The whole procedure is presented in detail in Additional file 3. After capture and manipulation, we recommend to let parent and chick rest and calm down for a few minutes in the corral to increase the chance that they stay together upon release. To release the birds in a particular direction, the cable ties of the edge facing the desired exit direction are unzipped and the corral sufficiently opened to allow the birds to go through (Additional file 5).

We used this method to capture an adult with its not-yet-moulted chick to increase our chances of recapture. Indeed, breeders with moulted chicks ready to fledge or with chicks having sufficient reserves to perform their moult and fledge on their own are more prone to end their breeding cycle, defined by the “abandon” of their chick (Robertson 1991). Devices were recovered after one to three foraging trips.

Please note that this corral capture procedure was also used to capture flock of chicks at the beginning of their moult to mark them with subcutaneous PIT in order to perform long-term population monitoring of the colony. Body mass and mortality rate of PIT-tagged chicks from equipped adults will be compared to these annual cohorts of 300 random chicks PIT-tagged each summer.

III.3.2.2. Single adult capture protocol

Two techniques can be used to capture a single adult emperor penguin, the choice depends on the behaviour of the bird while approaching, the availability of assistants, and the weather conditions.

As described above for the pair of an adult and its chick, the corral can be used to trap a single adult in a very similar way. Nonetheless, due to the fact that solitary birds are more mobile and usually more vigilant to their environment the corral method may be difficult, which is especially true during heavy winds or a blizzard.

An alternative and efficient technique is to use a crook to catch the bird (Additional file 6) as mentioned in Cockrem et al. (2008). The crook capture requires two people and in contrast to the corral protocol and the deployment of loggers can also be conducted in bad weather. Once the bird is isolated, one specialist places the crook around the neck of the bird preventing the penguin to escape by tobogganing, i.e. moving on its belly. Meanwhile, the other specialist grabs the tibiotarsi of the bird and holds them firm. The crook is gently removed and placed away from the capture site, and the penguin secured by the two specialists, one in front of the bird and one at the back. The crook-carrying specialist should be carrying the necessary supplies for manipulation in his/her backpack, because, after the capture, he/she will have his/her hands free, while the other specialist is still holding the bird.

We used this technique to recapture adults for device recovery or to capture non-breeding (e.g. moulting or post-moulting) adults.

III.3.2.3. Fledging juvenile capture protocol

For their first departure at sea, juvenile emperor penguins usually leave the colony in small groups. A group capture with the corral is, therefore, more efficient and potentially less stressful for the birds. The protocol is similar to the adult-chick-pair capture, but here an entire group of juveniles is slowly encircled by three corral bearers. As emperor penguins are social animals, it is likely that keeping the group together reduces the stress of manipulated individuals and facilitates the remainder of their travel towards the sea after release. Juveniles of interest are removed individually from the corral for the manipulation and returned afterwards. All juveniles are released together after all target animals have been handled.

III.3.3. Adult emperor penguin handling protocol

One specialist (S1) grabs the penguin's neck with his/her arm always above the beating flippers and, while kneeling down, pulls the penguin towards his/her body. The second arm goes above the junction between flippers and the body, against the penguin's chest, holding the bird firmly. It is crucial to always contain the head-beak-neck of the penguin, to prevent the bird from trying to strike with its beak. This procedure can be seen in detail in the Additional file 7. Once the bird is secured in this position, the second specialist (S2) approaches and bends the penguin's head towards the ground while S1 grabs the legs above the ankles to lay the bird on its belly. When the bird is laying on the ground, S2 kneels over the bird with its head between (below) the legs of S2. In this position, the bird is immobilised. It is crucial that the flippers, the most fragile part of the bird, are unrestrained and untouched, throughout the whole process. If an assistant is available, he/she can hold the legs of the birds and stretch them (foot soles pointing towards the sky). Working with three people allows S1 to deploy the loggers seated next to the penguin and reduces manipulation time. Most penguins stay quiet in this position with some few second long bursts of intense activity: a gentle but firm pressure on the back and pulling the foot soles upper and further from the ground helps to calm the bird.

III.3.4. Equipment protocols

During manipulation, the bird's eyes were always covered with a hood to reduce stress level (Casper 2009) and birds were handled at distance from the edge of the colony to avoid conspecifics' disturbance (usually > 40 m, thus well above the 5 m limit recommended in the General guidelines produced by the Antarctic Treaty Consultative Meeting (ATS 2020)).

III.3.4.1. Short-term deployment: back-taped loggers

Before starting with the attachment, we recommend to use a cardboard stencil and waterproof tape that is a bit larger than the logger to demarcate the precise location of the equipment and the placement of the strips of adhesive tape on the penguin (see this in detail Additional file 8). Following studies from Wilson et al. (1989, 1997b) and numerous subsequent short-term studies on other penguin species (Ropert-Coudert et al. 2003, Chiaradia et al. 2007, Pichegru et al. 2011, Le Vaillant et al. 2013, Poupart et al. 2017), we used a rounded knife to lift a few feathers from the back of the penguin and insert pre-cut strips of waterproof adhesive tape (e.g. Tesa® tape 4651, Beiersdorf AG, Hamburg, Germany). The number of strips depends on the logger's length. To strengthen the bond between strips, it is ideal if the strips overlap each other by 50%. To further reinforce the attachment, we added glue (e.g. cyanoacrylate glue, Loctite 401, Loctite, Henkel AG., Düsseldorf, Germany) between the adhesive part of the tape strips and the logger. Cable ties (e.g. Panduit, Panduit Corp, Illinois, USA) should be tightened with a cable tie gun. The size and number of cable ties used depend on the logger characteristics. Some glue is applied to secure their lock, which should be positioned on the side of the logger, near the lower end, to reduce drag. For a deployment period of more than one month, we recommend to add glue on top of the tapes. After manipulation is completed, we recommend to mark the bird before release with a hair-dye painted number that will last until the following moult (e.g. Schwarzkopf, Palette dark-blue N°909, Henkel AG., Düsseldorf, Germany; Fig. 32).

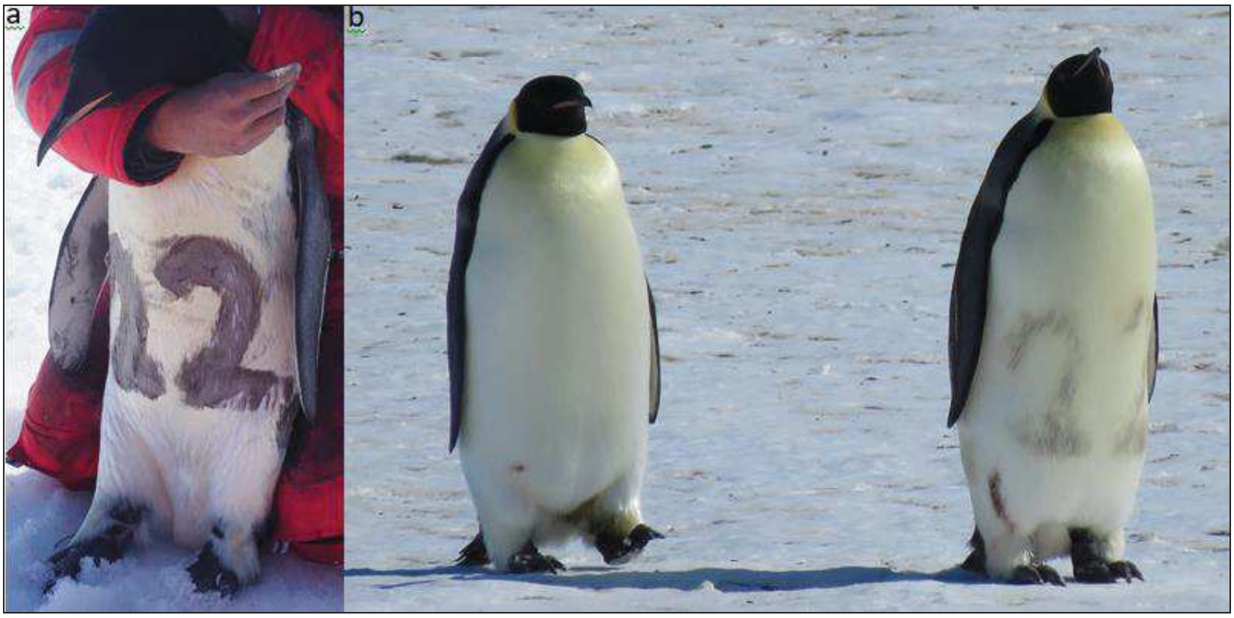

Fig. 32. Painted number on emperor penguin. a Fresh painted number on "bird 22". **b** The same marked bird after a 10 months deployment period. Notice the marks on its right leg. The other bird is a non-painted random emperor penguin.

We used this technique to deploy GPS-Acc-VHF (Axy-Trek from TechnoSmArt) and TDR (g5+ from Cefas) devices (see Table 4 for technical details and Fig. 33a to view an equipped bird) on adult emperor penguins at the end of their breeding cycle. It took 7 and 3 minutes respectively to deploy them (see respective movies of deployments in Additional files 8 and 10). We used four strips of tape and two cables ties (PLT1.5M-C0 142*2.6 mm) for the GPS-Acc-VHF and two strips of tape and two cable ties (PLT1M-C0 99*2.5 mm) for the TDR. The shape of the Axy-Trek logger was customised by the manufacturer to include two thin promontory ends, at the head and at the tail of the device, which facilitate cable tie attachment.

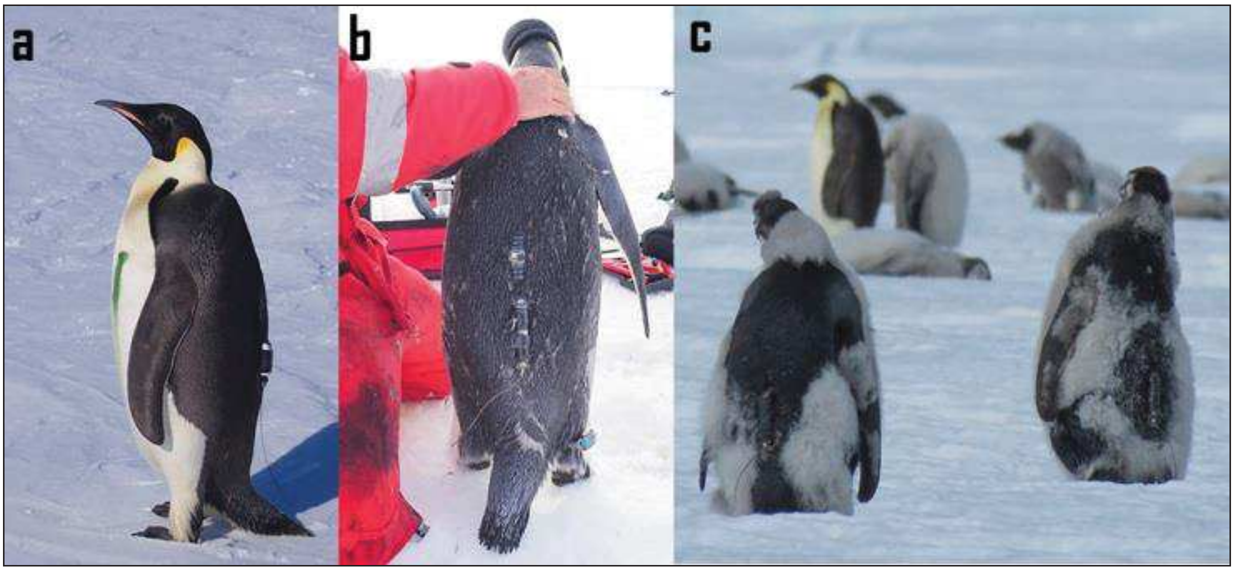

Fig. 33. Pictures of the different instrumentations performed. a. Adult emperor penguin equipped with back-taped loggers (a TDR in the middle of the back and a GPS underneath). The green line on the bird's belly is non-permanent marking. **b.** Adult emperor penguin equipped with back-glued loggers (an accelerometer in the middle of the back and ARGOS satellite transmitter underneath) and a leg-banded logger on its right foot. **c.** Two juvenile emperor penguins both equipped with a back-taped-epoxied logger.

III.3.4.2. Long-term deployment: back-glued loggers

According to protocols from previous studies (Wienecke et al. 2010, Thiebot et al. 2013, Kooyman et al. 2015), that conducted long-term deployment of biologgers on the back of penguins, we fixated the lower side of the loggers directly to the feathers using cyanoacrylate glue (Loctite 401). The attachment was secured with polyamide cable ties as described above (Fig. 33b).

We used this technique to deploy Spot-367 ARGOS loggers from Wildlife Computers and accelerometer (WACU) from MIBE-IPHC-CNRS on adults close to finishing their moult (Fig. 34). In an attempt to increase the duration deployment of the ARGOS logger, a rubber cable tie (Panduit, ERTM-C20), flexible and resistant to cold and pressure was added and positioned at the middle of the device. The accelerometer was positioned higher on the back of the penguin with approximately 3 cm between both loggers. Each deployment took about 8 minutes.

Fig. 34. Adult emperor penguin at the end of its moult.

III.3.4.3. Long-term deployment: back-taped-epoxied loggers

Similar to the short-term deployment protocol, the logger is attached to the feathers using pre-cut lengths of Tesa® tape on the entire logger length (sparing exposed sensors if any). The overlap between tape strips is reinforced with cyanoacrylate glue (Loctite 401). We recommend using two polyamide cable ties around the head and one at the bottom of the logger to secure the attachment. The supernumerary cable tie on the head is added for extra safety. Once all the adhesive strips and cable ties were fixated, we applied epoxy adhesive (Loctite EA 3430) on the mounting (sparing exposed sensors if any) to reinforce the waterproofness and robustness, adapting methods from other studies (Wilson et al. 1997a, Pütz et al. 2014). This manipulation takes approximately 20 minutes, but it prevents the use of glue directly onto the animal and its feathers. The attachment procedure is shown in the Additional file 12.

We performed this deployment on fledging chicks. We selected the individuals most advanced in their moult, i.e. presenting no more down on their back (Fig. 33c). The lower survival rate of the juveniles during the first year at sea compared to adults (Williams 1995), their non-return to breeding colonies before several years (Mougin and Van Beveren 1979) and their unfinished growth, prevent the use of other types of externally attached devices.

III.3.4.4. Long-term deployment: leg-banded loggers

To reduce drag and behaviour disturbance induced by devices on the back of penguins, we developed a leg-band (bracelet) for mounting TDR-loggers on emperor penguins. This development was guided by the *Refinement* principle from the Three Rs framework (Russel and Burch 1959) and inspired by

Ratcliffe et al. (2014) and our experience on Global Location Sensors (GLS) deployments on Adélie penguins.

We designed two similar types of bracelet, a first version that we deployed (Fig. 33b), and a second version incorporating slight changes and improvements. A detailed manual of the mounts is provided in Additional file 13. We designed the bracelet to mount a Lotek Lat 1800 TDR (see Table 4 for specifications) but the bracelet can be easily adapted to other types of TDR.

The TDR is fixed to a rubber cable tie (Panduit, ERTM-C20) covered with heat-shrinkable sheath and attached around the bird tibiotarsus by closing the cable tie just above the ankle, like a bracelet. A built-in lock prevents the cable tie to tighten itself after deployment. The bracelet fits loosely with ~1 cm space between the bracelet and the leg. The shape of emperor penguin's legs prevents the bracelet from spinning around the leg. When properly set up and attached (Additional file 13), the attachment does not interfere with egg or chick placement on the bird feet during the breeding season. Deployment time is less than 3 minutes. On retrieval, the bracelet is easy and quick to remove (within a few seconds) by cutting the rubber cable tie with pliers.

III.4 Results

III.4.1. Short-term deployment: back-taped loggers

In 2017-2018, 16 deployments were performed: 10 between November 27th and December 2nd, of which 6 devices were recovered and redeployed between December 10th and 12th. None of the devices of the second deployment session were recovered, resulting in 38% recovery.

In 2018-2019, 20 deployments were performed, 10 between November 05th and 07th, which all were recovered and redeployed between November 25th and December 6th. Six devices of the second deployment were recovered, resulting in 83% recovery. We conducted intense VHF and visual (binocular) surveys for equipped birds (ca. every 4 hours), thus we are confident that we retrieved all the loggers from returning birds. All VHF units of recaptured birds were working and unequipped birds have been regularly identified afterwards by their hair-dye painted number on their chest.

Bird feathering on recovery was intact and no physical damage on the bird or on the device was apparent. All loggers were still securely attached, even after the longest deployment of 25 days (Table 9). Our recovery rate for November (90%) is similar (z-test, $p\text{-value} > 0.05$) to those of previous studies at this period (Table 9). The recovery rate from December 2018 (30%), despite being higher, is statistically similar to what Robertson (1991) recorded for deployments performed in December on the opposite side of Antarctica (near Australia's Mawson Station) with a loss rate of 89%. The probability to recover a device deployed in December is significantly lower (z-test, $p\text{-value} < 0.05$) than in November.

Table 9. Comparison between at-sea-ecological studies that equipped emperor penguins over the last 30 years.

Category of deployment	Season	Age class	Type of device	Device dimension (mm)	Device weight (g)	Recovery	Mean duration (days)	Sd (days)	Range	# deploy	# recup	% recup	Publication	Study site and year
long-term	*W-Jan/Feb*	*ad*	*Argos*	*140x55x16*	*195*	*no*	*66*	*52*	*15-133*	*7*	*0*	*0*	*Kooyman et al. 2004*	*Ross Sea 2000*
long-term	*W-Mar*	*ad*	*Argos*	*109x32x26*	*100*	*no*	*114*	*98*	*12-**323***	*20*	*0*	*0*	*Goetz & Kooyman 2018, 2015*	*Ross Sea 2013*
long-term	W-Jan	ad	Argos Acc tdr	107x18x21 70x16x16 36x13x10	45 10 9	yes	**150**	30	118-201	8	4	**50**	This study	Atka Bay 2018
long-term	*W-Dec*	*juv*	*Argos*	*NA*	*120*	*no*	*64*	*12*	*43-81*	*8**	*0*	*0*	*Kooyman et al. 1996 and 2007*	*Cape Washington 1994, 1995, 1996*
long-term	*W-Dec*	*juv*	*Argos*	*NA*	*NA*	*no*	*113*	*49*	*41-160*	*7**	*0*	*0*	*Wienecke et al. 2010*	*Taylor glacier 1996*
long-term	*W-Dec*	*juv*	*Argos*	*NA*	*NA*	*no*	*121*	*55*	*38-189*	*10*	*0*	*0*	*Wienecke et al. 2010*	*Auster 2007*
long-term	*W-Dec*	*juv*	*Argos*	*NA*	*62*	*no*	*112*	*77*	*38-255*	*5**	*0*	*0*	*Thiebot et al. 2013*	*Pointe Géologie 2010*
long-term	*W-Dec*	*juv*	*Argos*	*NA*	*62*	*no*	*193*	*93*	*30-344*	*13**	*0*	*0*	*Labrousse et al. 2019b*	*Pointe Géologie 2014*
long-term	W-Jan	juv	Argos	107x18x21	45	no	**233**	108	73-**382**	8	0	0	This study	Atka Bay 2019
short-term	*S-Nov*	*ad*	*Argos tdr*	*78x50x23 67x17x17*	*105 30*	*yes*	*7*	*1*	*2-19*	*15*	*10*	*67*	*Zimmer et al. 2010*	*Pointe Géologie 2005*
short-term	*S-Nov*	*ad*	*Acc*	*128x27 or 122x22*	*101 or 73*	*yes*	*14*	*4*	*8-20*	*12*	*11*	***92***	*Watanabe et al. 2012*	*Cape Washington 2005*
short-term	S-Nov	ad	GPS tdr	105x38x18 35x12	60 7	yes	**16**	6	9-**25**	21	18	90	This study	Atka Bay 2017 & 2018
short-term	*S-Dec*	*ad*	*tdr*	*NA*	*NA*	*yes*	*NA*	*NA*	*NA*	*19*	*2*	*11*	*Robertson, 1991*	*Auster & Taylor glacier 1988*
short-term	S-Dec	ad	GPS tdr	105x38x18 35x12	60 7	yes	14	6	9-18	15	4	30	This study	Atka Bay 2018 & 2019

Only post-moult long-term deployments, i.e. pre-nuptial/pre-winter travels (beginning in Jan-Feb-Mar) and breeding short-term deployments, i.e. Nov-Dec, are considered in this table. Other studies have deployed devices specifically between May and October, i.e. breeding period only (Ancel et al. 1992, Kirkwood and Robertson 1997, Wienecke and Robertson 1997, Rodary et al. 2000a, Zimmer et al. 2007b, Labrousse et al. 2019a) or at the end of austral summer (end of December-January) trying to locate moulting areas (Kooyman et al. 2000, Wienecke et al. 2004). W-Mon = Winter-month of deployment, S = summer, ad = adult, juv = juvenile. NA = not available. For studies on juveniles, duration below 30 days have been removed since those short periods of deployment are mostly thought to be due to predation. For Kooyman and Ponganis (2007), only not hand-fed chicks have been considered. The corrected numbers of deployments are indicated by a star (*). In bold, the greatest values within a category of deployment. In italic, data from other studies.

The average mean mass of PIT-tagged chicks from the annual cohort and chicks from equipped adults were similar (Table 10). The mean mass of PIT-tagged chicks from the annual cohort in the second year was significantly lower (p-value < 0.05) than the mean mass of PIT-tagged chicks from the annual cohort in the first year. Albeit the mean mass of chicks from equipped adults in the second year was also lower than the mean mass of chicks from equipped adults in the first year, there were no statistical differences (p-value > 0.05) due to the small sample size (ANOVA were carried out after a log-transformation of the data to meet the assumptions of normality).

Table 10. Comparison of the mean mass of PIT-tagged chicks from the annual cohort and chicks of equipped adults.

Summer season	**PIT-tagged chicks from annual cohort** (mean ± sd in kg)	**Chicks of equipped adult** (mean ± sd in kg)
End of Nov. 2017	11.8 ± 2.4 (N=300)	11.7 ± 2.6 (N=16)
End of Nov. 2018	10.2 ± 1.9 (N=300)	10.2 ± 2.3 (N=20)

Concomitantly to the deployments, the survival rate of chicks was assessed both summers (Table 11). Dead chicks were counted on-site throughout the summer seasons, while alive chicks were counted using ClickPoints software (Gerum et al. 2016) at the end of December on ultra-high resolution panoramic pictures obtained with the SPOT penguin observatory (Richter et al. 2018a). Twice as many dead chicks were enumerated in December 2018/2019 as in December 2017/2018 (731 and 350, respectively). The ratio of dead chicks (5.2%) on the colony in 2017/2018 was thus significantly lower (8.8%) than in the subsequent year (z-test, p-value < 0.05). This increase in chick mortality rate was also noticeable for equipped adults, since 1 chick of the 16 tagged birds was found dead the first summer season (2017-2018), and 4 chicks over 20 from equipped adults were found dead the second summer season (2018-2019).

Table 11. Number of dead and alive emperor penguin chicks over the two summer seasons.

Summer season	**Dead chicks**			**Alive chicks**
	CEB	**PIT**	**Total**	**Total**
2017/2018	1 (16)	7 (300)	350	6352
2018/2019	4 (20)	14 (300)	731	7606

The number of dead (CEB, PIT, Total) and alive (Total) chicks over the two summer seasons at Atka Bay colony are provided. Dead chicks: CEB = chicks of equipped birds, PIT = Passive-Integrated-Transponder-tagged chicks not including the CEB, Total = total number of dead chicks found on the colony during the summer seasons (from November to January), Alive chicks: Total = number of alive chicks counted end of December on pictures. Numbers in brackets are the number of individuals manipulated for each study.

III.4.2. Long-term deployment: back-glued loggers

Our study is the first to report recapture of emperor penguins after a whole-winter deployment (January to November). Identified by the number painted on their chest (Fig. 32), 4 of the 8 birds equipped in January 2018 were resighted and recaptured in November 2018 (Table 9). All of them had lost the devices on their back. Instead, there was a line of missing/broken feathers (Fig. 35). No injury was detected.

This finding explains why contact with all ARGOS devices was lost during the winter. The mean transmission period was 150 ± 30 days (range 118-201 days, Table 9), significantly exceeding the previous average deployment durations of 66 (Kooyman et al. 2015) (p-value > 0.05, ANOVA) and 114 days (Goetz et al. 2018) (p-value < 0.05, ANOVA) from all previous similar studies.

Fig. 35. Back of the 4 penguins having lost their back-glued loggers during the winter.

III.4.3. Long-term deployment: back-taped-epoxied loggers

Noteworthy, three of the 8 juveniles equipped in January 2019 transmitted until their annual moult in January 2020. None of the birds did return to their native colony for moult; an observation congruent with the conjecture that juveniles of 1.5-years of age do not come back to moult at their colony of origin for the first year (Mougin and Van Beveren 1979, Labrousse et al. 2019b). This tracking period of a full year, from January 2019 to January 2020 (Table 9) is the longest documented deployment duration for the genus Aptenodytes and presumably for any penguin species since the deployments lasted from one moult to the next. None of the 5 remaining birds were spotted on colony despite visual search in summer 2019/2020. One device stopped transmitting after 73 days while the four others lasted between 142 and 185 days resulting in an average deployment duration of 233 ± 108 days. This average deployment duration is longer than any previously reported ($p\text{-value} > 0.05$, ANOVA, see Table 9 for mean ± sd values) but not significantly compared to Labrousse et al. (2019b), ($p\text{-value} < 0.05$, ANOVA).

III.4.4. Long-term deployment: leg-banded loggers

Our study is the first to perform a year-round deployment and data collection on emperor penguins. The 4 adults recaptured without their back-mounted loggers were still carrying their leg bracelet mounted TDR, providing an unprecedented record of an entire year of high frequency (1 Hz) depth and temperature logs for emperor penguins.

For all recaptured birds, the leg-bracelet mounting did not present any damage, the bracelet and the TDR were at the same position of their deployment, suggesting that the device did not rotate around the leg during the deployment period. However, all recaptured birds had lost a few feathers especially on the inside part of the leg and showed signs of abrasion in the form of a slight reddening of the skin and peeling under the bracelet area. Two of them had small sore spots on their tarsi. No limping was observed before or after removal. An illustrated comparison between an equipped and an unequipped leg after recovery can be found in the Additional file 14.

III.5 Discussion

We presented three techniques to capture and/or recapture emperor penguins, as well as four different procedures to externally attach various biologging devices on an emperor penguin. To our knowledge, the two methods of capture/recapture using a corral have not been described in the scientific literature. Two of the four deployment methods presented, the back-taped-epoxied logger and the leg-banded logger, are new developments for this species. With the description of those new or refined methods and detailed assessment of their impacts on the birds wellbeing, paired with an exhaustive documentation (pictures, movies and slideshows exposed in the multiple additional files), we aim to facilitate, standardise and thus enhance future research on this species.

III.5.1. Capture and handling

All capture techniques presented in this study yield minimal colony disturbance regardless of the period of the breeding cycle. The described handling is safe for birds and handlers, and only a minimal number of trained personnel is required, which is an important consideration when conducting fieldwork in remote places like Antarctica.

We recommend using those techniques to capture and manipulate emperor penguins at a breeding site and urge users to share their improvements and modifications. We also recommend the use of the corral if no member in the field team is accustomed to handling a crook or a hook on at least one penguin species.

We are confident that the use of an easy-removable corral opens new perspectives for research in different fields (demography, comparative physiology, evolutionary ecology) that require, for instance, catching pairs of breeding adults at the beginning of the austral winter.

III.5.2. Deployments

III.5.2.1. Short-term deployment: back-taped loggers

Our study is the first to report the deployment of GPS devices on emperor penguins. GPS devices have already been deployed on penguins (Mattern et al. 2005, Trathan et al. 2008, Poupart et al. 2017, Le Guen et al. 2018), yet never on emperor penguins on which only ARGOS devices (Zimmer et al. 2007b, 2010, Sato et al. 2011, Watanabe et al. 2012) or dive-pattern-analysis related loggers (Robertson 1991, Sato et al. 2011, Watanabe et al. 2012) have been deployed during the late chick-rearing period, presumably due to a combination of technical and logistical constraints. The increased temporal and spatial resolution of GPS loggers in comparison to ARGOS devices, combined with their lower cost that allows to sample a greater number of birds, can facilitate a better understanding of foraging activities and behaviour at a finer scale, thus improving fundamental knowledge about this iconic species.

The methods presented herein allow the deployment of high-resolution data acquisition loggers with a high probability of recovery once the phenology of the colony has been assessed, for instance by the size and moulting stage of chicks. At Atka Bay, the best deployment period is in November with a logger recovery rate of 90%. The low recovery rate (38%) during the 2017-2018 season can be explained by logistical issues we encountered and not the deployment technique. An unexpected late on-site arrival led to late deployment of 11 loggers in December 2017, compared to 4 in December 2018, and consequently to a substantial loss of devices. The higher mortality rate (Table 11) and the lower body condition of the chicks in 2018/2019 compared to 2017/2018 (Table 10) suggest that the environmental conditions were harsher the second summer, explaining the higher number of dead chicks from equipped birds in the second year of this study.

To optimise the recovery rate of devices deployed at the end of the breeding season and minimise potential impact on chicks, we recommend to deploy devices on adults with medium-sized chicks at the very beginning of chick moult. Supported by the secure attachment of the presented technique, we furthermore suggest increasing deployment time rather than to recover loggers and redeploy them.

III.5.2.2. Long-term deployment: back-glued loggers

Our study is the first to document the recapture of a long-term equipped emperor penguin and thus the first able to assess (i) the state of the bird, (ii) the state of devices, and (iii) provide evidence explaining the loss of signal from communicating-satellite-relayed loggers reported in previous studies. Until now, five studies had performed long-term deployments on emperor penguins right after the moult (Table 9), all using ARGOS platforms and cyanoacrylate glue to attach the logger directly to the back-feathers of the birds. None of the birds were resighted. Two deployments were made on adults (Kooyman et al. 2015, Goetz et al. 2018), three on chicks (Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b).

Our results show that both glued devices, the ARGOS transmitter and the small accelerometer, which vary substantially in size and weight (Table 4), were lost in the same manner on all birds. We speculate that the cyanoacrylate glue rigidifies the feathers, which then become brittle and break with either the continuous birds' movements and/or their attempts to remove the device. Wilson et al. (1997b) also observed this device-sized hole in the feather layer after winter deployment on four Magellanic penguins (*Spheniscus magellanicus*) using epoxy instead of cyanoacrylate glue. In our study, five of the eight ARGOS signals were lost while birds were on fast ice at the breeding side, thus not in the water for several weeks. The longest duration of deployment (201 days, Table 9) was recorded for the only bird that did not spend any extended time on ice. When the birds remain on the fast ice at their breeding colony, they are exposed to extremely cold temperatures, up to -50°C in Atka Bay (Richter et al. 2018a). We assume that, such cold temperature could have two different effects. Either the cyanoacrylate induced brittle feathers become very weak when exposed to such cold temperatures and, therefore, are easier to break during the penguins' movement, or the brittle feathers do not provide the proper isolation against the cold, thus altering the heat transfer and/or thermoregulation of the bird (as observed on pup grey seals (*Halichoerus grypus*) by McCafferty et al. (2007)). This could lead to the animal preening their feathers fiercely and thereby removing the logger by breaking/removing the brittle glued feathers. In addition, blizzards may have caused the accumulation of ice around the loggers, amplifying the above effects and tearing the device off (Kooyman and Ponganis 2004, Kooyman et al. 2015). However, we suggest that the huddling behaviour of emperor penguins (Prévost 1961, Gilbert et al. 2006) would prevent ice accumulation in the middle of the winter. Another possible explanation could be the timing of deployment. Devices were attached just at the end of the moult, a time when feathers may not yet be fully developed despite a meticulous bird selection process (Fig. 34). Their growth after deployment could potentially have added some slack and thus reinforced the pull on the feather shafts, ultimately leading to their breakage after few months. The loss of back feathers undoubtedly leads to a diminution of insulation that causes a greater heat loss. The resulting increase in energetic needs reduces fasting capabilities and forces the birds to compensate by finding more prey items when they return at sea to forage in order to replenish their reserves while accumulating food for their chick. As body reserves management is critical for this species, any significant heat loss is likely to impact breeding success.

The ARGOS locations of the birds throughout the year allow to determine if an animal attempted to breed (according to its location and behavioural pattern at sea and at the breeding site during the winter breeding period). Three of the four recaptured birds attempted to breed. Amongst those, only one succeeded and was observed several times with its chick during the summer season. The fourth recaptured bird did not attempt to breed in that year. Two of the four birds that were not recaptured, did not return to Atka Bay colony in that year and did not attempt to breed at another colony. The remaining two birds did return to Atka Bay colony for breeding. These two non-recaptured breeders were not resighted despite intensive searching efforts throughout the season (two daily checks of two hours each per day with two specialists screening the colony with binoculars). The risk of premature death is unlikely as survival is high on adult emperor penguins (Jenouvrier et al. 2012). This suggests that they either skipped or failed breeding and, therefore, were not present at the colony in November/December 2018. Nevertheless, the possibility that these two breeding birds were successful breeders that we did not detect and recapture cannot be excluded. First, the colony counts at least 12500 breeding pairs (Fretwell et al. 2012, Richter et al. 2018a), which makes visual detection difficult. Second, days of harsh weather conditions prevent binocular checks, sometime for several days in a row. Late chick-rearing emperor penguins spend only few hours at the colony (Robertson 1991), 22.5 hours in average for birds from this study, thus it is possible that we did not manage to recapture birds that were actually successful breeders.

We interpret the low number of successful breeders (1 over 3 or 5 that attempted a reproduction) amongst equipped birds as the consequences of the additional costs induced by the attachment technique to glue the device directly on the feathers, and thus reduced chance for successful breeding. In tagging procedures, the ethical principle of *Refinement* from the Three Rs (Russel and Burch 1959), i.e. the use of methods which decrease any adverse effect, should apply. Thus, we claim that the loss of the device and resulting consequences for the birds are unacceptable and that our findings combined with the ones from Wilson et al. (1997b) should prevent further use of glue directly on the birds feathers for long-term deployment on penguins as it is currently practiced. Instead, we propose an alternative technique.

III.5.2.3. Long-term deployment: back-taped-epoxied loggers

Due to the results of the long-term deployment performed in 2018 as highlighted above, we adapted the deployment methodology for the 2019 deployment. Logistical constraints forced us to leave the field before the first moulting adult emperor penguin on site had fully moulted. We therefore focused on a second long-term deployment objective of our research project on the distribution at sea according to the age-class. We employed the back-taped-epoxied technique on juveniles, who so far had only been tagged using the back-glued method so far (Table 9).

Three of the juveniles (40%) retained their device for an entire year, thus achieving the longest duration of back-mounted logger deployment possible in penguins. The previous longest durations recorded for juvenile emperor penguins were of 344, 298 and 271 days (Labrousse et al. 2019b) with one bird (6% of the deployments) approaching the one year length duration. The mean duration of our long-term deployments (233 ± 108 days) with the taped-epoxied technique is longer than any previously reported on juvenile or adult emperor penguins (Table 9). Therefore, we are confident that the technique presented is a significant improvement for tracking of penguins and understanding their activities at sea.

Some of the previous studies using glue on juveniles approached long-term attachment duration. Nevertheless, in addition to the possible loss of feathers and insulation previously discussed, the glue has the potential to cause thermal skin burns (Walker et al. 2012). Juveniles are more vulnerable than adults as their foraging skills (including their ability to dive, to capture prey, and to find productive feeding grounds) are not yet fully developed, and their experience to escape predators is also minimal (Wanless et al. 2007, Orgeret et al. 2016, Enstipp et al. 2017). The additional cost induced by a glued device may negatively impact the survival of the juveniles during their first months in their new marine environment that they experience for the first time. As a result, for studies requesting the deployment of back-mounted devices on penguins for long-term duration, the use of glue on feathers should be entirely avoided, and we recommend to use instead a mix of Tesa® tape strips (feathers' side) and epoxy (on the strips covering the device) to reinforce adhesion.

We did not show that this attachment will last on adult emperor penguins as long as for juveniles. An early departure from the field due to logistical constraints prevented us to deploy this new technique on fully moulted adult emperor penguin. Adult emperor penguins experience very harsh environmental conditions on the sea ice, especially at their breeding site, during winter with temperatures below −50°C and wind speeds above 150 km/h at Atka Bay (Richter et al. 2018a). Mean deployment durations on adults are less than six months (Table 9) and need to be improved to cover the entire breeding cycle to justify the disturbance. We are convinced that new techniques should be tested such as the more efficient and less impacting one presented in this study for juveniles.

III.5.2.4. Long-term deployment: leg-banded loggers

We developed and tested a leg-band TDR mount to enable year-round deployments on adult emperor penguins. The deployed leg-band TDR mount was the first to successfully collect high frequency (1 Hz), pressure and temperature data in this species during the whole year. This data will allow a detailed analysis of foraging activities and water column exploitation over a full year for the same birds.

Leg-band mounted devices had already been deployed on penguins (Bost et al. 2009b, Thiebot and Pinaud 2010, Ballard et al. 2010, Dunn et al. 2011, Ratcliffe et al. 2014, Thiebot et al. 2019), but not yet on the emperor penguin species. Often, the condition of the birds at retrieval are not mentioned, however, some of the studies reported similar leg irritations (Dunn et al. 2011, Ratcliffe et al. 2014; T. Raclot pers. com.; Houstin, Fournier, Le Bohec, unpublished observations) as the ones we observed in this study. The commonly accepted flying bird banding technique is also known to cause unintentional damage like sores, inflammation, or even loss of feet in extreme cases (Pierce et al. 2007, Griesser et al. 2012, Costantini and Møller 2013), thus the irritations observed here can be considered as a minor impact.

We suggest that the use of a non-continuous heat-shrink tubing and the glue around the head of the rubber cable tie created a small ledge in the otherwise smooth surface that irritated the birds' leg-skin. From this observation, we have designed an improved version for the second season (Additional file 13), which could not be tested due to early departure from the field site. The continuous heat-shrinkable sheath in the updated bracelet attachment will likely reduce friction between the leg and the bracelet and ideally avoid skin irritation. If feathers are still lost, we expect the tibiotarsus to be less irritated and the occasional development of sores prevented. To prevent the formation of glue flakes, glue will only be applied inside the cable tie's closure, with parsimony, and not around the whole head.

At retrieval, the mounting did not show any damage or sign of wears and is expected to last several years before the elastomeric cable tie breaks. Consequently, before deploying such a system, a strategic plan for its retrieval is crucial. Emperor penguins are non-nesting seabirds, breeding freely on sea ice within a mobile colony (Richter et al. 2018a), which makes the recapture of birds difficult, especially after more than one year when the annual moult removed any externally painted-markings. Due to their PIT-tag, all birds manipulated can be life-long identified by automatic detection systems, without requiring recapture or visual observation (Gendner et al. 1992, 2005, Le Bohec et al. 2007) and without long-term deleterious effects of flipper-banding for life (Gauthier–Clerc et al. 2004, Dugger et al. 2006, Le Maho et al. 2011). Such automatic detection systems have been successful at detecting emperor, Adélie and king (*Aptenodytes patagonicus*) penguins over the last years at the Pointe Géologie archipelago and Crozet and Kerguelen archipelagos (Le Bohec, Houstin, Chatelain, Courtecuisse, unpublished observations; Cristofari et al. 2018). Such a system will be deployed at Atka Bay colony the next coming season to improve our retrieval ratio of 50%, while the ones for nesting birds stand between 60 to 90% (Bost et al. 2009b, Ballard et al. 2010, Thiebot et al. 2011a, 2015, Dunn et al. 2011, Ratcliffe et al. 2014). This technological improvement will allow us in the years to come to recapture birds even after several years of deployment like for nesting birds (Ratcliffe et al. 2014, T. Raclot pers. com.; Houstin, Fournier, Le Bohec, unpublished observations).

Specifically with this bracelet technique, multi-year deployments might be considered. Scientific programmes running in Antarctica are not always able to return several years in a row, and this technique of deployment offers some flexibility. Solutions still need to be developed for communicating devices that need to get out of water regularly to send or receive telemetry (GPS, ARGOS) or for biologgers that would record too noisy data when positioned on the leg. However, for small data loggers, that are able to record environmental variables (e.g. hydrostatic pressure, water conductivity and temperature, environmental luminosity) on a multi-year scale (Enstipp et al. 2017, 2019), the leg-band technique is an interesting alternative.

III.6 Conclusions

The deployments presented in this study deliver long-term biologging data that provide highly valuable insights about emperor penguins’ distribution in the Weddell Sea and in the Atlantic sector of the Southern Ocean, where they had never been studied before and are essential for assessing the adaptive potential of the species globally. Ethical concerns raised by the use of measuring devices on wild animal are not new (Wilson and McMahon 2006) and a recent review (Forin-Wiart et al. 2019) addressed the current pros and cons on attachment issues. To ensure data is of exemplary quality from a scientific and ethical point of view, the potential deleterious effects of deployment procedures (capture-attachment-recapture) must be assessed and mitigated.

Emperor penguins have been equipped with loggers over the last thirty years, however, there is no specific methodological publications either on the critical “how” question nor on detailed capture and recapture processes. Attachment procedures are occasionally more detailed but with contrasting results of deployment durations and no conclusions about the outcomes for the birds and the devices.

This study is the first to provide such highly detailed and proven procedures to capture/recapture and externally attach telemetry devices on emperor penguins. We, therefore, consider this study as major advancement by (i) stating clearly the impact of using glue for biologging device attachment on penguins, not only emperor penguins, (ii) helping to assess long-term loggers loss reasons (notably ARGOS transmitters), (iii) presenting two customised less invasive attachment techniques of biologging devices on emperor penguins in detail, and (iv) explicitly providing techniques to capture and handle emperor penguins with a limited amount of disturbance as well as a maximum of safety and efficiency. This publication is intended to serve as a resource to facilitate future research on this iconic species, and urge researchers to share their improvements in order to keep implementing a high standard framework for the study of emperor penguins.

This study also encourages researchers and journals to give more exposure to fieldwork methodology in scientific publications not specifically methodology oriented, in particular to techniques developed and tested but not successful in the field. We are convinced that too much time and resources are allocated to the development of techniques already tested but not shared because of their failure. Tests, errors and failures are inherent of research and should be, to some extent, valued as significant results; a practice that would benefit to both scientists and animals.

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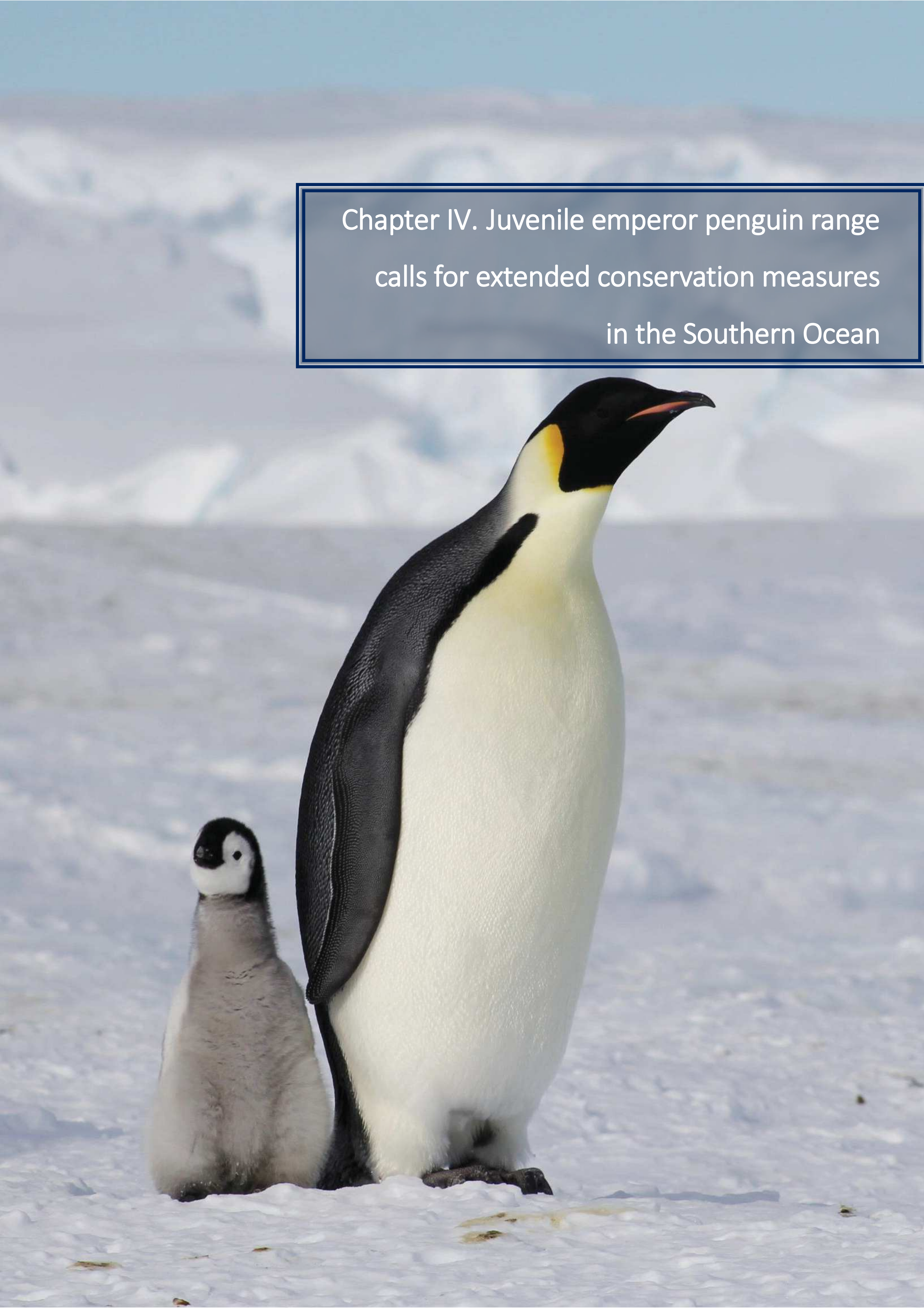
Availability of data and material

All data generated or analysed during this study are included in this published article and its supplementary information files available in the "Publishing Network for Geoscientific & Environmental Data" (PANGAEA) via https://doi.pangaea.de/10.1594/PANGAEA.913447.

Additional files list

- ✓ Additional file 1 (.pdf): Table S1. General information on the loggers deployed including the logger type, name, dimensions and weight, as well as the manufacturers name and location (Table 4 of this manuscript)
- ✓ Additional file 2 (.mp4): Movie S1. PIT-tagging of an adult emperor penguin
- ✓ Additional file 3 (.mp4): Movie S2. Capture of an adult-chick pair
- ✓ Additional file 4 (.mp4): Movie S3. Weddell seal disturbance on the emperor penguin colony
- ✓ Additional file 5 (.mp4): Movie S4. Release of an adult-chick pair
- ✓ Additional file 6 (.mp4): Movie S5. Capture of a single adult with the crook
- ✓ Additional file 7 (.mp4): Movie S6. Adult emperor penguin handling
- ✓ Additional file 8 (.mp4): Movie S7. Back-taped GPS deployment
- ✓ Additional file 9 (.pdf): Fig. S1. Marking of an emperor penguin with a painted number (Fig. 32 of this manuscript)
- ✓ Additional file 10 (.mp4): Movie S8. Back-taped TDR deployment
- ✓ Additional file 11 (.pdf): Fig. S2. Adult emperor penguin at the end of its moult (Fig. 34 of this manuscript)
- ✓ Additional file 12 (.mp4): Movie S9. Back-taped-epoxied logger deployment - epoxy spreading
- ✓ Additional file 13 (.pdf): Slideshow S1. Leg-banded TDR mounting manual
- ✓ Additional file 14 (.pdf): Slideshow S2. Leg-banded TDR deployment and recovery

Chapter IV. Juvenile emperor penguin range calls for extended conservation measures in the Southern Ocean



Juvenile emperor penguin range calls for extended conservation measures in the Southern Ocean

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IV.1 Abstract

To protect the unique and rich biodiversity of the Southern Ocean, conservation measures such as marine protected areas and fishery management zones have been implemented. Based on the known habitat distributions of key species of the ecosystems including emperor penguins and other top predators, the establishment of several additional protection zones are currently being considered. However, the presence of such species at sea is often insufficiently sampled. Indeed, current distribution models focus on the habitat of adult animals and neglect that immatures and juveniles can inhabit vastly different areas. Here, we show that conservation efforts in the Southern Ocean are insufficient for ensuring the protection of highly mobile species like the Emperor penguin. We find that juvenile emperor penguins spend the vast majority (~90%) of their time outside the boundaries of proposed and existing marine protected areas, and that their distribution extends up to 1500 km north of the habitat range as defined by the International Union for Conservation of Nature (IUCN) that curates the Red List of Threatened Species. We argue that for successful strategic conservation planning based on long-lived sentinel and umbrella species such as seabirds and marine mammals, the habitat range of all age classes must be considered.

IV.2 Introduction

Anthropogenic environmental changes lead to upheaval even in remote and apparently untouched ecosystems such as the Antarctic and its circumpolar Southern Ocean. Top marine predators such as seabirds and marine mammals play a pivotal role in marine ecosystems (Hammerschlag et al. 2019, Pimiento et al. 2020), and any disruptions in their abundance and distribution have a major impact on the ecosystem functioning and resilience (Myers et al. 2007, Graham et al. 2018). At the same time, top predators are key indicators of the ecosystem's health because of their high position in the trophic cascade and the vast, ocean basin-scale habitat of individual animals (Maxwell et al. 2013, Hazen et al. 2019, Hindell et al. 2020). Thus, they react particularly sensitive to disturbances in the food web and are therefore important bioindicators of environmental changes. The health, abundance and distribution of top marine predators are consequently key metrics in ecosystem-based management, e.g. for the designation and the design of marine protected areas and systematic conservation planning (Ronconi et al. 2012, Ballard et al. 2012, Maxwell et al. 2013, Hays et al. 2019).

Effective conservation plans require comprehensive consideration of the complete at-sea distribution of the species, including each life-history stage (Carneiro et al. 2020). However, the distribution of juvenile and immature animals, which are an essential part of the total population, is difficult to assess and is therefore often neglected. This is especially true for polar ecosystems, where remoteness and the extreme environmental conditions induce technical and logistical constraints for data collection (Fedak 2013).

Polar ecosystems currently experience significant impact due to global changes (Stark et al. 2019). Measurable negative effects on polar wildlife have already occurred, such as population decreases of numerous seabird species (Trivelpiece et al. 2011, Barbosa et al. 2012, Ropert-Coudert et al. 2018), including the complete loss of colonies of one of the most emblematic species of the Antarctic, the Emperor penguin ((*Aptenodytes forsteri*); Trathan et al. 2011a, Fretwell and Trathan 2019). The vanishing of these colonies has been attributed to strong El Niño events, rise in local mean annual air temperature, strong winds, and/or decline in seasonal sea ice duration. Climate change is also expected to result in human access to new ice-free fishing areas (Rintoul et al. 2018, Rogers et al. 2020), whereby seabirds and marine mammals will have to compete for food with industrial fisheries and may even become by-catch (González-Zevallos and Yorio 2006, Trathan et al. 2015, Crawford et al. 2017). The accumulation of anthropogenic pressures on these fragile ecosystems urgently requires effective protective measures (Chown and Brooks 2019, Brooks et al. 2020a).

The Southern Ocean is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The CCAMLR's mandate includes the implementation of direct conservation measures such as the establishment of Marine Protected Areas (MPAs) and the regulation of the fishing industry, through quota allocations and gear limitations. Conservation measures within the CCAMLR are adopted on the basis of the best scientific data available, amongst which are the distribution and demography of marine predators (CCAMLR 2018a, 2019a, Teschke et al. 2019). Similarly, the International Union for Conservation of Nature (IUCN)'s Red List of Threatened Species is built upon a range of scientific data that help to define the habitat range of each species, which serves as a reference for political decisions on the implementation of conservation measures. Consequently, an uncertain distribution range might lead to inadequate decisions for the future protection of the species.

As of today, 12% of the waters inside the CCAMLR boundaries are protected (Brooks et al. 2020a). For years, CCAMLR members have been discussing the implementation of the three new MPAs adjacent to the Antarctic continent, without reaching agreement. If these new MPAs are eventually established, this would increase the percentage of the protected waters of the Southern Ocean to only 22%, which is insufficient compared to the 30% protection target as recommended by the IUCN to ensure an ecologically representative and well-connected systems of MPAs. Even then, assessments and recommendations are based on limited and partially flawed data. For instance, in the Atlantic sector of the Southern Ocean, which is home to one-third of the global emperor penguin population, very little is known about their at-sea distribution since no tracking studies have been conducted in this region.

The emperor penguin population is currently estimated at ca. 270 000 breeding pairs spread over 61 identified colonies around the Antarctic continent (Trathan et al. 2020, Fretwell and Trathan 2020). The species is severely threatened by global warming and expanding fishing activities in the Southern Ocean (Trathan et al. 2015, 2020), facing the risk to be nearly extinct within this century 100 years (Jenouvrier et al. 2019). The most effective action to protect emperor penguins from impacts of climate change would be a reduction in anthropogenic greenhouse gas emissions (Jenouvrier et al. 2019, Trathan et al. 2020). Also the establishment of marine protected areas across its range would help to mitigate the anthropogenic impact (Trathan et al. 2020).

Marine conservation efforts need spatially-explicit movement data throughout each life-history stage, but little is known about the early life at sea of emperor penguins, even though this is a critical phase in their life and crucial for the viability of the global population (Jenouvrier et al. 2005). To date, only 48 juvenile emperor penguins have been tracked in total, and at-sea distribution data of juveniles are available only for the Ross Sea (10 animals; Kooyman and Ponganis 2007) and for East Antarctica (38 animals; Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b). However, for the designation of MPAs, it is fundamental to know their distribution at the circum-Antarctic scale (Hays et al. 2019, Carneiro et al. 2020, Hindell et al. 2020).

To bridge this gap in knowledge, we equipped eight 6-months-old emperor penguin chicks with ARGOS satellite platforms that sent the locations of the birds several times each day. We also incorporated into our analysis the distribution of all previously tracked juvenile emperor penguins (Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b) in order to assess the habitat used by the juvenile emperor penguin at a global scale and contribute towards a fuller assessment of the species distribution to be incorporated into conservation planning.

IV.3 Material and Methods

IV.3.1. Study site and instrumentation

Our study was conducted at the Atka Bay emperor penguin colony (70°37’S, 08°09’W) in close vicinity (~ 10 km) to the German Antarctic research base “Neumayer Station III”. In January 2019, we equipped eight 6-month-old chick emperor penguins with satellite communicating SPOT-367 ARGOS platforms (Wildlife Computers, Redmond, WA 98052, USA). The ARGOS platforms were programmed to transmit their identification every day at 4, 6, 10, 16, 19 and 21:00 GMT, corresponding to time points with optimum ARGOS satellite coverage over the Weddell Sea area (ARGOS CLS, Toulouse, France). Fledglings with no more down on their back (Fig. 33c) were captured on their departure to sea with a corral (Fig. 31).

To minimize drag, ARGOS platforms (107*18*21 mm, 45g, Table 4) were deployed on the lower back of the birds (Culik and Wilson 1991, Bannasch et al. 1994). The streamlined devices were attached to the feather with adhesive tape (Tesa® tape 4651, Beiersdorf AG, Hamburg, Germany) and secured with three cable ties (Panduit PLTM1.5M-C0 142*2.6mm, Panduit Corp, Illinois, USA). We then applied epoxy glue (Loctite EA 3430, Loctite, Henkel AG., Düsseldorf, Germany) on the mounting to increase waterproofness and robustness (Wilson et al. 1997b, Pütz et al. 2014).

IV.3.2. Estimation of the at-sea distribution of juvenile emperor penguins from the Atka Bay colony

IV.3.2.1. Location filtering

ARGOS locations are associated with spatial error ellipses. These spatial errors can range from a few hundred metres to several kilometres (Costa et al. 2010b, CLS 2016). Erroneous locations were filtered out using a speed filter from the R package ‘*argos filter*’ (Freitas et al. 2008) with the maximum travel speed fixed at 15 km/h following similar studies on emperor penguins (Wienecke and Robertson 1997, Labrousse et al. 2019b).

IV.3.2.2. Interpolation of locations at a regular time step

We used a state-space modelling approach (Johnson et al. 2008) to estimate hourly locations. Specifically, a Kalman filter, which accounted for location error, was applied using the R package '*crawl*' (Johnson 2014), and Continuous-time Correlated Random Walk (CRW) models were used to predict locations at a regular time step interval of 1 h (Johnson et al. 2008, Heerah et al. 2019).

IV.3.2.3. Estimation of the colony-specific distribution area for juvenile emperor penguins

In addition to the eight birds tracked in our study, 48 juvenile emperor penguins from four different colonies have previously been tracked (Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b); see Table 12 for the details on the colonies. Data of these previously acquired bird journeys are available as maps in the respective publications. We georeferenced these tracking maps using the QGIS software. We subsequently plotted the main corner points encompassing the tracks of all birds from each colony. We obtained the distribution of juvenile emperor penguins by computing the concave hull envelope for each dataset (Fig. 27) using the '*ConcaveHull'* plugin (Moreira and Santos 2007). Envelopes from the same colony (Thiebot et al. 2013, Labrousse et al. 2019b) were merged to consider only one polygon per colony (referred to as distribution area), including one for the Atka Bay colony. The size of each distribution area was calculated with the '*raster'* function from the R package (Hijmans and van Etten 2020) and is reported in Table 12. Due to the significant overlap of Auster and Taylor Glacier juvenile distribution (Wienecke et al. 2010) and the close (132 km) vicinity of the two sites (Ancel et al. 2017), for visualization purposes, the tracks of the birds from Auster and Taylor Glacier colonies are shown in the same polygon in Fig. 36. However, the distribution areas were computed separately for each colony.

IV.3.3. Ecological features

The locations of the Southern Ocean fronts and the Antarctic Circumpolar Current boundaries (ACC; Orsi et al. 1995) were downloaded from https://gis.ccamlr.org (CCAMLR 2019b).

The bathymetry at one-minute horizontal spatial resolution was obtained from the ETOPO1 Global Relief Model provided by the NOAA National Geophysical Data Center (Amante and Eakins 2009).

Sea ice concentrations (ranging from 0 to 100%) were obtained from Advanced Microwave Scanning Radiometer (AMSR-2) satellite estimates of daily sea ice concentration at 3.125 km resolution from the University of Bremen (https://seaice.uni-bremen.de/data/amsr2/, Spreen et al. 2008b). The sea ice edge contour was defined by the 15% sea ice concentration isocline (Fig. 38; Cavalieri 1991, Stammerjohn and Smith 1997).

The maximum and minimum median sea ice extent between 1981-2010 presented in Fig. 36 were obtained from the National Snow and Ice Data Center NSDIC (Fetterer et al. 2016) implemented in the '*Quantarctica3'* package (Matsuoka et al. 2018) of the QGIS software.

IV.3.4. Management features

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) planning domains and existing Antarctic Marine Protected Areas (MPAs) were obtained from https://gis.ccamlr.org (CCAMLR 2019b). The proposed Weddell Sea Marine Protected Area boundaries (WSMPA; CCAMLR 2018a) and the proposed East Antarctic Marine Protected Area boundaries (EAMPA; CCAMLR 2019a) were obtained from www.mpatlas.org (Marine Conservation Institute 2020). The Domain 1 MPA proposal (CCAMLR 2018b) was drawn from www.mpatlas.org (Marine Conservation Institute 2020). The South Georgia and South Sandwich Islands Marine Protected Area (SGSSIMPA) and the sub-Antarctic MPAs boundaries were downloaded from www.protectedplanet.net (UNEP-WCMC 2020).

The International Union for Conservation of Nature (IUCN)'s range of the Emperor penguin species was obtained from www.iucnredlist.org (Birdlife International 2018).

IV.3.5. Assessing the overlap between bird distribution and management zones

The average residence time that each of the birds equipped in our study spent inside existing or proposed management zones of the Southern Ocean was computed on a daily, weekly and monthly basis, and averaged over the total tracking period.

We tested if the observed monthly-averaged residence time changed significantly over the course of a year using the Kruskal-Wallis rank sum tests. For all tests, the significance threshold was set at $p=0.05$. Statistical analyses were performed using the software R v. 3.5.0 (R Core Team 2018) and QGIS v. 2.18.18 (QGIS Development Team 2017) with the data package '*Quantarctica3*' (Matsuoka et al. 2018).

IV.4 Results

Tracking data from our study show that juvenile emperor penguins from the Atka Bay colony commonly travel beyond 50°S (the lowest recorded latitude was 48.37°S), which is 600 km further north than previously recorded (Table 12). Two birds reached the sub-Antarctic South Georgia and South Sandwich Islands' region in late June and stayed there at least until July when their ARGOS platforms stopped transmitting, demonstrating that the presence of juvenile emperor penguins in sub-Antarctic area should be considered not an extreme but regular behaviour, at least in the Atlantic sector of the Southern Ocean. All tagged juveniles reached the Southern Boundary of the Antarctic Circumpolar Current (ACC), and 5 of out of 8 birds remained for prolonged time periods (> 46 days) between the southern ACC boundary and the Antarctic Polar Front where Antarctic waters meet the relatively warmer sub-Antarctic waters. One bird even travelled north of the Polar Front. The penguin tracks over a full year (polygon encompassing the area covered by the tracks) covered an area of 5.1 millions km^2 (Fig. 36 and Fig. 37, Table 12), nearly 1.4 times larger than the largest previously reported distribution of juvenile emperor penguins from a breeding colony Table 12).

Table 12. Tracking studies of juvenile emperor penguins at sea.

Colony	Colony coordinates	Colony population estimate*	Number of birds	Mean tracking duration (days)	Maximal distance from colony (km)	Northernmost latitude reached	Distribution area (millions km^2)	% in ACC	% in SO - Treaty limit	% in IUCN	% in CCAMLR	% in MPAs	Publication
Cape Washington	74.58 S, 165.48 E	11808	10	64	2845	56.9°S	1.7	54.6	73.5	14.6	73.5	4.4	Kooyman et al. 2007
Pointe Géologie	66.66°S, 140.00°E	2456	21	171	3503	53.76°S	3.6	75.9	62.7	35.8	98.0	13.5	Labrousse et al. 2019b Thiebot et al. 2013
Auster	67.38°S, 64.03°E	7855	10	121	2343	56.25°S	3.3	60.7	79.1	61.4	100	6.7	Wienecke et al. 2010
Taylor Glacier	67.47°S, 60.88°E	519	7	113	1570	54.23°S	1.7	87.3	67.7	43.4	100	9.3	
Atka Bay	70.62°S, 08.15°W	9657	8	221	2474	48.37°S	5.1	19.3	60.7	51.4	99.2	16.3	This study
Mean	/	*6459*	*11.2*	*138*	*2547*	/	*3.1*	*59.6*	*68.7*	*41.3*	*94.1*	*10.0*	/
sd		*4798.3*	*5.6*	*59.9*	*707.9*		*1.4*	*25.9*	*7.6*	*17.7*	*11.6*	*4.9*	

Colony details (location and size), tracking survey metrics (duration, distance, distribution), percentage of the distribution area that is falling within the main conservation and management areas (IUCN, CCAMLR, MPAs), and oceanographic features of the Southern Ocean (SO/Treaty limit, ACC). * Number of breeding pairs (Fretwell and Trathan 2020). ACC: Antarctic Circumpolar Current; SO: Southern Ocean (*i.e.* at the parallel of 60°S as defined in the Antarctic Treaty); CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources; IUCN: International Union for Conservation of Nature; MPAs: Marine Protected Areas.

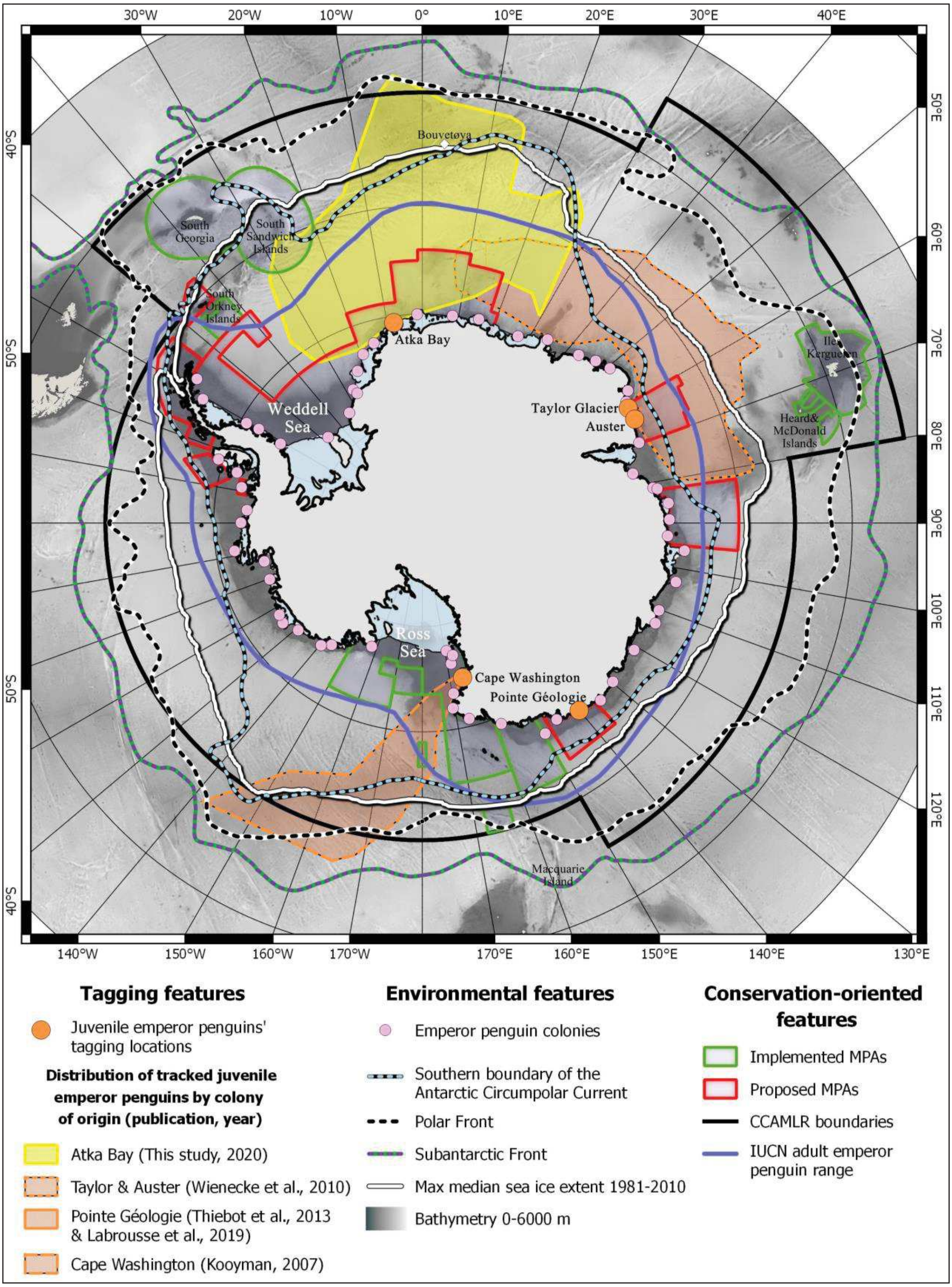

Fig. 36. Overlap between existing and planned conservation zones and the distribution of juvenile emperor penguins tracked to date in the Southern Ocean. Distribution areas of juveniles are indicated by coloured polygons. MPAs: Marine Protected Areas; CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources; IUCN: International Union for Conservation of Nature.

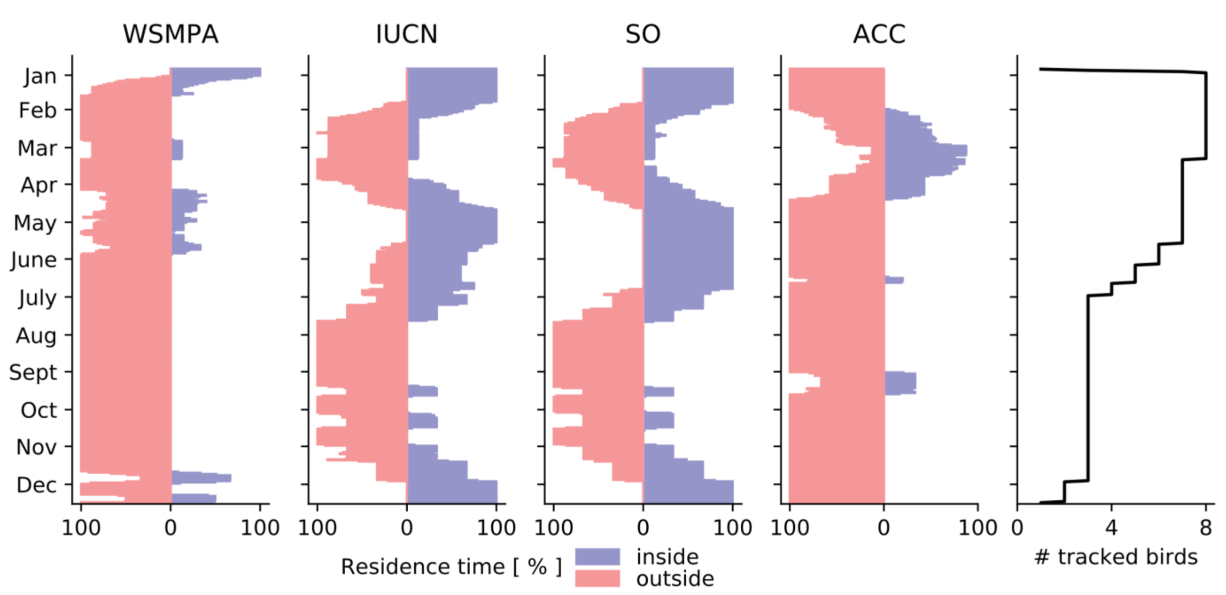

Fig. 37. Proportion of time that the eight tagged juvenile emperor penguins from the Atka Bay colony spent either inside or outside the main conservation and management bodies of the Atlantic sector of the Southern Ocean. Daily average across all individuals computed over hourly data points. WSMPA: Weddell Sea Marine Protected Area; IUCN: International Union for Conservation of Nature; SO: Southern Ocean (i.e. at the parallel of 60°S as defined in the Antarctic Treaty); ACC: Antarctic Circumpolar Current.

The seasonal travel pattern of the juvenile penguins from our data set resembles those of the other colonies. At the end of the summer, after leaving their colony of origin, juveniles migrate northward towards and into the Antarctic Circumpolar Current where, in our study, they remained on average for 37 ± 24 days (mean ± SD). Juvenile emperor penguins commonly range outside the limits of the Southern Ocean (*i.e*. the parallel of 60°S as defined in the Antarctic Treaty, hereafter referred to as SO-Treaty) with some birds wandering outside the CCAMLR boundaries (Fig. 36 and Table 13). In late fall, i.e. end of March/April, they migrate southward towards the pack-ice where they spent the winter (Fig. 37).

The individual juvenile emperor penguins from our study spent only 51.1 ± 13.3 % of their time inside the species' habitat range defined by the IUCN, which has been established based on the estimated adult distribution. Moreover, the percentage of time spent inside the designated habitat range showed large and highly significant variations across months (p<1e-05; Fig. 37). In deep winter (in August), all tracked juvenile penguins were outside the IUCN range, whereas in January and May, they were mostly within the IUCN range. The most distant location occurred at 1260 km north of the IUCN range. Data from other colonies followed a similar pattern (Table 12), whereby 38.8 ± 19.4% of the distribution areas of juvenile emperor penguins fall within the IUCN range. Juveniles from Cape Washington colony in the Ross Sea reached the furthest distance ever recorded (1500 km) outside the IUCN range.

Table 13. At-sea distribution metrics for the 8 juvenile emperor penguins equipped with ARGOS platforms at Atka Bay in January 2019.

ID	Start trip	End trip	Trip duration (days)	Max distance from colony (km)	Date of max distance from colony	Yearly travelled distance[1] (km)	Mean daily distance[1] (km)	%[2] in ACC	%[2] in SO - Treaty limit	%[2] in IUCN	%[2] in WSMPA	%[2] in SGSSI MPA
65787	11/01/19	29/12/19	352	2287	21/03/19	15593	44.3	14.4	59.3	40.1	16.9	0
65788	13/01/19	03/07/19	171	2390	10/04/19	NA	NA	28.8	44.4	36.6	10.7	5.6
65789	12/01/19	24/03/19	71	1484	26/02/19	NA	NA	0	18.1	81.6	29.8	0
65790	12/01/19	12/12/19	334	2176	05/04/19	13452	40.3	16.8	54.2	42.8	5.3	0
65791	12/01/19	01/06/19	140	1518	20/03/19	NA	NA	11.1	17.5	72.0	11.0	0
65792	11/01/19	13/07/19	183	1519	20/03/19	NA	NA	6.5	28.8	49.8	12.7	7.5
65793	12/01/19	18/06/19	157	2149	04/03/19	NA	NA	41.3	47.7	49.4	6.3	0
65794	10/01/19	01/01/20	356	2474	07/03/19	18326	51.5	19.3	48.5	50.6	5.3	0
Median (date) or Mean values	*12/01/19*	*08/07/19*	*220.5*	*1999.6*	*20/03/19*	*15790.3*	*45.4*	*18.0*	*55.3*	*48.9*	*10.6*	*1.4*
sd	*0.9*[3]	*109.8*[3]	*110.4*	*421.3*	*15.1*[3]	*2443.0*	*5.7*	*11.3*	*15.1*	*13.3*	*7.5*	*3.8*

[1] Yearly travelled distance was computed using one location every 6 hours (in km), [2] % of time spent during the trip duration, [3] in days. ACC: Antarctic Circumpolar Current; SO: Southern Ocean (*i.e.* at the parallel of 60°S as defined in the Antarctic Treaty); IUCN: International Union for Conservation of Nature; MPA: Marine Protected Area; WSMPA: Weddell Sea MPA.

Based on our and previous tracking data, the habitat range defined by the IUCN is severely underestimated. A similar argument can be made also for the current and planned Marine Protected Areas discussed by the CCAMLR, as on average only 10.0 ± 4.9% of the estimated distribution areas fall within the MPAs' boundaries (Table 12). For instance, juvenile emperor penguins from the Atka Bay colony, which is located inside the proposed Weddell Sea Marine Protected Areas (WSMPA, the largest currently proposed MPA in the Southern Ocean), left the MPA's boundaries after 9 ± 4 days of northward migration in January and remain only 10.6 ± 7.5% of their time inside the boundaries with significant variations across months (p<1e-04; Fig. 37). Only in January before they left the colony, and in December, when they returned to the Antarctic continent to moult, did they spend a significant amount of time inside the WSMPA (47.9 ± 23.8 % and 31.1 ± 13.4 %, respectively). All tagged penguins were outside the WSMPA's boundaries in February and between July and November (Fig. 37).

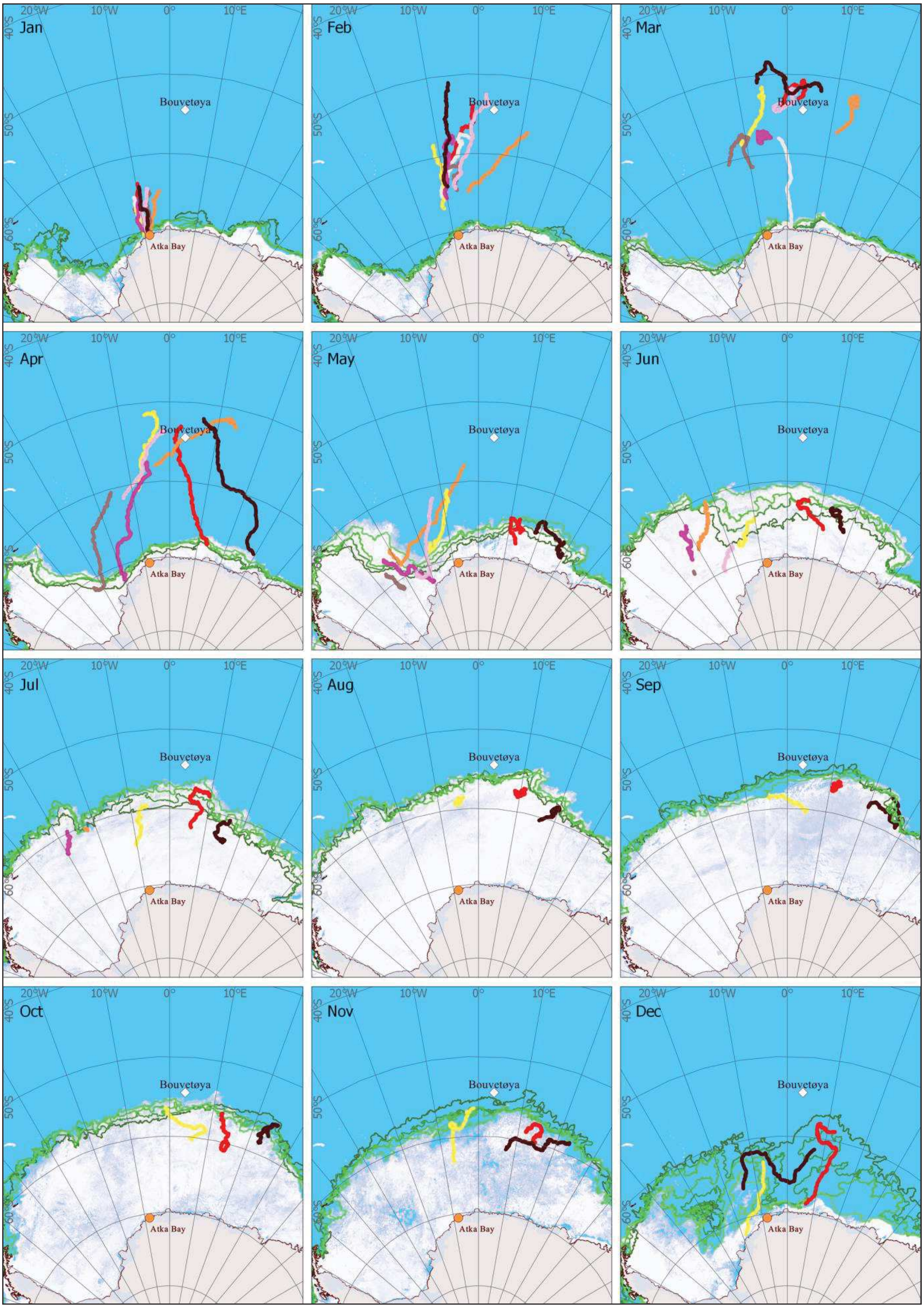

Fig. 38. Monthly tracks of the 8 juvenile emperor penguins tagged at Atka Bay in 2019. Sea ice concentration is shown for the last day of each month. Sea ice extent is indicated by the green lines for the 4th, 11th, 18th, 25th of each month as indicated by the gradient colour scale from dark green (4th) to light green (25th).

IV.5 Discussion

As a top marine predator, emperor penguins are a key umbrella species of the Southern Ocean's ecosystem (Le Bohec et al. 2013). Monitoring their population size and distribution at sea is therefore essential for the planning of biodiversity conservation measures. The common approach for designating boundaries of marine protected areas focus on protecting breeding birds and colonies (Sherley et al. 2013, Boersma et al. 2019). However, we argue that this is not sufficient and point out that the habitat range of juvenile penguins requires a particularly high level of protection. Juveniles are more vulnerable than adult animals as their foraging skills (including their ability to dive, to capture prey, and to find productive feeding grounds) are not yet fully developed, and their experience to escape predators is minimal (Wanless et al. 2007, Orgeret et al. 2016, Enstipp et al. 2017). Moreover, juvenile survival can have a critical impact on the population dynamics especially in long-lived species (Stearns 1992). Emperor penguins start breeding at the age of 4-5 years old at the earliest, lay only one egg per pair and year, and only have an annual 55% chance to bring a chick to fledging (Jenouvrier et al. 2010). This low fecundity makes the survival of immature individuals, which represent only about one quarter of the total population (Jenouvrier et al. 2005), particularly critical for the recruitment into the breeding population and thus the species viability (Abadi et al. 2017). Moreover, the dispersal behaviour of juveniles - in contrast to adults - is one of the main processes by which long-lived species will be able to adapt to the ongoing rapid environmental change and allow them to explore possible alternative feeding and breeding grounds (Gienapp and Merilä 2018). Therefore, for successful strategic conservation planning, the habitat range of all age classes must be considered.

Our tracking data are the first of its kind in the Atlantic sector of the Southern Ocean and in West Antarctica. Together with the tracking data from four other emperor penguin colonies distributed across Eastern Antarctica (Fig. 36; Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b), our findings reveal that juveniles spend a considerable amount of time outside the species' IUCN range and outside the limits of existing or planned MPAs in the Southern Ocean (Fig. 36, Table 12 and Table 13). Consequently, if protection measures would be based on the current IUCN range, as it stands, it would lead to inadequate and inefficient decisions for the future protection of the species. Furthermore, all studies including ours have found that the ACC area is visited by the vast majority of the tagged juveniles during their first journey after hatching, with some birds swimming as far north as the Antarctic Polar Front, which appears to act as an ecological constraint. The penguins' dispersive behaviour, tied to the most vulnerable stage of their life, leads them outside the SO-Treaty and CCAMLR limits in waters where they are more likely to encounter and compete with fisheries (Fig. 36). In accordance with the CCAMLR's ecosystem-based fisheries management approach, whose effectiveness has been recently questioned (Watters et al. 2020), the presence of this critical fragment of the emperor penguin population must be considered by the CCAMLR when allocating fishing quotas and zones. Noteworthy, several CCAMLR fishing states are lobbying for an increase of the spatial and temporal distribution of catches and fisheries (Cordonnery and Kriwoken 2015, Brooks et al. 2016, Trathan et al. 2018).

From an evolutionary perspective, it is noticeable that the fledglings of the two sister species from the Aptenodytes genus are aiming for the same feeding ground during their first year of life while adults forage in separate ecological niches (Williams 1995). Our tracking data show that the northern part of the range of juvenile emperor penguins overlaps in time and space with the range of juvenile king penguins ((*Aptenodytes patagonicus*); see Orgeret et al. 2019) for tracking details of juvenile king penguins). It is reasonable to think that these findings apply for other sectors of the Southern Ocean with sub-Antarctic islands (Fig. 52).

Most of our current knowledge about the breeding behaviour, life-history and demographic parameters of emperor penguins is based on the monitoring of a single colony at Pointe Géologie, Terre Adélie (Jenouvrier et al. 2005). This and our findings on the distribution at sea highlight the necessity to further compile baseline data for the species and all its life-history stages in presently uncharted regions (especially in West Antarctica, around the Peninsula, and in other parts of the Weddell Sea), to optimize and assess the implementation of future conservation measures on emperor penguins. Such pan-Antarctic data could also answer the current debate about the panmictic status of the Emperor penguin species, i.e. the connectivity between breeding colonies (Cristofari et al. 2016, Younger et al. 2017). The existence of several metapopulations or of a unique population connected around the whole of Antarctica could imply different conservation strategies.

While growing body of evidence indicates the ongoing and near future extinction threats, Trathan and colleagues (Trathan et al. 2020) recently advocated for a reclassification of the Emperor penguin on the IUCN Red List from the current “Near Threatened” status to “Vulnerable” or “Endangered”, as well as a classification of the Emperor penguin as an “Antarctic Specially Protected Species” by the Antarctic Treaty. Our data emphasize the need to include all age-classes and age-specific threats into the classification assessment and into the design of a new strategic framework for conservation in the Southern Ocean (Carneiro et al. 2020, Hindell et al. 2020). In the context of the vast habitat range of emperor penguins and also other marine top predators (Raymond et al. 2015, Staniland et al. 2018, Hindell et al. 2020), we furthermore argue in favour of globally integrated systems of marine protected areas (Hannah 2010). This can be achieved by combining migratory corridors with static and dynamic MPAs (i.e. MPAs that rapidly evolve in space and time in response to changes in the ocean and its users; see details in Maxwell et al. (2015), in order to create an ecological connected network that would provide a robust protection to the Southern Ocean (Brooks et al. 2020a). Without an aggressive effort to introduce effective dynamic management of the Southern Ocean it is virtually certain that Antarctica's biodiversity and its most iconic species will be irrecoverably lost.

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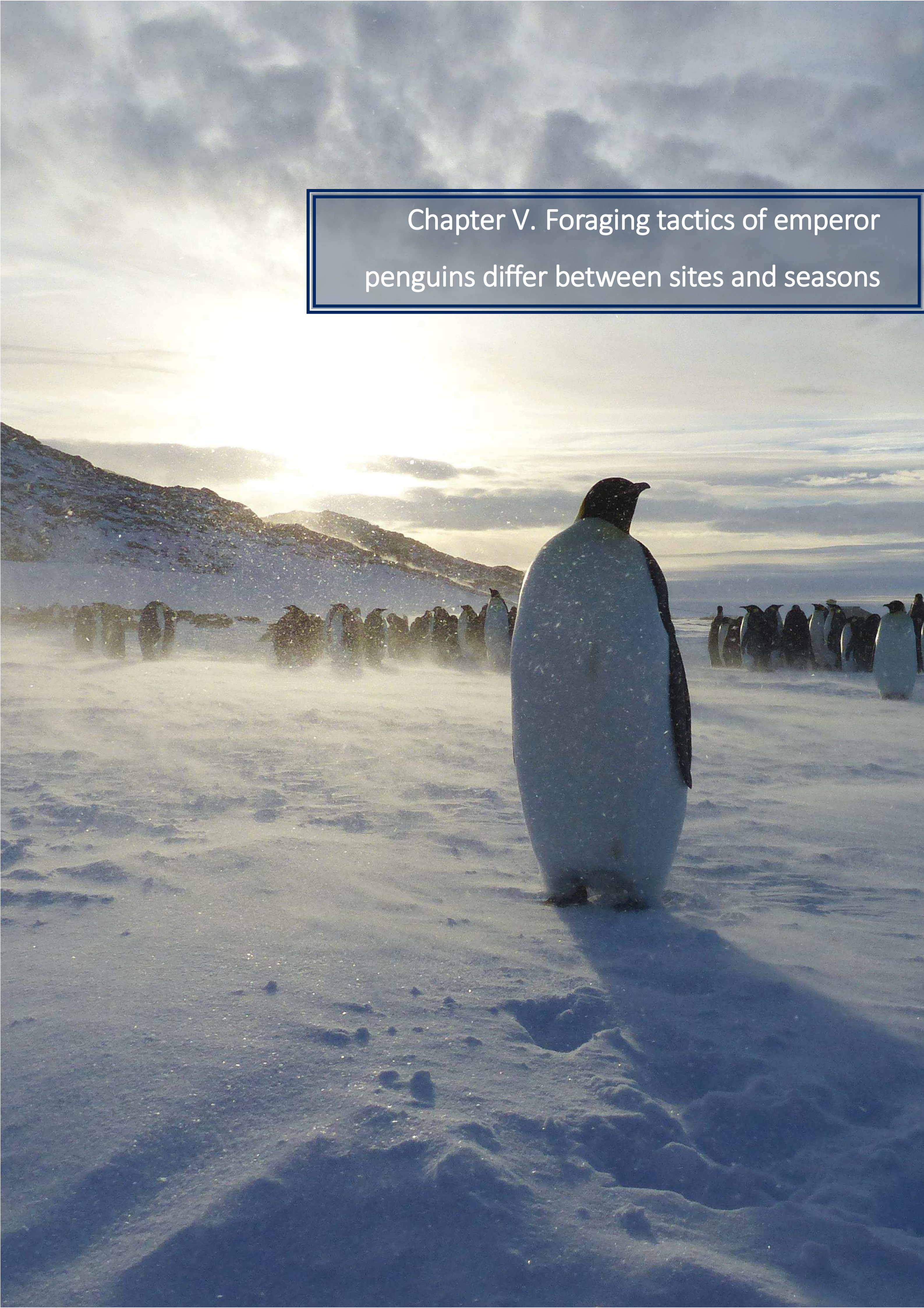
Chapter V. Foraging tactics of emperor penguins differ between sites and seasons



Foraging tactics of emperor penguins differ between sites and seasons

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Contrary to Chapters 3 and 4, the work from Chapter 5 is still in preparation and has not been submitted yet. Here, we present preliminary results and ongoing analyses that will be completed and confirmed.

V.1 Abstract

Despite being one of the most iconic seabird species of Antarctica, knowledge of the distribution at sea and of the fine-scale foraging behaviour of the Emperor penguin is fragmented and limited.

The species is however threatened by the ongoing climate change and the resulting projected sea-ice loss in a very near future around Antarctica. How the species will respond to global change is still uncertain. Acquisition of baseline data on the distribution and activities at sea of the species through the entirety of the life cycle, across all life-history stages, and at different breeding locations around the continent, are required to refine our understanding and the predictive models.

Here, we assessed and revealed the distribution of juvenile and adult emperor penguins in the Atlantic sector of the Southern Ocean throughout the year. We also investigated the fine-scale vertical foraging behaviour of adults from this area. The seasonal distribution and the foraging strategies identified were then compared to data previously collected in an antagonistic environment in the d'Urville Sea region in East Antarctica.

We showed that juvenile and adult emperor penguins from the Atka Bay colony in the Atlantic sector of the Southern Ocean were segregated in time and space throughout the year. We found that chick-rearing adults from Atka Bay colony used a core area 20 times smaller than juveniles and 5 times smaller than post-moult pre-breeding adults from this region. Adults from Atka Bay colony performed shallower dives in average than adults from Pointe Géologie. We also identified a switch in the diving effort of the adults from Atka Bay at the beginning of the summer: they appeared to perform 'day-time diving effort' strategy until end of October, and switch to a 'night-time diving effort' strategy for the rest of the season; a strategy that was not expressed by the adults from Pointe Géologie. These results suggest that different prey items are targeted between the birds from the two localities.

Such baseline information are crucial as they are intended to serve as science-based add-ons for the proposed MPAs around the continent (i.e. in the Weddell Sea and Dronning Maud Land region, in East Antarctica) that have been under intense negotiations for years.

V.2 Introduction

The abundance and distribution of marine organisms is highly heterogeneous over a wide range of spatial and temporal scales (Mann and Lazier 2005). Global change leads to many environmental disruptions for marine organisms (IPCC 2019) that are expected to result, for the very least, in shifts in species' distribution and interaction (Cheung et al. 2009, Poloczanska et al. 2013, Constable et al. 2014, IPCC 2019). However, monitoring changes of all the species that composed an ecosystem is logistically difficult. To address this challenge, ecologists use sentinel species, especially meso- and top predators such as seabirds and marine mammals (Burger 2006, Durant et al. 2009, Hazen et al. 2019), because they often forage over very large oceanic areas and stand near the top of the trophic networks. As such, they are exposed to a wide range of environmental conditions and integrate and amplify the changes occurring at lower levels of the food web over multiple trophic and spatio-temporal scales (Croxall et al. 2002, Frederiksen et al. 2007). The monitoring of top predator species can also help to identify and provide valuable insights into the zones of ecological importance (Block et al. 2011, Raymond et al. 2015, Reisinger et al. 2018, Maxwell et al. 2020, Hindell et al. 2020). As a result, marine predators have been recognised as a crucial component of spatial and ecosystem-based management, such as Marine Protected Area (MPA) design and systematic conservation planning (Ronconi et al. 2012, Maxwell et al. 2013, Hays et al. 2019). Assessing and understanding how marine top predators exploit their environment is therefore of particular interest.

Marine predators are challenging to observe at sea (Hooker et al. 2007). Their underwater behaviour cannot be easily observed while they move in three dimensions (i.e. horizontally and vertically by diving) and over time. As a result, accessing and assessing their movements to investigate their habitat use and preference or their foraging behaviour, require the use of animal-borne devices. The rapid and ongoing progress of biologging technology (Rutz and Hays 2009) in terms of miniaturisation, design optimisation, storage capacity and power consumption (Ropert-Coudert et al. 2009a, Portugal and White 2018) as well as the improvement of the quantity, the quality and the accessibility of remotely sensed data (Palumbi et al. 2003) has led to fundamental advances in ecology of marine predators (Bograd et al. 2010, McIntyre 2014, Roncon et al. 2018). Marine top predators generally feed on patchily-distributed prey resources over a range of spatial scales (Young et al. 2015). By studying simultaneously spatial locations of animals as well as the depth ranges they move in and tied them to the environmental conditions encountered, it is possible to determine the characteristics making areas profitable for foraging predators (Turchin 1991). Advances in technology now allow to examine small-scale movements and fine scale-vertical behaviour that are crucial to apprehend scale-dependent adjustments and foraging decisions of far-ranging predators (Dragon et al. 2012).

Living and feeding from the oceans, seabirds play a major role in the ecosystems, consuming several hundred tons of prey per year (Ballerini et al. 2014, Southwell et al. 2017). Among them, penguins constitute the dominant component of the avian biomass of the Southern Ocean (Llano 1978). Despite being one of the most iconic seabird species of Antarctica, the knowledge on emperor penguins distribution and foraging behaviour is still fragmented. For instance, in the Weddell Sea area, home of 33% of the population (Fretwell et al. 2012, Teschke et al. 2016b), apart from the presence and locations of breeding colonies, very little is known about the horizontal distribution at sea and the fine-scale vertical foraging behaviour of the species (Ancel et al. 1992, Kooyman and Kooyman 1995, Kirkwood and Robertson 1997, Wienecke and Robertson 1997, Zimmer et al. 2007b). As a sea-ice obligate species (Ainley et al. 2005), emperor penguins are particularly threatened by global change (Jenouvrier et al. 2012, 2014, 2019, Trathan et al. 2020), notably to changes in the dynamic of sea ice and its associated food web (Ainley et al. 2010b, Trathan et al. 2011, Constable et al. 2014, Fretwell and Trathan 2019).

How the species will respond to global change is still uncertain (Goetz et al. 2018, Jenouvrier et al. 2019, Trathan et al. 2020). To refine our understanding and improve the power of predictive models, it is necessary to acquire baseline data on the current behaviours and strategies at sea and on land of emperor penguins through the entirety of their life cycle, across all life-history stages, and also at different breeding locations spanning around the continent (Goetz et al. 2018, Trathan et al. 2020). Indeed, specific environmental conditions exist at each emperor penguin colony (i.e. distance to oceanic fronts, persistence of sea ice in time and space, seaward extent of Antarctic continental shelf, presence of specific oceanic currents like gyres, local weather like air temperature, snowfall, wind speed and direction) and may be affected differently by the ongoing and future impacts of climate change. Such heterogeneity is likely to lead to dissimilar responses and various population trajectories between sites (Kooyman and Ponganis 2017, Jenouvrier et al. 2019). Such information could also serve as science-based add-ons for the proposed MPAs around the continent (i.e. in the Weddell Sea and Dronning Maud Land region, in East Antarctica and in Peninsula) that have been under intense negotiations from years (Brooks et al. 2020a) as well as for the establishment of relevant and effective conservation measures in the Southern Ocean for an uncertain future (Teschke et al. 2016a, Trathan et al. 2020, Rogers et al. 2020).

Studies on the emperor penguins' diet suggest an opportunistic feeder through time and space since diet composition varies enormously with time of year and location (see references in Trathan et al.

2020). They can dive up to 564 m (Wienecke et al. 2007) for as long as 32 minutes (Goetz et al. 2018) to prey on pelagic and/or benthic fishes (especially the Antarctic silverfish (*Pleuragramma antarcticum*)), squids (mainly the arrow squid (*Psychroteuthis glacialis*) and the Antarctic neosquid (*Alluroteuthis antarcticus*)), and crustaceans (particularly Antarctic krill (*Euphausia superba*)) (Green 1986, Offredo and Ridoux 1986, Klages 1989, Piatkowski and Pütz 1994, Robertson et al. 1994, Pütz 1995, Kirkwood and Robertson 1997, Cherel and Kooyman 1998, Zimmer et al. 2007a, Cherel 2008). As other penguin species (Wilson 1993, Pütz and Bost 1994, Ropert-Coudert et al. 2006), emperor penguins have been suggested to be visual hunters. Such hypothesis was based on the analysis of the diving patterns of birds during winter, a time of the year during which they dive primarily during the day (Kirkwood and Robertson 1997, Zimmer et al. 2008). The diving activity of those birds increased with the length of the day. Most foraging dives of emperor penguins occur between the surface and 150 m deep and lasts less than 10 minutes (Kirkwood and Robertson 1997, Zimmer et al. 2007b, 2008), even though deepest dives have been documented across different sites (Kooyman and Kooyman 1995, Wienecke et al. 2007, Zimmer et al. 2010). Recent findings suggest that they access their foraging habitat by diving in small openings, including cracks, flaw leads and ephemeral short-term polynyas (Labrousse et al. 2019a). To date, only one study, performed in the Ross Sea region, monitored the diving behaviour of the same individuals (non-breeding birds only) right after the moult and through the winter, but with non-continuous and summarised dive profiles collected through ARGOS system (Goetz et al. 2018). Previous studies monitored the diving behaviour of adult emperor penguins for short periods, only a couple of months, either in winter or in summer (Kirkwood and Robertson 1997, Rodary et al. 2000a, Wienecke et al. 2007, Zimmer et al. 2008, 2010). Consequently, the detailed diving behaviour of individuals over a full year and the consistency of their foraging strategies over a year are still unstudied, while improving our understanding of these strategies and their drivers is required, especially as changes in the spatio-temporal availability of prey can be expected to increase with global warming and its consequence on oceanic processes.

Our study had several objectives: (i) to identify the at-sea distribution of emperor penguins in the Atlantic sector of the Southern Ocean, where the implementation of a new MPA (the Weddell Sea MPA) is being discussed, but where no tracking data have been recorded so far; (ii) to investigate potential variability in habitat use according to different life-history stages throughout the season to encompass – if possible – all breeding cycle stages and get a global picture of the emperor penguins' distribution in this area; (iii) to combine these novel information with datasets previously collected in Adélie Land, where the implementation of a new MPA (the East Antarctic MPA) is also being discussed, in order to assess emperor penguins' use of proposed MPAs so as to refine the scientific knowledge that can serve as an evaluation of the current and future proposed protected areas; (iv) to explore the environmental factors influencing the distribution at sea of emperor penguins in these two regions; (v) to examine the diving behaviour of adult emperor penguins in order to study changes in foraging strategies according to their breeding phases (pre-breeding/fall, incubation/winter and in chick-rearing) and status (non-breeder, failed breeder, successful breeder) and their locations (Atka Bay, Dronning Maud Land *versus* Pointe Géologie, Adélie Land). This last part is still preliminary and requires further investigation to validate our hypotheses and draw valid conclusions.

V.3 Material and Methods

V.3.1. Study sites and instrumentation procedures

V.3.1.1. Tracking data

To examine the seasonal distribution at sea of emperor penguins, we compiled tracking data from two colonies obtained over several years of sampling. We used tracking data from 38 individuals equipped at the Atka Bay colony (AB; 70.61°S, 08.15°W; near Neumayer Station III) between 2017 and 2019, and tracking data from 33 individuals equipped at the Pointe Géologie colony (PG; 66.67°S, 140.01°E; near Dumont d'Urville station) between 1998 and 2005 (see Table 3 and Table 5 for details). Tracking data from 2005 were previously published in Zimmer et al. (2007b).

Birds from AB were instrumented either with ARGOS platforms or GPS systems as exposed in Chapter III and birds from PG were instrumented with ARGOS platforms as explained in Zimmer et al. (2007b) (Table 14). Birds were instrumented across different life-history stages (i.e. fledging chicks/juveniles, adults), breeding status (i.e. breeding, non-breeding) and phases (i.e. pre-breeding, incubating, chick-rearing, moult) corresponding to different seasons (fall, winter, summer), resulting in five study groups (Table 14).

Deployments on adults were carried out over the summer during the late chick-rearing stage (adABs and adPGs groups), over the fall (after the moult) when birds were mostly not breeding (adABf group), and also in winter during the breeding season at Pointe Géologie colony (adPGw group).

Table 14. General information on tracking device deployments.

Study group	Life-history stage	Colony	Season	Tracking period	# inds	# trips	Tracker type
juvABy	juv	AB	year	Jan 2019-Jan 2020	8	8	ARGOS - SPOT-367 Wildlife Computers
adABf	ad	AB	fall	Jan-Aug (May)* 2018	8	10 (8)*	
adABs	ad	AB	summer	Nov-Dec 2018	16	32	GPS - Axy-Trek TechnoSmArt
	ad	AB	summer	Nov-Dec 2017	6	7	
adPGs	ad	PG	summer	Nov 2005 Jan-2006	18	28	ARGOS - Splash & SPOT-5 Wildlife computers
adPGw	ad	PG	winter	May-Sep 2005	3	4	ARGOS - ST-10 Sirtrack
	ad	PG	winter	May-Jul 2001	3	3	
	ad	PG	winter	Jul-Oct 1998	9	19	

The first column indicates the five study groups, as an aggregation of the three following columns: *Status* refers to the life-history stage of birds (juv = juveniles, ad = adults), *Colony* to the colony of equipment (AB = Atka Bay colony, PG = Pointe Géologie colony), and *Season* to the period of tracking (y = year, f = fall, s = summer, w = winter). Thus, for instance, the group *juvABy* refers to juveniles equipped at Atka Bay colony and tracked during a whole year.
* Platforms were programmed to stop emitting between April 25th and May 20th when birds were expected to be at their breeding site. All platforms restarted but they eventually stopped through the winter. By the time they stopped, only two birds were located outside the colony. The locations obtained after the April-May stop were considered as part of new trips.

V.3.1.2. Diving data

Juveniles were not equipped with Time-Depth Recorder (TDR) devices, while adults from Atka Bay were equipped with two different types of TDR (see Chapter III). We deployed Cefas g5+ TDR on chick-rearing birds (the one equipped also with GPS) and Lotek Lat 1800 TDR on birds that were equipped with ARGOS platforms. Both types of loggers were programmed to record depth and temperature at 1 Hz frequency with a 30 cm resolution and 1% accuracy. Equipment procedures are described in Chapter III.

Amongst the birds monitored in November 2005, 4 birds were equipped with Splash Argos platforms that also recorded diving depth every 2 seconds with a 50-cm resolution. The dive data and deployment procedure were already published in Zimmer et al. (2007b, 2008, 2010). General information on TDRs are summarised in Table 15.

Table 15. General information on TDR deployments.

Study group	Life-history stage	Colony	Season	Tracking period	# inds	# trips	Tracker type	TDR *Frequency, resolution*
adABf	ad	AB	year	Jan-Nov 2018	4	4	ARGOS	Cefas g5+ *1 HZ, 30 cm*
adABs	ad	AB	summer	Nov-Dec 2017 & 2018	22	32	GPS	Lotek Lat 1800 *1 HZ, 30 cm*
adPGs	ad	PG	summer	Nov 2005	4	4	ARGOS	Wildlife Computer Splash *0.5 Hz, 50 cm*

For the study group column: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter.

V.3.2. Spatial analysis

V.3.2.1. Location filtering and separation of tracking datasets per individual into foraging trips

Given the heterogeneity of the trackers and years, locations were sampled at different and irregular time intervals and associated with different spatial errors. Specifically, ARGOS locations were associated with classes in increasing order for birds from PG (Z, B, A, 0, 1, 2, 3) and associated with error ellipses for birds from AB, spatial errors ranging from several kilometres to few hundred metres (Costa et al. 2010b, CLS 2016), while GPS trackers have an accuracy inferior to 100 metres.

Erroneous locations were filtered out using a speed filter from the R package 'argos filter' (Freitas et al. 2008) with the maximum travel speed fixed at 15 km.h^{-1} following (Wienecke and Robertson 1997, Labrousse et al. 2019b). Periods spent at the colony (within a 5 km radius) were removed from analysis for all birds. Similarly, locations during the moulting periods of the three juveniles tracked throughout the year were removed prior to the analysis, as birds were not foraging. The moulting periods were identified by plotting the curve of the mean daily distance travelled as a function of time, and by checking the last inflexion point, indicating that the birds stopped travelling and started moulting. Indeed, according to the literature, when moulting (between December and March for an average of 30 days, Groscolas 1978), emperor penguins remain out of water on ice floes or coastal fast ice (Kooyman et al. 2004). As such, their daily distance travelled switch from several tens of kilometres a day to almost none, an abrupt behavioural change easily detected on tracked birds. The device then falls off with the feathers to which it was attached and get lost.

V.3.2.2. Interpolation of locations at a regular time step

We used a state-space modelling approach (Johnson et al. 2008) to estimate hourly locations. Specifically, a Kalman filter, which accounted for location error, was applied using the R package '*crawl*' (Johnson 2014), and Continuous-time Correlated Random Walk (CRW) models were used to predict locations at a regular time step interval of 1 h (Johnson et al. 2008, Heerah et al. 2019).

V.3.2.3. Identification of heavily used area

We analysed each study group according to the procedures developed by Lascelles and colleagues (Lascelles et al. 2016). For each dataset, we estimated the 50% (i.e. core area) and 90% (i.e. home range) (Börger et al. 2006) kernel utilisation distributions (UD ; Worton 1989), and we used a smoothing factor (in km) that corresponds to the scale of interaction of the birds with the environment. This smoothing factor is estimated from the peak of variance in first passage time (FPT), which assesses the time taken by an individual to cross the area of a circle of 5-150 km around each location (Fauchald and Tveraa 2003, Scheffer et al. 2010, Widmann et al. 2015, Lascelles et al. 2016, Vacquie-Garcia et al. 2017). Then, the value of FPT at each location was computed (with the relevant threshold for each study group) as a measure of residence since locations were interpolated on a regular time-step.

V.3.3. Dive analysis

V.3.3.1. Dive identification

Dive extraction from pressure data collected by the TDRs was carried out with the MT-Dive software (Multi Trace-Dive, Jensen Software Systems, Laboe, Germany). By looking at the inflexion points along the surface, the software splits the record into dives. Dives are then analysed sequentially and various parameters either extracted or computed. Up to now, we specifically focused on the maximum dive depth, the dive duration, the time spent at the bottom of the dive (bottom duration), the number of undulations (wiggles) per dive, and the post-dive duration in order to assess diving and foraging activities and performances of equipped birds. This analysis considers for the moment only the dives deeper than 5 m.

V.3.3.2. Dive metric computation

The bottom phase of a penguin dive, in contrast to the descending and ascending phases, is the phase in which penguins are most likely to hunt (Chappell et al. 1993, Zimmer et al. 2007b). The start and end of bottom phases were defined as the first and last time the rate of change of depth became < 0.5 m/s during a dive. Such parameters allow maximising the detection of wiggles occurring during the part of dive slightly ascending. The current literature on penguins proposes that most of the predation events happening during the bottom phase are indicated by the wiggles (Rodary et al. 2000b, Simeone and Wilson 2003, Ropert-Coudert et al. 2006, Halsey et al. 2007, Zimmer et al. 2007b). Wiggles correspond to deviations of the depth at 3 points on which the vertical speed drops below 0m/s (inflexion points) and with a change of depth above a threshold depending on the resolution of the TDR used. Adapting the method from Simeone and Wilson (2003), we defined a wiggle as a change in 1 second of at least 0.75 m compared to the mean rate of the previous 3 seconds, unless an undulation had already occurred within this 3-second time window. The value of 0.75 m is more than twice the resolution of TDRs used on AB birds and 1.5 times the resolution of TDRs used on PG birds. The number of wiggles per dive depending on the dive duration, we computed a proxy of foraging effort called Attempts of Catch Per Unit Effort (ACPUE; Zimmer et al. 2010, Le Guen et al. 2018), which is the ratio of the number of wiggles by the bottom time. We also computed a second proxy, the diving efficiency (DE), which is the ratio of the bottom duration by the sum of the dive time and the post-dive surface interval time (Ydenberg and Clark 1989, Zimmer et al. 2008, Le Guen et al. 2018).

V.3.3.3. Foraging dive characterisation

Then, foraging dives were defined as dives to any depth showing a bottom phase with wiggles, or dives to depths > 20 m or duration > 60 s in the absence of such wiggles (Rodary et al. 2000b). To classify dives without any wiggle and of maximum depth < 20 m, we assumed that penguins foraging at shallow depth would not spend much time in transit from the surface to the foraging depth and consequently would have a faster descent phase than travelling dives (Rodary et al. 2000b). We looked at the distribution of the speed of descent and, unlike (Rodary et al. 2000b), we could not find a bimodality. As such, we kept dives with a speed superior to the third quartile (0.62 m/s). Other dives were considered as travelling dives and remove from subsequent analysis.

V.3.3.4. Benthic dive estimation

Emperor penguins have been shown to perform benthic dives (Rodary et al. 2000a, Zimmer et al. 2008, Goetz et al. 2018). To assess if such behaviour was performed by our birds, dive locations were determined by linking dive time with time along the track line and linearly interpolated to the nearest minute (Goetz et al. 2018) with the function '*redisltraj*' from the R package '*adehabitatLT*' (Calenge and Royer 2020). Then, we extracted the bathymetric depth at each dive location and subtracted this value from the maximum dive depth. The resulting difference was then divided by the bathymetric depth. When the maximum dive depth was deeper than the bathymetric depth, the bathymetric depth was changed to the dive depth. Dives with value between 0.8 and 1 were classified as 'benthic' and all other dives as 'pelagic' (Goetz et al. 2018).

V.3.3.5. Diving effort characterisation

At the trip scale[15], we focused on the diving effort per unit of time, i.e. the number of dives made per hour (in local time) of each group. The diving profiles of adABf birds (year-round TDR datasets) allowed to identify the period out of water. Switch between periods of diving or absence of diving gave us an indication on the sex of the birds and if they attempted to breed or not. We assessed their breeding success by direct observations at the colony at the end of the breeding season in November/December. For breeding birds, the extended periods without any dive are likely to correspond to period spent at the colony, while, for non-breeding birds, we can only affirm that they are not diving. The yearly data were divided into trips separated by an extended period (several days in a row) out of water (Fig. 49). However, one of the birds did not exhibit any extended period without diving between September and its recapture in November. We, therefore, manually split this period in two different trips at the date where we identified a switch in the diving effort, i.e. a change in the distribution of dives during the day. Each trip of each bird was then assigned one type of the two diving effort patterns.

V.3.4. Management and environmental feature analysis

V.3.4.1. Management features

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)'s planning domains and existing Antarctic Marine Protected Areas (MPAs) were obtained from https://gis.ccamlr.org (CCAMLR 2019b). The proposed Weddell Sea Marine Protected Area boundaries (WSMPA; CCAMLR 2018a) and the proposed East Antarctic Marine Protected Area boundaries (EAMPA; CCAMLR 2019b) were obtained from www.mpatlas.org (Marine Conservation Institute 2020). The Domain 1 MPA proposal (CCAMLR 2018b) was drawn from www.mpatlas.org (Marine Conservation Institute 2020). The South Georgia and South Sandwich Islands Marine Protected Area

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[15] Diving effort was investigated weekly, but the trip scale kept the observed pattern, see results.

(SGSSIMPA) and the sub-Antarctic MPAs boundaries were downloaded from www.protectedplanet.net (UNEP-WCMC 2020).

The International Union for Conservation of Nature (IUCN)'s range of the Emperor penguin was obtained from www.iucnredlist.org (Birdlife International 2018).

V.3.4.2. Residence time

To assess the intensity of use of features related to conservation management in the Southern Ocean by the tracked birds, we averaged the proportion of time they spent monthly inside each feature, referred hereafter as 'residence time'. We also computed the residence time per individual over the total tracking duration for each bird. Additionally, for each study site and each management feature, we computed the proportion of the distribution area falling inside the boundaries of a particular feature with the R package '*raster*' (Hijmans and van Etten 2020).

V.3.4.3. Environmental features

(i) Habitat features

To examine the importance of bathymetric depth, the bathymetry covariate at one-minute horizontal spatial resolution was obtained from the ETOPO1 Global Relief Model provided by the NOAA National Geophysical Data Center (Amante and Eakins 2009). We calculated the slope covariate in degree for each grid cell from the bathymetry values of the eight neighbouring cells using the '*terrain*' function from the R package '*raster*' (Hijmans and van Etten 2020).

We divided the Southern Ocean in three habitat types to take into account the effect of bathymetry and water movements: 1) The continental shelf break was considered as the area along the continent below the 1000 m isobaths (Knox 2007, Nicholls et al. 2009). We then used the classification of Douglass and colleagues (2014) to segregate 2) the Antarctic continental slope area (roughly areas around the continent ranging between 1000 and 4000 m) from 3) the deep ocean (abyssal plain) characterised by a smooth bathymetric slope and depth > 4000 m. Each penguin location was attributed to one of the classes, and the proportions by study group were computed.

(ii) Sea ice

Sea ice concentration values (ranging from 0 to 100%) at particular locations for AB were extracted from Advanced Microwave Scanning Radio meter (AMSR-2) satellite estimates of daily sea ice concentration at 3.125 km resolution from the University of Bremen (https://seaice.uni-bremen.de/data/amsr2, Spreen et al. 2008). Sea ice concentration values for PG were extracted from estimates of daily sea ice concentration at 12.5 km resolution from the Institut Français de la Recherche pour l'exploitation de la Mer (IFREMER, ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/).

To account for spatial variability of sea ice, we additionally computed the sea ice concentration over a delineated area whose radius is the value of the smoothing factor that corresponded to the scale of interaction of the birds with the environment, as described previously in the location data processing (page 147). We also computed the percentage of sea ice > 90% over the area as a measure of full sea ice concentration and absence of cracks and daily polynyas used by emperor penguins to dive and forage (Labrousse et al. 2019a). The distance of the tracked penguins from the sea ice edge were calculated, using the R package '*geosphere*' (Hijmans et al. 2019), as the minimum distance between penguin positions and the sea ice edge contour defined by the 15% sea ice concentration isocline (Cavalieri 1991, Stammerjohn and Smith 1997). This isocline defines the sea ice extent. Contours corresponding to outlying floes or polynyas were removed during extraction to prevent bias in the sea ice edge distance computation with QGIS *'r.contour.step'* tool. Positive values indicated that the bird was inside the sea ice area.

(iii) Oceanographic conditions

The Southern Ocean fronts and the Antarctic Circumpolar Current boundaries (ACC; Orsi et al. 1995) were downloaded from https://gis.ccamlr.org (CCAMLR 2019b). The shortest distance to the Southern Antarctic Circumpolar Current Front (SACCF) of the ACC (Orsi et al. 1995) was computed for juveniles at each location.

(iv) Extraction process

To account for location error when extracting environmental variables, we used the fitted CRW model to create a dataset of 100 simulations of each location and individual bird (Johnson et al. 2008). The 100 values for the bathymetry, slope, sea ice concentration covariates, and distances associated with each possible location were first extracted and then averaged, giving a mean value for each location along the mean track (Heerah et al. 2016).

V.3.5. Statistical analysis

Except for the dive analysis, analyses were performed using the software R v. 3.5.0 (R Core Team 2018) and QGIS v. 2.18.18 (QGIS Development Team 2017) with the data package '*Quantarctica*' (Matsuoka et al. 2018).

V.3.5.1. Residence time

We tested the statistical effect of the individuals and of the months on the residence time within the management features using Kruskal-Wallis rank sum tests. When a significant difference was measured among individuals or months, the Tukey's 'Honest Significant Difference' multiple comparison of means test was used to identify which individual(s) or month(s) differed from others (Thiebot et al. 2013, 2019).

V.3.5.2. Dive analysis

To determine the relationship between the diving effort strategy of the adABf[16] birds and their main diving metrics (e.g. bottom time, dive maximum depth, dive efficiency, number of wiggles, dive duration, and ACPUE), we fitted a Generalized Linear Mixed Model (GLMM) using the '*glmer*' function from the R package '*lme4*' (Bates et al. 2015). Exploratory variables were first normalised with a Cox Box Power transform and their correlation assessed with the use of the variance inflation factor (VIF) and a threshold of 3, as well as with the Pearson correlation coefficient with a threshold of 0.6. (Zuur et al. 2010). As a result, the dive duration and the number of wiggles were discarded from the analysis. Models were fitted with Binomial distribution, and birds were included as random effects to account for inter-individual variability. The model selection was performed using the '*dredge*' function from the R package '*MuMIn*' (Kamil Barton 2020).

V.3.5.3. Assessing the influence of environmental factors on the distribution

We used Generalized Additive Mixed Models (GAMMs) to identify nonlinear functional relationships between species distribution and environmental conditions (Zuur 2009). We explored relationships between FPT and key physical variables (i.e. sea ice concentration, distance to the fronts and sea ice edge, day of year, bathymetry, slope, and habitat) using a Gaussian distribution with the identity link function. For each model, only the variables not highly correlated (< 0.8) were used and standardised after checking of outliers (Vacquie-Garcia et al. 2017). The response variable was log transformed prior to analysis to correct for non-Gaussian distribution and a correlation term was added to take into account the temporal correlation (Zuur 2009). Individual trips and colonies were included as random factors. GAMMs were computed separately for juveniles and for adults because of their highly different patterns of distribution that likely involved different variables that we did not want to confound. Model selection could not be conducted using Akaike's Information Criterion (AIC) due to

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[16] Our preliminary analysis focused only on one group (the adults from Atka Bay during the fall ; adABf) for the moment.

the presence of the autocorrelation term (Van Rijn et al. 2020). We used adjusted R^2 and percent deviance explained to evaluate model performance (Zuur 2009) with the help of the '*comparML*' function from the R package '*itsadug'*. Model assumptions pertaining to GAMMs, including normality and homogeneity of variance, were checked using plots of residuals against fitted values (Zuur 2009, Zuur et al. 2010, Wood 2017). GAMMs were computed with the R package '*mgcv'* (Wood 2017). For the study group 'adABf', only the time period spanning from January to April was considered since only two non-breeding birds were still transmitting afterwards and were therefore not representative of the group anymore.

V.4 Results

Detailed general information per birds, such as deployment and tracking durations or distance to colony are reported in Table 13 for juvenile emperor penguins from Atka Bay and in the Table 16 below, which also includes general information on diving metrics, for adult emperor penguins from Atka Bay (AB) and Pointe Géologie (PG).

Table 16. General information and at-sea metrics of adult emperor penguins from Atka Bay (AB) and Pointe Géologie (PG).

Study group	Bird and trip ID*	Status	# locations	Start trip	End trip	Trip duration (days)	Max distance from colony (km)	Date of max distance from the colony	% in MPA	# dive kept	Max dive depth (m)	Max dive duration (min)	Proportion of benthic dives
adABf	44837	nb	2173	25/01/2018 11:00	25/04/2018 23:00	90.5	1025	23/04/2018	100			NA	
	44839_1	nb	2197	24/01/2018 11:00	25/04/2018 23:00	91.5	1348	25/04/2018	81.7				
	44839_2	nb	2009	20/05/2018 05:00	13/08/2018 21:32	83.7	1547	21/07/2018	11.5				
	44842	b	1658	26/01/2018 17:00	05/04/2018 18:00	69.0	351	22/03/2018	98.9				
	44843	b	1760	24/01/2018 11:00	07/04/2018 18:00	73. 3	486	31/03/2018	94.5				
	44836	b	2027	25/01/2018 05:00	19/04/2018 15:00	84.4	308	20/03/2018	100	21670	381	13.3	0.3**
	44840	b	1907	27/01/2018 05:00	16/04/2018 15:00	79.4	257	27/02/2018	100	24448	446	19.5	1.5**
	44841	b	1991	26/01/2018 17:00	19/04/2018 15:00	82.9	275	22/03/2018	86.6	18282	284	**29.7**	0**
	44844_1	nb	2107	27/01/2018 05:00	24/04/2018 23:00	87.8	410	29/03/2018	100	35863	472	21.7	0.3**
	44844_2	nb	905	20/05/2018 05:00	26/06/2018 21:00	37.7	550	26/06/2018	100				
adABs	0602949	b	140	28/11/2017 17:00	04/12/2017 12:00	5.8	97	02/12/2017	100	777	252	13.2	0.4
	7740383	b	150	30/11/2017 13:00	06/12/2017 18:00	6.2	360	06/12/2017	100	1157	225	9.2	0
	7740387	b	172	01/12/2017 16:00	08/12/2017 19:00	7.1	143	05/12/2017	100	820	238	12.1	0
	7740392_1	b	89	01/12/2017 19:00	05/12/2017 11:00	3.7	86	02/12/2017	100	653	262	9.9	0.2
	7740392_2	b	63	05/12/2017 19:00	08/12/2017 09:00	2.6	103	08/12/2017	100	490	358	9.8	0.8
	7740427	b	147	02/12/2017 16:00	08/12/2017 18:00	6.1	80	08/12/2017	100	794	412	17.7	1.5
	7740429	b	175	02/12/2017 23:00	10/12/2017 05:00	7.2	122	03/12/2017	100	956	449	16.0	11.2
	7740091_1	b	118	06/11/2018 10:00	11/11/2018 07:00	4.9	78	07/11/2018	100	729	271	10.0	0
	7740091_2	b	126	12/11/2018 02:00	17/11/2018 07:00	5.2	97	15/11/2018	100	783	374	15.3	0.1
	7740093_1	b	125	06/11/2018 05:00	11/11/2018 09:00	5.2	96	08/11/2018	100	771	444	11.3	1.9
	7740093_2	b	164	12/11/2018 02:00	18/11/2018 21:00	6.8	133	15/11/2018	100	779	480	13.1	20.2
	7740101_1	b	161	08/11/2018 17:00	15/11/2018 09:00	6.7	59	11/11/2018	100	883	417	10.2	5.4
	7740101_2	b	160	16/11/2018 04:00	22/11/2018 19:00	6.6	94	16/11/2018	100	896	448	12.5	4.1
	7740097_1	b	160	07/11/2018 15:00	14/11/2018 06:00	6.6	101	11/11/2018	100	1139	241	15.0	0.2
	7740097_2	b	262	15/11/2018 08:00	26/11/2018 05:00	10.9	190	19/11/2018	100	2044	260	11.3	0
	7740115_1	b	213	08/11/2018 20:00	17/11/2018 16:00	8.8	192	14/11/2018	100	1651	370	14.4	0.2
	7740115_2	b	182	18/11/2018 22:00	26/11/2018 11:00	7.5	133	24/11/2018	100	1418	292	11.2	1.2
	7740099_1	b	174	07/11/2018 11:00	14/11/2018 16:00	7.2	102	11/11/2018	100	1176	364	17.1	3.2
	7740099_2	b	168	15/11/2018 13:00	22/11/2018 12:00	7.0	143	16/11/2018	100	1015	430	11.6	17.4
	7740099_3	b	148	23/11/2018 13:00	29/11/2018 16:00	6.1	82	24/11/2018	100	785	460	9.9	35.9
	7740095_1	b	133	07/11/2018 03:00	12/11/2018 15:00	5.5	150	09/11/2018	100	1303	228	18.6	0.1
	7740095_2	b	211	13/11/2018 18:00	22/11/2018 12:00	8.8	146	16/11/2018	100	1670	224	12.2	0

	7740095_3	b	175	23/11/2018 11:00	30/11/2018 17:00	7.2	135	26/11/2018	100	1246	231	11.9	0.5
	7740113_1	b	158	07/11/2018 15:00	14/11/2018 04:00	6.5	140	09/11/2018	100	1144	452	13.0	1.8
	7740113_2	b	158	15/11/2018 23:00	22/11/2018 12:00	6.5	101	17/11/2018	100	980	384	12.5	0.2
	7740113_3	b	177	24/11/2018 01:00	01/12/2018 09:00	7.3	147	26/11/2018	100	1189	398	11.5	1.3
	7740119_1	b	152	08/11/2018 21:00	15/11/2018 04:00	6.3	113	12/11/2018	100	1076	446	12.6	0.7
	7740119_2	b	165	16/11/2018 01:00	22/11/2018 21:00	6.8	103	20/11/2018	100	917	471	12.6	0.5
	7740119_3	b	183	24/11/2018 09:00	01/12/2018 23:00	7.6	116	26/11/2018	100	1076	404	12.1	0.1
	7740129_1	b	102	27/11/2018 21:00	02/12/2018 02:00	4.2	64	29/11/2018	100	577	450	24.8	5.6
	7740129_2	b	85	02/12/2018 19:00	06/12/2018 07:00	3.5	59	05/12/2018	100	471	440	26.6	11.7
	7740123	b	208	28/11/2018 06:00	06/12/2018 21:00	8.6	127	02/12/2018	100	1188	346	19.3	0
	7740127	b	234	27/11/2018 13:00	07/12/2018 06:00	9.7	138	05/12/2018	100	1663	456	15.3	2.5
	7740122_1	b	78	26/11/2018 20:00	30/11/2018 01:00	3.2	55	28/11/2018	100	369	381	14.6	9.2
	7740122_2	b	68	30/11/2018 22:00	03/12/2018 17:00	2.8	49	03/12/2018	100	253	459	21.9	27.3
	7740122_3	b	94	04/12/2018 09:00	08/12/2018 06:00	3.9	68	06/12/2018	100	463	**497**	20.0	15.2
	7740125	b	229	28/11/2018 19:00	08/12/2018 07:00	9.5	126	30/11/2018	100	1355	405	15.1	1.8
	7741031	b	307	01/12/2018 01:00	13/12/2018 19:00	12.8	130	11/12/2018	100	1783	478	24.5	0.8
	7740946	b	401	03/12/2018 15:00	20/12/2018 07:00	16.7	115	18/12/2018	100	1564	389	14.5	7.5
adPGs	F18-60047_1	b	145	14/11/2005 08:00	20/11/2005 08:00	6.0	86	18/11/2005	100	1151	339	12.9	10.5
	M10-60048_2	b	219	06/11/2005 08:00	15/11/2005 10:00	9.1	130	10/11/2005	100	1629	401	10.6	34.5
	P5-60046	b	189	02/11/2005 04:00	10/11/2005 00:00	7.8	82	05/11/2005	100	952	227	13.2	**62.8**
	P8-60047	b	151	03/11/2005 05:00	09/11/2005 11:00	6.2	71	06/11/2005	100	911	438	13.0	30.7
	F2-60037	b	172	01/11/2005 08:00	08/11/2005 11:00	7.1	90	04/11/2005	100			NA	
	F19-60047_1	pm	1011	01/12/2005 05:00	12/01/2006 07:00	42.1	838	18/12/2005	18.2				
	F20-60037_2	b	185	28/11/2005 09:00	06/12/2005 01:00	7.7	110	01/12/2005	100				
	F20-60037_3	b	530	07/12/2005 06:00	29/12/2005 07:00	22.0	566	20/12/2005	60.0				
	F20-60037_4	pm	339	01/01/2006 06:00	15/01/2006 08:00	14.1	624	08/01/2006	0				
	F7-60041_1	b	207	07/11/2005 19:00	16/11/2005 09:00	8.6	80	11/11/2005	100				
	F7-60041_2	pm	1221	25/11/2005 02:00	14/01/2006 22:00	50.8	569	11/12/2005	74.0				
	M12-60050	b	61	04/11/2005 20:00	07/11/2005 08:00	2.5	66	07/11/2005	100				
	M13-60042	b	55	19/11/2005 01:00	21/11/2005 07:00	2.2	48	19/11/2005	100				
	M14-60043	nb	1068	06/11/2005 20:00	21/12/2005 07:00	44.5	353	05/12/2005	93.4				
	M15-60044	nb	1174	06/11/2005 12:00	25/12/2005 09:00	48.9	924	04/12/2005	30.2				
	M4-60039_1	b	419	03/11/2005 00:00	20/11/2005 10:00	17.4	130	10/11/2005	100				
	M4-60039_2	b	223	24/11/2005 05:00	03/12/2005 11:00	9.2	112	30/11/2005	100				
	M4-60039_3	b	117	05/12/2005 14:00	10/12/2005 10:00	4.8	109	06/12/2005	100				
	M4-60039_4	b	81	13/12/2005 03:00	16/12/2005 11:00	3.3	112	15/12/2005	100				
	M4-60039_5	pm	781	19/12/2005 01:00	20/01/2006 13:00	32.5	439	07/01/2006	49.3				

	P1-60036	b	551	01/11/2005 04:00	24/11/2005 02:00	22.9	316	19/11/2005	100	
	P16-60045	nb	1521	07/11/2005 02:00	09/01/2006 10:00	63.3	542	03/12/2005	69.4	
	P17-60046	b	199	14/11/2005 05:00	22/11/2005 11:00	8.2	150	18/11/2005	100	
	P3-60038_1	b	180	01/11/2005 23:00	09/11/2005 10:00	7.5	57	05/11/2005	100	
	P3-60038_2	b	147	11/11/2005 07:00	17/11/2005 09:00	6.1	57	16/11/2005	100	
	P3-60038_3	b	257	18/11/2005 09:00	29/11/2005 01:00	10.7	101	22/11/2005	100	
	P3-60038_4	pm	676	02/12/2005 05:00	30/12/2005 08:00	28.1	751	26/12/2005	27.1	
	P6-60040	nb	1661	03/11/2005 03:00	11/01/2006 07:00	69.2	537	10/01/2006	87.7	
adPGw	13865-2005	b	1772	17/05/2005 13:00	30/07/2005 08:00	73.8	61	08/06/2005	100	NA
	13866-2001	b	730	21/05/2001 14:00	20/06/2001 23:00	30.4	133	09/06/2001	100	
	13869-2001	b	1155	17/05/2001 14:00	04/07/2001 16:00	48.1	133	17/06/2001	100	
	13869-2005	b	460	24/07/2005 12:00	12/08/2005 15:00	19.1	62	05/08/2005	100	
	13870-2005_1	b	1332	19/05/2005 00:00	13/07/2005 11:00	55.5	93	02/06/2005	100	
	13870-2005_2	b	259	21/08/2005 22:00	01/09/2005 16:00	10.8	63	27/08/2005	100	
	13873-2001	b	536	23/05/2001 15:00	14/06/2001 22:00	22.3	108	08/06/2001	100	
	16925-1998	b	271	22/07/1998 11:00	02/08/1998 17:00	11.2	49	24/07/1998	100	
	16927-1998_1	b	346	19/07/1998 10:00	02/08/1998 19:00	14.4	52	22/07/1998	100	
	16927-1998_2	b	169	19/08/1998 20:00	26/08/1998 20:00	7.0	62	26/08/1998	100	
	16928-1998_1	b	250	23/07/1998 08:00	02/08/1998 17:00	10.4	46	26/07/1998	100	
	16928-1998_2	b	62	16/08/1998 08:00	18/08/1998 21:00	2.5	34	17/08/1998	100	
	16928-1998_3	b	421	26/08/1998 21:00	13/09/1998 09:00	17.5	55	28/08/1998	100	
	16929-1998_1	b	383	17/07/1998 23:00	02/08/1998 21:00	15.9	47	24/07/1998	100	
	16929-1998_2	b	135	08/08/1998 08:00	13/08/1998 22:00	5.6	21	09/08/1998	100	
	16929-1998_3	b	107	18/08/1998 18:00	23/08/1998 04:00	4.4	18	20/08/1998	100	
	16931-1998	b	205	16/08/1998 07:00	24/08/1998 19:00	8.5	47	23/08/1998	100	
	17196-1998	b	672	18/07/1998 20:00	15/08/1998 19:00	28.0	84	13/08/1998	100	
	17197-1998	b	440	18/07/1998 09:00	05/08/1998 16:00	18.3	58	21/07/1998	100	
	17198-1998_1	b	543	18/07/1998 07:00	09/08/1998 21:00	22.6	52	23/07/1998	100	
	17198-1998_2	b	378	18/08/1998 18:00	03/09/1998 11:00	15.7	92	31/08/1998	100	
	17198-1998_3	b	823	08/09/1998 11:00	12/10/1998 17:00	34.2	223	30/09/1998	100	
	17199-1998_1	b	348	18/07/1998 10:00	01/08/1998 21:00	14.5	57	21/07/1998	100	
	17199-1998_2	b	176	10/08/1998 13:00	17/08/1998 20:00	7.3	49	13/08/1998	100	
	17199-1998_3	b	221	27/08/1998 16:00	05/09/1998 20:00	9.2	54	31/08/1998	100	
	17199-1998_4	b	154	08/09/1998 11:00	14/09/1998 20:00	6.4	52	11/09/1998	100	

b = breeding bird, nb = non-breeding bird, pm = pre-moult trip. * = for birds that made several trips, the number of the specific trips is indicated after the "_" symbol, ** = metric computed only over the period during which ARGOS platform was sending locations. For the study group column: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter. Maximum recorded dive metrics are in bold.

V.4.1. Spatial analysis

V.4.1.1. Distribution at sea

(i) Journey of juvenile emperor penguins from Atka Bay

The distribution of the eight equipped juveniles in Atka Bay (juvABy; Fig. 39) covers a vast area (UD 50% = 0.6 million of km², Table 17), stretching over 3000 km from east to west and 2500 km from north to south. They travelled north when leaving the colony in mid-January 2019, reaching their northernmost latitude (maximum at 48.5°S) between the end of February and the beginning of April, being at 1500 to 2400 km from the colony (Table 13). Five of them went north of the maximal sea ice extent (Fig. 38) and spent several weeks above the bathymetric "plateau" structure located around Bouvet Island.

One of the birds expressed a very different behaviour than the seven others. This bird was the first to turn south. On March 16th, this individual was located at the sea ice edge, only 30 km off the coast while the other juveniles were still within the ACC, 1400 km north of the coastline. The signal of its ARGOS platform was lost on March 24th on the sea ice edge, 80 km north of Sanae emperor penguin colony.

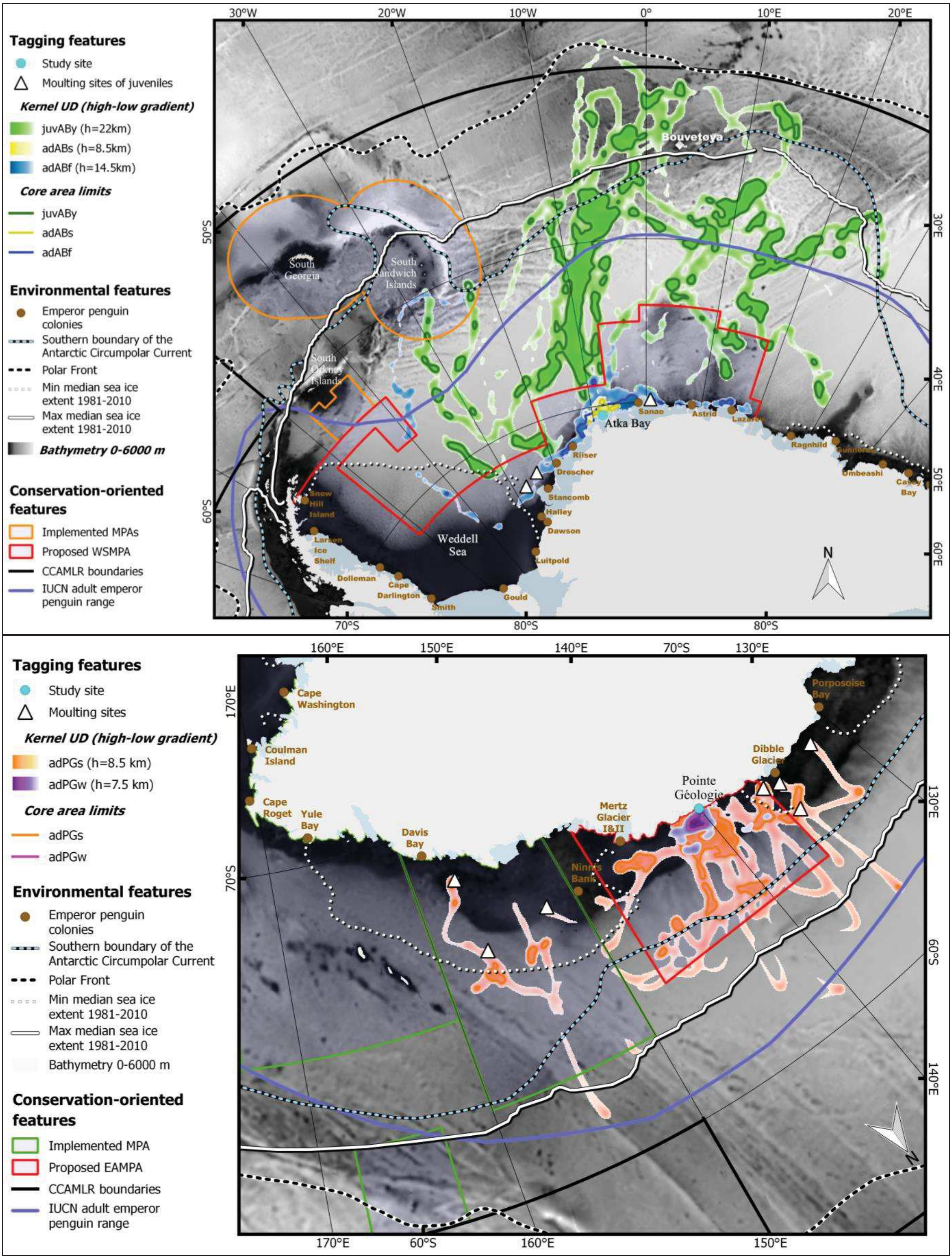


Fig. 39. Distribution (Kernel UD) of study groups equipped at Atka Bay (up) and Pointe Géologie (bottom). 'h' corresponds to the scaling factor used in the kernel estimation for each group. The black part of the background corresponds to the shelf area (1000 m isopleth). For the Kernel UD nomenclature: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter.

The seven other juveniles turned South in March/April and entered into the sea ice between mid-April and mid-May. From this time on, they split in two groups. Both groups remained in the pack ice, within 100-300 km of the sea ice edge (Fig. 40) over the abyssal plains (Fig. 41) for the rest of their tracking period. One group, made of four juveniles, went into the Weddell Gyre and their signal got lost one by one in June-July, while they were heading northward following the sea ice edge during its expansion. The other group, made of the three other juveniles, remained for the whole winter around 1000 km north-northeast of Atka Bay. In December, they followed the sea ice edge during the sea ice retreat southward. They eventually moulted near the continent between mid-December and mid-January (Fig. 39). None of them returned to moult at their native colony. One moulted on the fast ice east of Troll Tunga and Sanae emperor penguin colony, at 360 km from Atka Bay, while the two others moulted at approximately 650 km southwest of Atka Bay in the vicinity of Stancomb and Drescher emperor penguin colonies.

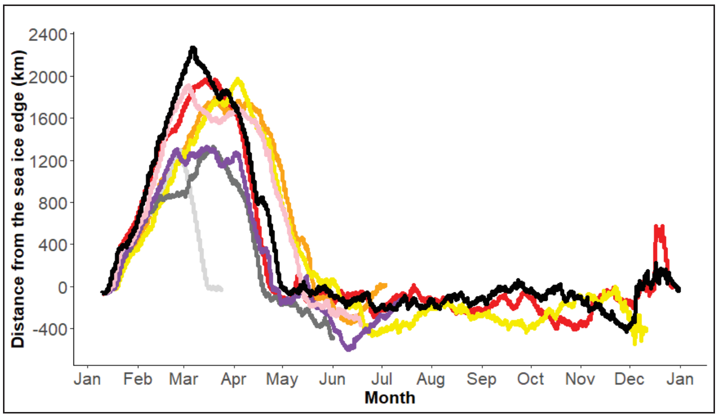


Fig. 40. Distance from the sea ice edge over the course of the year for juvenile emperor penguins equipped in AB in January 2019. Each coloured line represents one bird.

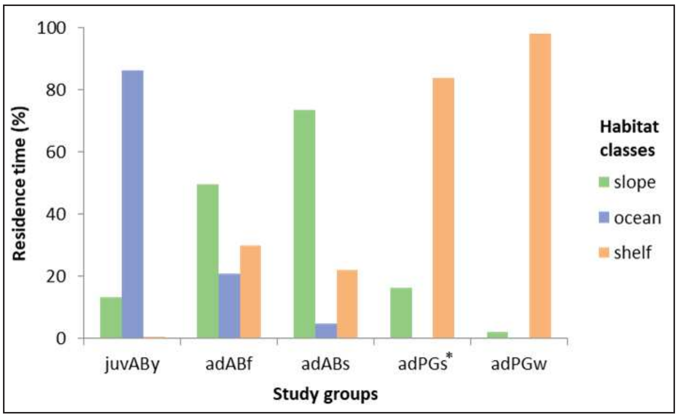


Fig. 41. Proportion of time spent in the different classes of habitat per study groups. * = only breeding birds were considered. For the study group classes: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter.

(ii) Adult emperor penguins from Atka Bay

In the Atlantic sector of the Southern Ocean, adults during fall (adABf) used a core area 15 times smaller than juveniles (juvABy) and 5 times bigger than adults in summer (adABs; Fig. 39). The latter mostly stayed in a radius of 200 km around the colony (median of maximum distance from the colony = 113 km, Table 17), over the shelf and the continental slope, while adABf birds also exploited the water column above the abyssal plains (21% of their time in average; Fig. 41).

Noteworthy, one of the non-breeding adABf birds went into the Weddell Gyre, following a similar pattern to the juveniles a year later, while the two others non-breeding adABf birds stayed along the Antarctic continent. Signals from ARGOS platforms of adABf birds were all lost during the winter.

Table 17. Distribution metrics of study groups.

Study group	juvABy	adABf	adABs	adPGs	adPGw
Home range size (UD 90% in km²)	2 619 470	258 268	26 552	199 371	11 309
Core area size (UD 50% in km²)	624 868	40 661	8 270	37 118	1 788
Maximum distance from the colony (km)	2474	486* / 1547^	360	316* / 924^	223
Median of mean max distance from the colony (km)	1834	304* / 1026^	113	101* / 569^	56

* only breeding birds are taken into account, ^ only non-breeding trips are taken into account. For the study group: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter.

(iii) Adult emperor penguins from Pointe Géologie

In the d'Urville Sea, adults in summer (adPGs) used an area 20 times bigger (Table 17) than adults in winter (adPGw; Fig. 39). The wintering foraging area of birds from PG (adPGw) was situated east of the colony, between their colony and the persistent Mertz polynya, with a median of maximum distance from the colony of 56 km. This area was exclusively over the shelf and consistent between years (Labrousse et al. 2019a). Part of the trips (16.3%) of breeding adults from adPGs group was situated over the continental slope (Fig. 41). None of the two groups from PG exploited areas above abyssal plains.

V.4.1.2. Residence time

Juveniles from Atka Bay (juvABy) spent the majority of their tracking time outside of the existing and proposed MPAs (86.1 ± 8.6%), being only present in the proposed WSMPA in January and in December (Fig. 37, see Chapter IV for details). Two birds were inside the SGSSI MPA in late June. They stayed there at least until July when their ARGOS platforms stopped transmitting. The three juveniles equipped with an ARGOS platform that transmitted the whole year moulted inside the WSMPA.

By contrast, from the date of their equipment in January until May, the eight post-moulting adult emperor penguins equipped from Atka Bay (adABf) spent in average 94 ± 5% of their tracking time inside the proposed WSMPA boundaries. Only two of the birds, both non-breeding birds, were still tracked in June. One of them was inside the proposed WSMPA, travelling along the continent, while the other one left the proposed WSMPA following the Weddell Sea Gyre. This last bird reached the SGSSI MPA in mid-July (Fig. 39 and Fig. 41). The signal of this bird was lost inside the SGSSI MPA in mid-August.

All the adults in chick-rearing from Atka Bay (adABs) and all the birds in a breeding stage at Pointe Géologie (adPGw and adPGs breeding, see Table 14) stayed within the boundaries of the relevant MPA, the proposed WSMPA and EAMPA, respectively (Fig. 39 and Fig. 41). In East Antarctica, only non-breeders and pre-moulting birds crossed the boundaries of the proposed EAMPA. Seven adults from adPGs were tracked until their moult in January. Three of them moulted inside the western part of the adjacent Ross Sea Region MPA. The four others went west of the proposed EAMPA, with only one bird moulting inside its boundaries (and being inside for less than a kilometre, Fig. 39).

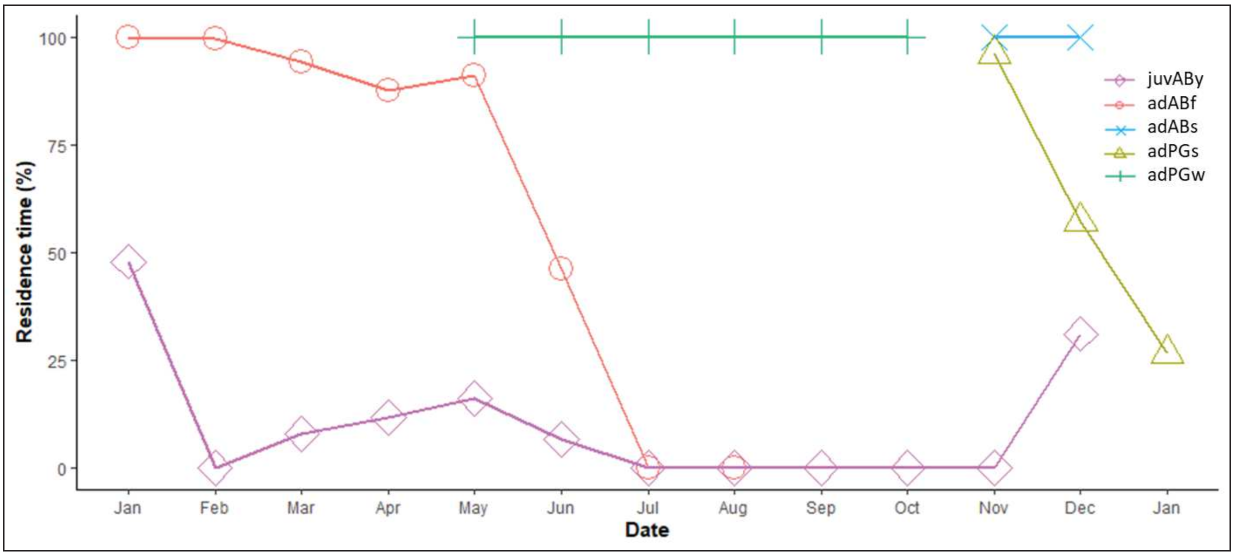


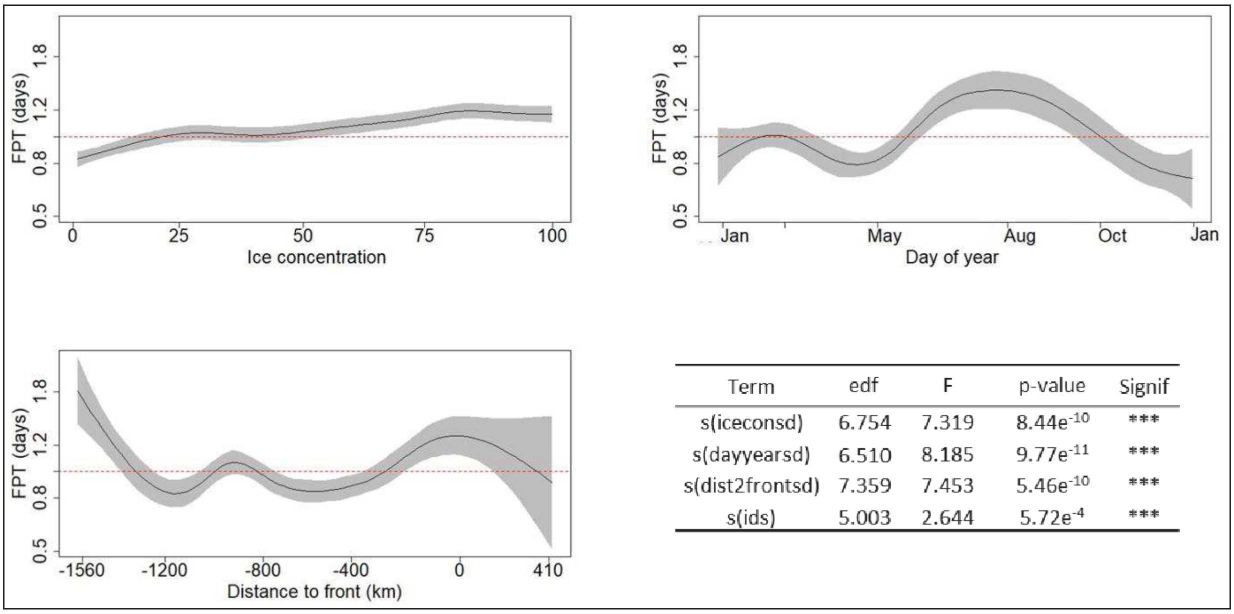
Fig. 42. Monthly proportion of time spent, over the year, by each study group in the relevant proposed Marine Protected Areas: the Weddell Sea MPA (WSMPA) for Atka Bay (AB) birds and East Antarctic MAP (EAMPA) for Pointe Géologie (PG) birds. For the study group classes: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter.

V.4.1.3. Environmental drivers of the time spent in an area

(i) Juvenile emperor penguins

We found a significant effect of the sea ice concentration, the day of the year, and the distance to the Southern Antarctic Circumpolar Current Front (SACCF) on the time spent by the juvenile emperor penguins from Atka Bay in an area (i.e. the first passage time, or FPT; see GAMM results in the Table of the Fig. 43). The bathymetry and the slope as well as the distance to the sea ice edge were not retained in the best model.

The time spent per area (FPT) increased linearly with the sea ice concentration. The season also influenced the FPT with higher values occurring during the winter, meaning that birds were moving less in winter. On the contrary, birds spent less time per area (lower FPT values) at the beginning and the end of the year. The effect of the distance to the SACCF on the FPT showed a more contrasting pattern. There was no clear tendency, except at the very extreme values of the range. Intermediate values of the FPT, from 400 to 1200 km south of the front (negative sign), included data from the heart of winter as well as from the trips at the beginning and end of the year.



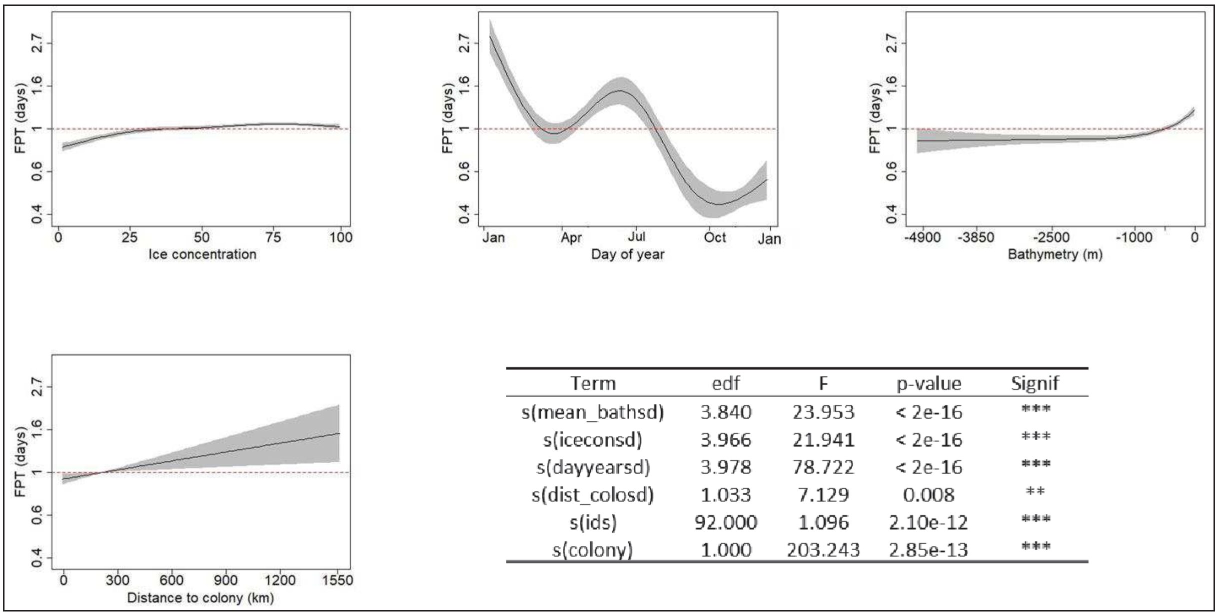
Term	edf	F	p-value	Signif
s(iceconsd)	6.754	7.319	$8.44e^{-10}$	***
s(dayyearsd)	6.510	8.185	$9.77e^{-11}$	***
s(dist2frontsd)	7.359	7.453	$5.46e^{-10}$	***
s(ids)	5.003	2.644	$5.72e^{-4}$	***

Fig. 43. Results of the best model of the GAMM analysis illustrating the functional relationship between the FPT value at each location and the significant variables for juveniles (i.e. sea ice concentration, day of the year, and distance to the Southern Antarctic Circumpolar Current Front). Negative value of the variable ‘Distance to front’ indicates that the birds are located south of the front. Thin grey line indicates 95% confidence intervals. The table is the model output of the best GAMM model (R^2-adj = 0.294 ; deviance explained = 29.5%). Significance is indicated by stars with *** < 0.001 ; edf = estimated degrees of freedom.

(ii) Adult emperor penguins

We found that the time spent by adult emperor penguins from Atka Bay and Pointe Géologie in an area (FPT) was significantly influenced by the sea ice concentration, the day of the year, the bathymetry, and the distance to colony (see GAMM results in the Table of the Fig. 44). The gradient of bathymetry, the habitat as well as the distance to the sea ice edge and the proportion of ice > 90% were not retained by the model selection.

Adult emperor penguins spent more time (higher FPT values) in area with high concentration of ice. Higher values of FPT were observed at the beginning of the year with a decreasing trend between January and April. Then, the residence time increased through the beginning of the winter with a peak in mid-July. Finally, the time the adults spent per area during the chick-rearing period was lower than in winter. We found higher FPT values over the shelf area (i.e. bathymetry between 0 and 1000 m). Finally, the time spent by the adult emperor penguins per area increased with the distance to their colony. Nevertheless, the incertitude is high and the confidence interval increasing after 600 km. Values above this threshold should not be considered since 89% of the data collected are within 600 km from the colony, amongst which all the data from breeding or post-moulting birds. For instance, no difference was found in the median of the mean maximal distance from the colony between the chick-rearing birds of Atka Bay and Pointe Géologie (Mood’s median test, p-value = 0.5; Table 17), the birds being located within ca. 200-km radius around the colony.



Term	edf	F	p-value	Signif
s(mean_bathsd)	3.840	23.953	< 2e-16	***
s(iceconsd)	3.966	21.941	< 2e-16	***
s(dayyearsd)	3.978	78.722	< 2e-16	***
s(dist_colosd)	1.033	7.129	0.008	**
s(ids)	92.000	1.096	2.10e-12	***
s(colony)	1.000	203.243	2.85e-13	***

Fig. 44. Results of the best model of the GAMM analysis illustrating the functional relationship between the FPT value at each location and the significant variables for adults (i.e. sea ice concentration, day of the year, bathymetry, and distance to the colony). Thin grey line indicates 95% confidence intervals. The table is the model output of the best GAMM model (R^2-adj = 0.455 ; deviance explained = 45.5%). Significance is indicated by stars with *** < 0.001 and ** < 0.01 ; edf = estimated degrees of freedom.

V.4.2. Foraging analysis

V.4.2.1. Diving effort estimation

The results presented in this section are preliminary and require further investigation and validation.

General statistics (mean ± SD) of the main diving metrics, i.e. the maximum dive depth, the dive duration, the time spent at the bottom of a dive, the dive efficiency (ratio of the bottom duration by the sum of the dive time and the post-dive surface interval time), the number of wiggles and the ACPUE (ratio of the number of wiggles per dive per the bottom time) per study groups are presented in Table 18. Remarkably, we collected the first year-round diving data at high-resolution frequency (1 Hz) on the same adult emperor penguins (N = 4, adABf group[17], Table 15) resulting in the detection of 106 980 dives (100 263 foraging dives). Therefore, for this study group adABf, TDR datasets have been divided in four subgroups to take the seasonality into account (see details in Table 18).

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[17] For birds from the adABf group, the ARGOS platforms transmitted until the winter, while we collected year-round data with the TDRs for four of the birds (Table 14 and Table 15).

Table 18. General statistics (mean ± SD) of the main diving metrics per study group equipped with TDRs.

Study group	Max depth (m)	Dive duration (min)	Bottom time (min)	Dive efficiency (%)	Number of wiggles	ACPUE
adABf1* (N=4)	42.1 ± 43.1	2.8 ± 1.4	1.4 ± 0.9	37.6 ± 17.8	2.3 ± 2.2	1.5 ± 1.3
adABf2*(N=4)	43.7 ± 49.9	3.1 ± 1.9	1.5 ± 1.3	37.5 ± 20.3	2.3 ± 2.5	1.4 ± 1.3
adABf3* (N=4)	52.6 ± 54.7	3.6 ± 2.2	1.8 ± 1.4	37.7 ± 19.3	3.1 ± 3.1	1.6 ± 1.4
adABf4*(N=4)	53.3 ± 55.4	3.4 ± 1.8	1.6 ± 1.1	35.4 ± 18.6	2.7 ± 2.9	1.6 ± 1.3
adABs (N=22)	UA	UA	UA	UA	UA	UA
adPGs (N=4)	122.0 ± 73.1	4.9 ± 2.1	1.9 ± 1.1	29.9 ± 16.0	1.2 ± 1.8	0.5 ± 0.7

ACPUE = Attempt of Catch Per Unit Effort (ratio of the number of wiggles by the bottom time). For the study group classes: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter. * = sub-groups from the adABf study group made to correspond with the season of monitoring. adABf1 = monitored from January to April (fall; also corresponding to the post-moult/pre-breeding period). adABf2 = monitored from May to August (deep winter). adABf3 = monitored from September to mid-October (spring). adABf4 = monitored from mid-October to their recapture in November (summer). UA = under analyses. Artefacts in the data from the TDRs still have to be cleaned.

Foraging dives occurred throughout the trips of adult emperor penguins at each study site and for every season (Fig. 45).

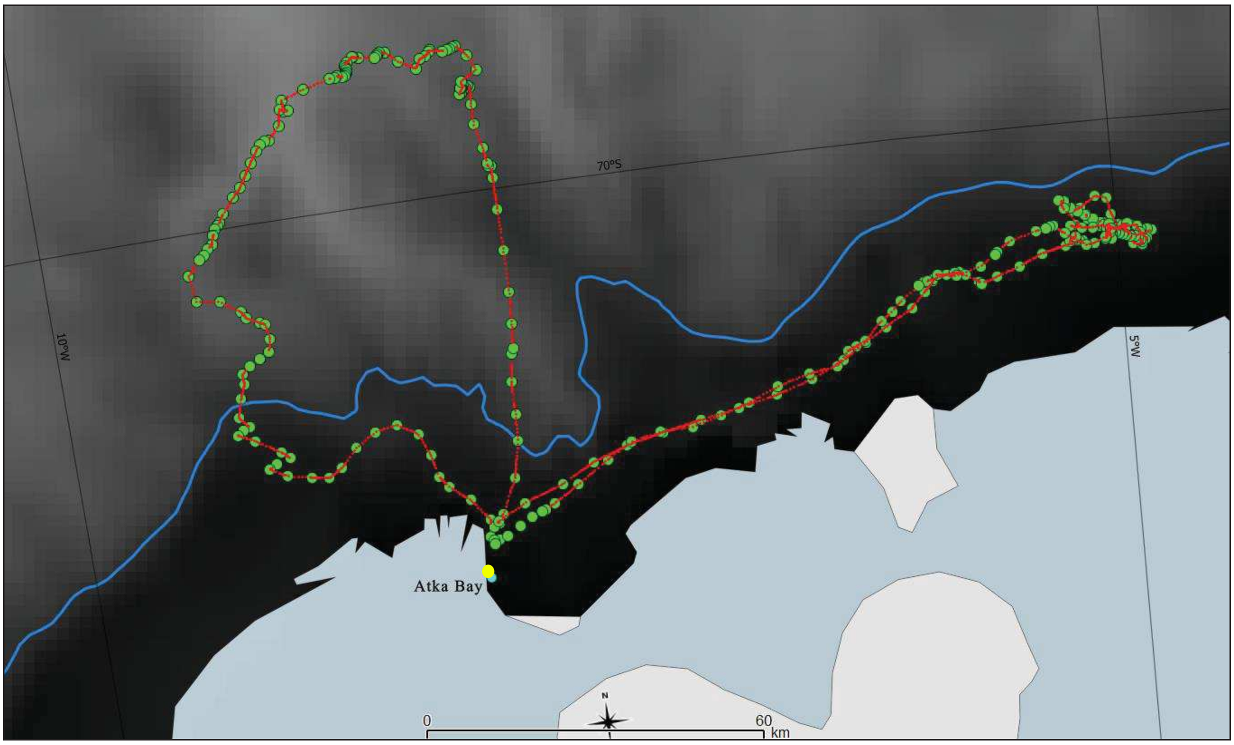

Fig. 45. Interpolated locations of the foraging dives (small red dots) along the two trips of the bird "7740093" equipped with GPS and TDR devices at Atka Bay in November 2018. Large green dots are hourly locations. The blue line is the 1000 m isopleth delineating the shelf break, and the bathymetry is in the background in grey scale. The first trip to the north extends beyond the shelf area and counts only 2% of benthic dives, while the second trip east of the colony remains over the shelf habitat and count 20% of benthic dives.

The study of the mean maximum dive depth per hour of each study group reveals a contrasting pattern between Atka Bay birds (adAB groups) and Pointe Géologie birds (adPGs group; see Fig. 46 and Table 18). The mean depth of foraging dives is significantly lower for the birds from Atka Bay colony than for the birds from Pointe Géologie colony (Wilcoxon test, $p < 0.001$). Additionally, chick-rearing birds from Pointe Géologie (adPGs) dove deeper during the day-time hours than at night-time hours, while the pattern is reversed for chick-rearing birds from Atka Bay (adABf4 and adABs). Birds from Atka Bay present a consistent pattern through the day for the rest of the year.

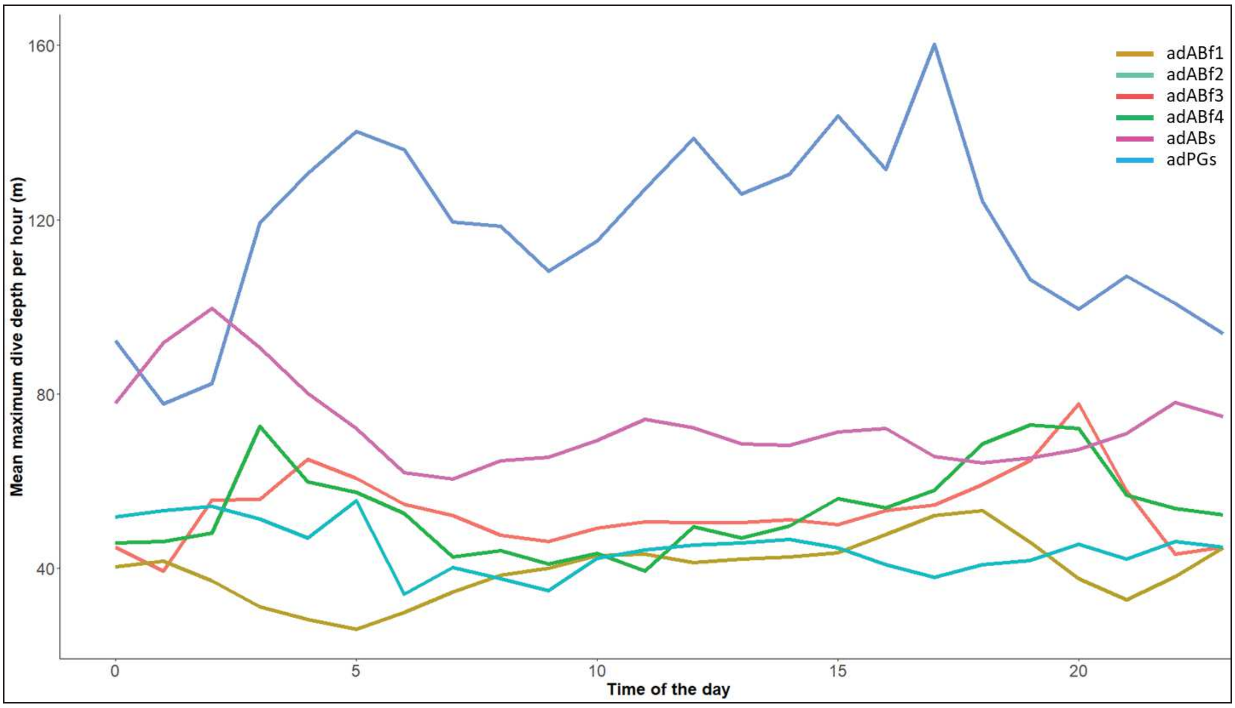

Fig. 46. Mean maximum dive depth per hour per study group equipped with TDRs. For the study group classes: juv = juveniles, ad = adults, AB = Atka Bay colony, PG = Pointe Géologie colony, y = year, f = fall, s = summer, w = winter. adABf1 = monitored from January to April (fall; also corresponding to the post-moult/pre-breeding period). adABf2 = monitored from May to August (deep winter). adABf3 = monitored from September to mid-October (spring). adABf4 = monitored from mid-October to their recapture in November (summer).

V.4.2.2. Behavioural patterns identification

We identified two daily diving patterns. In the first one, referred herein as 'day-time diving effort' strategy, the majority of the dives occurred during day-time hours, while a lower diving effort (fewer dives per hour) took place during night-time[18] hours. The second one, referred herein as 'night-time diving effort' strategy, is characterised by two peaks of diving effort, one in the middle of the day and the other one during night hours with a decrease in intensity between the two peaks of activity.

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[18] In November and December, the night is no more present at these latitudes. Night-time hours referred therefore to hours between 8 pm and 4 am.

The ‘day-time diving effort’ strategy was displayed by adABf birds from January to October as well as by adPGs birds in November (Fig. 47 for adABf and Fig. 48 for adPGs). The ‘night-time diving effort’ strategy was displayed by adABf birds in November as well as by adABs birds in November/December (Fig. 47 for adABf and Fig. 48 for adABs).

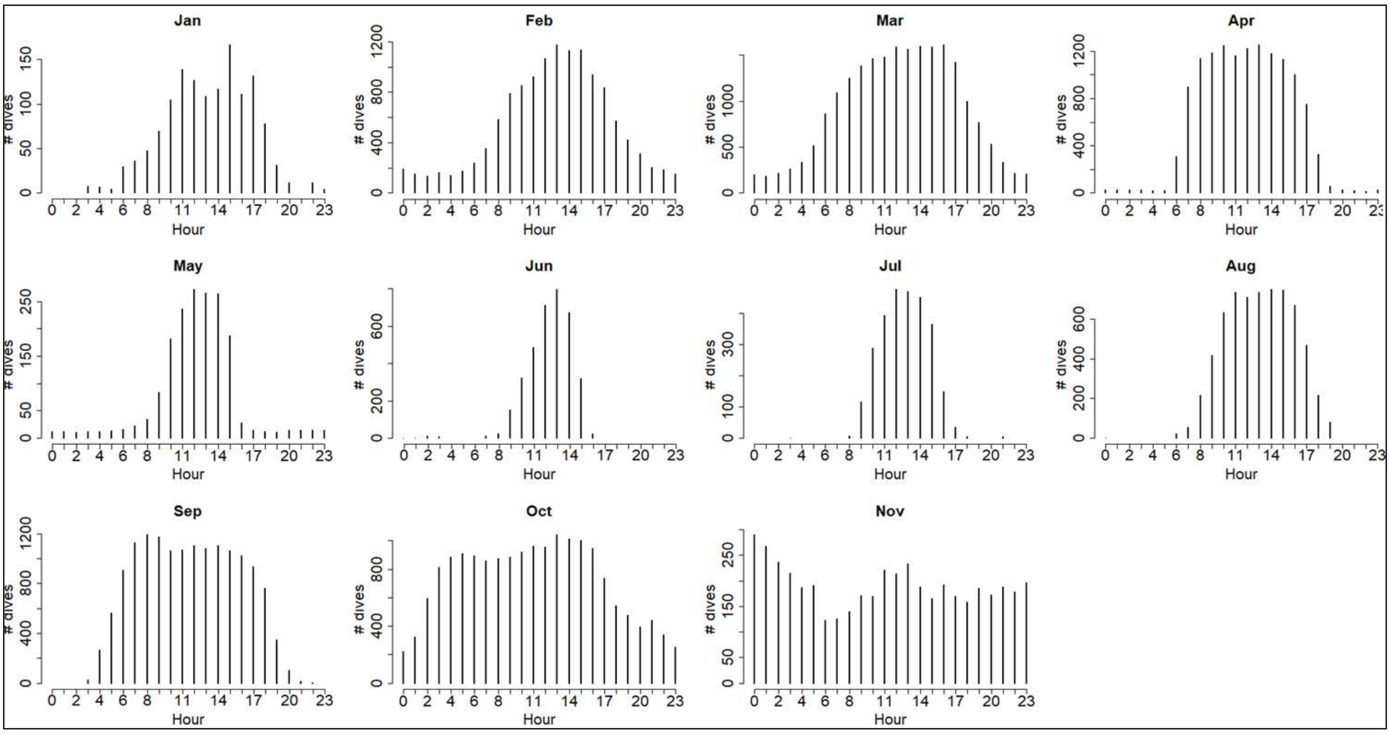

Fig. 47. Averaged hourly diving effort per month of the adult emperor penguins from Atka Bay equipped just after their moult for the whole year (adABf).

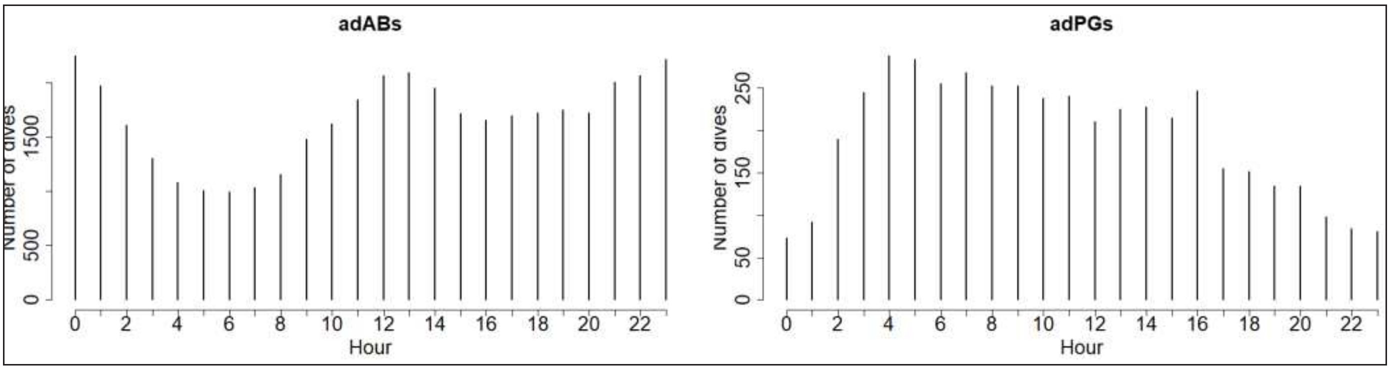

Fig. 48. Averaged hourly diving effort of the adult emperor penguins from Atka Bay equipped in November/December (adABs) and from Pointe Géologie equipped in November (adPGs).

In a preliminary analysis, we aimed to explore if the diving strategies we previously observed ('night-time diving effort' and 'day-time diving effort') could be explained by particular diving metrics. The best GLMM model retained all the diving parameters (i.e. the bottom time, the dive maximum depth, the dive efficiency, and the ACPUE) as descriptor of the daily diving patterns.

Table 19. Results of the best model of the GLMM analysis illustrating the functional relationship between the diving effort strategy (i.e. 'night-time diving effort', 'day-time diving effort') and the diving metrics.

Variable	Estimate	Std. Error	z value	Pr(>|z|)	Signif
Bottom time	0.44871	0.01495	30.008	< 2e-16	***
Max depth	-0.15733	0.02058	-7.645	2.09e-14	***
Diving efficiency	-2.95857	0.13953	-21.204	< 2e-16	***
ACPUE	0.29125	0.02121	13.729	< 2e-16	***

Variables were first normalised with a Cox Box Power transform. Significance is indicated by stars with ***< 0.001.

V.4.2.3. Benthic *vs* pelagic dives

Adult emperor penguins from Atka Bay performed less benthic dives than those from Pointe Géologie (z-test, $p < 0.001$; Table 17). For the periods during which the TDR datasets and the concurrent ARGOS tracking data were available (i.e. January to April) to extract the bathymetry, the adults from Atka Bay (adABf) performed only 0.5 ± 0.7% of benthic dives in average (Table 17). Similarly, during the chick-rearing period, the adABs birds made in average 3.9 ± 5.4% of benthic dives. On the contrary, 34.6 ± 21.5% of the dives from the chick-rearing adults equipped with TDRs at Pointe Géologie (adPGs) were benthic.

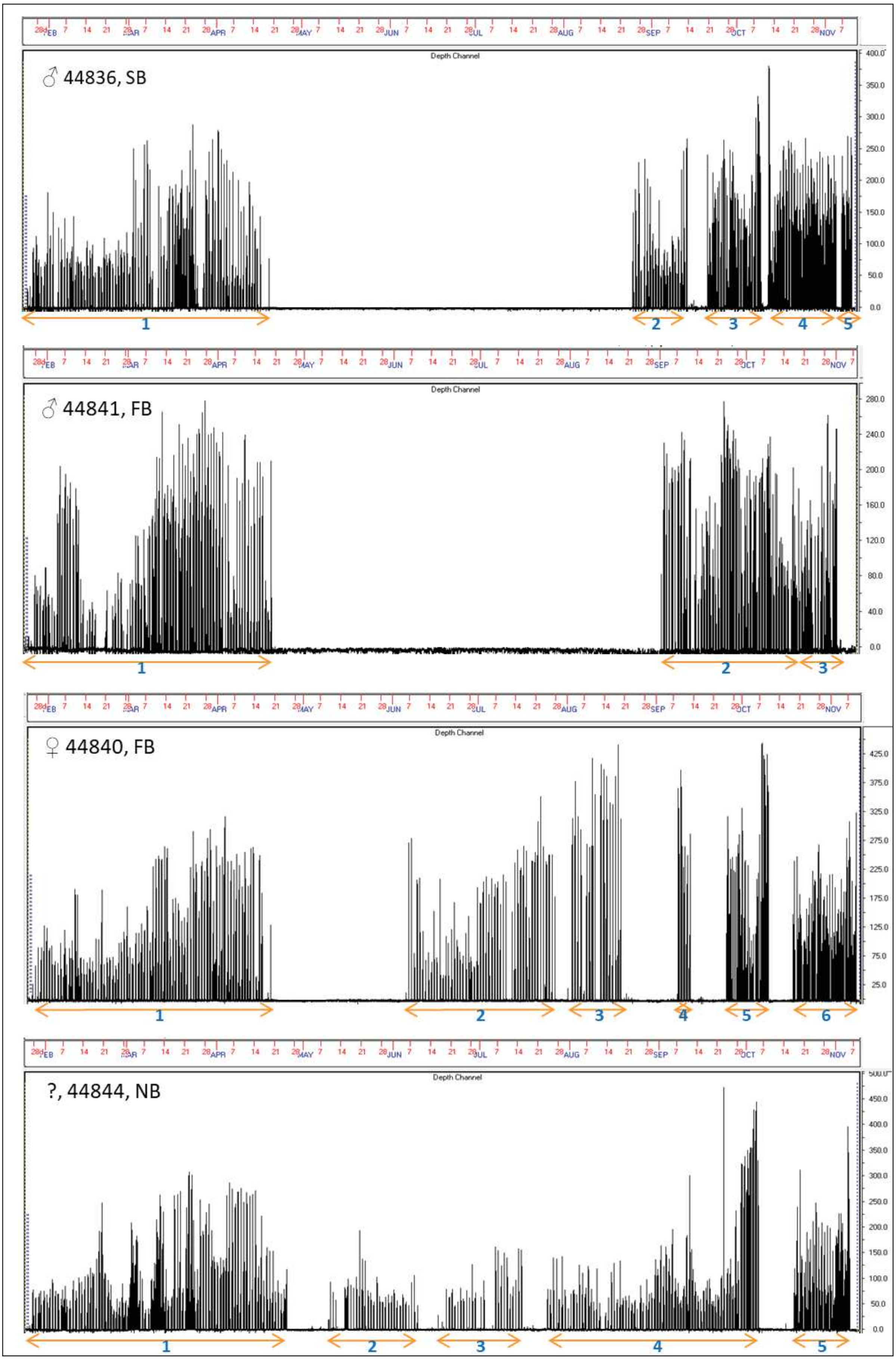

Fig. 49. Diving profiles of the four adult emperor penguins from Atka Bay equipped year-round with a TDR. For each profile, the x-axis represents the time and the y-axis the depth reached. The first profile on top belongs to a successful breeding male (long fasting period in winter and several absences of diving period in October and November). The second profile belongs to a male that was in breeding failure (no absence of diving period in October and November). The third profile belongs to a female that was in breeding failure (confirmed in the field). The last one is a non-breeding bird (no fasting period in winter) of unidentified sex. Trips are indicated by blue arrows and numbers.

V.5 Discussion

V.5.1. Distribution at sea, habitat and Marine Protected Areas use

Our study shows that juvenile and adult emperor penguins from the Atlantic sector of the Southern Ocean were segregated in space through the year. Juveniles dispersed and spent their first year at sea, several hundred kilometres away from the colony of origin. On the contrary, breeding adults remained in the close vicinity of the colony, even before the breeding season started (Table 17). Similar at-sea spatial segregation between juveniles and adults has been observed at the four other emperor penguin colonies where tracking of adults and juveniles has been performed (see Zimmer et al. (2007b), Thiebot et al. (2013), Labrousse et al. (2019b, 2019a) for Pointe Géologie colony; Kirkwood and Robertson (1997), Wienecke et al. (2010) and Wienecke and Robertson (1997) for Auster and Taylor colonies, and Ancel et al. (1992), Kooyman and Ponganis (2007) for Cape Washington colony). Such habitat-use segregation between different life-history stages is common in seabirds as revealed by studies in penguins, albatrosses and a few other large procellariforms (Clarke et al. 2003, Péron and Grémillet 2013, Weimerskirch et al. 2014, Fayet et al. 2015, Campioni et al. 2016, Orgeret et al. 2019).

Additionally, our results suggest that adult emperor penguins from Atka Bay express a comparable seasonal movement behaviour than adults from other colonies (Ancel et al. 1992, Kirkwood and Robertson 1997, Wienecke and Robertson 1997, Zimmer et al. 2007b, Labrousse et al. 2019a). For instance, the breeding adults from Atka Bay are foraging within ca. 200-km radius around the colony during the chick-rearing season, similar to what we also found for Pointe Géologie birds. Post-moult trips of adults from Atka Bay are also analogous to what Kooyman and colleagues (2004) reported in the Ross Sea between January and June.

Atka Bay and Pointe Géologie colonies are both situated within proposed MPAs that run alongside the continent, the WSMPA and the EAMPA, respectively (Fig. 39; CCAMLR 2018a, 2019b). We found that the life-history stage, the breeding status, and the season highly influenced the residence time of emperor penguins inside these MPAs. Juveniles spent the vast majority of their time outside the WSMPA, while breeding birds from both breeding colonies remained inside the relevant MPA boundaries. Breeding adults are indeed constrained spatially and temporally as they must return to the colony to provision their offspring (Ropert-Coudert et al. 2004). The situation is more contrasted for non-breeding birds. Only one of the three adults from Atka Bay, which did not try to breed, left the WSMPA during the winter, while 86% of the adults from Pointe Géologie tracked until their moult crossed the EAMPA boundaries to moult. Three of them eventually moulted in the adjacent Ross Sea region MPA. Such findings reveal that emperor penguins (and not only juveniles, as already highlighted and discussed in Chapter IV) commonly range outside existing and proposed MPAs. If the Ross Sea region MPA and the WSMPA would procure shelter for moulting birds of these regions (Kooyman et al. 2000), our results from Pointe Géologie reveal that important moulting areas (some were also identified in (Kooyman et al. 2000) would still be lacking protection if the proposed EAMPA was to be accepted. During their moult, emperor penguins must remain out of the water for approximately a month (Groscolas 1978, Williams 1995). Thus, they are highly dependent of stable platforms of ice that are still accessible between January and March. We, thus, recommend that MPA boundaries also include ice shelves, adjacent fast ice, and pack ice to secure potential moulting areas by preventing additional anthropogenic pressures to the physiological stress induced by the moult (Trathan et al. 2020). Juveniles, non-breeding immatures and adults that skip breeding also represent a non-negligible segment of emperor penguin populations (Jenouvrier et al. 2005, Abadi et al. 2017, Trathan et al. 2020) and of seabird populations in general (Carneiro et al. 2020). However, they are often not considered in MPA planning that focuses mainly on breeding colonies, like for the proposed WSMPA (Teschke et al. 2016a, CCAMLR 2018a). In that context, our analysis reveals the importance of building a connected network[19] of MPAs (e.g. WCPA/IUCN 2007, Hannah 2010) for such highly dispersive components of the populations, to ensure continuity in the protection process throughout the life cycle of the individuals (Grüss et al. 2011, D'Aloia et al. 2017).

In addition to the need of protected corridors between MPAs of the EAMPA, and between the EAMPA and the Ross Sea region MPAs to, at least, access suitable moulting areas, our results from Atka Bay colony also highlight the importance of a global management of connected network of MPAs in the Atlantic sector of the Southern Ocean. Indeed, some of our juveniles and non-breeding (and probable immature of 1.5 year-old, see page 182) birds reached the South Georgia and South Sandwich Islands MPA distant of 1150 kilometres from Atka Bay.

Noteworthy, we lost the signal of the five birds from Atka Bay that went into the Weddell Gyre, four juveniles and the probable immature mentioned above. Contrastingly, the three juveniles that stayed in the pack ice north of Atka Bay kept their device for a full year. As such, the technique of attachment on juveniles seems robust and does not appear to be the most plausible cause of signal loss, unlike for adults (see page 109). There is no clear environmental explanation either, the two groups were both foraging into the pack ice and resting on ice floes. Yet, leopard seals are known to prey on emperor

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[19] IUCN defines an MPA network as: '*a collection of individual MPAs or reserves operating cooperatively and synergistically, at various spatial scales and with a range of protection levels that are designed to meet objectives that a single reserve ca not achieve*' (WCPA/IUCN 2007).

penguins (Hiruki et al. 1999)[20] but sightings never happened at sea during the winter. However, studies on leopard seal movement and activities over the winter in the Weddell Sea region (Nordøy and Blix 2009, Staniland et al. 2018) reveal the presence of leopard seals in the Gyre region at the same time of the year than the birds for which we lost the signal. On the contrary, there is no recorded presence of leopard seals in the area where the signals of the equipped birds were not lost. As such, we suggest that the birds present in the Weddell Gyre may have been subject to predation events. Predation events by killer whales (*Orcinus orca*) could also be a possibility (Andrews et al. 2008) although killer whales have been spotted only once during the winter in the vicinity of emperor penguins in East Antarctica (Gill and Thiele 1997).

V.5.2. Environmental drivers of the time spent in an area

We showed that both juveniles and adults spent more time in areas (FPT) with high sea ice concentration (Fig. 43 and Fig. 44). Such finding is in coherence with their resting behaviour on ice floes especially at night in winter (Wienecke and Robertson 1997, Zimmer et al. 2007b, Wienecke et al. 2010, Goetz et al. 2018, Labrousse et al. 2019b, 2019a), as illustrated by the high values of FPT for both groups in winter. Then, juveniles and adults present dissimilar patterns for the rest of the year, which might reveal the influence of different environmental parameters encountered by these two life-history stages during these periods.

For the juveniles, low values of FPT were observed i) at the beginning of the year, which corresponds to the round trip between the Antarctic continent and the Southern Antarctic Circumpolar Current Front (SACCF), and ii) at the end of the year, when the juveniles were following the sea ice retreat. These results suggest that, during those periods, juveniles were moving around a lot and mostly travelling, being located between 1400 km (i.e. the distance between Atka Bay and the SACCF) and 200 km south of the front. Conversely, high FPT values were observed i) in March, which coincides with the relatively high values of FPT recorded between 200 km south and 200 km north of the SACCF, and points to a high effort of foraging activities in this area, and ii) during the winter period, when the birds spend most of the day resting on the sea ice, as highlighted above. Between June and October, the birds were situated at distances between 1400 km and 200 km south of the SACCF. Due to the confounding effect of the travelling periods and of the winter period, FPT values for those intermediate distances do not show any specific trend. In contrast, in May, the birds were at the southernmost part of their trip, the only period during which they were distant to more than 1400 km

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[20] See also https://www.youtube.com/watch?v=skoWevMUemc&list=RDEhsTCvLI5O4&index=19

to the SACCF. This is when and where they were encountering the sea ice habitat and starting to exhibit high FPT values, which could be interpreted as resting behaviour on ice floes. Note that the values of FPT corresponding to the birds being located more than 200 km north of the SACCF cannot be interpreted due to the high dispersion of the confidence interval (CI). Such CI dispersion might be explained by the fact that three of the five juveniles that went north of the SACCF, exhibited high FPT values for few days, suggesting high effort of foraging activities in this area, while the rest of their trips in this zone consisted of travelling period with low FPT values.

High FPT values of adults at the beginning of the year (January to April) concerned only the adults from Atka Bay after the moult and before the breeding season (adABf), when they need to replenish their reserves, thus accessing and remaining in very productive zones to forage. A more detailed analysis will help us to explain the decreasing trend observed over the season, by investigating if the birds adjusted their spatial and/or diving behaviour during this period (e.g. increased diving effort, increased distance travelled per day). The winter's high values of FPT, marked with a peak in July and August, concerned only one bird from Atka Bay (adABf group) and the females from Pointe Géologie during the winter (adPGw). As we have already shown, birds from Pointe Géologie had a small distribution area (Table 17) and foraged only few hours a day (Zimmer et al. 2008), resting on the pack-ice for most of the time, limiting the daily travelled distance to a minimum. During the chick-rearing period in summer, the birds used a wider area than in winter (Table 17) while diving day and night (Fig. 47 and Fig. 48). This mobility on short-time periods resulted in the lower FPT values recorded for this time of the year. The higher FPT values over the shelf (i.e. bathymetry between 0 and 1000 m) were heavily influenced by the high winter FPT values exhibited by the birds from Pointe Géologie (adPGw) and from Atka Bay right after the moult (adABf).

V.5.3. Foraging behaviour

Our unique datasets on depth use and diving behaviour of adult emperor penguins in the Atlantic sector of the Southern Ocean suggest a change in the diving effort of the birds at the beginning of the summer (late October – early November). Adult birds from Atka Bay switched from a 'day-time diving effort' strategy expressed from January until the last week of October, to a 'night-time diving effort' strategy at the end of October and beginning of November[21].

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[21] Birds were recaptured and devices removed on November 8th, 9th and 11th (two birds) 2018.

All but one of the chick-rearing adults from Atka Bay equipped in November and December expressed only the ‘night-time diving effort’ strategy, in 2017 as well as in 2018. Recording the same type of diving effort at the same period of the year, two years in a row, hints towards a common behavioural pattern for this period at this colony. Logistical constraints of fieldwork in Antarctica make it unlikely that we will soon be able to deploy TDRs on breeding adult emperor penguins in October to confirm the switch observed on the year-round monitored birds. Interestingly, the only chick-rearing individual that expressed a ‘day-time diving effort’ strategy also displayed different movement behaviours: the bird was the only chick-rearing bird to move inside a pair of inlets, ~100 km west of Atka Bay, and dove and rested in this specific area for 10 days, i.e. half of its trip. The other birds stayed off the coast to forage, only coming back towards the continent when they returned to their colony.

Our preliminary analyses on the year-round-monitored adults from Atka Bay (adABf) suggest that these daily diving patterns performed at the trip scale can be described by diving parameters such as the maximum dive depth, the time spent at the bottom of the dive, the number of catching attempt (ACPUE), and a measure of the diving efficiency. The next step will be to perform the analysis with the diving data from chick-rearing birds from Atka Bay to assess if their diving parameters are similar to those of the ‘night-time effort’ strategy of the post-moult/pre-breeding birds.

Previous study performed on the diving behaviour of emperor penguins in winter at Pointe Géologie (Zimmer et al. 2008) showed a ‘day-time diving effort’ strategy similar to the birds from Atka Bay in winter, with most of the dives occurring between 6 am and 6 pm (Fig. 47). The birds from Pointe Géologie studied in early summer also presented a ‘day-time diving effort’ strategy, even though dives are more scattered during the day (Fig. 48; Zimmer et al. 2008). The birds monitored in winter and in summer at Pointe Géologie were not the same birds, but they were equipped the same year. Yet, we do not detect a change in the diving effort, the majority of the dives occurring in the middle of the day for both seasons. Birds from Pointe Géologie dove deeper in average than Atka Bay birds (Fig. 46 and Table 18). Foraging chick-rearing birds from Pointe Géologie exploited the water column only over the continental shelf, at depth where they can and do perform benthic dives. In contrast, the shelf around Atka Bay is narrow (~20 km wide off the coast of Atka Bay *vs* 100 km wide off the coast of Pointe Géologie, Fig. 23) and steep. The seabed being quickly out of reach of the diving emperor penguins from Atka Bay, the opportunities to perform benthic foraging strategy is therefore very limited in this sector, as suggested by the low amount of benthic dives performed by all the birds from Atka Bay in summer and fall.

Overall, our results suggest that different prey items are targeted between the birds from Pointe Géologie and those from Atka Bay. Given the behaviour of the birds from Pointe Géologie presented in this study and given the previous studies that described birds from Pointe Géologie as ichthyophagous in summer (Offredo and Ridoux 1986, Cherel 2008), Zimmer and colleagues (2008) proposed that the birds fed primarily on Antarctic silverfish. Results from Atka Bay will require further investigations and analyses to confirm our hypotheses. Debate is still ongoing about krill diel migration and depth to which they can be found (Flores et al. 2012, Siegel 2016), and it is likely that there is considerable variability depending on the environment and time of year (Cresswell et al. 2009). However, several studies found that swarms in the Atlantic sector of the Southern Ocean had mean depths between 30 and 80 m (Godlewska 1996, Lascara et al. 1999, Siegel 2016), and they agreed that 95% of the krill range below 200 m (Siegel 2016). Given the mean low depth of the foraging dives performed by emperor penguins from Atka Bay in winter, we propose that birds primarily fed on krill during this period. The switch of diving effort in late October, and the second peak of foraging activity at night in summer remains unclear. Some studies in the Scotia Sea and offshore of South Georgia found a reverse diel pattern of krill migration, with patches being at greater depth at night than during the day (see Tarling et al. (2018) and references therein). However, why would penguins increase their diving effort by diving more and deeper to target the same prey species? Studies in the Weddell Sea (Klages 1989, Pütz 1995) and in the Ross Sea (Goetz et al. 2018) regions suggested two different pelagic feeding strategies in emperor penguins. They hypothesised that the diving birds target krill during shallow dives, while they prey on mesopelagic fish (especially the Antarctic silverfish) and squid during deeper dives. Increasing the dive depth requires longer recovery periods and decreases the diving efficiency of the birds (Kooyman and Ponganis 1998, Zimmer et al. 2010). However, fish is more energetically valuable than krill (Ainley et al. 2003, Ruck et al. 2014), especially at depth since biggest Antarctic silverfish are found above the seabed (Mintenbeck and Torres 2017). In the Ross and Weddell Sea regions, Antarctic silverfish represent as much as 90% of the ichtyofauna (La Mesa and Eastman 2012, Vacchi et al. 2017), and they are generally found over the continental slope and inner-shelf depressions at water depths below 200 m (Klages 1989, Plötz et al. 2001, Lancraft et al. 2004, Mintenbeck and Torres 2017). As such, we hypothesise that chick-rearing birds from Atka Bay exhibited both strategies over the course of the day, foraging on krill at shallow depths during the day and on fish at greater depth at night-time hours.

Although preliminary, these analyses suggest a change in diet during the austral summer for emperor penguins breeding in Atka Bay. Environmental seasonality (e.g. decrease in sea ice thickness, retreat of the sea ice, increase of day length) is likely influencing the abundance, the diel distribution and the type of prey available in an area, leading to a switch in the foraging strategies performed by the birds during the course of the year. Emperor penguins from Atka Bay appear to be mostly pelagic feeders along the year, but during the chick-rearing period, they may adapt their foraging behaviours to different prey items (i.e. shallow, medium, and, to some extent, benthic dives).

Chapter VI. General discussion

In a review about the conservation status of the Emperor penguin, Trathan and colleagues (2020), advocated for an "*Action Plan (that) should also include priorities for telemetry work to help determine where and when, and which demographic categories of emperors are at greatest risk in relation to threats at sea*".

Although initiated prior to this publication, the studies that compose my PhD project are part of that stream of thought. The aim of my PhD thesis was, through the use of telemetry, to enhance our knowledge and understanding about the at-sea ecology, i.e. distribution as well as activities, of the Emperor penguin, and this specifically in an area where such questions had not been studied before and where conservation stakes are high. My PhD project is part of a larger programme with the main objectives to (i) ensure a fundamental knowledge of the species by collecting unprecedented data that can answer unresolved questions, and to (ii) start long-term monitoring at sea and on land through systematic data collection observatories set up all around the Antarctic continent to monitor changes resulting from anthropogenic pressures. In this Chapter, I will summarise the main results obtained during my PhD work and consider them in a more general perspective. First, I will focus on the new knowledge gathered on the distribution and behaviour at sea of emperor penguins. Then, I will discuss the importance to collect such data within an ethical, standardised and reliable framework. Finally, I will consider the use of tracking data for conservation purposes in the Southern Ocean. I will conclude by investigating future research perspectives raised by the results obtained during my PhD project.

VI.1 Global overview on the at-sea distribution and activities of the Emperor penguin

VI.1.1. A partially filled distribution

Up to now, 61 known colonies of emperor penguins have been identified around the Antarctic continent (Fig. 16; see review in Wienecke (2011), Trathan et al. (2020) and in Fretwell and Trathan (2020)). During my PhD, we collected tracking data on adult and juvenile birds from one colony settled at Atka Bay in the Atlantic sector of the East Antarctica, and we used previous data on juveniles and adults collected on four others colonies: at Cape Washington in the Ross sea sector, and at Taylor Glacier, Auster, and Pointe Géologie in the Indian sector of the East Antarctica (Fig. 36; Zimmer et al. 2007b, Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Goetz et al. 2018, Labrousse et al. 2019b).

In a recent review about tracking studies in the Southern Ocean, Hindell and colleagues compiled several datasets that they managed to obtain on emperor penguins (Hindell et al. 2020, Ropert-Coudert et al. 2020). Noteworthy, they mostly considered adult datasets except for Auster and Taylor colonies were they also used juvenile tracking information. Adult datasets were from three other colonies (Amanda Bay in the Indian sector of the East Antarctica, and Ross and Coulman Islands in the Ross sea sector) and from few birds equipped directly on the sea ice in the Ross Sea. To our knowledge, Fig. 50 shows the maximum extent of all the tracking data available on emperor penguins (but not every single emperor penguin’s track).

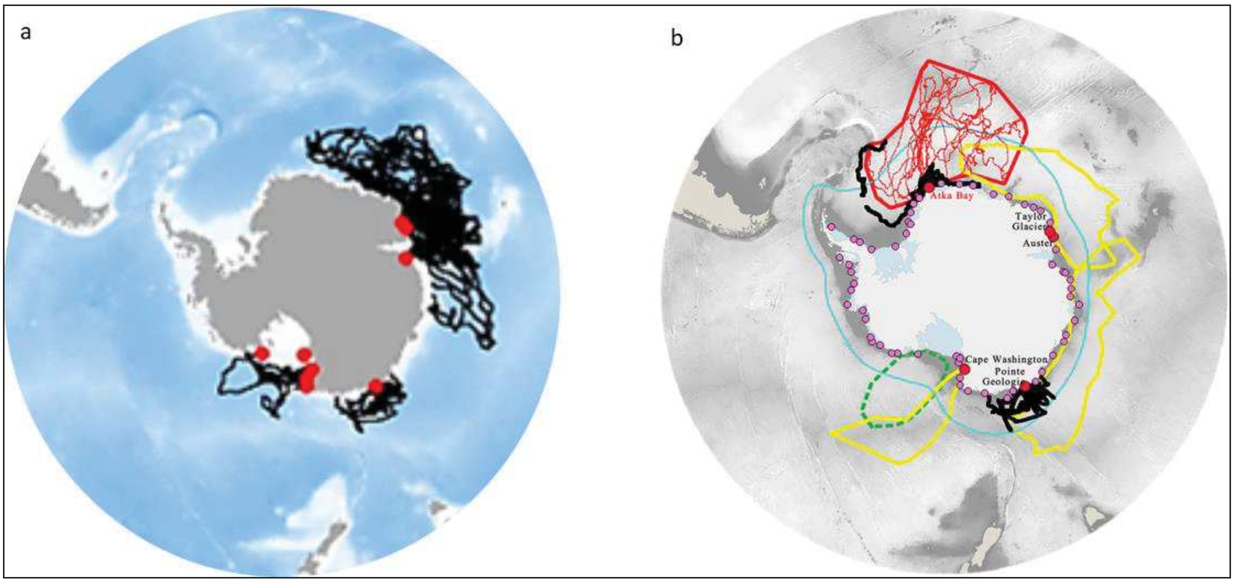

Fig. 50. Emperor penguin tracking data overview. (a) Data used in Ropert-Coudert and Hindell studies (Hindell et al. 2020, Ropert-Coudert et al. 2020). Adapted from Ropert-Coudert et al. (2020). (b) Data used in my PhD thesis. Tracks are in black, except tracks obtained during my PhD project on juveniles equipped in Atka Bay: thin red lines correspond to their tracks and the red outlined polygon to their distribution area. Yellow outlined polygons represent the distribution areas of juveniles equipped and tracked at other colonies. The green dashed outlined polygon represents the distribution areas of non-breeding birds from Goetz et al. (2018) and was obtained thanks to the method described page 126. Study sites where equipment has been performed, are indicated with red dots, while pink dots correspond to other emperor penguin colonies. The International Union for Conservation of Nature (IUCN) range is represented by the thin blue line.

The comparison between the two maps highlights the contribution of the data gathered during my PhD project to the general knowledge on the emperor penguins' distribution at sea. We provide the first tracking data (adults and juveniles) in the Atlantic sector of the Southern Ocean (including the Weddell Sea region), which is home to more than a third of the breeding population of emperor penguins (Fretwell et al. 2012, Teschke et al. 2016b).

These maps also emphatically reveal the geographical gap of knowledge in the distribution at sea of the Emperor penguin. Tracking data are particularly missing in the Bellingshausen and Amundsen seas of the West Antarctica sector, around the Peninsula, and in the deepest part of the Weddell Sea since no tracking has ever occurred in these sectors of the Southern Ocean, for any life-history stage.

VI.1.2. A 2-D differential use of the Southern Ocean between adults and juveniles, but consistent across breeding sites

Many studies on seabirds focus on the distribution and habitat use of adult animals and neglect that immatures and juveniles can inhabit vastly different areas (Carneiro et al. 2020). The studies (Chapter IV and Chapter V) on emperor penguins performed during my PhD project confirm the results of previous studies, and reveal different use of the Southern Ocean between juvenile and adult emperor penguins.

The seasonal travel pattern we found in the post-fledging juvenile emperor penguins from Atka Bay, Queen Maud Land, resembles those of the other colonies (Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019b). At the end of the summer (i.e. February), after leaving for the first time their colony of origin, juveniles migrate northward towards and into the Antarctic Circumpolar Current (ACC, Fig. 37). This northward exploration can be observed even for the juveniles from Atka Bay and Cape Washington despite the remoteness of the ACC from the continent/colonies in these regions (Fig. 37). Remarkably, none of the birds ventured far north of the Polar Front (PF) that most likely acts as an ecological boundary. In late fall (i.e. April), juvenile emperor penguins migrate southward towards the Antarctic continent and reach the pack ice where they spend the winter and spring, moving northward as the sea ice extends (Fig. 38). The following summer (i.e. November), juveniles follow the southward contraction of the pack ice. According to our tracking data of juveniles up to their annual moult, the first data of this kind reported so far, one-and-a-half-year-old juveniles moult in late December-January near the Antarctic continent, hundreds of kilometres from their colony of origin[22] (Chapter V, Fig. 39). Only a few juveniles (i.e. birds with white chin and white/yellow auricular patches) have been observed moulting at Atka Bay or at Pointe Géologie colonies during our fieldwork sessions, but it was, of course, not possible to determine if they belonged to these colonies as they were not marked. Similarly to adults, > 1-year-old juvenile emperor penguins appear to engage their moult on consolidated part of the sea ice, fast ice or even ice shelf (Houstin, Le Bohec, unpublished observations). Juveniles and adults have also been spotted to moult together in the pack ice deep inside the Weddell and Ross Seas (Kooyman et al. 2000).

Overall, adult emperor penguins from Atka Bay reveal similar behaviour in their seasonal 2-D movements than adults from other colonies (Ancel et al. 1992, Kirkwood and Robertson 1997, Wienecke and Robertson 1997, Zimmer et al. 2007b, Labrousse et al. 2019b). We showed that their distribution at sea is mostly constrained by the breeding status of the birds and the distance between the breeding colony and the limit of the continental slope over which they forage presumably in ephemeral polynya, cracks and leads where the productivity is high (Chapter V). Right after their moult, adults range further to reach foraging grounds (probably more productive) to build up their reserve for the next breeding season. They explore areas, which they cannot reach during the breeding season, near other colonies or at the margin of the continental slope (up to 486 km, Fig. 39). The ARGOS deployed on the post-moult adults from Atka Bay stopped transmitting between May and July

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[22] The three juveniles from our study moulted at the following southern latitude: 69.8°, 72.9°, and 73.4°.

for breeding birds. Thus, we could not collect data on breeding birds after their return to the colony for the courtship and incubation phase. Nevertheless, as for adults breeding at Pointe Géologie (median of maximum distances to the colony = 56 km, Table 17), between May and September, breeders from Atka Bay are also likely constrained around the colony.

The tracks we collected at Atka Bay during the chick-rearing period reach the limits of the maximum extent determined by the model of probability of occurrence of breeding emperor penguins[23] developed by Teschke and colleagues (2016b, 2019), with some parts of the tracks at the very edges of the boundaries (Fig. 51). Given the few (but only available for the region) data we collected, we suggest that this model underestimates the probability of occurrence of breeding birds, at least over the chick-rearing period. In the deep winter, if breeding emperor penguins from the Atlantic sector of the Southern Ocean exhibit the same habitat use behaviour than the ones in the d'Urville Sea (Chapter V), then the tracks of breeding birds would fall within the model boundaries.

In the case of non-breeding birds, either individuals in post-moult period (i.e. January to April before breeding) or birds that chose not to breed during the winter, the model is not trustworthy: emperor penguins from Atka Bay range commonly outside the predicted area of presence (Fig. 51). In our study, like in the study carried out in the Ross Sea (Goetz et al. 2018), non-breeding adults express two different habitat-use strategies: either they spend the winter foraging along the Antarctic continent (N =2), or travel clock-wise in the Weddell Sea Gyre (N = 1). Consequently, such model shall not be used to infer the probability of occurrence of emperor penguins in the area.

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[23] The model of probability of occurrence that used to estimate the distribution at sea of breeding emperor penguins in the Weddell Sea region assumes that "*the probability of an emperor penguin being present at a certain geographical locality depends on three major factors, the overall density of penguins in the wider area* (e.g. colony size)*, the distance from the colony, and the sea ice conditions,* i.e. *to which extent entry into the water is possible*" (Fig. 51; Teschke et al. 2016b, 2019). In the absence of tracking data on emperor penguins from the Weddell Sea region, the distance parameter is based on the winter distribution of male emperor penguins from the Pointe Géologie colony (Zimmer et al. 2007b). A distance model weighted by the penguin density (estimates from Fretwell et al. 2012) was combined with a sea ice concentration model considering the mean sea ice concentration between June and January from 2002 to 2011.

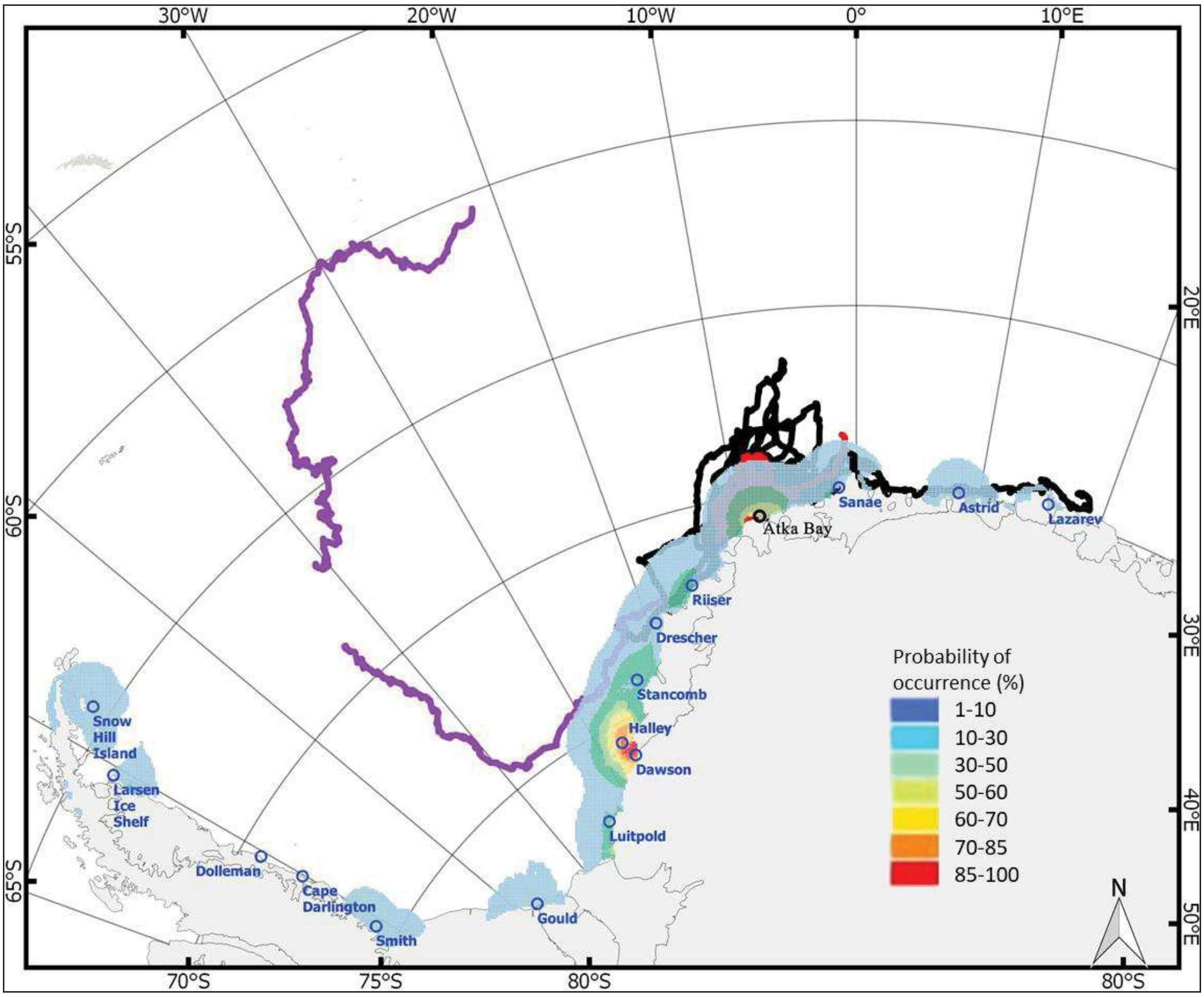

Fig. 51. Probability of occurrence of breeding emperor penguins in the Weddell Sea region overlaid on adult tracks obtained during my PhD project. The probability of occurrence and their colour scale were obtained from Teschke et al. (2016b, 2019). Red tracks are from chick-rearing adults (GPS datasets obtained in November/December) and black lines are from non-breeding birds (ARGOS datasets obtained between January and August). The purple track belongs to the non-breeding adult that exhibited a Gyre habitat-use strategy[24].

VI.1.3. Inferring the reasons for the dispersion of juveniles

Interestingly, juvenile emperor penguins from Atka Bay are heading northward, on the open sea, at a time when adults are spreading along the continent, over the continental shelf and slope, to replenish their reserves after the annual moult and before breeding (Chapter V, Fig. 39). Then, in April, while

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[24] The mass and the morphological characteristics (flippers, beak and feet lengths) of this bird were not extreme. However, its auricular yellow patches appeared to us slightly smaller and lighter than the ones from the other post-moulting birds that we were able to find and capture on the colony. The coloration of auricular patches has been shown to be indicative of birds' age for the sister king penguin species (Nicolaus et al. 2007). Additionally, the habitat-use strategy displayed by this bird is strikingly similar to the one displayed by our equipped fledglings and dissimilar from the two other non-breeding birds. As such, we suggest that this bird might actually be an immature of 1.5 year old.

juveniles are back in the vicinity of the Antarctic continent, adult emperor penguins are at the colony to mate and breed. This finding suggests that these two life-history stages might not overlap in their distribution over the year and until the annual moult period (December to February) during which they gather in the same habitat (Houstin, Le Bohec, unpublished observations; Kooyman et al. 2000). At-sea spatial segregation of conspecifics according to age-class is not uncommon in other southern oceanic bird and mammal species (Field et al. 2005, Weimerskirch et al. 2006, Trebilco et al. 2008).

Noteworthy, ranging so far north (up to 48.5°S for one juvenile of Atka Bay) during their dispersion in fall, our results reveal that juvenile emperor penguins overlap in space and time with juvenile and possibly non-breeding adult king penguins (Fig. 52). The two species of the Aptenodytes genus split up 3 million years ago (Cole et al. 2019). However, in contrast to emperor penguins, king penguins have not been tracked within the pack ice area during winter, but only up to its edge (Orgeret et al. 2019). Given the similarities in size and diving ability between juvenile emperor penguins and king penguins (Kooyman et al. 1992a, Ponganis et al. 1999), it is likely that juvenile emperor penguins forage on the same prey species, i.e. lantern fish (myctophids) and squids than king penguins when they forage at their northern range (Wienecke and Robertson 2002, Wienecke et al. 2010); a diet drastically different to the one they were being fed with (i.e. krill and Antarctic silverfish) by their parent (Klages 1989, Robertson et al. 1994, Kirkwood and Robertson 1997, Cherel 2008).

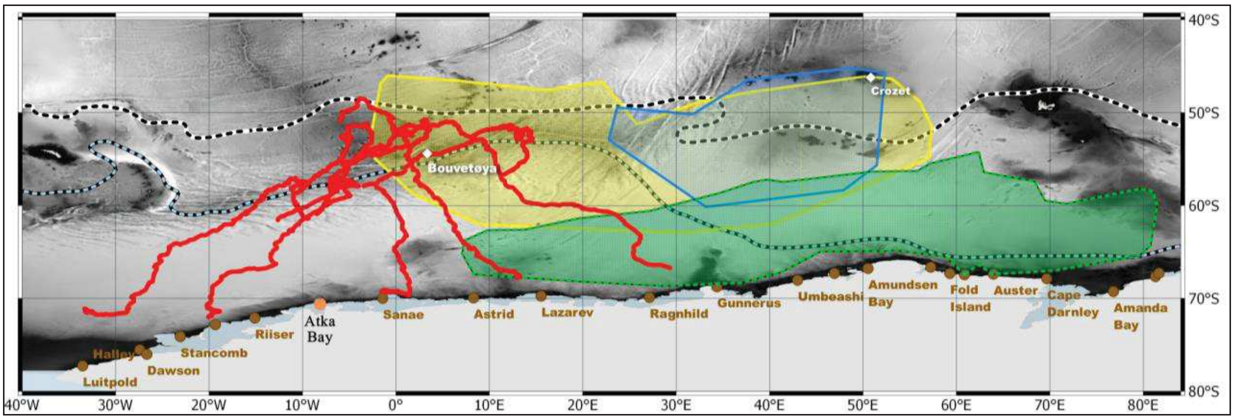

Fig. 52. At-sea distribution of juvenile emperor and king penguins and of non-breeder king penguins tagged with ARGOS platforms in the Atlantic and Indian sectors of the Southern Ocean. Tracks from March and April of juvenile emperor penguins equipped at Atka Bay in 2019 are in red (N = 8). The at-sea distribution area, during the fall season (March/April/May), of juvenile (N = 17) and non-breeding (N = 6) king penguins equipped at Crozet archipelago in 2013/14 and 2014/15 is represented by a yellow and blue polygons, respectively (Orgeret et al. 2019). The at-sea distribution area of juvenile emperor penguins (N = 17) equipped at Auster and Taylor colonies is represented by a green polygon (Wienecke et al. 2010). Brown dots are emperor penguin breeding colonies. Dashed lines are from top to bottom the Polar Front and the Southern Boundary of the Antarctic Circumpolar Current. The white line is the median maximum sea ice extent between 1981 and 2010 and the greyscale background represents the bathymetry.

Post-natal dispersal has been shown to be partially pre-determined in various species, for instance, in flying seabirds (de Grissac et al. 2016, Yoda et al. 2017), sea turtles (Scott et al. 2014), seals (Bornemann et al. 2000, Tosh et al. 2015), or some penguin species like the King penguin (Pütz et al. 2014, Orgeret et al. 2019). As suggested by Thiebot et al. (2013), the northward-directed movement into the ACC of all tracked juvenile emperor penguins might be driven by innate mechanisms. What triggers the southward return of juvenile emperor penguins remains also unclear. Several non-exclusive hypotheses can be at stakes including physiological maturation (e.g. increase in body insulation as shown in king penguins (Enstipp et al. 2017) or in O_2 storage capacity as suggested by Ponganis et al. (1999) and shown in seals (Thorson and Boeuf 1994)), development of foraging skills (e.g. Ponganis et al. 1999, Orgeret et al. 2016, Grecian et al. 2018), a switch in diet or of the prey distribution over the seasons (Charrassin et al. 2002, Matthysen 2012), intra- and inter-specific competition for food resources (Burns and Kooyman 2001, Ballance et al. 2009, Ainley et al. 2010a), as well as predation avoidance regarding, for instance, the leopard seals or killer whales (Ainley and Ballard 2012). The survival rate of emperor penguins over their first year at sea is relatively low (40%, Abadi et al. 2017). In comparison, the return (and thus survival) rate of juvenile king penguin is between 68–87% (Saraux et al. 2011b). Yet, juveniles are more sensitive to environmental factors than adults, and juvenile survival can have a critical influence on the population dynamics especially in long-lived species (Stearns 1992). Given the ecological upheavals that are expected in a near future as a result of global change (see page 38), an improved understanding of the factors that influence juvenile emperor penguins' survival during their dispersion should, therefore, become a research priority in order to predict as accurately as possible the future demographic trends of the species.

VI.1.4. Adaptive capacity through behavioural flexibility in foraging to cope with a changing environment

Adult emperor penguins are associated with the pack ice both during the breeding (Wienecke and Robertson 1997, Zimmer et al. 2007b) and post-breeding seasons (Kirkwood and Robertson 1997, Rodary et al. 2000a, Kooyman et al. 2004, Wienecke et al. 2004). They access their foraging grounds from small openings, including holes, cracks, flaw leads, and ephemeral short-term polynyas; the sea ice restricting their access to the water (Zimmer 2007, Labrousse et al. 2019a). Once immerged, they search for food items that is patchily distributed, both horizontally and vertically (Wienecke and Robertson 1997, Zimmer 2007). The diving data we collected on adult emperor penguins in the Weddell Sea region and the Atlantic sector of the Southern Ocean (Chapter V) are the first of their kind, since the activities at sea of the species had never been studied in this area, home of a third of the global population. Indeed, to date, studies on the diving behaviour of emperor penguins occurred essentially in the Ross Sea (Ancel et al. 1992, Kooyman and Kooyman 1995, Goetz et al. 2018), in the d'Urville Sea (Ancel et al. 1992, Zimmer et al. 2007b, 2008, 2010), and along the Mawson coast (Kirkwood and Robertson 1997, Wienecke and Robertson 1997). Emperor penguins exhibit dive capacities, both in terms of dive duration and maximum dive depth, similar to those of marine mammals such as Weddell seals (Burns and Kooyman 2001).

The exploration of the foraging behaviour of diving birds using proxies of the daily diving effort (i.e. the distribution of dives throughout the day and the depth of dives) allowed us to investigate the diet of the emperor penguins from the Atlantic sector of the Southern Ocean. Indeed, our unprecedented year-round high-resolution complete datasets (N = 4) suggests a switch in the diving effort strategy of the birds in late October (from a 'day-time diving effort' strategy before the summer to a 'night-time diving effort' strategy in summer). The prevalence of this second strategy in summer was confirmed by the equipment of chick-rearing birds in summer (except one bird, all (N = 22) exhibited this pattern). We interpreted this switch as a change in the diet of the birds, and we suggest that they forage on krill during the day, while the dives occurring at night hours in the 'night-time diving effort' strategy indicate a higher predation effort on fish exhibiting a diel vertical migration (Mintenbeck and Torres 2017) and of a higher energetic value for the birds (Ainley et al. 2003).

Our study in that sector of the Southern Ocean supports the hypothesis of an existing flexibility in the foraging behaviour of the Emperor penguin giving birds the ability to adapt their diet according to season, year and location. For instance, it has been shown that emperor penguins from Auster colony switched from a fish diet in 1988 to a krill diet in 1993 (Kirkwood and Robertson 1997), while birds from Pointe Géologie presented a fish diet in two studies 20 years apart (Offredo and Ridoux 1986, Cherel 2008). The prey availability may vary with seasons and years due to environmental factors like sea ice extent and thickness, water salinity, or light quantity. However, the physical environment of each locality also influences the prey composition of an area and may offer different perspectives for emperor penguins according to their breeding sites. For instance, the shelf around Atka Bay is narrow and steep (Zimmer et al. 2007b, Jerosch et al. 2016, Labrousse et al. 2019a), while the shelf in the Ross Sea and the d'Urville Sea is wide (Anderson 1999, Beaman et al. 2011) and presents particular bathymetric features (called 'banks') between 200 and 500 m of depth aggregating bentho-pelagic fish within reach of emperor penguins. As Goetz et al. (2018) in the Ross Sea, we showed that birds from Pointe Géologie perform benthic dives, a strategy not expressed by the large majority of our birds in the Atlantic sector of the Southern Ocean. As a result, both physical and geographical environmental differences in localities may lead to various foraging strategies expressed by the individuals within the species. Consequently, foraging but also general behavioural strategies observed at a given breeding site might not be generalised to colonies form other regions. Additionally, multi-year data on a same breeding site are required to investigate the consistency of the strategies with regards to environmental stochasticity and more persistent changes.

Although unique, the year-round diving datasets we obtained are from a small sample size (N = 4), which does not allow to draw strong conclusions regarding differences in sex and breeding status. In addition, the absence of tracking data over the winter prevents us from getting a fully comprehensive understanding of the foraging behaviour of emperor penguins from Atka Bay. Therefore, we could not investigate the effect of sea ice and the presence of ephemeral short-term polynyas on the spatial and diving behaviour of the birds from this region.

Noteworthy, in all the emperor penguins foraging related studies listed here, including ours, the sub-ice foraging behaviour was not considered. Shallow dives are very common in emperor penguins (Cherel and Kooyman 1998), and they are mostly considered as non-foraging dives, travelling dives, or part of the recovery from an oxygen debt (Kooyman and Kooyman 1995, Kirkwood and Robertson 1997). They are, therefore, classically removed from the foraging analyses based on the wiggles' detection at depth. However, such sub-ice foraging behaviour has been documented on emperors (Ponganis et al. 2000) as well as on Adélie penguins (Watanabe and Takahashi 2013) and is highly suspected on Weddell seals (Watanabe et al. 2006). Moreover, the occurrence of cryopelagic fish and krill species as well as scavenger amphipods in the diet of emperor penguins has also been reported (Offredo and Ridoux 1986, Klages 1989, Pütz 1995, Cherel and Kooyman 1998). Surface or shallow-depth foraging seabirds in the Ross Sea are known to feed on a similar diet and on Antarctic silverfish (Ainley et al. 1984, Mund and Miller 1995, Cherel and Kooyman 1998). In conclusion, as Cherel and Kooyman (1998), we consider that there is no reason to believe that emperor penguins would not forage on sub-ice prey and at shallow depths as well, and this behaviour will need to be investigated (see Perspectives page 208).

VI.2 Acquisition of baseline data and set up of a global monitoring in the context of global change

VI.2.1. Global change and emperor penguins

There is growing evidence that ongoing climate change is adversely affecting penguin populations on a global scale (Ainley et al. 2010a). Recent studies on the two major Antarctic species - the Adélie penguin (Jenouvrier et al. 2012, Cimino et al. 2016, Ropert-Coudert et al. 2018) and the Emperor penguin (Jenouvrier et al. 2009b, 2012, 2014, 2019, Trathan et al. 2011) - have highlighted their exposure to environmental changes, and the vulnerability of the Emperor penguin to changes in sea ice extent, formation, and persistence.

Sea ice monitoring by satellites is on-going since 1978 (Stammerjohn et al. 2012, Parkinson 2019). Contrasting trends have been observed depending on the Antarctic sector considered (Stammerjohn et al. 2012, Parkinson 2019). Sea ice extent and persistence have been decreasing in the West Antarctic Peninsula sector since records started (Massom and Stammerjohn 2010, Stammerjohn et al. 2012)[25], while a reverse trend has been observed in the Ross and the Weddell Seas (Stammerjohn et al. 2012, Parkinson 2019). Moreover, despite some uncertainties, models project sea ice loss over the 21st century in all scenarios (Roach et al. 2020).

Top predator species have already been negatively impacted by environmental changes. For instance, declines in populations of Chinstrap and Adélie penguins in Western Antarctic peninsula, as well as of Antarctic fur seals (*Arctocephalus gazella*) around South Georgia, has been associated to a decrease in krill biomass, their main prey species (Forcada et al. 2006, Trathan et al. 2007, Trivelpiece et al. 2011, Lynch et al. 2012). Sightings of Weddell seals have also been reported to have declined In the western Antarctic Peninsula (Siniff et al. 2008). Moreover, direct environmental impacts have already been monitored on emperor penguins' colonies with the loss of two breeding colonies associated with sea ice decline and fast ice alteration (Trathan et al. 2011, Fretwell and Trathan 2019). Birds may have relocated to other colonies or sites, as it has been shown for the Mertz colony after the Glacier Tongue calving in 2010 (Ancel et al. 2014) and for the Ruppert Coast colony that relocated from sea ice to an

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[25] See also https://www.climate.gov/news-features/understanding-climate/understanding-climate-antarctic-sea-ice-extent

ice shelf in 2012 (Fretwell et al. 2014). Yet, if sea ice, and specifically fast ice, around Antarctica tends to disappear in the near future due to global warming, suitable areas for relocation for breeding might shrink (Trathan et al. 2020). Indeed, to access ice shelves that can be up to several tens of meters above the sea ice level, emperor penguins require the presence of snow bridges connecting the shelf and the sea ice (Zitterbart et al. 2014). In the absence of sea ice, such bridges are unlikely to be present.

Emperor penguins are tied to sea ice not only for their breeding ground, but also for feeding. Their main prey species (krill and Antarctic silverfish) have both larval stages dependent on sea ice (Mintenbeck and Torres 2017, Atkinson et al. 2019). The disturbance of the sea ice cycle is thus likely to negatively affect these prey populations in terms of abundance, structure, size, quality, and distribution (Piñones and Fedorov 2016, Mintenbeck and Torres 2017), and/or to lead to temporal mismatch between their availability and the critical phase of the breeding cycle of these predators (e.g. the very demanding chick-rearing period). If food resources were to be limited, then emperor penguin populations would indubitably decrease. However, myctophids or demersal notothenioids might progressively replace krill and Antarctic silverfish in areas where sea ice disappears and water temperature rises (Mintenbeck and Torres 2017). Given their opportunistic behaviour and diving capacities (Chapter V), it is worth considering that emperor penguins will probably be able to adapt, to some extent, their diet accordingly.

The ongoing global change has already started to affect Southern Ocean ecosystems (Constable et al. 2014, Gutt et al. 2014) and emperor penguins (Trathan et al. 2011, Fretwell and Trathan 2019). However, each emperor penguin colony presents specific environmental conditions (e.g. distance to oceanic fronts, persistence of sea ice in time and space, seaward extent of Antarctic continental shelf, presence of specific oceanic currents, like gyres, that may lead to contrasting population trajectories (Jenouvrier et al. 2014, 2019, Kooyman and Ponganis 2017).

VI.2.2. A limited knowledge and amount of data on the most iconic species of Antarctica

Our understanding of climate change impacts on emperor penguins is fragmented (Ainley et al. 2010b, Larsen et al. 2014). Most of our current knowledge about the breeding behaviour, life-history and demographic parameters of emperor penguins (e.g. breeding date, breeding cycle duration, survival and reproductive rates) is based on the monitoring of a single colony at Pointe Géologie, Terre Adélie, monitored continuously since 1952 (Prévost 1961, Jenouvrier et al. 2005, Barbraud et al. 2011).

However, heavy flipper banding scheme was carried out in the 70’s and 80’s (Jenouvrier et al. 2005), while it has been later shown to negatively affect survival and breeding success (Gauthier–Clerc et al. 2004, Dugger et al. 2006, Saraux et al. 2011a, Le Maho et al. 2011). Thus, biodemographic parameters, trends and conclusions from flipper-banded dataset gathered in this colony until the 2000’s are questionable and should be interpreted with caution (Cristofari et al. 2016). Yet, to evaluate the overall trend of a species and the amplitude of its adaptive capacities, it is crucial to monitor over the long-term more than one population breeding in different ecosystems; a trend from a single colony may not be a good environmental sentinel (Kooyman and Ponganis 2017). However, to date, only a few other long-term time series of colony size exists for other colonies than Pointe Géologie (Trathan et al. 2020), and Kooyman and Ponganis (2017) demonstrated that colonies should be counted every year at a regional scale, given the high yearly fluctuations of colony size they recorded in a 12-years census over 7 colonies in the Ross Sea.

In addition to these time series, other studies have been conducted on the species (see Table 20), including satellite censuses (Fretwell et al. 2012, LaRue et al. 2014), population genetics (Cristofari et al. 2016, Younger et al. 2017), investigations on the colony functioning (Zitterbart et al. 2011, 2014, Gerum et al. 2013, Richter et al. 2018a), the huddling behaviour and its associated thermoregulation physiology (Le Maho 1977, Gilbert et al. 2006, 2007, McCafferty et al. 2013, Richter et al. 2018b) as well as some diving physiology experimentations (Kooyman et al. 1992b, Ponganis et al. 2009, Sato et al. 2011, Williams et al. 2011, Wright et al. 2014). Finally, the spatial distribution at sea and the foraging-related studies resulting in the global overview presented in this thesis, concern about 10 colonies for adults and 5 colonies for juveniles.

Table 20. Summary of the main research topics on emperor penguins and their level of knowledge achieved in the literature.

Research topics	Level of knowledge
Census/Population size	1[a]
Population dynamics/Demography	
✓ Vital rates	1[b]
✓ Dispersion (empirical)	0
Life-history traits/strategies	
✓ Trade-offs	1[b]
✓ Pedigrees	0
Population genetics	
✓ Gene flow	1[c]
✓ Genetic diversity	1
Genomics of Adaptation and Speciation	0-1[c]
Demographic history	1-2[c]
Behavioural studies	
✓ Foraging/Prospection/Migration	
- Winter	
○ Unknown age/history	0-1
○ Known age/history	0-1
- Summer	
○ Unknown age/history	0-1
○ Known age/history	0
✓ Sexual selection	
- Acoustics	1-2
- Ornaments	0
Ecophysiological studies	
✓ Fasting/Energy reserve management	2-3
✓ Breeding costs	1-2
Other stressors than climate change	
✓ Contaminants/Microplastics	0-1[c]
✓ Fisheries	0
✓ Diseases	0

Level of knowledge: 0 = Null/quasi-Null ; 1 = Low ; 2 = Medium ; 3 = High

[a]: a few colonies have been monitored on the long-term (through aerial images or direct counts). Global population of the species is estimated mainly through satellite images, therefore, time series are very short.

[b]: one colony initially monitored with flipper-banded birds over the 61 colonies. Electronic long-term monitoring (micro-tagged birds detected by automatic identification systems) started in 2009/2010 in Pointe Géologie (Adélie Land) and in 2017/2018 in Atka Bay (Queen Maud Land).

[c]: investigations initiated by our research team.

This inventory highlights the cruel lack of available data on general ecology and life-history processes in emperor penguins, not mentioning physiological insights. In other words, the bottom of the pyramidal structure to set up adequate conservation measures (Fig. 2) is very narrow and fragmented. Given the rapid on-going global changes, without baseline data in space and time on demographic trends, distribution and general ecology of emperor penguins, it will be soon impossible to disentangle changes owing to natural environmental stochasticity from those due climate upheavals or more direct anthropogenic disturbances (e.g. fisheries, tourism, pollution, or geopolitical pressures for scientific station multiplication; see Maxwell et al. 2013, Brooks et al. 2016, Trathan et al. 2018). Such an initial state of knowledge is also a prerequisite to frame conservation objectives and to their efficiency (Mihoub et al. 2017, Ropert-Coudert et al. 2020).

VI.2.3. Building up a new framework

VI.2.3.1. Setting up long-term monitoring programmes

Concerned by these shortcomings from the very beginning of this thesis, one of our first and main objectives was to set up a second worldwide long-term monitoring programme of micro-tagged emperor penguins; the first one having been implemented in 2009/2010 by the team at the Pointe Géologie colony based on the RFID methodology we developed in the King penguin from Crozet archipelago. Atka Bay colony has been chosen for several reasons. First, as highlighted in Chapter 2 (page 70), Atka Bay and Pointe Géologie colonies present contrasting population size, a slightly shifted phenology as well as contrasted environmental characteristics (e.g. winds regime, shelf configuration, and oceanographic conditions), and are, therefore, optimal for comparisons. Second, since 2013, a remote-controlled camera observatory (developed by Zitterbart and colleagues, see Richter et al. 2018a) monitors on land the emperor penguins' colony of Atka Bay, providing already population census and phenological data. Finally, Atka Bay colony is situated nearby a research station that enables logistic supports, an elementary asset to ensure continuous monitoring over time.

Similar to what we set up at the Pointe Géologie emperor penguins' colony, a close monitoring of the phenology and demography of the colony has been initiated in 2017 and is now carried out through and over years in order to establish long-term time series. Annual cohort of 300 fledging chicks is electronically marked every year with subcutaneous passive integrated transponder (PIT, page 95) that allows life-long identification by automatic detection systems (page 95). Classical vital rates can then be estimated to perform population dynamic analyses and assess population trends, and to predict population trajectories under the projection of different environmental scenarii. Additionally, every 3 years and over 2 years, the distribution and activities at sea of ca. 70 adults and juveniles are investigated in order to track and interpret fluctuations of their distribution and activities at sea over time in regards to environmental drivers. Such programme is a novelty much needed on emperor penguins while similar projects have been running for years on Adélie and king penguins (Péron et al. 2012, Le Guen et al. 2018) or on other predators of the Southern Ocean. For instance, Weimerskirch and colleagues (2012) linked the southward shift of wandering albatrosses over 20 years to the poleward shift of the westerly winds. Southern elephant seals are also the focus of several long-term monitoring programmes. An eleven-years time series described the effect of the inter-annual variability in sea ice advance and concentration on seals' foraging behaviour (Labrousse et al. 2017) while a seven-years time series revealed the long-term fidelity of individuals to the same foraging areas, suggesting limited behavioural adaptations to rapid environmental changes (McIntyre et al. 2017). Tracking behavioural changes (variation of e.g. the foraging ranges, diving strategies, diet) of individuals and populations over successive years within a monitoring framework, which also gives us access to life-history and genetic data, has the potential to vastly improve our knowledge and understanding of occurring changes (Le Bohec et al. 2013). However, data from animal-borne sensors must be collected in such a way that animal behaviour is still representative and unbiased so that conclusions drawn are valuable.

VI.2.3.2. An old and fragmented at-sea ecology literature

Despite the fact that emperor penguins have been equipped with biologgers for half a century (Kooyman and Campbell 1971), there were no specific publication dedicated on the capture and equipment protocols of non-anaesthetised emperor penguins in the field. This information is most of the time not mentioned in the scientific literature, or with very limited details (see Chapter III for review). During my PhD project, techniques of captures and logger attachments, seen on the field during my overwintering and discussed beforehand with experts working on emperor penguins and/or with biologging, have been initially used. However, we discovered that some of these techniques were unsuccessful, inefficient or even damageable for the animals, and, for most of them, their potential impacts have not been fully assessed. Typically, potential adverse effects of the commonly-used technique of gluing the logger to the back feathers of emperor penguins for long-term deployment were not evaluated, given that until our study, such equipped bird had never been resighted. Some of the techniques presented in this very limited and fragmented literature are, therefore, out of date and should not be considered as reference anymore. For instance, the rugby-like catch technique mentioned to capture adult emperor penguin (

Fig. 53; Robertson 1991, Zimmer 2007) should not be used, as stressed by ethic committees like the one of the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux) in France (Fournier pers. com.) due to the level of risk and stress induced for the birds.

Fig. 53. Catch of an adult emperor penguin by rugby-like tackling at the edge of the penguin colony of Pointe Géologie, Adélie Land. Adapted from Zimmer (2007). See also https://www.youtube.com/watch?v=RxgScMyZDXI.

VI.2.3.3. The development of new methodologies

Noteworthy, several studies have been published recently on best tagging practices in different taxa (see, for instance, Horning et al. (2019) on pinnipeds, or Andrews et al. (2019) for cetaceans). As stated by Andrews and colleagues (2019) "*As tag designs and tagging methods develop, information about the most successful refinements and innovations should be shared to facilitate the use of techniques that are most appropriate for a project and that minimise any potential adverse effects on tagged animals*". In other words, to ensure that the data collected are of exemplary quality from a scientific and ethical point of view, the potential deleterious effects of the deployment procedures and the devices must be assessed and mitigated.

Thus, in the context of fragmented knowledge on emperor penguin tagging, in Chapter III, we presented three techniques to capture and/or recapture emperor penguins with minimal disturbance: adult-chick pair capture with a corral, fledging juveniles capture with a corral, and capture of an adult with a crook. Two of those are new to the literature (the coral captures), while the last one is for the first time exposed in a movie. Additionally, we shared two deployment methods that are novel procedures and have ensure the longest deployment duration ever performed for this species (382 days). Above all, being the first to resight long-term equipped birds on which devices had been glued on the back feathers, we showed that the loggers and the feathers to which it was attached were missing. We thus revealed that the classical technique used for long-term deployment on emperor penguins is detrimental to the bird and answer the question of Kooyman and colleagues (2015) who provided only few months of data: "*Why ARGOS devices stopped transmitting over the winter?*". We illustrated our work with an exhaustive documentation made of slideshows and movies to make our work transparent and easily reproducible. We also encourage regular updates of this material.

Chapter III was not initially planned at the beginning of my PhD project. As mentioned earlier, the Chapter was born from discovering the damage to the animals and gaps in literature. Therefore, it was obviously not design with predefined protocols to answer methodological questions about welfare impacts or ethical questions in wildlife experiments. For instance, the timing of each handling step together with an ethogram should be developed and used to monitor birds' behaviour and stress level throughout the manipulation. Moreover, although we were able to highlight the loss of feathers and its unambiguously detrimental effect for the birds' insulation, it was not possible to properly assess the degree of disturbance caused to the birds due to the lack of control birds. "Does the loss of feathers alter the capacities of the birds to cope with winter fasting period? Do the birds increase their diving efforts to compensate the heat loss? Ultimately, does feathers' damage impact their breeding success or their survival?" are still pending questions without this control group. Another methodological difficulty was linked to the deployment of several instruments on the same bird, which prevents us from disentangling with certainty the impacts of each logger. Those are well known issues relevant to biologging studies (Beaulieu et al. 2010, Vandenabeele et al. 2011, Forin-Wiart et al. 2019). Unfortunately, there are still no device on the market designed to collect simultaneously all the data (location, pressure, and acceleration), at the frequency and for the duration we needed to use, to address our research questions. By deploying several devices on the same bird, we minimised the number of birds disturbed (the "Reduction" principle from the Three Rs - *Replacement, Reduction, Refinement* - framework; Russel and Burch (1959)) even though we possibly increased the amount of disturbance per bird.

VI.2.3.4. Calling for future methodological improvement and standardisation

The alternative techniques we developed during my PhD project (leg-band attached TDR and back-taped-epoxied GPS) have given encouraging results (Chapter III). For the first time on emperor penguins, these methods allowed to successfully collect year-round data leading to unprecedented insights into the species' behaviours (Chapter IV and Chapter V). Yet, logistical constraints prevented us from testing the most updated version of the leg-band attached TDR that incorporated latest improvements to reduce bird disturbance[26]. However, we will be able to test these updates within the next years and deployment sessions planned through the long-term monitoring programme (see page 192). Given the promising results and the detrimental impacts of the classical deployment techniques, we opted for the principle of precaution and shared our techniques and results (Chapter III submitted to Animal Biotelemetry) to prevent avoidable animal disturbance and/or suffering in future projects (Hawkins 2004).

While biologger characteristics have undergone rapid progress (e.g. size, shape, weight, power consumption; see Wilson and Vandenabeele 2012, Portugal and White 2018), deployment techniques have stagnated (at least in emperor penguins), leading to incomplete datasets owing to technical and logistical constraints. We demonstrated that continuous improvement and refinement are fundamental and achievable. Our work does not pretend to be a collection of best practices, but intends to provide a baseline (resource) for the development of a standardised, reproducible, efficient and ethical framework for future deployments on the species, as well as to provide comprehensive data while ensuring minimal disturbance to equipped individuals. The continuous enhancement of equipment protocols, ensuring the expression of genuine natural behaviours and their recording over meaningful duration, will greatly improve our understanding of wildlife ecology and allow the design of

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[26] Detailed descriptions of the systems have been deposited in PANGAEA repository and are available at https://doi.pangaea.de/10.1594/PANGAEA.913447.

adequate conservation and management measures. For instance, thanks to our new leg-band attachment technique of TDR on adult emperor penguins, we have been able to identify the change in diving effort that occurred in late October, suggesting a concomitant switch in diet (Chapter V). With the classical gluing technique, the device would have been lost too early to detect this behavioural flexibility in emperor penguins. Similarly, thanks to the long-term attachment technique we developed for juveniles, we identified the importance of the South Georgia and South Sandwich Islands MPA for juvenile emperor penguins as well as the moulting sites and the complete annual pattern of the ocean use of this life-history stage. Such finding would have not been possible with the use of previous techniques.

Finally, during my PhD project, my involvement in the development of equipment techniques resulted in the perception that various methods have been elaborated and tested (not necessarily *in-situ* on wildlife) and then abandoned because they revealed unsuccessful. We deplore the fact that these developments are (hardly) ever reported, resulting in the investment of a lot of resources and time to develop similar techniques that will prove to be equally unsuccessful. We are convinced that it would be beneficial to give more exposure to fieldwork developments and methodology in scientific publications to improve and facilitate experimental designs and their results - a practice that would benefit both, animals and scientists. This should not only be the burden of researchers but also a change of paradigm of editors and journals. Tests, errors and failures are inherent of research and thus should be, to some extent, valued as significant results. Their highlighting would also contribute to make research more transparent to people in those time of mistrust towards science, the clarity of information being the focus of conservation researchers (McMahon et al. 2012).

VI.3 Biotelemetry on emperor penguins and conservation measures in the Southern Ocean

VI.3.1. Emperor penguins commonly range outside marine protected areas

The tracking data gathered during my PhD project together with the previous ones extracted from the literature reveals that emperor penguins are marginally present in specific protection zones of the Southern Ocean (Chapter IV and Chapter V). We showed that juveniles spent the vast majority of their time outside of the extents of proposed or existing marine protected areas (MPAs), and their distribution extends up to 1500 km north of the species range used by the IUCN to evaluate the global conservation status of the species. We also showed that non-breeding and post-breeding adults (e.g. moulting birds of Pointe Géologie) commonly range outside those areas. Similar observations can be made in the Ross Sea area, except that the MPA has already been implemented. One third (3 on 9) of the non-breeding adults tracked over the winter in this region (Goetz et al. 2018) spent the majority of their time outside the Ross Sea region MPA, like the juveniles tracked from Cape Washington (Fig. 54; Kooyman and Ponganis 2007).

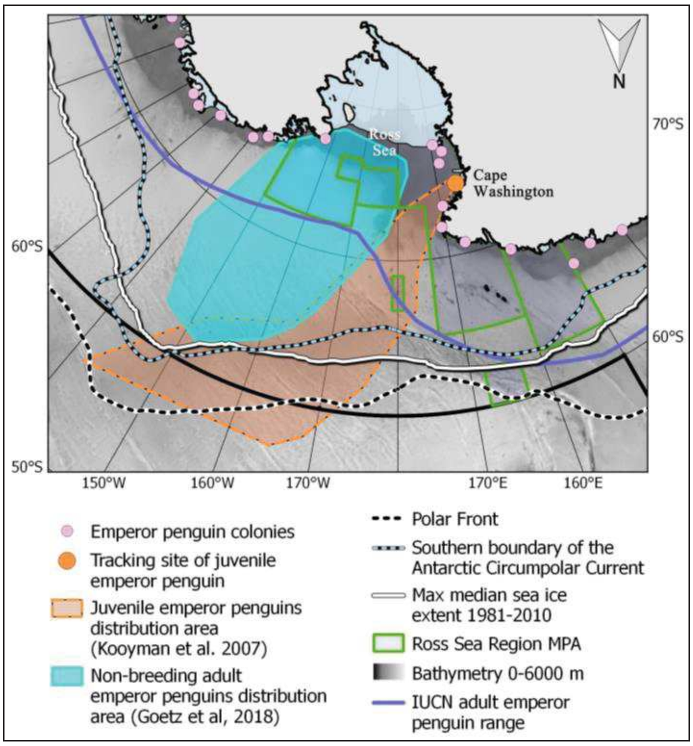

Fig. 54. Distribution areas of juvenile and non-breeding adult emperor penguins in the Ross Sea Region Marine Protected Area.

VI.3.2. Only breeding sites matters in current MPA planning

The monitoring of emperor penguin juveniles has been called since years to become a priority (Trathan et al. 2011); however, tracking studies of juveniles are relatively rare (to date, five studies on five colonies, including ours (Kooyman and Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013, Labrousse et al. 2019a; see Chapter IV). This shortcoming holds not only for penguins but also for other seabirds, sea turtles, and marine mammals. The main reasons are that biologgers' recovery is more difficult and biologgers' size is often less suitable for juveniles (Hays et al. 2016). Juvenile distributions are therefore usually not considered, while they are of primary importance for conservation plans and species viability (Carneiro et al. 2020).

For penguins, the common approach for designating boundaries of MPAs focuses on protecting breeding birds and colonies (Sherley et al. 2013, Boersma et al. 2019). As a result, 32 of the 61 emperor penguin colonies (52%) are situated within planned or existing MPAs. In the Weddell Sea Marine Protected Area (WSMPA) proposal, only models of probability of occurrence of breeding adults (see footnote page 182) were considered to assess emperor penguin's distribution (Teschke et al. 2016b, CCAMLR 2018a). As a consequence, important pelagic areas for juvenile and non-breeding adult emperor penguins are lacking consideration. For instance, in the southern Atlantic region of the Southern Ocean, the Antarctic Circumpolar Current (ACC) region is not included in the proposed

WSMPA (CCAMLR 2018a), while we showed that the area was critical for the juveniles (Chapter IV). We already stressed the importance of juvenile survival for the species viability (see also Abadi et al. 2017). On the other hand, the proportion of non-breeding adults and how often emperor penguin adults skip breeding still remains unknown (Goetz et al. 2018). Barbraud and Weimerskirch (2001) stated that, at Pointe-Géologie colony, '*the number of breeding pairs represents 80% of the overall population size*'. However, this assessment might stand for Pointe Géologie colony only. Additionally, it is unclear if this statement reflects the proportion of birds at the colony site (breeding birds and birds that failed to find a partner), or also include birds at sea that did not return at the colony site for breeding at the beginning of the season. In the first case, there is no estimation of the number of non-breeding birds that remained at sea to skip breeding. With climate change impacts, the proportion of non-breeding emperor penguins is likely to increase. Indeed, as long-lived species, we expect that adults in poor conditions may favour their own survival by skipping breeding opportunities (i.e. if they did not succeed to accumulate enough body reserves before breeding), as it has been shown in albatross species (Jouventin and Dobson 2002). As such, the number of birds commonly out of existing and planned marine protected areas is likely to increase with future global upheaval, while they would be in need of more protection. Another level of protection afforded by the Annex V of the Protocol on Environmental Protection to the Antarctic Treaty System (ATS 1991) is the designation of an area as an Antarctic Specially Protected Area (ASPA). To date, eight ASPAs including emperor penguins colony have been designated (Trathan et al. 2020). However, they provide only very limited protection at sea, the designation of MPAs having been historically left to the CCAMLR[27] (Chown et al. 2017, Trathan et al. 2020).

VI.3.3. The challenging position of the Convention on the Conservation of Antarctic Marine Living Resources

With only two operational MPAs since 2009 and three under consideration (Table 1), the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) is falling short on its initial ambition (Cordonnery and Kriwoken 2015, Cordonnery et al. 2015, Nicoll and Day 2017, Trathan and Grant 2020) to establish a harmonised regime for the protection of the Antarctic marine environment. The three proposals (CCAMLR 2018a, 2018b, 2019a) for the establishment of the new MPAs have been

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[27] Over 72 existing ASPAs, only nine, all of them less than 1,000 km^2, have a marine component (Chown et al. 2017). Entry to an ASPA is prohibited without a permit, and activities must be conducted in accordance with the Management Plan of the area (ATS 1991).

under intense international negotiations for years and the size of the potential protected areas substantially reduced (Sylvester and Brooks 2020, Brooks et al. 2020b), while it took five years of negotiations to delimit the Ross Sea region MPA status and its size was reduced of 40% to satisfy some Member countries with high economic interest in fisheries (Brooks et al. 2020b). With a limited duration of 35 years, the Ross Sea MPA shall not even be considered as an MPA in regards to IUCN status, some of the species having longer life span (Brooks et al. 2016, 2020b, Nicoll and Day 2017). Indeed, this duration violates the "long-term conservation" objective fixed in the definition of an MPA[28]. Not to mention the fact that areas of primary importance to safeguard predators were left unprotected to accommodate fishing (Brooks et al. 2016).

Noteworthy, 60% of the protected areas within CCAMLR boundaries are inside nationally managed MPAs (Table 1). This observation highlights the difficulty to manage areas beyond national jurisdiction (ABNJ)[29] due to the very different views between members on how marine ecosystems should be managed (Rogers et al. 2015, Cordonnery et al. 2015, Brooks et al. 2020b). Initially created with the purpose of long-term conservation, CCAMLR appears on the brink of becoming only a fisheries management entity (Nicoll and Day 2017, Trathan et al. 2020). As an illustration, the investigation of the CCAMLR's Conservation Measures of the 2016-2017 season reveals that 76% of the measures focused on fisheries management, while 14% concerned species/habitat protection and 10% both categories (Nicoll and Day 2017). Some Members are pressing for increased quotas, and for permitting fishing within closed management areas (Brooks et al. 2016, Trathan et al. 2020). Those Members are reversing the initial CCAMLR approach: to prevent fishing, they are now demanding that sufficient data should be available to show that fishing is damaging the ecosystem (Brooks et al. 2016, Trathan et al. 2020). Against the advice from the CCAMLR's Scientific Committee, Russia also initiated research fishing for toothfish in the Weddell Sea in 2013 and 2014 (Brooks 2013, Teschke et al. 2016a). Additionally, a recent study in Antarctic Peninsula (Watters et al. 2020) suggests that the precautionary approach[30] to the management of the fisheries (i.e. reaching sustainability of fisheries without jeopardizing the structure and functioning of the ecosystem) does not yield the expected protection. Even if catches are sustainable, the presence and activities of fisheries are suggested to disrupt the

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[28] IUCN defines an MPA as : "*A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.*", while long-term conservation is defined as : "*managed in perpetuity rather than a short term or a temporary management strategy.*" (WCPA/ICUN 2019).

[29] Areas of the oceans for which no one nation has sole responsibility for management (referred also as 'high seas'). They represent ~2/3 of the oceans (IUCN website).

[30] "*CCAMLR's precautionary approach requires that management decisions should have a low risk of long-term adverse effects*" (Nicol and Foster 2016).

structure of krill swarms or their distribution in the water column, which, in turn, affect the performance of krill-dependent penguins that forage in the area (Watters et al. 2020). Together with our findings in emperor penguins, such studies highlight the current limitations of the protection measures in place in the Southern Ocean. Clearly, current CCAMLR measures and intents are not sufficient to ensure the protection of highly dispersive species that cross distinct ecoregions. Even though the acceptance of proposed MPAs would greatly improve the representativeness of Antarctic biodiversity (Brooks et al. 2020a), the broad-scale region zoning used in the designation process of MPAs by the CCAMLR (Brooks et al. 2020a) is too coarse to fully encompass the heterogeneity of southern ecosystems. For instance, the ACC system, critical habitat for many species (Tynan 1998, Bost et al. 2009a), including juvenile emperor penguins (Chapter IV), is not considered in planned CCAMLR MPAs. Additionally, the ecological spatial connectivity between MPAs (UN 2002, WCPA/IUCN 2007, Carr et al. 2017) is a component currently absent from CCAMLR framework (CCAMLR 2011). Increasingly recognised as a major ecological criterion in the design of effective conservation plans (Carr et al. 2017, Laffoley et al. 2019, Balbar and Metaxas 2019), this network of connected MPAs in the Southern Ocean would ensure a continuity of protection to individuals and species that move through the seascape. With such a complementary approach, the CCAMLR could design MPAs including critical habitats that are still unprotected like the ACC area.

VI.3.4. Management alternatives

VI.3.4.1. Hot-spot areas

To make the best use of tracking data and translate them into management policy, a wide spread approach is to combine tracking data from different top predator taxa and to estimate the areas where they concentrate (see review in Hays et al. 2019 and Hindell et al. 2002, Block et al. 2011, Raymond et al. 2015, Dias et al. 2017, Reisinger et al. 2018, Harrison et al. 2018, Heerah et al. 2019). Those regions, called “hotspot of biodiversity”, can be designated under different names in the literature, but all referring to the “hotspot” concept. Here, is a non-exhaustive list of the nomenclatures used in marine studies: Ecologically or Biologically Significant Marine Areas (EBSAs; CBD 1992, Clark et al. 2014, Dunstan et al. 2016), marine Important Bird Areas (mIBAs ; BirdLife International 2010, Lascelles et al. 2016, Dias et al. 2017, Heerah et al. 2019), or Area of Ecological Significance (AES; Hindell et al. 2020). Such areas of top predator concentrations are indicative of predictable abundance and/or diversity of lower trophic organisms, and, therefore, require specific management consideration (Block et al. 2011, Raymond et al. 2015, Ropert-Coudert et al. 2020). Presence data can also be implemented into predicting models of suitable habitats in order to estimate probability of presence in non-sampled areas (Raymond et al. 2015, Ropert-Coudert et al. 2020). The main drawback of this latter approach is that the bias in data sampling is not easily corrected, and predictions are not always reliable. Moreover, data encompassing the full life-history stage (Carneiro et al. 2020) and the entire life cycle of individuals are required to properly assess the species' distribution in time and space. For instance, the critical importance of the ACC region for the Emperor penguin would have not been discovered if only adult data were considered (Chapter IV). We also confirmed the importance of the continental slopes and shelf areas for foraging adult emperor penguins replenishing their reserves in summer (Chapter V). However, these areas where the sea ice may retreat in the near future could be stormed by fishing vessels (Teschke et al. 2016a), although those habitats are critical for emperor penguins' feeding, but also breeding and moulting (Chapter V).

Protecting biodiversity is likely to require the development of ground-breaking and creative concepts in environmental management. New approaches have emerged in the last two decades, but their diffusion and practical implementation in the field are still limited.

VI.3.4.2. Dynamic management

Currently, most of the marine management approaches (e.g. quota setting, MPAs) are relatively static, while the Southern Ocean is a highly dynamic system in time and space. A shift towards the need of a more dynamic ocean management[31] emerged during the last two decades (Hyrenbach et al. 2000, Maxwell et al. 2015), concurrently with the quality of biologging data and the remote sensing of environmental data by satellite. A good example of this flexible management is *TurtleWatch*, launched in 2008 (Howell et al. 2008). A daily map of the preferred habitat of Loggerhead sea turtles (*Caretta caretta*), defined by water temperature, is transmitted to fishing vessels so that they can avoid these areas preventing by-catch of the endangered turtles. The model was developed by integrating tracking data from 1997 to 2006. Similarly, the *WhaleWatch* management tool (Hazen et al. 2017) combines 14 years of tracking data to build a habitat model and to predict current estimates of abundance of blue whales (*Balaenoptera musculus*) using remotely sensed variables. An application shares the data with vessels in order to avoid strikes. Such examples are not readily to the Southern Ocean context, but might serve as inspiration for the CCAMLR and the researchers involved in tracking studies, especially in the context of fisheries development (Brooks et al. 2016, Trathan et al. 2020). Management measures may only be necessary at particular period (e.g. during a species' breeding season, during a moulting period) and in certain areas. Additionally, dynamic MPAs could be used to protect dynamic

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[31] Management that changes rapidly in space and time in response to the shifting nature of the ocean and its users, based on the integration of new biological, oceanographic, social and/or economic data in near real-time (Maxwell 2015).

oceanographic habitats critical for ecosystem functioning (such as fronts, currents, or eddies), or to protect individual species or groups of species (Hyrenbach et al. 2000, Maxwell et al. 2015).

Global change will lead to environmental disruption (Collins et al. 2013, IPCC 2019, Rogers et al. 2020) that will, in turn, alter the distribution and abundance of interacting species (Reed et al. 2010, Constable et al. 2014, Dunn et al. 2019). For instance, the ACC system is expected to shift southward in response to ocean warming (Collins et al. 2013). Thus, it is crucial that future conservation measures are adaptive and not tied to coordinate boundaries, but associated with environmental parameters. Our study on juvenile emperor penguins showed that they are wandering within the ACC limits during two months at the end of the summer right after fledging. The protection and management policies could, therefore, be limited in time but also in space, with specific measures implemented for critical colonies. Critical colonies could be either colonies experiencing a decrease in population size or colonies expected to act as refugia for the species in the context of global changes (i.e. colonies from the Weddell Sea and Ross Sea regions; Ainley et al. 2010b, Jenouvrier et al. (2017, 2019)), or colonies from which individuals are or will be in the near future competing with fisheries.

VI.3.4.3. A need of a governance for the common good

While calls are increasing for a more aggressive protection of ABNJ (Warner 2009, O'Leary et al. 2016, Dias et al. 2017), the Southern Ocean appears to be a perfect place for ambitious conservation action due to the international framework and agreements linked to the Antarctic Treaty, and to the relatively small amount of anthropogenic activities in this area, up to now. In an international context burdened by the tensions generated by the threat of climate change, CCAMLR members have the opportunity to send an ambitious message by banning all industrial activities from the Southern Ocean, like the Antarctic Treaty (ATS 1959) did for the continent. Such a measure would be the second best action to ensure the protection of these polar and subpolar regions, the first being the diminution of greenhouse gases emissions (Trathan et al. 2020). This is unlikely to happen given that CCAMLR Members fishing states outnumber the non-fishing States by a ratio of 5:3 (Brooks 2013, Smith and Jabour 2018), leading to intense negotiations each year regarding new MPA proposals (Sylvester and Brooks 2020).

Noteworthy, the existing and planned CCAMLR MPAs are mostly out of the ACC region, while the ecological importance and productivity of the frontal system of the ACC is well established (Tynan 1998, Bost et al. 2009a, Trathan and Grant 2020). On the contrary, the countries owning islands situated within the ACC have established MPAs and conservation measures, with the exception of Norway around Bouvetoya Island (Fig. 10). These countries are also most of the ones leading the proposals for new MPAs around Antarctica (Table 1). This highlights the difficulties for an international organisation based on consensus to act in the interest of all when national interests are given priorities by some Member states (Cordonnery et al. 2015, Brooks et al. 2016). Despite a relative shortness of the Antarctic science-policy communication pathways (Hughes et al. 2018), like in the rest of the oceans where only 1.2% of the high seas have been designated in MPAs (Visalli et al. 2020), the management of ABNJ collides with political and economic barriers and interests (Smith and Jabour 2018). In definitive, much remains to be done to make the Southern Ocean an area of peace and science like the continent it encircles.

VI.4 Future research perspectives

The studies carried out during my PhD project have improved the knowledge and understanding about the at-sea ecology of the Emperor penguin. To start the long-term monitoring of a new colony in a region where emperor penguins' at-sea distribution was unknown, we made an intense use of biologging and improved capture and tagging techniques on different life-history stages of the species. Our findings reveal a much larger extent of the species distribution than previously assessed and highlight the current lack of protection of the species. Our preliminary analyses on the foraging activities of the species suggest various strategies between sites, seasons, and birds. Nevertheless, the methods we developed can (and should) still be improved while numerous ecological questions are still pending.

VI.4.1. Field methods

VI.4.1.1. Equipment

As outlined in Chapter III, the improvement or development of new equipment techniques are still needed for emperor penguins. The success of the back-taped-epoxied technique on juvenile emperor penguins advocates for the use of this technique on adults before any other. Similarly, the testing of the updated version of the leg-band should also be a priority. Given the logistic constraints of field studies in Antarctica and the promising results of the leg-band techniques on other penguin species (Bost et al. 2009b, Thiebot et al. 2011, Ratcliffe et al. 2014; Houstin, Le Bohec, unpublished observations), we recommend that the development of such long-term attachment system should be considered with emperor penguins.

The RFID systems that will be deploy in Atka Bay the next coming season, have been very successful at detecting emperor penguins at Pointe Géologie colony and are expected to give similar results in Atka Bay. These systems are communicating with field workers when a micro-tagged bird is detected. Thus, in addition to the collection of micro-tagged cohorts' detection data for population dynamic analyses, they will be precious tools for the recapture of equipped birds (which are also systematically micro-tagged) and, thus, for the device recovery over the years.

Tracking technology is also likely to continue its on-going enhancement. For instance, the new generation of ARGOS satellites is being developed and should be fully operational by ~2023 with 20 dedicated nanosatellites[32]. The main benefits of this network of nanosatellites will be an increased bandwidth, an enhanced capacity, new modulations of the signals and high data rate transmissions for wildlife tracking[33] . In other words, it will be possible to send more efficiently a bigger amount of data. The Fastloc® technology, similar to a low-power-consumption and fast-acquisition-time GPS, is also expected to reach a size ethically compatible with a deployment on emperor penguins, enabling longer-term deployments with higher acquisition rate. Together with less disruptive long-term attachment techniques, this new technology will greatly improve our understanding of the foraging activities in space and time, with a more accurate correspondence between locations and dives and, thus, with environmental variables.

VI.4.1.2. Capture

Our easy-removable and light corral allows the simultaneous capture of several individuals in the field. This might be especially useful for research requiring simultaneous equipment and/or marking of individuals, whether breeding pairs or adult-chicks pairs with chicks of any age. For instance, by equipping with GPS-TDR-Acc biologgers both partners of breeding pairs simultaneously, it will be possible to study the different foraging tactics exhibited within breeding pairs and, more precisely, if (and how) compensation mechanisms exist between partners during the chick-rearing period, if one of the partners is less performant at sea. The simultaneous equipment with GPS or acoustic recorders of an adult and its chick will, for instance, help us to investigate how their spatial interactions (e.g. how an adult is able to find its chick in a colony of several thousand individuals, at which distance) change over the winter, especially if coupled with a camera observation system like SPOT (for *Single Penguin Observation and Tracking* ; Richter et al. 2018a) or the micrObs (for *mobile micro-observatory ;* Richter et al. 2018b, Gerum et al. 2019; Annex A and Annex B) observatories. Using acoustic tags, it would be possible to investigate the ontogeny of chick calls and the recognition process between adult-chick pairs. Yet, the main disadvantage of our corral lies in the number of people needed to handle it (i.e. 3 persons). Knowing that two persons are sufficient to handle and equip an emperor penguin, it would be advantageous to develop a technique requiring only two people.

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[32] See https://www.cls-telemetry.com/argos-solutions/the-future-of-argos-argos4ng/ and https://www.cls-telemetry.com/production-underway-on-kineis/

[33] https://wildlifecomputers.com/blog/new-argos-satellite-launching-in-2019/

VI.4.2. Spatial distribution and conservation implications

VI.4.2.1. General distribution

We highlighted that, to date, no tracking of emperor penguins ever occurred in the western part of Antarctica, from the eastern Ross Sea to the Peninsula (*via* the Amundsen and Bellinghausen seas) and deep inside the Weddell Sea (Fig. 50). The first priority should, thus, be to track birds from colonies in these areas. Moreover, until now, immature emperor penguins (i.e. 1.5 to ~2.5 years old) have never been equipped with biologgers. We, therefore, do not know the at-sea distribution and diving behaviours and strategies of this life-history stage. However, due to its at-sea behaviour similar to our juveniles and the doubt we had regarding the coloration of ornaments, we suggest that one of the post-moult birds we tracked from Atka Bay could be an immature emperor penguin of 1.5 year old, even though it is currently impossible to validate this hypothesis (Fig. 51). As such, the tracking of birds of this age would require marking them at the beginning of their moult and managing to monitor them (if they stay in the study area) until the end of their moult when devices could be deployed. Telemetric data on all life-history stages are essential to assess and monitor, in time and space, the risks these different categories are facing. This baseline knowledge is fundamental for discussing future conservation measures for the species as well as monitoring future changes. If considered by the policy bodies and broadcasted, this information should also be of great importance in the discussion of current - and hopefully future - proposals on spatial and ecosystem-based management, such as MPA design and systematic conservation planning, in the Southern Ocean.

VI.4.2.2. The connectivity between colonies

Due to discordance on minimal sample size and analytical methods to use, population genetic studies led to an intense debate on the existence of one global population or several metapopulations (at least four) of emperor penguins, and on the connectivity between breeding colonies (Cristofari et al. 2016, Younger et al. 2017). Tracking data obtained to date on juvenile emperor penguins suggest that birds from the Ross Sea region might not travel as far as George V and Adélie Lands (and vice versa (Thiebot et al. 2013, Labrousse et al. 2019b)), but would remain in the Ross Gyre (Fig. 50; Kooyman and Ponganis 2007) ; whereas juveniles from the Weddell Sea region might not be able to cross Drake Passage in an anticlockwise direction and to reach the West Peninsula due to the strength of the ACC and the presence of the Weddell Gyre (Chapter IV; Fig. 4). The same applies to breeding and non-breeding adults tracked so far for these sectors (Fig. 50). On the contrary, the distribution at sea of birds born or breeding in the East Antarctica, from Dronning Maud Land to Adélie Land, overlaps (Fig. 36) enabling the existence of mixing populations in this area. Tracking studies on colonies at the edge of the gyres might help answering such primordial questions for risk assessment and conservation measures design. For instance, if no dispersive event between sectors is observed and if the existence of several populations is demonstrated, then a priority will be to avoid local extinction of specific colonies to preserve every single population as a genetic unit, even small ones (Moritz 1994, Palsbøll et al. 2006). On the contrary, if there is only one global population spanning around the continent, the focus might be to preserve the main colonies or the ones situated in the more favourable habitats, i.e. future potential refugia, in the context of global change.

VI.4.3. Foraging behaviour and strategies

VI.4.3.1. Further analyses of the data collected during my PhD project

Some of the data collected over the course of my PhD project have been only partially analysed, while others were collected for future use. Their future analysis will improve our knowledge on the foraging strategies of adult emperor penguins.

The diving dataset from chick-rearing birds equipped with back-taped GPS-TDR in Atka Bay will be reanalysed and compared with the unique diving dataset from adults equipped leg-band attached TDR over the full year. Given the similar diving effort strategy that we identified between these two groups at the beginning of summer, we expect their diving parameters (dive depth and duration, diving efficiency, Attempts of Catch Per Unit Effort or ACPUE) to be similar (Chapter V). Additionally, by resampling the diving datasets from Atka Bay birds at the frequency of those used at Pointe Géologie, we will be able to compare at-sea activities and foraging strategies observed at Pointe Géologie and Atka Bay during the chick-rearing period. We expect to confirm our preliminary results of different diving behaviours (pelagic *vs* benthic) and to emphasise the difference of diet between the two regions, notably through a detailed comparative analysis of the ACPUE index (Le Guen et al. 2018; Zimmer et al. 2010), a proxy of foraging effort.

Additionally, the analyses of the blood samples at capture and recapture of the equipped adults and their chicks (e.g. stable isotope analyses), together with stomach samples from dead chicks (e.g. direct prey species identification), will provide information on the trophic level and diet of emperor penguins from Atka Bay colony at least during the chick-rearing period. The diet determination will also help us to refine our understanding of the diving profiles and diving parameters.

The GPS of the chick-rearing birds from Atka Bay was also paired with a 3-axis accelerometer. Such data can deliver great insights on how animals change behaviour as a function of space and, therefore, on the influence of the environmental conditions they encounter during their foraging trips. They can easily be used to estimate general activity time-budget (e.g. walking, resting, diving, porpoising ; see Watanabe et al. 2012). We are convinced that such data can be used to detect catching events with more accuracy (due to the frequency of recording) than the methods using depth and wiggles data from TDR, as it has been shown in other diving top predators (Viviant et al. 2009, Carroll et al. 2014, Watanabe et al. 2014, Vacquié-Garcia et al. 2015, Jeantet et al. 2018). However, before using proxies from acceleration, prior analyses are required to correlate signals identified in the datasets with proven behaviours. Without such validation, we consider that the interpretation of the results might be biased (Jeantet et al. 2020). To perform such validation, the method consists of synchronising a video recording with the corresponding signals from the accelerometer. This can be realised either in captivity (Yoda et al. 2001) or in the wild with the concomitant deployment of an accelerometer and externally attached camera (Van Dam et al. 2002, Watanabe and Takahashi 2013, Thiebot et al. 2016). However, behaviours display in captivity are not representative of all the behaviours expressed in the wild (Jeantet et al. 2018), while the video recordings are limited to short-term studies. Indeed, in order to record prey capture attempts and investigate foraging activities, the video-recorder needs to be placed on the head of the animal-borne individual, which induces significant disturbance (Culik and Wilson 1991, Culik et al. 1994, Kay et al. 2019) incompatible with long-term deployment. Additionally, memory and power consumption are still technological limits preventing the long-term deployment of such devices (Heylen and Nachtsheim 2018). The combination of supervised learning algorithms and multi-signal analysis tools are being developed (Jeantet et al. 2020) and should provide automated and reliable identification of the various behaviours exhibited by diving animals. However, calibration data are still required and not available on emperor penguins. Future analyses of such datasets should allow a better assessment of predation attempts, and we expect the detection of such events outside of the bottom phase. Indeed, the investigation of sub-ice foraging behaviour should receive specific attention, since it has been shown to occur for emperor (Ponganis et al. 2000) and Adélie (Watanabe and Takahashi 2013) penguins, while the frequency and the importance of such behaviour has not yet been estimated and is currently neglected as already highlighted ~25 years ago (Cherel and Kooyman 1998).

One of the main interests of decoding behaviours and space usage is ultimately to get enough information to build conservation management decision. A current useful tool is the environmental (or ecological) niche modelling (Aarts et al. 2008, Kearney and Porter 2009, Scales et al. 2016). The niche modelling aims at making inferences over space and time on the favourable habitats available for a species (Aarts et al. 2008, Kearney and Porter 2009). Prior to the modelling, the analysis of habitat selection (i.e. an estimation of the magnitude from which the distribution of the habitat use (i.e. where the species is present) differs from the distribution of the habitat available (i.e. where the species could be present); see Aarts et al. 2008, Labrousse et al. 2019a) is performed. This step reveals insights about the studied population (e.g. preference of diving towards specific depth, preference of area with a high concentration of ice for resting) that are used to make prediction at other sites or at larger scale (Aarts et al. 2008, Kearney and Porter 2009). Such knowledge does not only improve our understanding of animal behaviour (Scales et al. 2016, Labrousse et al. 2019a) and ecology, but also provides valuable planning tools for conservation measures.

Labrousse et al. (2019a) performed such a study on emperor penguins from Pointe Géologie and Auster over several winter. Their analyses revealed that, despite differences in the habitat availability between the two sites, they consistently targeted the same type of features in a dynamic environment: the ephemeral polynyas while avoiding icebergs areas. The analysis of our data under such a framework, in a new environment and seasons, and with various life-history and breeding stages, would greatly enhance the understanding of the ecological niche of the species around the Antarctic continent. This will provide conservation and management bodies with relevant information to ensure the species protection.

VI.4.3.2. Cutting-edge technologies

In a recent study, video cameras with built-in microphones were deployed on king, gentoo (*Pygoscelis papua*) and macaroni (*Eudyptes chrysolophus*) penguins (Thiebault et al. 2019). All the recorded vocalisations were emitted during feeding dives, and half of them were directly associated with hunting behaviour. The exact function of these vocalisations (e.g. by-product of physiological need, group coordination, role in the capture process) still needs to be assessed and requires further investigation. This behaviour (at-sea vocalisations) still needs to be proven for emperor penguins. It would be valuable to know, as noise pollution at sea is a rapidly increasing threats for many marine species globally.

It would also be interesting to investigate social interactions of emperor penguins at sea. African penguins (*Spheniscus demersus*) have been recently shown to hunt in groups thanks to video recordings (McInnes et al. 2017), while Adélie penguins have been recorded exhibiting underwater group behaviour (Takahashi et al. 2004) and emperor penguins are also often seen in groups when spotted at sea (Kooyman and Campbell 1971). The use of acoustic loggers can also serve this purpose. For instance, the use of microphone-camera loggers on gentoo penguins suggests that off-shore vocalisations resulted in group association of birds that subsequently foraged at the same patch of prey (Choi et al. 2017). In our study, two juvenile emperor penguins tagged together entered the water at the same time, however, due to the ARGOS locations uncertainty, we could not confirm that they entered in the water at the exact same location.

Finally, ongoing research and technological development lead to the emergence of new biologgers that may refine or even revolutionise our understanding of marine ecosystems. For instance, a new prototype of biologger has been recently tested on Weddell seals (Heerah pers. com.). Using sonar-like technology, the logger is designed to measure sea ice sickness as well as to detect prey and their shape for subsequent identification. Improvements in sea ice data remote detection (e.g. resolution, thickness, temporality) and of bathymetry resolution (Hindell et al. 2002b), matching the fine-scale resolution of dataloggers, would also greatly contribute to refine our perception of the spatial (horizontal and vertical) interactions of sub-ice diving animals with their environment. Accelerometer, acoustic and video recording tags have a huge potential - and have already started - to open up a new window on our understanding of the foraging behaviour of diving species. Their use on emperor penguins is still limited mainly due to logistical constraints, but is likely to spread with their technological improvement in miniaturisation, design optimisation, storage capacity, and power consumption.

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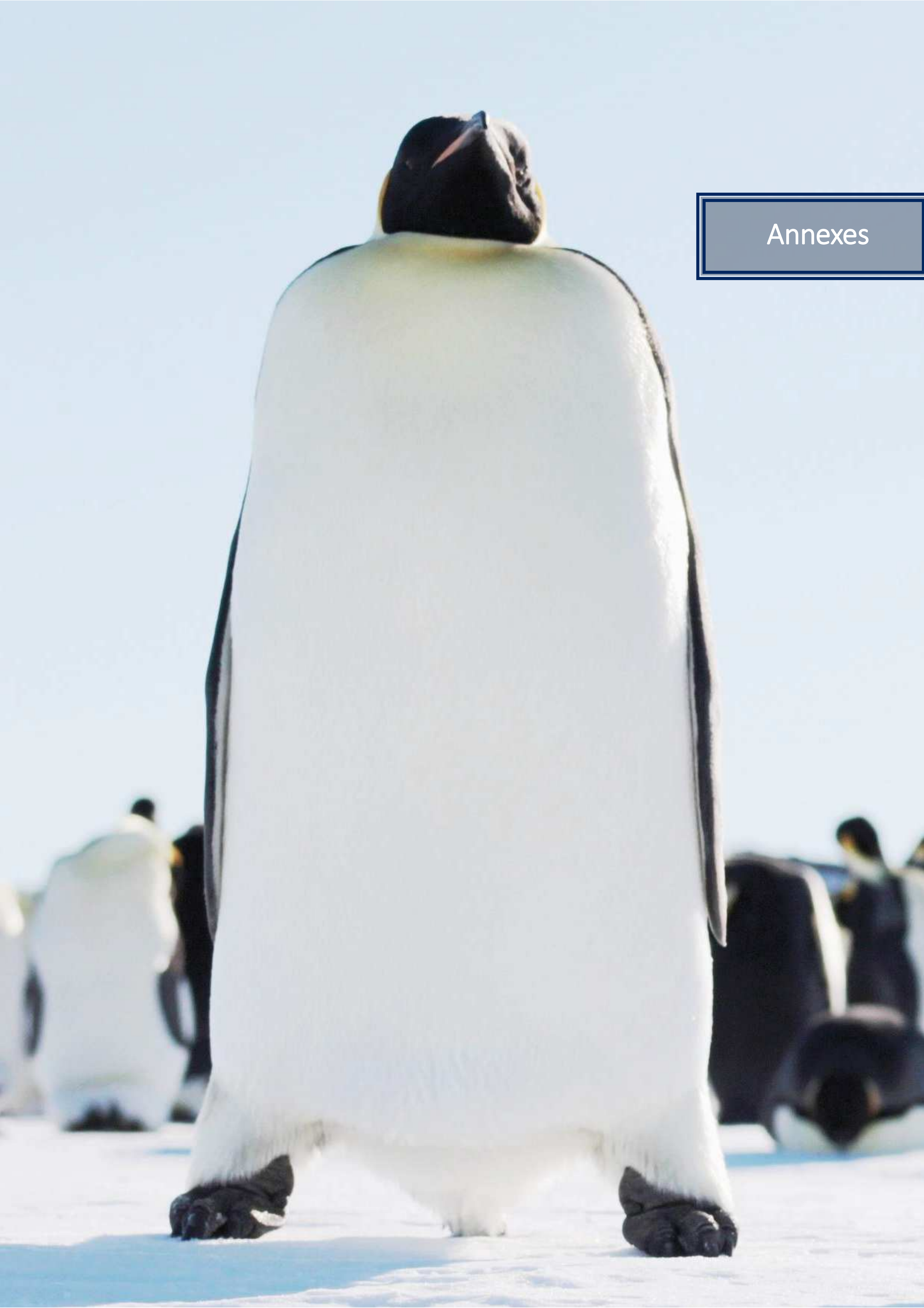

Annexes

Annex A. Phase transitions in huddling emperor penguins

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Phase transitions in huddling emperor penguins

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Abstract

Emperor penguins (*Aptenodytes forsteri*) are highly adapted to the harsh conditions of the Antarctic winter: they are able to fast for up to 134 days during breeding. To conserve energy, emperor penguins form tight groups (huddles), which is key for their reproductive success. The effect of different meteorological factors on the huddling behaviour, however, is not well understood. Using time-lapse image recordings of an emperor penguin colony, we show that huddling can be described as a phase transition from a fluid to a solid state. We use the colony density as order parameter, and an apparent temperature that is perceived by the penguins as the thermodynamic variable. We approximate the apparent temperature as a linear combination of four meteorological parameters: ambient temperature, wind speed, global radiation and relative humidity. We find a wind chill factor of $-2.9\ ^\circ\mathrm{C}\,(\mathrm{ms}^{-1})^{-1}$, a humidity chill factor of $-0.5\ ^\circ\mathrm{C}/\%$ rel. humidity, and a solar radiation heating factor of $0.3\ ^\circ\mathrm{C}\,(\mathrm{Wm}^{-2})^{-1}$. In the absence of wind, humidity and solar radiation, the phase transition temperature (50% huddling probability) is -48.2 °C for the investigated time period (May 2014). We propose that higher phase transition temperatures indicate a shrinking thermal insulation and thus can serve as a proxy for lower energy reserves of the colony, integrating pre-breeding foraging success at sea and energy expenditure at land due to environmental conditions. As current global change is predicted to have strong detrimental effects on emperor penguins within the next decades, our approach may thus contribute towards an urgently needed long-term monitoring system for assessing colony health.

Keywords: collective behaviour, phase transition, emperor penguin, huddling, climate variability, environmental conditions

S Supplementary material for this article is available online

(Some figures may appear in colour only in the online journal)

Introduction

Emperor penguins (*Aptenodytes forsteri*) breed during the Antarctic winter and survive temperatures below -50 °C and wind speeds exceeding 150 km h^{-1}. The male penguins fast for up to 134 days (Prévost 1961, Isenmann 1971) during mating and incubation until the females return from foraging. Therefore, the conservation of energy is critical for successfully incubating the unique egg until hatching. A key component for energy conservation is the formation of huddles (Le Maho 1977, Gilbert *et al* 2010), which are constantly reorganized to minimize energy loss (Zitterbart *et al* 2011, Gerum *et al* 2013). Huddles are densely packed groups of individuals that allow the colony to share body heat, reduce

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effective surface area, and shelter each other from the wind. Temperatures inside a huddle can reach up to 37.5 °C (Gilbert *et al* 2006). Previous studies reported that the likelihood of huddling increases with lower temperature and higher wind speed (Gilbert *et al* 2006, 2008), and with lower solar radiation (Ancel *et al* 2015).

The rearrangement of the colony structure during huddle formation is reminiscent of a phase transition in non-living matter. A phase transition in the context of an Emperor penguin colony describes the change between a solid state—corresponding to a dense huddle—and a liquid or gaseous state—corresponding to a loose configuration of individual penguins—in response to one or more external parameters (Canals and Bozinovic 2011, Vicsek and Zafeiris 2012) such as temperature, wind speed or solar radiation (figure 1).

In this study, we apply the concept of a phase transition to a penguin colony and study their huddling behaviour in response to short-term fluctuations of the following environmental parameters: ambient temperature, wind speed, relative humidity, and global solar radiation. We use the density of the colony as order parameter of the system to describe the phase, or state, of the colony. Density is extracted from time-lapse image recordings of an emperor penguin colony at Pointe Géologie, Antarctica (66°39′46.5″S 140°00′14.1″E). We define an ‘apparent temperature’ perceived by the penguins as a linear combination of the ambient temperature, wind speed (times a wind chill factor), relative humidity (times a humidity chill factor), and solar radiation (times a solar heating factor). We then model the colony state as a function of the apparent temperature, whereby we fit the influence of wind chill, humidity chill, and solar heating, and the range and transition point of the apparent temperature over which the phase transition occurs.

Material & methods

Data acquisition

We acquired time lapse photography recordings of the Pointe Géologie emperor penguin colony, adjacent to the French Antarctic research station Dumont d’Urville (66°39′46.5″S 140°00′14.1″E, figures 2(a) and (b)). Images are recorded by a mobile observatory (*micrObs*) over multiple days or weeks at frame rates of up to 1 frame per second (figure 2(c)).

We use a Panasonic DMC-G5 digital single lens mirrorless (DSLM) camera equipped with a 128 GByte SD card for storing jpeg images (4608 × 3456 pixel). The camera can be externally triggered and has an electronic shutter. Compared to a mechanical shutter, the electronic shutter does not suffer from wear and is not affected by low temperatures. Furthermore, the focus of this camera model can be set manually and remains fixed during deployment, as the lens does not automatically retract on power-off. A microcontroller (Arduino Nano) is used to control the power supply to the camera and to trigger the image acquisition. In addition, we measure ambient light and suspend image acquisition during night, which helps to conserve energy and data storage space. The microcontroller can be programmed via USB to support frame rates of up to one image per second. The system is powered by a lithium ion battery (7.3 V, 20 Ah) that is recharged by two 20 W solar panels. During the Austral winter, the solar panels are insufficient, and the battery is exchanged together with the SD cards every 3 days.

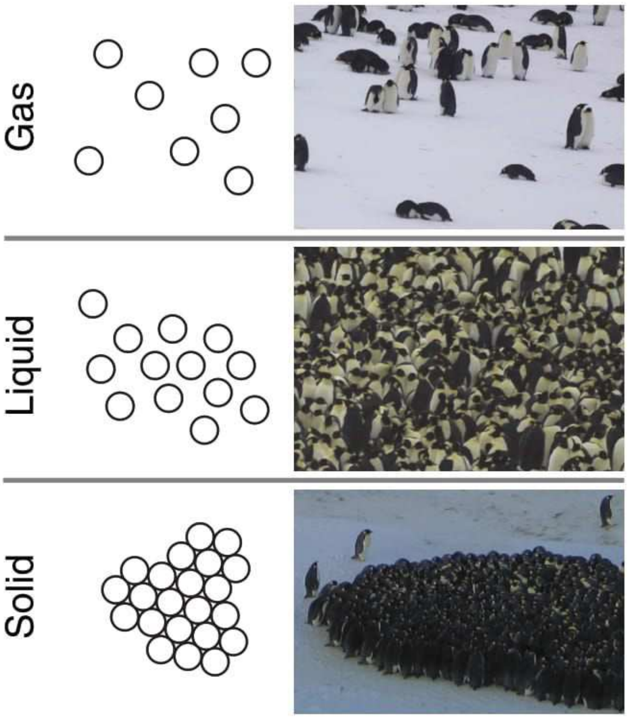

Figure 1. Comparison of phase (aggregation) states of non-living matter and states of emperor penguin colonies: In a gas-like state, individuals are loosely aggregated, and their motion is not impeded. In a liquid-like state, denser clusters without long-range order appear. In a solid-like state, individuals are arranged in a dense, quasi-hexagonal structure with long-range order, and individual motion becomes impossible.

The camera is mounted on a sturdy tripod, and the camera’s field of view can be adjusted to keep the moving colony in sight. The observatory can be carried by one person and can be erected in poorly accessible areas, e.g. on the rocky tips of the islands around Dumont d’Urville station.

Meteorological data, including air temperature, wind speed and wind direction, humidity and global solar radiation (the sum of direct and diffuse solar radiation) are acquired by the meteorological observatory (Météo France) at Dumont d’Urville (Ile des Pétrels, figures 2(a) and (b)). As the colony remains in close proximity to the base (less than 1000 m), these measurements are assumed to be representative for the conditions experienced by the colony.

Data preparation

We use the area covered by the colony as order parameter to quantify the state of the penguin colony. The minimum area corresponds to the highest density of the colony when all penguins are huddling (solid state), and the maximum area corresponds to the lowest density where nearly all penguins are scattered and only few, small huddling groups are present (liquid and/or gas state).

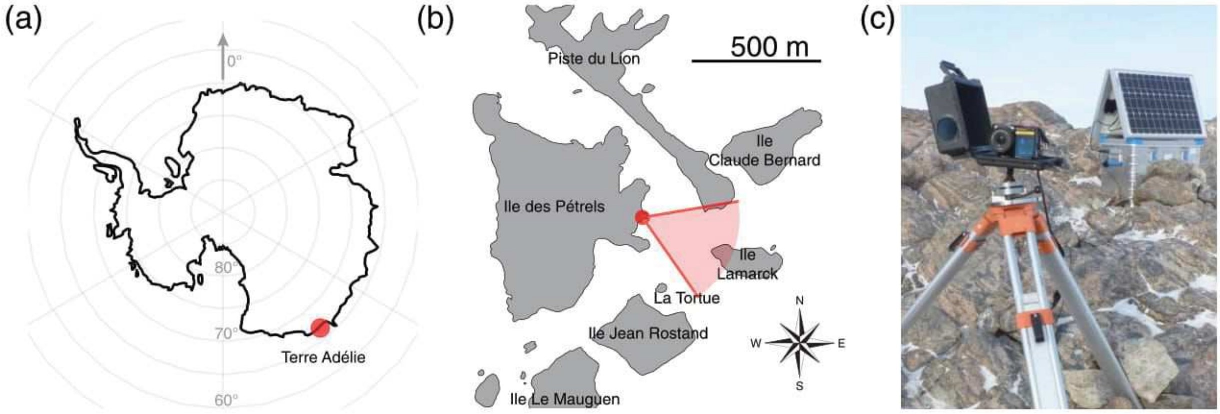

Figure 2. (a) position of the Pointe Géologie colony (b) position and field-of-view of the micrObs observatory. (c) The observatory is positioned on the rocky peaks of the surrounding islands for optimum viewing angle.

We limit our analysis to the time between mid-April and the end of May, a period with sufficient light to acquire low-noise time-lapse recordings over multiple hours, and varying environmental conditions where different phase states occur. Moreover, during this time period, we can assume that the influence of the breeding cycle on the penguins' huddling behaviour is minimal, because the animals just returned from several months of foraging and are well nourished. Also, there are no chicks present that could influence the huddling behaviour.

We selected only days for the analysis that fulfil the following conditions: good visibility over the whole day, and a quasi-stationary colony that predominantly remains in the field of view of the camera (figure 3(a)). Within the study period, we selected 8 out of 10 consecutive days (supplementary information table 1, supplementary figure S1 (stacks.iop.org/JPhysD/51/214002/mmedia)) that fulfil these criteria.

We extract the area occupied by the colony using an automatic image segmentation algorithm. The segmentation is based on an adaptive K-means clustering (Bradski, 2000) of pixel intensities (figure 3(b)). Pixel intensities are clustered into five groups. The group with the lowest mean intensity corresponds to the black plumage of the penguins. This approach proved to be robust to changes in illumination and shadows. To simplify the task, we manually masked rocks and heavily guano stained ground using ClickPoints (Gerum *et al* 2017a), and excluded them from the segmentation. One image every 3 min was analysed.

To correct for perspective distortions, we calculate the area represented by one pixel depending on its vertical (y-) position in the image. The calculation is based on the projection specified by the intrinsic and extrinsic camera matrix (supplementary figure S2, Gerum *et al* 2017b). The colony area is then calculated as the perspective-corrected area of the pixels belonging to the K-means group with the lowest intensity. We assume the number of penguins that are present within the field-of-view to be constant during the observed period. Therefore, we can normalize the colony area for the observed period by the maximum colony area across all evaluated days, after subtracting the absolute minimum colony area from every data point. The normalized area A_{norm} therefore varies between zero and unity. If we were to observe the colony from directly above (nadir), the colony area as defined here would simply be the sum of the area occupied by each penguin and hence remain constant regardless of colony density. At shallower viewing angles, however, penguins standing in the front occlude penguins standing further behind, and thus the colony area decreases approximately linearly with increasing density (supplementary figure S3). If we further assume the coexistence of two phases (huddles versus loosely clustered or free standing penguins), with each phase having an approximately constant average density, the normalized area is also a measure of the inverse huddling probability of the colony, with zero corresponding to the situation where (nearly) all penguins are in a huddle, and unity corresponding to the situation where (nearly) all penguins are free-standing.

Three simplifications were necessary for the automated evaluation of colony area and huddling probability: First, we cannot differentiate between the white plumage and the sea ice, resulting in a trend to underestimate the area especially at low densities. Second, because of the occlusion effect, a large huddle has a somewhat smaller area compared to multiple smaller huddles with the same total number of huddling penguins. Third, if the density of the penguins in the fluid/gas phase changes over time, this will change the degree of occlusion and hence affect the colony area (supplementary figure S3).

To reduce noise in the measurements, colony area and meteorological data are smoothed along the time axis using a least squares smoothing filter (first order Savitzky–Golay filter over 15 data points, Savitzky and Golay 1964) corresponding to a smoothing over 45 minutes (see figure 3(e)).

Model

To prevent overfitting of the limited data available (8 d, 3000 data points), we choose a simple two-stage model. First, we assume that the huddling state (or phase) of penguins as expressed by the normalized colony area changes only in response to an apparent temperature T_a. Second, we assume

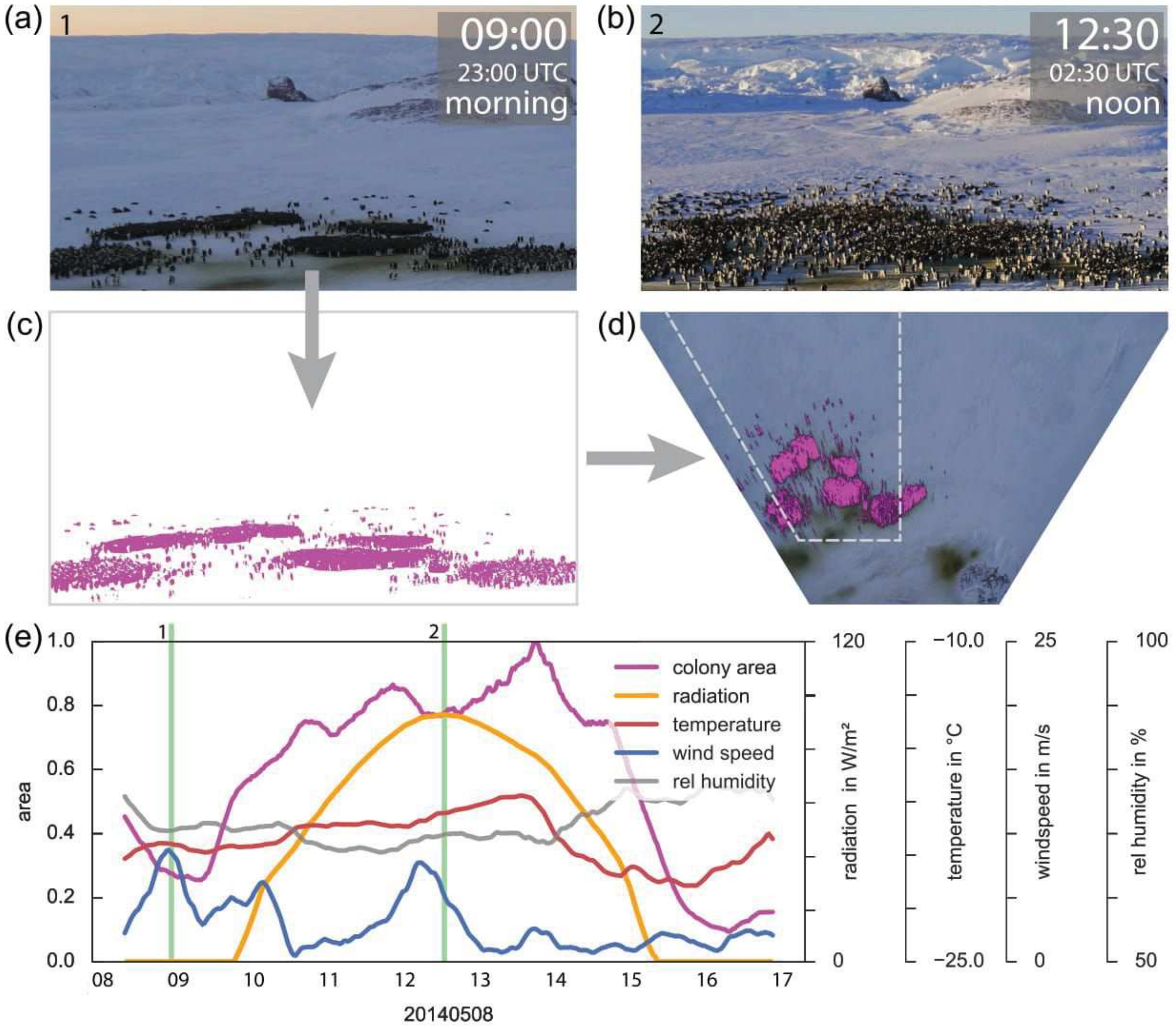

Figure 3. Images of the colony in the morning (a) and at noon (b); the change of the occupied area is clearly visible. The colony area is quantified based on a binary segmentation (c) followed by a correction of perspective image distortions (top-view projection) (d). Temporal fluctuations of normalized colony area (pink), temperature (red), wind speed (blue), global radiation (yellow) and humidity (grey) (e). See supplementary video SF1.

that the phase transition occurs as a monotonous function over a temperature range of T_a.

Apparent temperature. The apparent temperature T_a is expressed as a generalized linear model (equation (1)). Inspired by the wind chill factor for human temperature perception, the apparent temperature is defined as a combination of the environmental parameters ambient temperature (T), wind speed (W), global solar radiation (R) and relative humidity (H):

$$T_a = T + c_W W + c_R R + c_H H. \tag{1}$$

Except for ambient temperature T, all other environmental parameters are weighted by the model coefficients c_W (wind chill factor), c_R (solar heating factor) and c_H (humidity chill factor). We keep the apparent temperature dimensional (°C) so that the contributions of the meteorological factors can be expressed in units of °C per unit of the changing parameter. For example, an increase in wind speed of 5 m s^{-1} is perceived as a temperature reduction by 14.3 °C (see results).

Phase transition. We suggest that the normalized area A_{norm} occupied by the colony represents the huddling state and thus the phase of the penguin colony, where 0 corresponds to tight huddling or solid state, and 1 corresponds to a loosely clustered or liquid/gas state. The phase transits smoothly between 0 and 1 over a range of apparent temperatures according to a sigmoid function:

$$A_{norm} = \frac{1}{\left(1 + e^{-(T_a + T_{trans})/b_0}\right)}. \tag{2}$$

The phase transition point T_{trans} is the apparent temperature at which half of the penguins are in a huddle. The parameter b_0 denotes the apparent temperature range over which the phase transition occurs and hence defines the width of the sigmoid function.

Model training. The model parameters are determined using Bayesian inference, based on the probabilistic programming framework PyMC3 (v3.0) package for Python (Salvatier *et al*

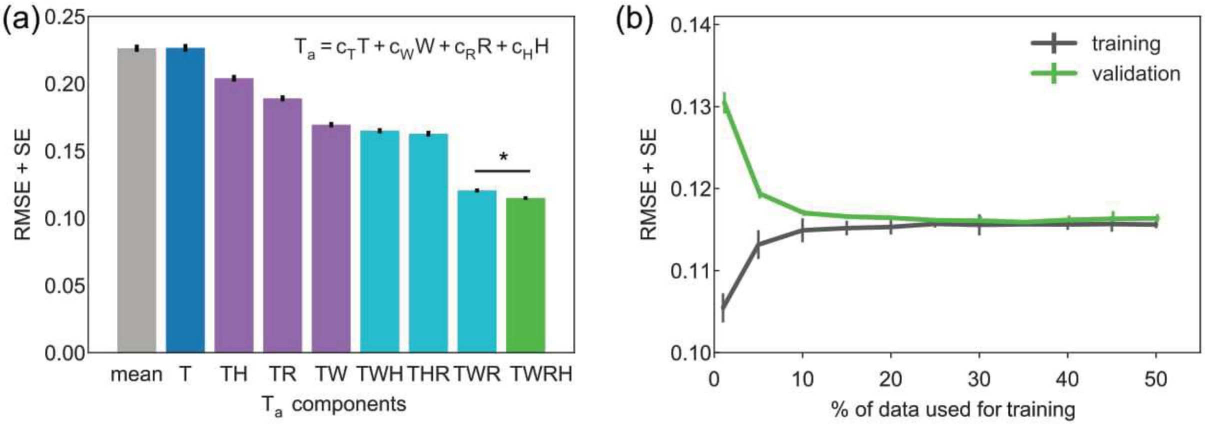

Figure 4. (a) root mean squared error (RMSE ± sd) for the prediction of the trainings dataset, depending on the environmental variables (temperature T, humidity H, wind speed W, global solar radiation R) included in the model. Coefficients of unused variables are set to zero. The improvement of the TWRH model over the TWR model is significant ($p < 0.05$). (b) RMSE (mean ± sd) of the model with 4 environmental parameters (TWRH) for training and independent validation dataset versus the percentage of data used for training. The standard error is calculated over all possible cross validation splits. The difference between training and validation error vanishes at 25%.

2015). In contrast to the classical frequentist approach, which provides a single value for each parameter, the Bayesian approach provides a parameter distribution, which is a direct measure of the uncertainty.

For model selection and parameter estimation, we use normally-distributed priors and a Metropolis-Hastings sampler (a Markov chain Monte Carlo method) to draw 100 000 samples to approximate the parameter distributions. We discard the first 10% of the samples (burn-in) to reduce the influence of the initial point estimate, which is used as a starting point for the sampling process. Predictions are drawn from the posterior parameter distributions and averaged over 1000 samples. For the final model, we draw $4 \cdot 10^6$ samples, discard the first 10^6 as burn-in and take every 10th sample to remove potential short-range autocorrelations that can occur as an artefact of the sampling process.

Model selection. To determine the importance of individual environmental parameters on the predictive performance of the model, we iteratively exclude parameters ($c_T = 1$; exhaustive combinations of c_W, c_R and c_H set to 0), and calculate the RMSE (root mean squared error) between the model prediction and the measured normalized colony area. We verify that we have sufficient data for the proposed model using a cross validation evaluation with increasing numbers of training samples. Data samples are considered sufficient when training and test error converge.

To quantify whether an additional parameter increases the model performance due to new information and not simply by increasing the degrees of freedom, we replace the value in question with a randomly sampled uniformly distributed variable and compare the model performance. Significance is tested using bootstrapping.

Predictive capability on the limited dataset is tested using a 'leave one out' training scheme (Hastie *et al* 2001), where the model is trained on n-1 of the n available sample days and is tested on the excluded day.

Results

Daily overview plots (figure 3(e) and supplementary figure S4) indicate a positive correlation between global radiation and the colony area, and a noticeable negative correlation with increasing wind speed. By contrast, daily changes in temperature and relative humidity are relatively small, and thus it is difficult to clearly discern a correlation with colony area. We do not consistently observe huddling below or above a threshold of any single meteorological variable.

We evaluate the effect of individual environmental parameters on the colony area by exhaustively iterating over all combinations and comparing the RMSE between the measured huddle area and the model (figure 4(a)). We find that ambient temperature (T, $\mathrm{rmse} = 0.228$) alone does not significantly ($p > 0.05$) improve the fit of the model to the data compared to the simplest model of a constant mean colony area. This is because the temperature shows only small variations over the course of each of the investigated days (supplementary figure S4). When we combine temperature with a second environmental parameter, however, we find a significant ($p < 0.05$) improvement of the model. Especially the combination of temperature and wind speed lead to the best results for two environmental parameters (TW, $\mathrm{rmse} = 0.169$), corresponding to a 25.6% improvement over a model with temperature as sole input variable. When we combine temperature with two parameters, we find a significant ($p < 0.05$) improvement only for the combination of temperature, wind speed and global radiation (TWR, $\mathrm{rmse} = 0.121$) with a further improvement of 28.4% compared to temperature and wind speed (TW). Including humidity as a fourth parameter leads to further small but significant ($p < 0.05$) improvement (TWRH, $\mathrm{rmse} = 0.115$) of 5.0% compared to the best model with three environmental parameters (TWR) (supplementary figure S5).

To verify that the model does not have too many degrees of freedom for the available amount of training data, we train the model on an increasing number of samples and evaluate

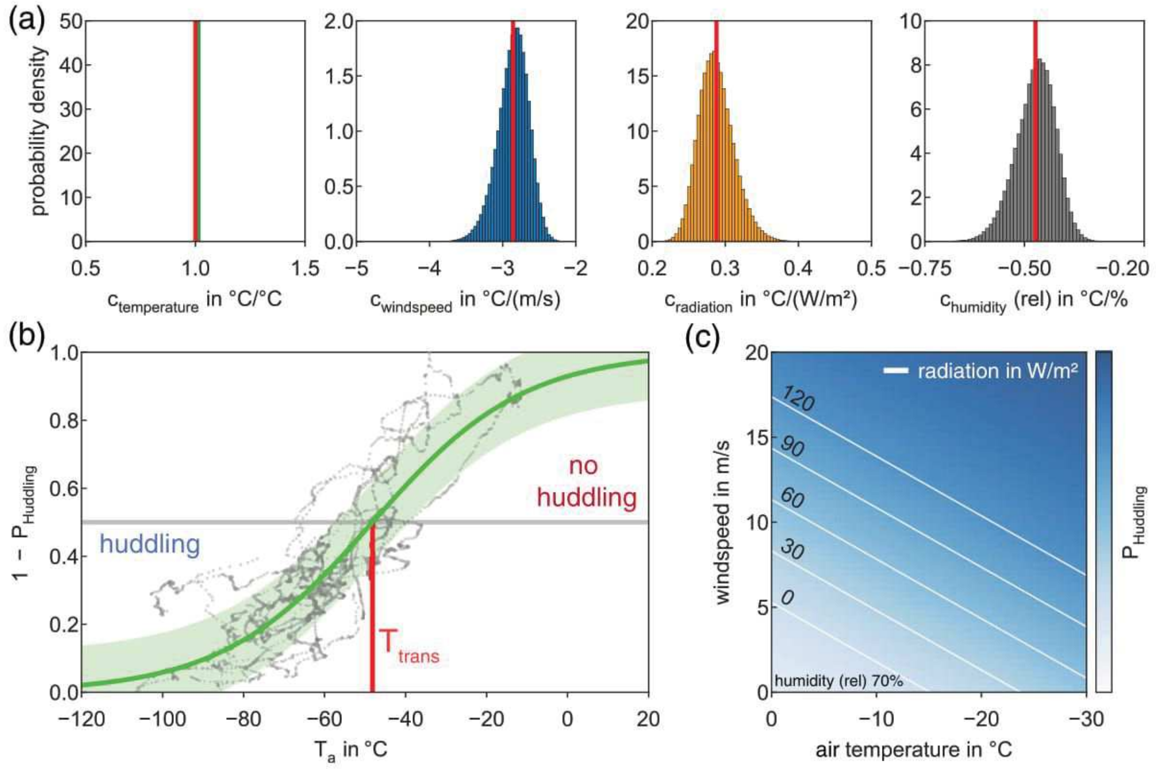

Figure 5. (a) distribution of model coefficients as estimated by Bayesian inference. The mean is shown by the red line. (b) Normalized colony area (corresponding to the inverse huddling probability) versus apparent temperature. Grey dots show the data from 8 days. The green line shows the model according to equation (2). Green shaded area indicates the standard deviation of the model. The red line indicates the apparent transition temperature T_{trans} where the huddling probability is 0.5. (c) Phase transition diagram for a fixed air humidity (70%). Lines of equal huddling probability (p = 0.5) for different solar radiation in a wind speed versus temperature diagram. Points with wind speeds and temperatures above the line have a huddling probability p > 0.5 as indicated by the blue shading.

Table 1. Model parameters based on the full dataset.

	c_T	c_W	c_R	c_H	b_0	T_{trans}
Unit	—	$°C\ (\mathrm{ms}^{-1})^{-1}$	$°C\ (\mathrm{Wm}^{-2})^{-1}$	°C/%	°C	°C
Mean	1	−2.857	0.288	−0.473	18.650	−48.167
Std	0	0.212	0.024	0.050	1.536	3.213
CV $\left(\frac{\sigma}{\lvert\mu\rvert}\right)$	—	0.074	0.083	0.106	0.082	0.067

the training and validation error (figure 4(b)). With less than 15% of the dataset used for training, we observe a large difference between the error of the training and validation dataset, indicating overfitting (a low error on the training data, but a larger error on the validation data indicates poor generalization). When more than 25% of the data set is used for training, however, the training and validation errors converge, indicating good generalisation and saturation of the model. We also performed a 'leave one out' evaluation where we train the model on the data from 7 d and validate the model on the remaining day for all possible combinations (see supplementary figures S6 and S7). This results in a mean RMSE of 0.115 ± 0.004 for the training data and 0.138 ± 0.043 for the validation data, demonstrating the predictive power of the model.

To determine the final model parameters ($c_T, c_W, c_R, c_H, T_{trans}, b_0$, see equations (1) and (2)), we sample the posterior distributions for the full dataset. Resulting parameter distributions are shown in figure 5(a) and table 1, the Bayesian sampling trace plot is shown in supplementary figure S8.

We set the temperature coefficient c_T to 1, which allows us to interpret all other coefficients as conversion factors towards an apparent temperature. The wind chill factor indicates a reduction in apparent temperature of $c_W = -2.857$ °C per 1 m s^{-1} wind speed increase. The solar heating factor indicates an increase in apparent temperature of $c_R = 0.288$ °C per W m^{-2} of global solar radiation. The humidity chill factor indicates a reduction in apparent temperature of $c_H = -0.473$ °C per % in relative air humidity. The coefficient of variation for these parameters (table 1 and figure 5(a)) agrees with our assessment from the model selection that key parameters are in the order wind speed, radiation, humidity (figure 4(a)).

Our model describes a transition from a solid to a liquid/gas state of the colony over a broad range ($b_0 = 18.65$ °C) of apparent temperatures (figure 5(b)), with a phase transition temperature of −48.167 °C where the probability is equal for both states. We can visualize the huddling probability in a phase transition diagram as shown in figure 5(c).

Discussion

In this report, we show that the huddling behaviour of emperor penguins can be described as a phase transition that is dependent on at least 4 environmental parameters: ambient temperature, wind speed, global solar radiation, and relative humidity. Using a linear combination of these environmental parameters, motivated by the concept of the wind-chill factor (Ames and Insley 1975, Siple and Passel 1999), we find an apparent temperature that controls the phase state of the colony. Moreover, we find that the transition from a high-density solid-like state (huddling) to a low density liquid/gas-like state (dispersed) occurs over a broad range of apparent temperatures.

Our findings are in agreement with the well-established notion that the primary purpose of emperor penguin huddling is to conserve energy and not, for example, a mechanism to protect against predators (Le Maho 1977). A previous study reported that average colony density was correlated with ambient temperature but not with wind speed (Gilbert *et al* 2008). Further experiments were performed with data loggers in combination with video recordings to investigate the influence of environmental parameters on the number of huddles and the mean number of individuals per huddle (Ancel *et al* 2015). This study reported a significant correlation of both measures with temperature, wind speed and radiation, but not with humidity. The correlation values, however, cannot be directly compared with our parameters as the huddling probability that we report is a combination of both, huddle number and number of individuals per huddle. Results of both previous studies are summarized in supplementary information table 2.

Based on measurements of the huddling probability extracted from time-lapse images, we have quantified the contribution of the following environmental parameters: ambient temperature, wind speed, global solar radiation, and relative humidity. We show that fluctuations of the huddling state cannot be explained by fluctuations of the ambient temperature alone. This is largely explained by the small temperature variations of ±5.0 °C over the course of 8 days (see supplementary figure S9), and less than ±3.0 °C over the course of any given day (see supplementary figure S4). By including additional environmental parameters, the model improves significantly. With four environmental parameters and two additional parameters describing the sigmoid shape of the apparent temperature range over which the phase transition process from a densely packed huddle to a loosely packed configuration occurs, we can account for approximately 50.7% of the huddling probability fluctuations. The remaining fluctuations that are not captured by our model are likely the result of physiological and behavioural processes. For example, even at low apparent temperatures, individual huddles might break up after exceeding an average lifetime of 1.6 h (SD = 1.7 h) (Gilbert *et al* 2006), which is thought to be triggered by individual penguins in a huddle that have sufficiently warmed up. This behaviour could be included in the model by tracking individual animals in the image data and thus considering their past huddling history. With the data presented here, tracking of individual penguins inside a huddle is impossible due to limited spatial and temporal resolution. Recent developments (Richter *et al* 2018) will provide a more suitable data basis for this analysis. We also tested if the model predictions can be further improved by introducing a time-delayed huddling response of up to 6 h to account for thermal inertia or physiological adaptation, but this did not lead to significant improvements (data not shown).

Most of the time, the penguin colony shows coexistence of solid phases (huddles) and liquid/gas phases (loosely packed or free-standing penguins). Thus, the phase transition from a solid to a liquid/gas state does not occur at a sharp apparent temperature. Instead, we find a sigmoidal relationship between huddling probability and apparent temperature, whereby the huddling probability decreases from 1 to 0 over an apparent temperature range of 140 °C, with a transition temperature of −48.2 °C at which the coexistence of solid and liquid/gas states is equally likely. The broad temperature range over which the phase transition occurs within the colony may be a combined effect of different transition temperatures for different individuals, a wide distribution of current skin temperatures among different individuals due to their individual huddling history and body constitution, or an oversimplification of our estimate of the apparent temperature as a linear combination of environmental parameters. Moreover, broadening of the temperature range over which the phase transition occurs may be caused by differences between the measured environmental conditions at the meteorological station and the colony site which is up to 1 km away. In particular westerly winds may be partially shielded by the close-by ~40 m high elevations of the Île des Pétrels, but since the dominant (76.9%) wind direction is easterly (45°–135°) where elevations reach maximally 22 m and are further (~300 m) away (figure 3(a), supplementary figure S10), we do not expect this to be a major confounding factor.

Despite these limitations, we propose that the model parameters, in particular the phase transition temperature, are indicators of the colony's energy budget/reserves. Physiological changes that naturally occur over the course of the breeding cycle (e.g. diminishing energy reserves and reduction in fat insulation, or the presence of chicks) will necessarily change the temperature perception and huddling behaviour (Robin *et al* 1998, Groscolas and Robin 2001, Ancel *et al* 2015), and hence the parameters of our model are valid only for the time span over which the training data was acquired. By continuously updating the training data over the course of the incubation part of the breeding season, we suggest that the time evolution of the model parameters, in particular the phase transition temperature T_{trans}, report the seasonal energy budget of the colony and may therefore help to predict colony foraging efficiency that will affect the breeding success of the population. Moreover, by monitoring these parameters over multiple years, we may gain a better understanding of how climatic changes or altered food supply may impact the foraging success reflected in the colony's energy reserves, and ultimately population dynamics (Jenouvrier *et al* 2014). Given the simplicity of the model and the ease with which huddling statistics can be automatically acquired using remote-controlled or autonomous observatories (Richter *et al* 2018), we believe that our method has the potential to become a valuable tool for large-scale colony monitoring.

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Annex B. MicrObs: a customizable time-lapse camera for ecological studies

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Hardware Article

micrObs – A customizable time-lapse camera for ecological studies

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A B S T R A C T

Camera traps for motion-triggered or continuous time-lapse recordings are readily available on the market. For demanding applications in ecology and environmental sciences, however, commercial systems often lack flexibility to freely adjust recording time intervals, suffer from mechanical component wear, and can be difficult to combine with auxiliary sensors such as GPS, weather stations, or light sensors. We present a robust time-lapse camera system that has been operating continuously since 2013 under the harsh climatic conditions of the Antarctic and Subantarctic regions. Thus far, we have recorded over one million images with individual cameras. The system consumes 122 mW of power in standby mode and captures up to 200,000 high-resolution (16 MPix) images without maintenance such as battery or image memory replacement. It offers time-lapse intervals between 2 s and 1 h, low-light or night-time power saving, and data logging capabilities for additional inputs such as GPS and weather data.

Hardware name	micrObs
Subject area	• Biological Science • Environmental Sciences
Hardware type	• Imaging tools • Field measurements and sensors
Open Source License	GPL CC-BY 4.0

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(*continued*)

Hardware name	micrObs
Cost of Hardware	440 € (minimal system: camera, control box, housing), 957 € full system (camera, control box, housing, battery, battery case, solar panel, charger, tripod, mounting)
Source File Repository	https://doi.org//10.5281/zenodo.3756718

1. Hardware in context

Automated imaging is widely used in ecological studies, e.g. for monitoring the occupancy of breeding sites in penguin colonies [1], collective movement of chickens [2], flocks of birds [3], mating of mosquitoes [4], hunting strategies in bats [5], grouping of midges [6], or the huddling of emperor penguins (*Aptenodytes forsteri)* [7]. The recording hardware used in such studies can vary from camera traps [1], semi-automatic camera systems [8], DSLR cameras with custom trigger electronics [9], to autonomous multi-camera arrays [10]. Also, requirements regarding frame rate and image resolution can vary greatly. For studies that focus on slowly changing parameters such as population size and breeding site occupancy, long image intervals (1 image per hour to 1 image per day) are sufficient, and accordingly the total number of acquired images remains small, with typically less than a few thousand images per camera and season. By contrast, behavioral studies require higher frame rates to identify individual motion and interaction between individuals, ranging from 1 frame per minute for studying breeding penguins [1,11] to video frame rates [4] or even high-speed cameras [6] for studying collective order in swarms of midges.

Unfortunately, frame rates between one frame per second to one frame per minute are often not available in commercial camera traps and time-lapse cameras, or if they are, longer recording periods of several days or weeks cannot be achieved for various reasons such as mechanical camera failure after 100,000 images [12]. This lack of long-term recording hardware is especially critical for studies in which the behavior of a species needs to be observed over a significant part of its annual cycle, for example emperor penguins that remain continuously at the breeding colony for over 130 days [10]. Another disadvantage especially of low-cost commercial systems is their poor image quality as regards image resolution and noise performance in low-light conditions.

Here, we present a low-cost, high-resolution, sturdy and water-resistant time-lapse camera system (micr0bs) (Fig. 1) based on customized consumer components. The camera system was designed to record time-lapse images continuously and autonomously at frame rates between 0.5 frames per second and 1 frame per day with an image storage capacity of

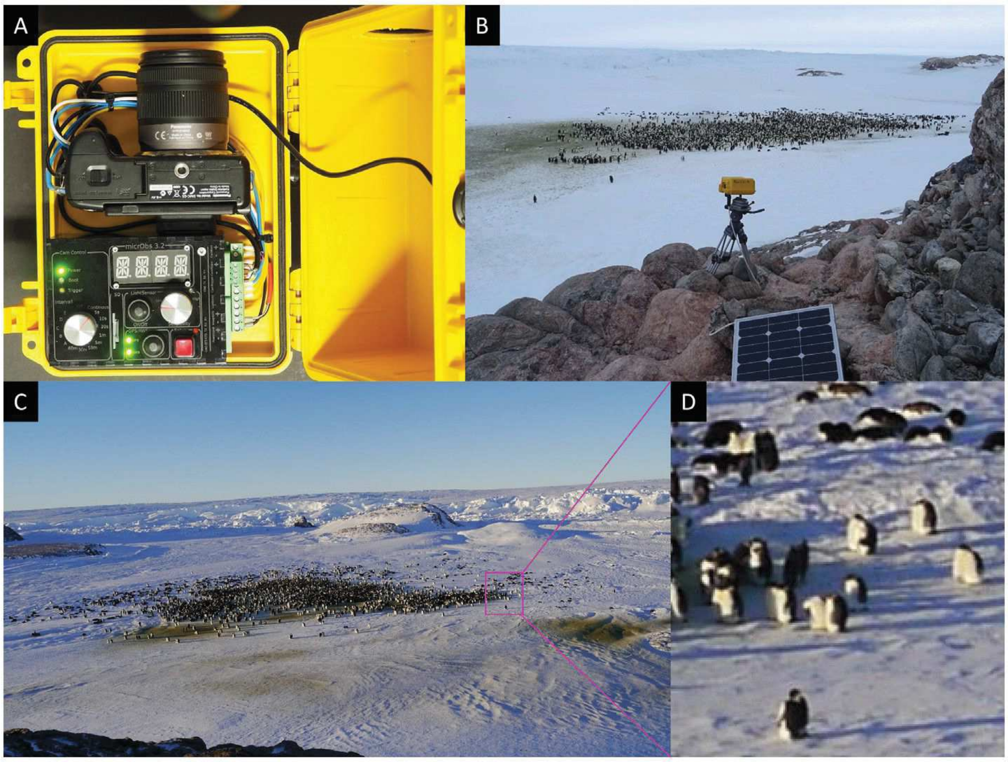

Fig. 1. micrObs recording system in the field. (A) The camera housing contains the control box and camera. (B) System deployed in the field at Pointe Géologie archipelago, Adélie Land, Antarctica (66°42′01″S 139°49′41″E, May 2019). The camera housing is mounted on a tripod with a pan/tilt ball mount. The system is powered by a 12 V car battery with a solar panel and charge regulator. (C) Image recorded with micrObs. (D) Enlarged detail: Individual animals are clearly distinguishable.

1024 GByte (~200,000 jpeg-compressed 16 MPix images). Furthermore, the system was optimized for minimum power consumption and offers auxiliary data logging capabilities, for example to record local weather conditions. micr0bs systems have been deployed since 2013 under the harsh climatic conditions of Antarctica and the Sub-Antarctic Islands, with some of the cameras having recorded more than 1 million images (Table 6).

2. Hardware description

The camera system was designed to handle a large range of time-lapse applications. This foremost includes a wide range of image recording rates (2 s–1 h), low power consumption and large image storage capacity to maximize runtime. The camera system offers auxiliary data logging capabilities, for example to record local weather conditions. We foresee the main applications to fall into one of the following categories:

- Continuous observation of individual behavior, e.g. tracking predation events in a seabird colony at high temporal resolution of 1 image every 5 s for 12 days
- Investigation of collective behavior events, e.g. observing penguin huddle formation at intermediate temporal resolution of 1 image every minute for 20 weeks
- Long-term monitoring of landscapes, aggregations, or population sizes of animals, e.g. observing nesting seabirds at low temporal resolution of 1 image per hour for 4 years

In addition to ecological studies there is a wide spectrum of other applications where micrObs could be used. Those include coastal boat traffic monitoring e.g. assessing area use of recreational (non AIS) vs. commercial ship traffic (with AIS), monitoring of local geophysical processes such as glacier and volcanic activity as well as geoscientific studies (e.g. snow coverage monitoring).

2.1. Camera choice

Existing solutions for automated image capture can be divided into four categories: camera traps, action cameras, consumer digital single lens reflex (DSLR) cameras, and computer-assisted image acquisition system based on industrial cameras. In Table 1 we compare representative examples of such systems to our approach (micrObs).

Table 1
Comparison of four time-lapse recording systems for frame rates between 1/s and 1/day. *Images per battery charge are calculated based on a 3Ah 12 V battery for comparability. References: [1][13], [2][18], [3][9], [4][16], [5][15], [6][20], [7][21], [8][22] [9][23].

System Type	Camera Trap	Action Camera	DSLR camera		Mirrorless camera
Name	Bushnell Impulse Trail	GoPro HERO8 + CamDo BlinkX	Cyclapse	Newbery & Southwell 2009	micrObs
Price	265 €[1]	692 € [4,5]	3372 € [2]	N. A. (~1000 €) [3]	957 €
Electrical Shutter	Yes [8]	Yes [5]	No	No [3]	Yes [9]
Mirror	No [8]	No [5]	Yes [7]	Yes [3]	No [9]
Camera	integrated [8]	GoPro Hero 8 [5]	Canon EOS-1500D / Rebel T7 [2]	Canon EOS-1300D / Rebel T6 [3,6]	Panasonic Lumix G5
Other Cameras Possible	No [8]	GoPro Hero 5 to 8 [4]	Yes [2]	Yes [3]	Yes
Image Resolution	8 MPix [8]	8 MPix [5]	24 MPix [7]	6.3 MPix [6]	15.9 MPix [9]
FOV (typical)	38° [8]	68°-122° [5]	23-63° [7]	23-63° [3]	23°-63°
Other Lenses Possible	No [8]	No [5]	Yes [7]	Yes [6]	Yes
Images per Battery Charge*	5400 [8]	2890 [4]	2100–3500 [2]	~3700 [3]	6400
Image Interval	1 min to 1 h [8]	0.5 s to 1 h [4]	1 s to 24 h [2]	1 h to 24 h [3]	2 s to 24 h
Max Image Storage	32 GB (SDHC) [8]	1024 GB (SDXC) [5]	1024 GB (SDXC) [7]	1024 GB (SDXC) [6]	1024 GB (SDXC) [9]
Reference Timing	GSM [8]	wifi & NTP server [4]	RTC [2]	RTC [3]	GPS
Power per Image	10 mWh [8]	40 mWh [4]	38.4 mWh [2]	6.9 mWh [3]	5.64 mWh
Standby Power Usage	0.96 mW [8]	10 mW [4]	100 mW [2]	0.96 mW [3]	122 mW
Regenerative Power	No	Solar (additional cost)	Solar [2]	Solar [3]	Solar
Open Source	No	No	No	No	Yes
Open Hardware	No	No	No	No	Yes
Hardware User Interface	Yes [8]	No	No	No	Yes
Light Sensor	Yes [8]	No	Yes [2]	No	Yes
GPS	Yes [8]	Yes [5]	No	No	Yes
Automatic Weather Station	No	No	No	No	Yes (optional)

Camera traps such as the Bushnell impulse trail [13] are designed for long deployment times, low energy uptake, and harsh environmental conditions. Typically, they are used to record a picture/video on demand after being triggered by motion or a thermal signal from a passing animal. These systems often support time-lapse imaging but cannot record more than several thousand images during a deployment period due to their limited memory capacity and battery lifespan. Furthermore, their image quality is limited by low-resolution lenses, small apertures, lack of automatic aperture and focus settings as well as small sensor sizes and low image resolution.

Action cameras such as the goPro Hero 8 [14] are primarily used for frame rates between 30 fps and 120 fps, but they also support time-lapse modes [15]. Similar to camera traps, they are limited by battery capacity and image storage capacity. There are solutions bypassing this issue with additional hardware [16,17]. However, further drawbacks of these cameras are their wide-angle lenses and small image sensors that perform poorly under low-light conditions.

The use of consumer DSLR cameras for time-lapse recordings is widespread in construction progress documentation [18]. In addition, there is a noncommercial system already in use to study penguin population dynamics [9,19]. These systems are closest to our requirement in image quality and range of time-lapse intervals. However, DSLR cameras suffer from mechanical wear of the mirror and shutter, which are moved during each image capture. This limits the lifetime of a DSLR camera to about 50,000 to 100,000 images. Furthermore, in extreme cold, DSLR fail mechanically: shutter and mirror move slowly, become stuck or damaged [11]. The DSLR in both systems can be replaced with a mirrorless interchangeable-lens camera with an electronic shutter, however, the relatively high cost of the commercial system and the absence of open soft- and hardware documentation for the noncommercial system remain an issue.

Custom image acquisition systems based on industrial cameras and controllers [10] are expensive, bulky, have a high energy consumption, and require the user to develop customized algorithms for the automatic control of aperture, gain, exposure time, and focus distance. Software and hardware for compression and management of the recorded images further increase the complexity.

Our "micrObs" imaging system is based on the Panasonic Lumix DMC G5, a commercially available digital mirrorless camera that offers an electronic shutter, external trigger, optional external power supply, and high-quality interchangeable fixed or adjustable focal length lenses with large aperture. We use a wide-to-medium angle telephoto lens (Panasonic H-FS014042E) with a focal length of 14–42 mm (28–48 mm in 35 mm equivalent). We use the manual focus option to set the focus point (usually to infinity). This prevents blurred images due to an unsuccessful autofocus search in scenes with poor light or poor visibility, and further reduces the number of moving parts.

2.2. Camera control

The recording system is controlled by an Arduino Nano microcontroller [24] mounted onto a custom printed circuit board. The microcontroller monitors battery voltage and ambient light conditions. It powers and boots the camera, and triggers the image acquisition (see Figs. 2 and 3). The microcontroller also logs the data from a GPS module, a weather station (AWS), or any other RS232-capable device, to an interchangeable memory card (microSD). We choose the Arduino over alternative controllers with lower power requirements because of the large user community providing existing hardware and software solutions such as the SD card board.

We control the camera's boot and shut down commands by replacing the camera's manual power switch with an electronic switch. This is necessary to ensure a proper shut-down sequence, as simply disconnecting the external power supply leads to an erroneous numbering of the recorded images.

A major limitation of a consumer camera is the inaccuracy of their image timestamps. Even if the camera's clock is set properly, it will drift noticeable during long-term deployments. Therefore, in addition to the image timestamp provided by the camera, we log the microcontroller time of each image trigger event in a file. To prevent time drift, we synchronize the microcontroller's clock once per hour (configurable) to UTC time provided by the GPS module. To reference the camera-provided image timestamp to the microcontroller-provided trigger time, we acquire two images with no (minimal) time delay each time the microprocessor's clock is synchronized.

For most applications, ambient light conditions will occasionally be insufficient for image acquisition, e.g. due to day-night cycles or weather changes. To save energy and storage space, micrObs measures the ambient light intensity with a photoresistor and interrupts recording if it falls below a user-defined threshold.

To simplify the camera setup procedure under poor weather conditions, the user can adjust the frame rate and illumination threshold via the front panel of the control box (see Fig. 1A). A display informs the user of image interval, current ambient illumination, illumination threshold, connected RS232 devices such as a weather station, battery voltage, availability and functionality of GPS, and memory card.

The control box can in principle control any camera that offers external power supply and shutter release. The voltage levels of the camera power supply and the shutter release are adapted to our camera model but can be changed by adjusting resistors R6 and R7 and the voltage converter TSR-2490 (see design file MainPCB.sch).

2.3. Other components

The housing of the recording system needs to withstand severe weather conditions like heavy rain, drifting snow or ice buildup as well long-term UV exposure. The housing is chosen as small as possible to reduce wind-induced vibrations. It

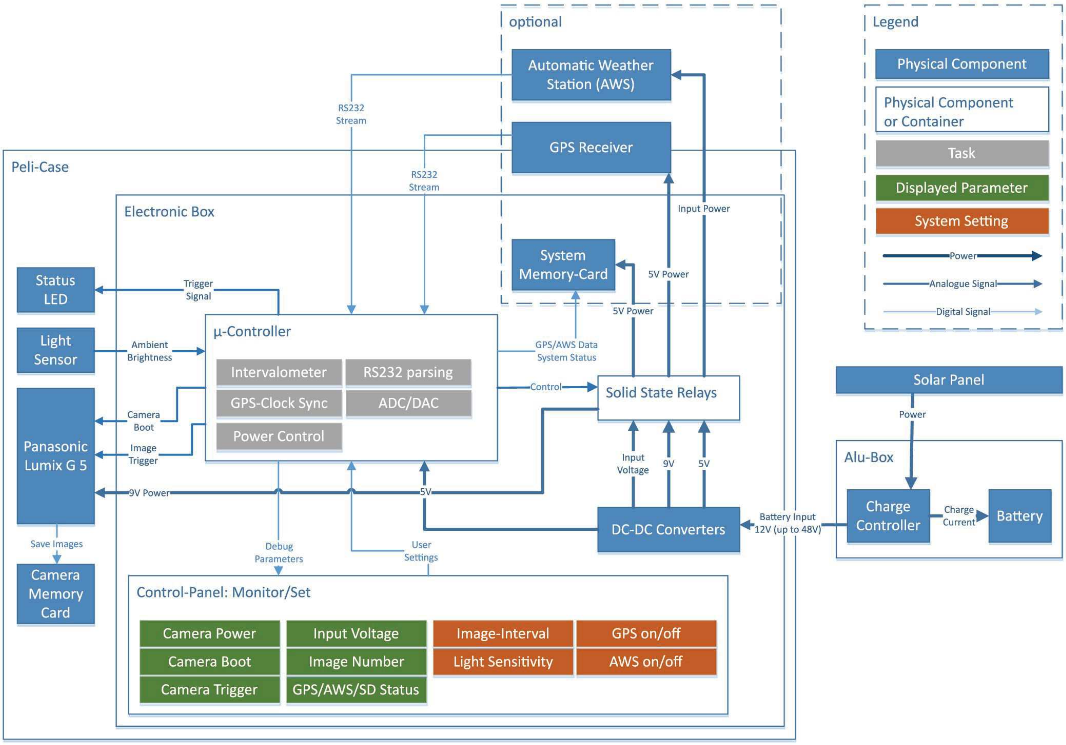

Fig. 2. Schematic of the camera control setup.

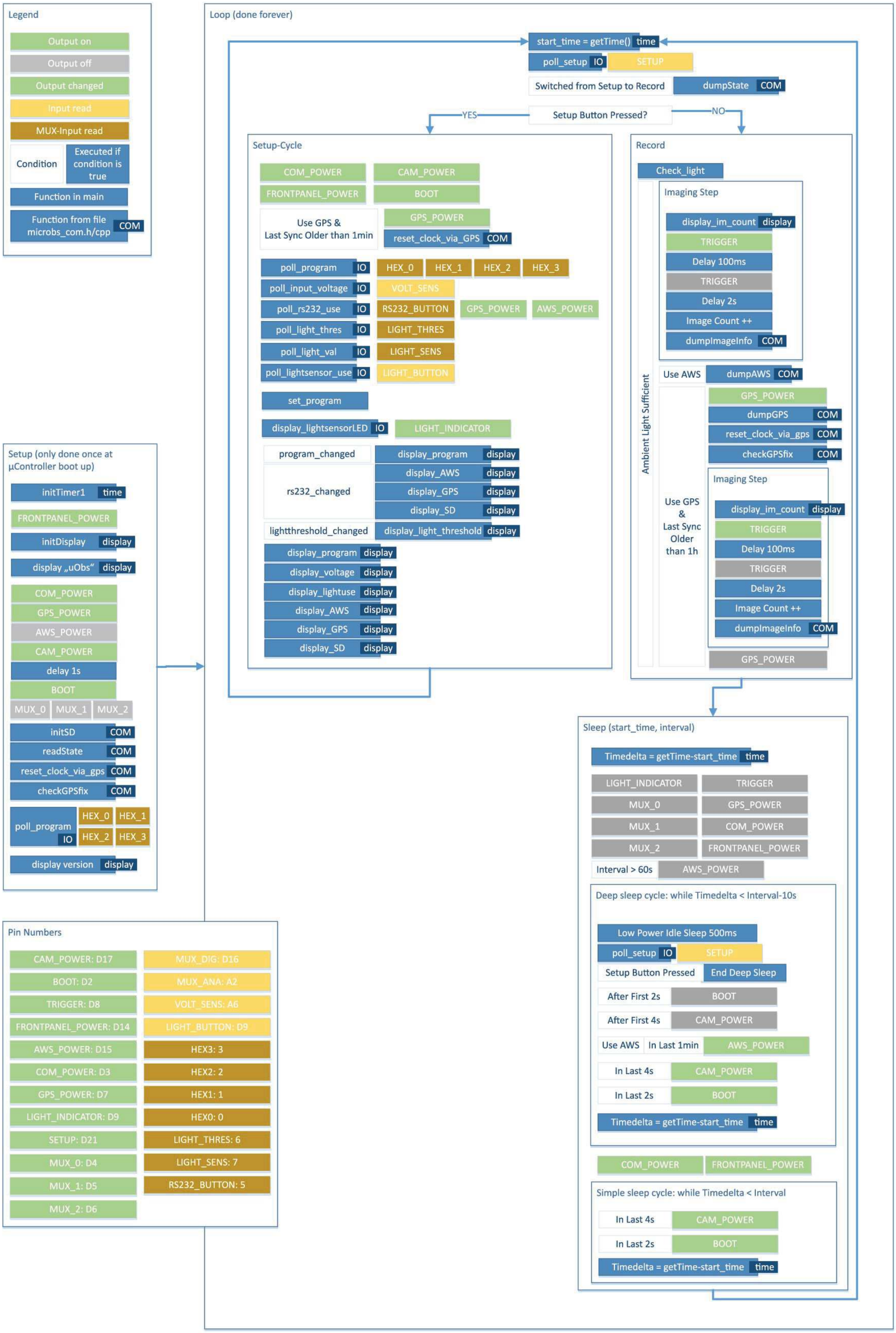

Fig. 3. Camera control software block diagram.

holds the camera, the control unit, and the GPS receiver (NL-604P, Navilock). We chose a plastic housing with rubber sealing (Protector 1150, Peli). Cables to the battery box and external weather station are connected to the controller via waterproof cable-glands. The cutout for the camera's viewport through the enclosure is covered with a standard 52 mm UV filter used for photography and sealed with a custom-made rubber gasket that is compressed to the enclosure by a bracket. The housing is water resistant (comparable to IP66 rating) but not submersible. It is attached to a tripod via a custom pan-tilt mount that is easily operable and fits most tripods. The tripod (berlan BST285A) used in our application is a standard surveillance equipment tripod and was chosen based on its low cost and light weight (aluminum construction).

If a rechargeable battery with solar panels is to be used, the solar panel is mounted on a separate aluminum box (Zarges) that also houses the charge controller and battery. For transportation, the camera case is designed to fit into the battery box as well. Depending on battery weight and size, transport and setup of the system is possible with one or two persons.

For the battery, we chose a deep cycle, non spillable, AGM (Absorbent glass mat) battery (Lifeline GPL-U1T), which, for our application, was the best compromise between weight (10.9 kg), price (170 €) and capacity (33 Ah, 12 V). A 30 W solar module (Offgridtec 3-01-001530) that fits on the aluminum box charges the battery with a 6 A 12 V charge regulator (Steca Solsum 0606). AGM batteries are very forgiving in cold environments and very safe to handle, thus the prime choice for our deployments. In deployment situations where weight is crucial the AGM battery can be directly replaced by a Lithium Ion battery which offers a higher energy density. We have previously used Lithium Ion batteries on several deployments.

3. Design files

3.1. Design file summary

The design file lists for the hardware and software components are shown in Tables 2 and 3. MainPCB.sch: Documentation file containing the circuit schematic for the custom electronic board.

MainPCB.brd: The print circuit board layout file of the main board of the control unit. Most manufacturers accept this filetype, otherwise it can be opened with the free version of AutoCAD Eagle, to derive other file types (e.g. Gerber files).

FrontPCB.sch: Documentation file containing the circuit schematic for the breakout board of the front panel.

FrontPCB.brd: The print circuit board layout file. See MainPCb.sch. Most manufacturers accept this filetype, otherwise it can be opened with the free version of AutoCAD Eagle, to derive other file types (e.g. Gerber files).

Enclosure.svg: Vector graphics file containing the plans for the control box. The control box can be laser cut from 3 mm acrylic glass using this file. It contains engraving paths as well as cutting paths. It can be opened and manipulated with the open source program Inkscape or similar software.

WindowMount.svg: Vector graphics file containing the plans for the camera window mount. The window mount can be laser cut from 3 mm acrylic glass and 1 mm chlorine free rubber using this file. It can be opened and manipulated with the free program Inkscape or similar software.

Table 2
Hardware design files.

Design file name	File type	Open source license	Location of the file
MainPCB.sch	EAGLE Circuit file	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
MainPCB.brd	EAGLE Board file	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
FrontPCB.sch	EAGLE Circuit file	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
FrontPCB.brid	EAGLE Board file	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
Enclosure.svg	vector graphic	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
WindowMount.svg	vector graphic	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
PanTiltMount.stp	step file with CAD drawing	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718

Table 3
Software files.

Design file name	File type	Open source license	Location of the file
Software.ino	Arduino Project/C++ Code	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_IO.cpp	C++ code	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_IO.h	C++ header	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_com_v0.cpp	C++ code	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_com_v0.h	C++ header	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_display_v0.cpp	C++ code	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_display_v0.h	C++ header	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_time.cpp	C++ code	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
microbs_time.h	C++ header	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
SoftwareLibraries	C++ libraries	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718
syncRenameFiles.py	python script	CC-BY 4.0	https://doi.org//10.5281/zenodo.3756718

PanTiltMount.stp: A step file containing the drawing of the pan and tilt mount. It can be opened with many CAD programs like SolidEdge, which we used for creating the drawing.

Software.ino: Arduino Project including main routine for micrObs. Project management.

microbs_IO.cpp: Get and set micrObs inputs and outputs. Handling of analog averaging and multiplexer.

microbs_IO.h: Settings and definitions of inputs and outputs.

microbs_com_v0.cpp: Communication with GPS, weather station and control box memory card.

microbs_com_v0.h: Settings and definitions of communication modules.

microbs_display_v0.cpp: Front panel routines for display and LEDs. Debug strings for display. Set/get methods for system settings (interval, light sensitivity, GPS/weather station activity).

microbs_displa_v0.h: Definitions for front panel routines.

microbs_time.cpp: Timing routines: interval timer, syncing with GPS, time display, reset functions.

microbs_time.h: Definitions of timing routines.

Software Libraries: Contains Open Source Libraries like Adafruit_LED_Backpack, Low-Power, SdFat.

syncRenameFiles.py: This file contains a self-explanatory (help function) python (version >3.4) script used to synchronize the recorded images from the camera memory card with the timestamps and meta information from the control box' memory card.

4. Bill of materials

We included a detailed bill of materials with the other design files (https://doi.org//10.5281/zenodo.3756718) and in Supplementary File 1.

The control box housing can be ordered from a laser cutting service or manufactured at a local fab lab using the provided drawings. The control box housing (parts C1-C8, see Fig. 4 in Supplementary File 2) is made out of 3 mm black cast acrylic glass (PMMA). The window parts W1 and W2 are made out of 3 mm acrylic glass, and W3 is made out of 1 mm thick chlorine free rubber.

The electronic parts and most of the smaller mechanical parts can be purchased through online retailers such as conrad.de or mouser.com.

Aluminum for larger mechanical components (e.g. for the tripod mount) can be purchased from a local hardware store. We manufactured the tripod mount at our institute's mechanical workshop.

The hardware costs for a minimum configuration of the system consisting of the enclosure box, camera, control electronics and GPS are 440 €. This does not include the costs for an external power supply (289 €) and tripod mounting (228 €). All prices include German VAT of 19%.

5. Building instructions

We provide a detailed step-by-step building instruction in Supplementary File 2. The instruction contains descriptions and pictures of the assembly of the control box, the customization of the camera, the construction of the front panel, a drilling plan for the outer housing, and a building instruction for the window mount. It does not contain instructions on how to cut acrylic glass, how to manufacture the pan and tilt mount, how to make a PCB from the design files or how to solder components. If an in-house workshop for these tasks is not available, they can be outsourced (e.g. Online PCB Services, Laser Cutting Services). In the following, we give a brief summary of the instructions:

Pry open the camera body and replace the hardware switch by two cables connected to the former hardware switch pads. Drill a hole in the camera body to feed-through the cables. Re-assemble the camera body. Replace the camera battery with the DC-adapter. (See chapter 2 in Supplementary File 2.)

Fabricate the acrylic glass parts (C1-C8) shown in Enclosure.svg and (W1, W2 × 2) shown in WindowMount.svg from 3 mm cast acrylic glass (PMMA) using a laser cutter. Fabricate the rubber sealing W3 shown in WindowMount.svg. Glue the enclosure from parts C2-C7 using an adhesive for acrylic glass (Acryfix, Evonic). Drill the M2 threads in the sides and the 6 mm countersunk holes in the top and bottom piece of the control box housing. (See chapter 4.1 in Supplementary File 2.)

Produce the Main PCB and Frontpanel PCB (printed circuit board) from the design files MainPCB.brd and FrontPCB.brd. Solder the electronic components (D1, IC1, Q1-Q9, R1-R23, REED, TSR-1-2450, TSR-1-2490, U1, X1, X2, Ca1, Ca2) to the main board. (See chapter 3 in Supplementary File 2.)

Mount the main board into the control box housing. Assemble the connectors for the weather station and GPS, mount them to the control box, and connect them to the main PCB. Assemble the front panel from the control box housing top acrylic glass piece (C7, C8 x2), the front panel circuit board, buttons (B1, B2, B3), hexadecimal encoder (H), potentiometer (M), knobs (K1, K2), display (D) and LEDs (L1-L7). Assemble the connector ribbon cable (MM) with the connectors (P4, P5). Connect front panel and main PCB. Put the SD card reader in the socket on the main board. (See chapter 4.2 in Supplementary File 2).

Flash the Arduino with the C++ software (software.ino) using the Arduino IDE software and a mini USB connector. Put the Arduino in the socket on the main board. Close the control box housing. Assemble the trigger cable from the core of the audio jack (P6) with two 0.5 mm^2 wires. Assemble the light sensor from the photoresistor (R0), the plastic mantle of the audio jack (P6) and two 0.5 mm^2 wires. Drill holes for the camera mount, window, light sensor, GPS, and power cable gland (T1, T2) in the housing. Assemble the window mount from the laser cut window mount parts (W1-W4) and secure it to the housing. Mount the camera and GPS inside the housing. Assemble the GPS connector plug. Connect the camera to the control box via the trigger cable, customized camera power switch cable, and dc adapter cable. Double check (!) the polarity of the camera power connection. (See chapter 5 in Supplementary File 2).

Connect the light sensor and GPS. Put a SD card in the camera and a micro SD card in the control box. Push the debug button and connect the control box to power. The system should boot, start up the camera, and display the system parameters. (See chapter 6 in Supplementary File 2)

We use the transport box as a housing for the battery and charge regulator and as a support for the solar panel. Detailed instruction for the customization of the transport box, wiring, mounting the solar panel and mechanically securing the battery are given in chapter 7 in Supplementary File 2.

6. Operation instructions

We include a user's manual in Supplementary File 3, which explains the setup in the field, front panel setup options and synchronization software. In the following, we describe the typical use case.

The battery box with the camera and tripod can be easily carried by two people. Remove the camera housing and solar panels from the transport box and connect cables to the outer sockets. For most applications, the camera should be positioned as high as possible above the imaged area to achieve a high observation elevation angle. This is usually associated with a high wind load. We reduce wind-induced shaking and tilting by attaching a heavy weight to the camera mount/tripod. For example, a tarpaulin or net can be attached to the tripod, which is then loaded with stones or other heavy material available on site. Alternatively, tent pegs can be used to secure the tripod.

The camera mount allows for $\pm 15^\circ$ of tilt and 360° of panning. For better access while setting pan, tilt, and recording parameters, the camera housing can be opened and closed without moving or touching the camera. To prevent ice buildup and remove water droplets from the lens, we suggest to position the micrObs in an exposed location facing the main wind direction. This was a very successful approach to keep the lenses clean during longer term deployments.

To adjust recording settings, first switch to setup mode by pressing the red setup button (red LED will turn on). The button will click and stay in the latched position. While in setup mode, no images are acquired. To resume time-lapse operation, click the setup button again (red LED will turn off).

While in setup mode, the control box' display shows the current parameters of the system: Image interval, ambient light threshold, GPS activity, weather station activity, μSD card presence and power supply voltage. To change those parameters, set the image interval, the GPS and weather station usage and the light sensor threshold using their respective control/button. The settings will be saved when the setup mode is exited.

After exiting the setup mode, recording will start immediately, and the control box will display the cumulative number of recorded images after each trigger event. The "Power" LED indicates the supply of the camera with power, the "Boot" LED indicates if the camera is switched on, the "Trigger" LED lights up shortly when an image is triggered.

If micrObs is disconnected from power intentionally or unintentionally (e.g. to exchange the battery), it is not necessary to reset any parameters. The control box saves the last setup on its μSD card and continues recording when re-powered. Likewise, the system resumes recording after a power loss, e.g. when connected to a variable power source like a photovoltaic panel. Control box memory card and camera memory card should always be exchanged together, to keep the timestamp and meta information synchronous with the recorded images. We provide a software tool for reordering and renaming of image files based on the timestamps from the control box' μSD card.

7. Validation and characterization

micrObs has 9 different time lapse intervals between 2 s (fastest) and 1 h implemented. The use of the light sensor, GPS, and a second RS232 device can be enabled or disabled. If needed, these default time lapse intervals can be changed in the Software.ino file, but 2 s is the fastest interval due to camera limitations. The performance characteristics and limitations with our configuration (12 V 30 Ah battery (3,600 Wh), 1 TByte memory card for the images) are:

- Capture more than 200,000 images (this requires recharging of the battery)
- Capture up to 64,000 images on a single battery charge
- Record for up to of 98 days on a single battery charge
- Relative deviation of the timer interval from the target value is less than 0.1%

7.1. Timing and power drain

We minimize the energy consumption of our recording system by optimizing the component uptime, keeping components only powered when necessary. Therefore, we switch-off the camera between two images if the image interval is larger than 10 s or when there is not sufficient ambient light (e.g. night, storm). Power consumption is 152.4 mW during the power-down phases (Fig. 4B). A single charge of a 3,600 Wh (12 V 30 Ah) battery lasts for up to 64,000 images recorded at the highest frame rate, or up 98 days when images are recorded at the lowest frame rate (if no additional RS232 device other than the GPS device is powered, see Table 5). The light sensor (to automatically turn-off recording during low-light conditions), GPS, and a second RS232 device can be switched on or off. The power consumption during the power-down phases can be further lowered to 122 mW by removing the microcontroller's status LEDs and removing the built-in power converter of the Arduino-controller, which are not necessary for operation. If solar power (with a small buffer battery) is sufficient to power micr0bs continuously (e.g. 3 W average consumption, 30 W solar panel), the system's maintenance interval is only limited by the camera's image memory card size. With a 1 TB memory card, the camera can capture more than 200,000 16 MPix 98% quality jpeg images.

micrObs supports any interval between 2 s and 49 days. 2 s is the minimum time necessary for the camera to save one image, hence the lower limit. 49 days is the maximum interval coverable with the microcontrollers 32-bit millisecond timer. However, 1 h is the sensible end of the interval range, where the user will not gain much deployment time by reducing the image frequency (e.g. 95 vs 98 days of deployment when switching from a 1 h interval to a 24 h interval, as shown in Table 5). Five positions of the interval switch are available for custom interval settings.

micrObs supports 9 different image intervals between 2 s and 1 h. Each image is provided with a GPS time stamp. We verified the image interval by measuring the timing accuracy of the Arduino's internal clock. In particular, we measured four different micrObs devices at four settings for the sleep timing (the time the system spends in deep sleep without interruption) and image intervals (the actual time between images): 0.5 s sleep at 1 h image interval, 0.5 s sleep at 10 s interval, 1 s sleep at 30 s interval, and 0.5 s sleep at 30 s interval. We then compared the Arduino's internal timestamp to a network time protocol-synchronized pc timestamp and found that the relative deviation from the target interval for each of the devices was below 0.1% (Fig. 4A).

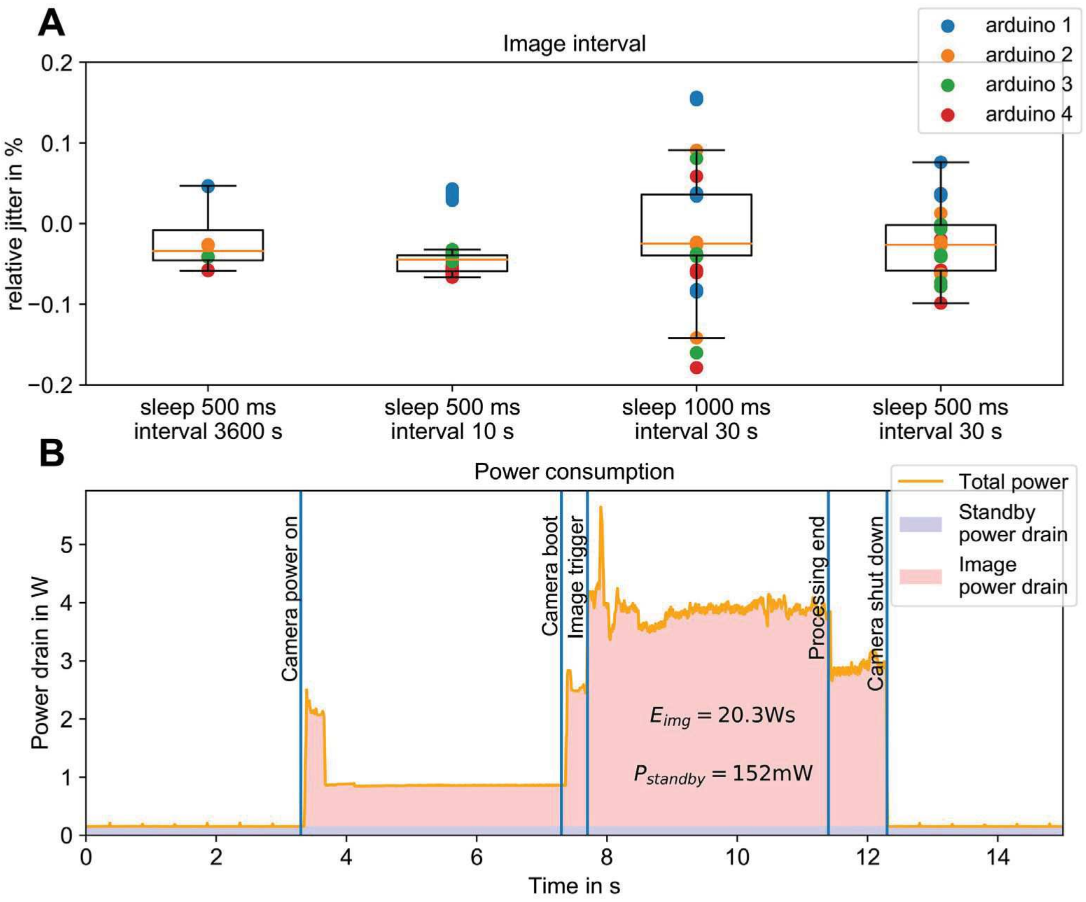

Fig. 4. Validation of time interval precision and power drain. (A) Deviation of the image interval relative to the target interval for different settings. Each point corresponds to an independent measurement, colors indicate the performance of different microcontrollers. The boxplot (median, 25 and 75 percentiles) shows the data pooled over all measurements from all microcontrollers for the same setting. Whiskers show the 1.5 interquartile range. (B) Power drain during image capture without GPS or other RS232 device. The pink area corresponds to the energy consumed for the capture of one image (20.3 Ws). The blue shaded area indicates the power consumption in standby mode (152 mW). Vertical lines indicate the phases of image capture initiated by the microcontroller. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

7.2. Field test

With five separate micrObs systems, we recorded time-lapse images of penguin colonies of three species (emperor penguins (*Aptenodytes forsteri*), Adélie penguins (*Pygoscelis adeliae*), and king penguins (*A. patagonicus*)) at three different locations: Pointe Géologie archipelago (Adélie Land, Antarctica), Kerguelen (Ratmanoff Cape), and Crozet (Baie du Marin on the Possession Island). During 6 years of operation, we recorded over 6 million images (see Table 6).

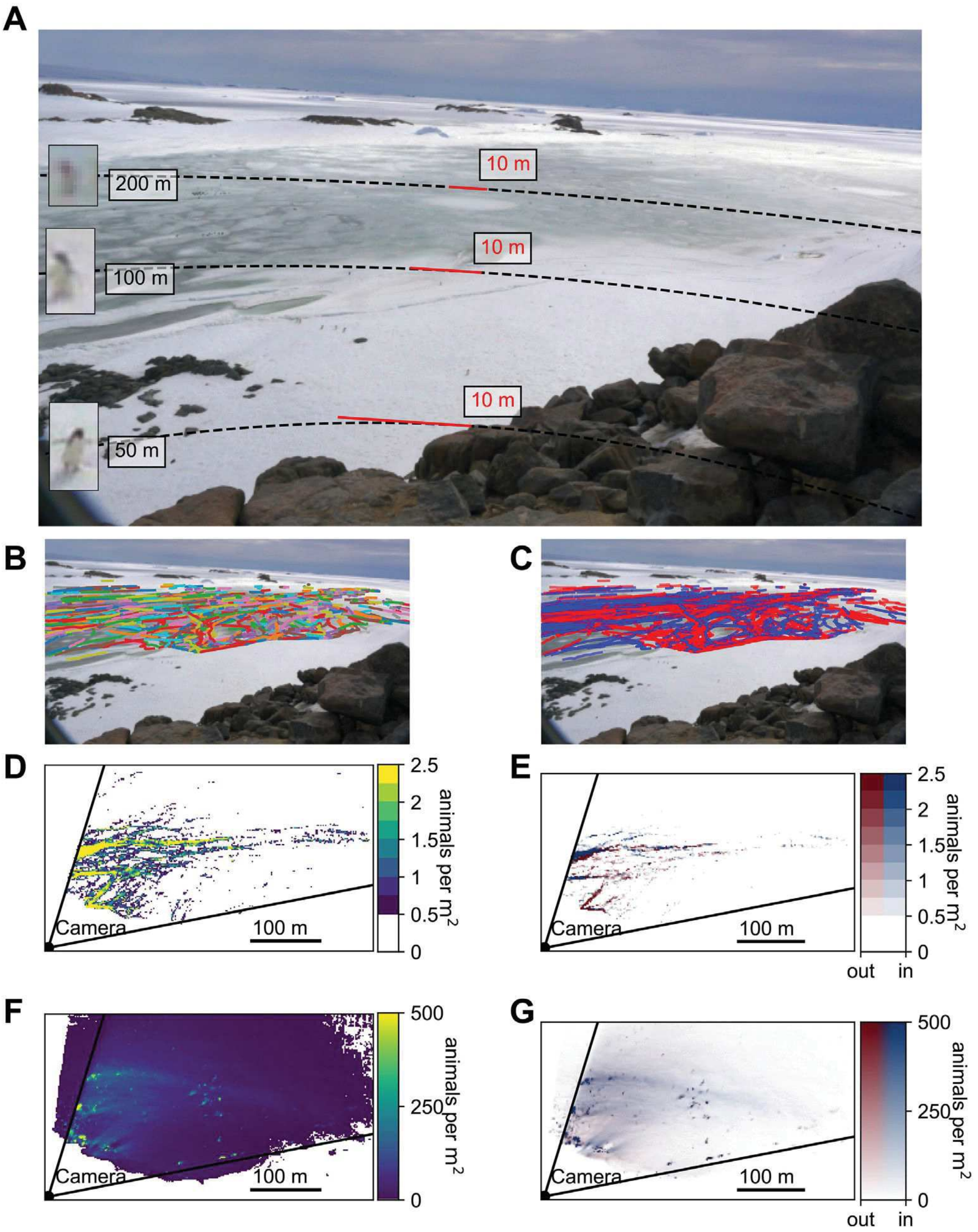

Fig. 5. (A) Image recorded with micrObs. The dashed curves show circles with distances of 50 m, 100 m, and 200 m around the camera. The solid red lines mark a line of 10 m length at the respective distances from the camera. Insets show examples of penguins at the respective distances. (B) and (C) are images recorded with micrObs overlaid with penguin tracks during a 17 min observation period. Each individual track in (B) is marked by a separate color. Colors in (C) indicate the track direction. Red tracks mark individuals leaving the colony to forage at the open sea (out), blue tracks mark individuals returning to the colony (in). (D) and (E) show *ortho*-projected maps, with colors indicating the cumulative animal density (number of detected animals per square meter integrated over a 17 min observation period). The solid lines mark the field-of-view of the camera. (D) shows the cumulative density of both outgoing and incoming animals, while (E) shows the cumulative density separately for outgoing (red) and incoming (blue) animals. (F) and (G) show the cumulative density over 21 days for outgoing and incoming animals together (F) or separately (G). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

7.2.1. Path finding in foraging Adélie penguins

During the austral summer, approximately 47,000 Adélie penguin pairs breed at Pointe Géologie close to the French Antarctic research station of Dumont d'Urville (Adélie Land, Antarctica) [25]. During breeding, adult penguins alternate between breeding and foraging, forming a continuous stream of thousands of penguins arriving and leaving their colony. Therefore, we persistently encounter trafficking individuals between the open sea and the breeding sites. We continuously observed an area of high traffic over 21 days. To achieve reliable tracking of animals (which are indistinguishable from each other), the distance between two individuals must not be greater than the distance one individual covers between two images. Therefore, the image interval of 2 s was selected to track the penguins, yielding 398,149 images in total.

Images were segmented into back- and foreground (penguins) using a ViBE filter [26]. Penguin positions were georeferenced using CameraTransform [27]. We tracked each of the detected objects with a Kalman filter [28]. We determined the cost for assigning new detections to tracks from the distance between the prediction made by the Kalman filter and the detection position. The assignment was done with the Hungarian method [29,30].

This object detection and tracking algorithm generated 7,413,146 detections of individuals, and 373,290 penguin tracks. Individual tracks of 1628 penguins during a 17 min recording period are shown in Fig. 5A. Penguin tracks separated into penguins arriving and leaving their colony site are shown in Fig. 5B.

We found that penguins use preferential pathways to commute over the sea ice on short time scales (Fig. 5C), creating "penguin roads". These penguin roads, however, were not stable over time but meander across the sea ice area during the 21 day recording period so that over time a substantial part of the sea ice area was utilized by the Adélie penguins (Fig. 5F). The high-density areas (yellow) in Fig. 5F represented points along the road where penguins frequently stopped and rested, resulting in a high area usage. We also found that animals leaving and returning to the colony prefered separate trails (Fig. 1D) to avoid collisions.

7.2.2. Ecological study on emperor penguins

micrObs was previously used in a published study that analyzed the behavioral response of emperor penguins to weather changes [7].

While breeding and fasting under the harsh conditions of the Antarctic winter, emperor penguins form tight groups to conserve energy [31]. This strategy, called huddling, is the key to their reproductive success. From micrObs time lapse recordings at 30 s time intervals, we measured the area covered by the animals to estimate the colony density. We then interpreted this density as an order parameter for studying colony phase transitions (from a dilute phase to a dense huddling phase) as function of an apparent temperature [7]. This apparent temperature is computed as a linear combination of four meteorological parameters (ambient temperature, wind speed, relative humidity, solar radiation) and serves as the thermodynamic variable in a phase transition model. The model predicts the colony's state depending on the environmental con-

Table 4
Short bill of materials.

Designator	Component	Number	Cost per unit - currency	Total cost - currency	Source of Material	Material type
Camera	Panasonic Lumix G5	1	99 €	99 €	mpb.com	other
Lens	Panasonic Lumix G Vario 14–42 mm Vario f/3.5–5.8 ASPH Mega OIS	1	64 €	64 €	mpb.com	other
housing	Pelicase 1150	1	42 €	42 €	pelishop.com	other
Battery	Lifeline GPL-U1T	1	170 €	170 €	akkuangebote.de	other
Charge Regulator	Steca Solsum 0606	1	20.99 €	20.99 €	conrad.de	other
Tripod	berlan BST285A	1	40 €	40 €	Bergland (ebay)	other
Photovoltaik Module	Offgridtec 30 W 12 V	1	44.90 €	44.90 €	amazon.de	other
GPS	Navilock NL-604P	1	65 €	65 €	amazon.com	other
Transport-Box	Zarges40877	1	140 €	140 €	zarges.com	other
DC-Adapter	Panasonic DWM-DCCG8	1	10 €	10 €	amazon.com	other
SD-Card Reader	SPIReader AZDelivery	1	2 €	2 €	amazon.com	other
MicroController	ArduinoNano	1	23 €	23 €	amazon.com	other
W4*	Walimex UV Filter 52 mm	1	5 €	5 €	amazon.com	other
C1, C2, C3, C4, C5, C6, C7, C8, W1, W2*	Acrylic glass 3 mm × 60 cm × 30 cm	1	6.58 €	6.58 €	Plattenzuschnitt24.de	acrylic
W3	chlorine free rubber 1 mm × 60 mm × 60 mm	1	18 €	18 €	amazon.com	rubber
MainPCB	MainPCB	1	30 €	30 €	multiCB	other
Frontpanel-PCB	Frontpanel-PCB	1	10 €	10 €	multiCB	other
Control Box	Electronic components	–	–	58.09 €	conrad/mouser	other
Control Box/Housing	Mechanical components	–	–	14.34 €	conrad	other
Mount	Mount components	–	–	48.12 €	hardware store	other
Transport Box Components	Mechanical and electrical components	–	–	52.93 €	hardware store	other
Sum				956.56 €		

* Part numbers such as W4, C2 etc refer to the parts shown in Fig. 4 in Supplementary File 2.

Table 5
Runtime and image memory usage for different recording intervals.

Image interval	# Images	Runtime (30Ah 12 V battery)	Camera memory usage
2 s	64 k	35 h	319 GB
5 s	64 k	88 h	319 GB
10 s	64 k	7 days	319 GB
30 s	56 k	19 days	277 GB
1 min	46 k	32 days	232 GB
5 min	20 k	69 days	100 GB
10 min	12 k	81 days	59 GB
30 min	4421	92 days	22 GB
1 h	2284	95 days	11 GB
6 h	391	97 days	2 GB
24 h	98	98 days	0.5 GB

Table 6
Operation statistics since 2013.

	Location	Species	# Images	Year
	Crozet	King penguin	126 k	2013
	Pointe Géologie	Emperor penguin	1,957 k	2014
	Kerguelen	King penguin	130 k	2014
	Pointe Géologie	Emperor penguin	968 k	2015
	Pointe Géologie	Adélie penguin	830 k	2015
	Pointe Géologie	Emperor penguin	519 k	2016
	Pointe Géologie	Adélie penguin	671 k	2016
	Crozet	King penguin	181 k	2016
	Pointe Géologie	Emperor penguin	402 k	2017
	Crozet	King penguin	269 k	2018
Total			6,053 k	6 years

ditions. For this study, we analyzed data from 8 days of recordings (2767 images) between 6th of May and 11th of May 2014 at DDU (see Table 4). The system operated in cold (average temperature −16.8 °C) and low illumination conditions (average solar radiation 1878 W/m^2). The 20 Ah battery was replaced every 3 days.

8. Future developments

While micrObs is well developed and has been used for several years in the field, we find a number of possible improvements: the image quality could be improved by replacing the Lumix G5 with another (probably more recent) mirrorless camera with electronic shutter. Cost and build time could be saved by replacing the hardware user interface with a wireless low-energy Bluetooth solution. Operators would apply the recording settings via a smartphone, tablet, or laptop on site. Unnecessary maintenance trips or data loss can be prevented by sending the observatory status (settings, battery voltage, number of images, last time image recorded) to a research station or satellite relays within a range of dozens of kilometers via a Long Range Wide Area Network (LoRaWAN) node. General processing capabilities could be added and power consumption could be reduced by replacing the Arduino Nano microcontroller with newer hardware such as the Arduino Nano 33, the pyboard v1.1., or Raspberry Pi Zero. We could enable software image stabilization and reduce effort in georeferencing objects in the image by adding position and motion sensors on the camera body, which track absolute and relative heading, tilt, and roll of the camera. A USB connection to the camera, capable of transferring recorded images to an external storage SSD via the controller, would further expand the recording time and ease of image time- and georeferencing.

CRediT authorship contribution statement

Alexander Winterl: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Sebastian Richter:** Conceptualization, Methodology, Validation, Writing - review & editing. **Aymeric Houstin:** Investigation, Writing - review & editing. **Anna P. Nesterova:** Investigation, Writing - review & editing. **Francesco Bonadonna:** Investigation, Writing - review & editing, Funding acquisition. **Werner Schneider:** Methodology, Validation. **Ben Fabry:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition. **CÕline Le Bohec:** Writing - review & editing, Supervision, Funding acquisition. **Daniel P. Zitterbart:** Conceptualization, Methodology, Software, Investigation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Human and animal rights

This study was approved by the French ethics committee (APAFIS#4897-2015110911016428 and APAFIS#9496-201707131540776) and the French Polar Environmental Committee of the Terres Australes et Antarctiques Françaises (TAAF project implementation and access permits #2012-117 & 2012-126, 2013-74 & 2013-82, 2014-116 & 2014-132, 2015-52 & 2015-105, 2016-76 & 2016-82, 2017-92 & 2017-102, 2018-116 & 2018-129, 2019-107 & 2019-115) and conducted in accordance with its guidelines.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ohx.2020.e00134.

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Annex C. Effects of individual characteristics and environmental conditions on foraging behavior of Adélie penguins (*Pygoscelis adeliae*)

Effects of individual characteristics and environmental conditions on foraging behaviour of Adélie penguins (*Pygoscelis adeliae*)

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Abstract

The general biology of the Adélie penguin (*Pygoscelis adeliae*), archetype of the penguin species, have been relatively well studied, however there is still a lack of knowledge regarding their foraging behaviours and how they vary (or not) with the fluctuations of the environmental conditions and individual characteristics, for instance. This study monitored more than hundred Adélie penguins during their breeding seasons 2017-18 and 2018-19 at Pétrels' Island, Pointe Géologie archipelago, Adélie Land (Antarctica). Adélie penguins of known-age and sex were equipped with storing-on-board data-loggers, including temperature-time-depth recorder (TDR) and Global Positioning System (GPS) devices, to have an insight into their diving behaviour. Various metrics of the foraging behaviour of the birds, such as diving depth, dive duration or trip length, were calculated, as well as their foraging efficiency (a proxy including information on wiggles and the bottom phase). Spatial distribution and foraging areas of the birds were also determined. Influence of breeding season and stage, sex and age-classes, and environmental conditions (sea ice and chlorophyll-a) on all the foraging variables was tested. We found that foraging efficiency differed mostly between breeding seasons and breeding stages. Older Adélie penguins showed a more 'targeted' foraging behaviour, with smaller foraging area and less travelling dives per trip than younger individuals. Breeding season and breeding stage are likely to influence foraging behaviour through variations in sea ice concentration, which was very different during both breeding seasons of the study. Our findings give a new multifactorial insight on a major component, the resource acquisition, of penguin ecology.

Key words: Adélie penguin, age, chlorophyll-a, foraging ecology, seabirds, sea ice, sex, Southern Ocean

Introduction

Polar ecosystems are fragile and sensitive because they host highly specialised organisms, which face particularly harsh and adverse conditions. Even small changes in the environmental conditions may have major impacts on the balance of the ecosystems (Smetacek and Nicol, 2005). Indeed, although marine ecosystems are well buffered thanks to the size of oceans and inertia of water, they are currently confronted with rapid changes that may have consequences on a large number of organisms (Smetacek and Nicol, 2005).

The Southern Ocean is composed of very rich and complex ecosystems (Llano, 1978; Smetacek and Nicol, 2005; Tynan, 1998); however, krill (mainly *Euphausia superba*), the basis and key component of the Antarctic food web (Adler et al., 2016; Atkinson et al., 2019, 2009; Llano, 1978), is temperature-sensitive and currently suffering from warming of the waters (Atkinson et al., 2009, 2019; Loeb et al., 1997; Nicol et al., 2000), leading to cascading effects on ecosystems as a whole. Living and feeding from oceans, high trophic level seabirds play a major role in the ecosystems, as meso/apex-predators consuming several hundred tons of prey per year (Ballerini et al., 2014; Southwell et al., 2017) and, among them, penguins constitute the dominant component of the avian biomass of the Southern Ocean (65 %), and 90 % of the total biomass of Antarctic (Llano, 1978). They are very specialised and particularly sensitive to changes in their environment (Ainley et al., 2010; Croxall et al., 2002; Forcada and Trathan, 2009; Le Bohec et al., 2008). The impacts of these changes can be both direct (e.g., local atmospheric effects) or indirect (e.g., changes in the dynamic of sea ice and/or of the food web) (Pershing et al., 2005).

Adélie penguins are sea ice obligate, except for their breeding sites, where they seek ice-free rookeries (Ainley, 2002). They are then mostly found on the pack ice, floating ice floes between which they have access to open water where they can dive and forage (Ainley, 2002). Penguins depend on relatively stable conditions, that determine food resources and the availability of breeding and moulting habitats (Forcada and Trathan, 2009). Variations of sea ice are, therefore, one of the greatest factors of influence on Antarctic (and some of the sub-Antarctic) penguin foraging behaviour (Croxall et al., 2002; Forcada and Trathan, 2009; Le Bohec et al., 2008; Wilson et al., 2001), including the timing of sea ice retreat, the presence of near-shore icebergs (Dugger et al., 2014; Lescroël et al., 2014) or polynyas (ice-free area within the ice cover), upwelling strength, and food availability (reviewed in Gao et al., 2019), as well as other environment variables such as the water temperature. Variations of sea ice also influence the food resource temporally and spatially: summer krill density correlates positively with sea ice extent (SIE) the previous winter, and it correlates with the chlorophyll-a concentrations (Chla) (Constable et al., 2014). Krill provides then a link between the physical environment, primary producers, and higher trophic levels in the Antarctic marine food web (Loeb et al., 1997). In Antarctic waters, Chlorophyll-a concentration is well correlated to the primary productivity and can explain up to 60 % of its variability (Dierssen et al., 2000; Nicol et al., 2000). The ocean primary production and the resulting marine biomass can therefore be assessed through the water Chla concentration (Ainley et al., 2005), varying seasonally and according to climatic factors.

All these variables are strongly related and influence the foraging behaviour of most marine organisms. Foraging for food is not an easy task: the ocean is wide, with unevenly distributed food (Shealer, 2001). During the breeding period, Adélie penguins have to cope with the environmental conditions to find enough food for their own body maintenance and for their chicks, and as central place foragers, they must return regularly to the colony to feed their chicks, limiting the available foraging area to the maximal distance they can go so that their chicks do not starve (Ainley, 2002, Nicol et al., 2008). Foraging success is usually determined by the net fat level of individuals (Kramer, 2001). However, as this measure might often be difficult to obtain, foraging efficiency (FE) is commonly used to determine the amount of energy gained by individuals during a foraging event (Le Guen et al., 2018; Lescroël et al., 2019; Weimerskirch et al., 2003; Zimmer et al., 2011).

The foraging efficiency implies maximising the energy input (food acquisition) and minimising the energy loss (food allocation and energetic expenditure, e.g., by swimming, Lescroël et al., (2019)). It is a major factor influencing the condition of an individual and the population dynamics, as it determines the amount of energy that can be invested in fitness-related activities, particularly breeding (Lescroël et al., 2019). It will hence strongly influence the survival and the resilience of the population. Age and sex are commonly argued to be major individual factors of change in feeding behaviour (Engen and Stenseth, 1989; Jaeger et al., 2014; Le Vaillant et al. 2012, 2013, 2016; Zimmer et al., 2011), reflecting differences in parental care (Beaulieu et al., 2009) or in experience; efficiency increasing in old individuals through learning (Wunderle, 1991) and may thus influence the foraging tactics of birds.

Older individuals might indeed have a greater experience, as they had time to learn where and how to find prey, on which environmental or social clues to rely; for example, the presence of other birds foraging in an area was used as clue by individuals to determine where food resources are more likely to be found (Shealer, 2001), or to dive deeper/longer, and to adapt their catching technique according to the type of prey (Grecian et al., 2018). They might also be more aware of the dangers of predation and of their own limits. In their breeding cycle, where mates regularly shift for the chicks' care and feeding at sea, the role and the importance of the sex is of primary interest, as both partners will go foraging at different periods, meaning different conditions at sea (Chappell et al., 1993a; Clarke et al., 1998). Both sexes also have different morphological and physiological capacities at different times of the breeding season (Ainley, 2002; Nicol et al., 2008). In the current trend of rapid environmental change, penguins might have to face new and rapid constrains and to adapt their behaviours.

It is often difficult to assess the exact food intake of such individuals, as they forage deep and far away from observation. Nevertheless, advances in technology permit us to equip birds with data-loggers, storing large amount of data while birds are travelling, such as depth, temperature, body position, localization, speed.

Moreover, the stable isotope analysis (SIA) technique has become more accessible in a wide range of topics, and in ecology, it is particularly interesting to assess the trophic level of individuals and the water masses where they feed, as it does not need high logistic and instrumentation and is relatively low time demanding (Jaeger et al., 2014). Indeed, as ingested nutrients become the molecular components of the tissues, differences in ingested food will be reflected in tissues like feathers and blood. The isotopic signature of Carbon and Nitrogen found in animal tissues might differ along a latitudinal and depth gradient and along the food chain (Cherel et al., 2007; Kokubun et al., 2015; Hobson, 1994). Thus, Carbon and Nitrogen isotopic ratios are commonly used as proxies to assess the foraging area and the place in the food web. By using this technique, we aim to determine if there is a preferential foraging area or isotopic niche, and to determine if birds may adapt their foraging area and/or diet according to environmental variations (e.g., sea ice variations). An isotopic niche can be defined as a bi-dimensional area including the localisation (assessed through $\delta^{13}C$) and the trophic level (assessed through $\delta^{15}N$).

The study of animal behaviour allows us to understand changes in the environmental conditions, as well as the individual conditions (e.g., diving capacity, breath-holding capability) affecting animal behaviour. These individual parameters are often related to factors such as age or experience, and sex. For example, Le Vaillant and colleagues, (2016) found that age affected foraging behaviour only during incubation stage, younger king penguins (*Aptenodytes patagonicus*) performing longer trips. Zimmer and colleagues, (2011) also found that intermediate-aged female little penguins (*Eudyptula minor*) were more efficient than younger and older ones during guard stage. Lescroël and colleagues, (2019) found that male Adélie penguins were more performant in foraging than females (i.e., they could capture more prey). They also found that age slightly affected foraging efficiency. However, literature is lacking regarding the comparison of foraging behaviour between old and young Adélie penguin breeders after hatching (Clarke et al., 2006, but see Lescroël et al., 2019), principally because it needs a long-term database allowing to know the age of individuals. In this study, we aim to explore this age-specific component of the foraging ecology in penguins.

The main objective of our study was to determine the effects of the environmental variability and of some individual characteristics on the foraging behaviour and efficiency displayed by Adélie penguins. We hypothesised that: i) foraging efficiency and food allocation to chicks, as described before, differ between individuals according to their age and/or their sex; ii) foraging efficiency is related to external/environmental factors (e.g., sea ice concentration and chlorophyll-a concentration); and iii) that birds may change/show a higher adaptability in their diet and/or foraging area according to their age and the environmental conditions. We respectively expect that: i) as older birds have more experience, they can be more efficient in foraging (Lescroël et al., 2019), and, given the difference of timing in the energetic needs of males and females along the breeding season, the foraging efficiency differs between sexes (Chappell et al., 1993a); ii) as krill populations correlate temporally with sea ice variations (Constable et al., 2014) and water temperature (Atkinson et al., 2019, 2009; Loeb et al., 1997; Nicol et al., 2000), food availability is temporally affected by changes is sea ice concentration; and as increasing chlorophyll-a reflects increasing primary productivity (Dierssen et al., 2000) and thus higher food resources, penguins foraging in areas of richer resource (Stephens and Krebs, 1986, cited in Evans et al., (2019)) reflect areas of high concentrations in Chla; iii) as older birds have more experience, they have the ability to adapt or change their foraging area and/or their diet to face changing environment conditions (e.g., they may go further to catch more qualitative food and adapt to changing spatial and temporal distribution of prey; Clarke et al., 1998).

Material and Methods

Permits and ethics statement

All animal handling procedures employed during the fieldwork were approved by the French ethics committee (APAFIS#4897-2015110911016428) and the French Polar Environmental Committee (TAAF permit #2017-92/102 & 2018-116/129) and conducted in accordance with its guidelines, also complying with French laws including those related to conservation and welfare.

Study species, study site, and instrumentation

The study was carried out at the Antavia Adélie penguin colony on Pétrels' Island, Pointe Géologie archipelago, Adélie Land, Antarctica (66°39'46"S; 140°00'07"E), close to the French Research Station "Dumont d'Urville" (DDU) (Figure 1).

Since 2006, chicks and adults from the colony are electronically marked with a Radio-Frequency Identification (RFID) PIT-tag (Passive Integrated Transponder with a unique identification number), and, since 2010, automatic identification and weighing systems have been installed to long-term monitor the electronically-marked individuals, to know and understand their movements, their fidelity, their breeding activities and their survival, and ultimately their population dynamics. In addition to producing a database containing all departures and arrival of each bird and their masses along all seasons, these systems allow us to work with birds of known-age and history. Thus, knowing the age of all birds marked as chicks, two age-classes were established: young individuals of 4 to 7 years old, and old individuals of > 10 years old. Birds were also sexed genetically (using blood samples). These birds of known-age and –sex were followed during two breeding stages (brooding and crèching) and for two breeding seasons (2017-2018 and 2018-2019, hereafter referred as 2018 and 2019, respectively).

Birds were externally equipped with storing-on-board data-loggers (model Axytrek from TechnoSmArt Europe S.r.l, 56x24x12 mm, 26 g in air, 600 mAh rechargeable battery) that included time-depth/temperature recorder (TDR) with a 0.1 °C and 5 mBar (~5 cm) accuracy, and Global Positioning System (GPS). Devices were positioned on the back of birds, on the lower back, just above the tail (in order to reduce drag), and maintained with Tesa®

tape. Birds were equipped twice when leaving the colony: first, during the brooding stage, when parents relay to go to feed at sea and keep the chick warm. During this stage, males and females shift every 2 to 4 days, bringing food to chicks. Second, during the crèching stage, when chicks can thermoregulate, and both parents are at sea so that chicks remain together in crèches. These *ca.* 15-days recording periods (average 13 days, ranging from 3.3 to 21 days) are referred hereafter as "breeding stage". Birds were recaptured and the device removed after several foraging trips, and data extracted from the data-loggers.

A total of 76 individuals were followed during the breeding season 2018 and 60 in 2019. However, usable data from only 60 individuals in 2018 and 56 in 2019 (116 birds in total) could be recovered, because of technical defects on some devices (some GPS or TDR devices misfunctioned, especially in 2018, or may have run out of battery), or because birds did not come back (Table 1). Over those 116 individuals, 13 have full data records for the two years of the study.

Foraging behaviour

Diving parameters

It is commonly admitted that penguins perform bimodal dives: short and shallow dives, without effective hunting activity, corresponding to travelling, and longer, deeper dives, with a proportionally longer deep duration during which occur effective hunting behaviour, corresponding to foraging dives (Bost et al., 1994; Kooyman et al., 1992; Ropert-Coudert et al., 2001; Weimerskirch, 1998; Williams et al., 1992) (see Appendix 1).

To define the depth discriminating between travelling and foraging dives, we used a log-survivorship analysis. For each year, the mean and variance among all trips of the breakpoint between the distribution of deep and shallow dives were very similar, with no effect of sex or age-class. Thus, the deep dive threshold was defined as the calculated average on all trips, namely 12.9 m for 2018 and 12.3 m for 2019. For further analysis, except mentioned, all dives shallower than this threshold were excluded.

Diving data were extracted from the TDR, and dive profiles were obtained using MT-Dive software (MultiTrace Dive Analysis, 2017.6.0.0, Jensen-Software). Some dive characteristics, like e.g., depth, speed, durations, were directly obtained through this software and the remainders were calculated with R software (3.5.3, R Development Core Team, 2019).

To correct for the drift of the pressure sensor, a zero-offset correction of depth time sequence was applied prior to the delimitation of dives (Luque and Fried, 2011), correcting depth by removing the difference between the maximum dive depth recorded from the logger and the maximum dive depth calculated by MT-Dive for each recording. Start and end of dives were considered from the last record at the surface, and dive duration as the time between dive start and end. Only dives deeper than one meter were considered, travelling dives being excluded. We defined foraging and travelling/non-foraging dives as following (based on Rodary et al., 2000): Foraging dives: any dive with bottom phase (see below) and wiggles *OR* depth > 12.9 m (2018) or 12.3 m (2019), threshold calculated as explained before *OR* duration > 60 s *OR* bottom phase, no wiggles and Rate Of Descent (ROD, see below) > 0.7 m/s ; Travelling dives: not foraging dives *AND* depth < 8 m *OR* duration < 60 s *OR* bottom phase, no wiggles and ROD < 0.7 m/s.

For each trip, we extracted the most relevant variables (see list in Table 2) and compared them between individuals according to breeding season (2018 or 2019), breeding stage (brooding or crèching), sex or age-class (as defined previously).

The bottom phase is defined as the flat part of the dive, approximately corresponding to the maximum depth, during which penguins are most likely to hunt (Rodary et al., 2000; Ropert-Coudert et al., 2007), and defined more precisely as the dive part when vertical speed is inferior to 0.25 to 0.20 m/s (resp. Carroll et al., 2014; Ropert-Coudert et al., 2007; Zimmer et al., 2008) and when the Rate Of Descent (ROD, which is the covered distance in a given amount of time) is less than 0.2 m/s (Rodary et al., 2000). The wiggles are short undulations occurring mostly during hunting, and were considered when the amplitude was superior to two meters.

A trip is composed of a succession of dives during a period, corresponding to food foraging/searching, called diving bouts. Ecologically speaking, a diving bout may be the sign of foraging in a given food patch i.e., at a given depth. Two diving bouts are separated by a period of resting on water surface or on ice floes, but may also be separated by a change in diving depth, meaning a change of prey patch (Mori et al., 2001). To separate a trip into bouts, we calculated the Bout Ending Criterion (BEC), using log-survivorship analysis according to Gentry et al. (1986). The survivorship analysis aims to assess an interval of time to expect before the happening of an event, in our case the maximum surfacing duration before the beginning of a new diving bout. The survivorship analysis is based on the analysis of the frequency of dive intervals, in order to assess the minimal duration between 2 diving bouts. The log-transformation allows to normalise the distribution. The obtained threshold, above-named BEC, was used in the MT-Dive to separate diving bouts. BECs too long or too short were optimised by visual inspection: trip dive profiles were visually checked, if some diving bouts were not well separated, or, at contrary, dives from the same diving bout were separated, BEC was manually adjusted. Most of the time, it appeared that BECs smaller than 500 s and greater than 1000 s were respectively too short and too long.

The foraging efficiency (FE) was assessed with the Attempting Catch Per Unit Effort (ACPUE; Le Guen et al., 2018), which corresponds to the number of wiggles (i.e., a proxy of the number of times the individual tried to catch food) divided by the bottom phase (i.e., a proxy of effective foraging duration), we could calculate the ACPUE either per trip, using the total number of wiggles and the total bottom duration, or the average of all dive-ACPUE.

Spatial parameters

Distances (maximum and total) were calculated after GPS records were linearly interpolated to the one second intervals in the *adehabitatLT* package in R (Calenge, 2006), and after applying a speed filter to the GPS data to remove erroneous locations (McConnell et al., 1992), with a maximal speed of 4.16 m/s. Duplicated and on-land locations were also removed.

During a trip, various factors can influence the behaviour of penguins, such as the sea ice conditions, the availability of food, the individual physiological or physical capacities. Penguins can change/adapt their response to changing environmental conditions in a very short time (Barreau et al., 2019; Rodary et al., 2000). Therefore, the trip time-scale we used is adequate to assess short-term behaviour changes and adaptability.

The bearing of each trip was determined for the first hour and at the furthest point of the trip (Whitehead et al., 2016) with the function *bearing* in the package *adehabitat* to determine if there was a preferential direction for the foraging trips among individuals.

Giving that one diving bout is considered to represent one patch of food, the repartition of the foraging behaviour along the trip was determined using diving bouts. Trip locations were firstly linearly interpolated, using the *redisltraj* function of the *adehabitat* package in R. Then, diving bouts were visualised along the trip.

Environmental parameters

Sea ice conditions

Sea ice conditions, assessed through Sea Ice Concentration (SIC), which is the fraction of ice covered by a minimum amount of sea ice (generally 15%), expressed in percentage, were locally determined in front of Pointe Géologie archipelago in the D'Urville Sea, through the mean monthly sea ice concentration data from IFREMER (*Institut Français de Recherche pour l'Exploration de la Mer*) database, available from 1991 to nowadays on the website: ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/antarctic/daily/netcdf/. The data are presented with a 12.5 x 12.5 km resolution. The mean monthly SIC was calculated in the vicinity of the study area, on a 435 km-radius area that is, a radius including all penguin trips recorded, up to the farthest North, East and West, using the software QGIS (QGIS® 3.4.4).

For each trip, an area of 10 km around the trajectory followed by each bird (obtained from a linear interpolation of the GPS points) was delimited using QGIS and the mean sea ice concentration of this area was calculated using the zonal statistic function on QGIS. This 10-km area was divided in a first 5-km buffer zone, 5 km each side of the interpolated trajectory, and in a 10-km buffer zone, from 5 to 10 km each side of the trajectory (Figure 2). A ponderation was applied to calculate the mean sea ice: values from the 5-km zone counted two times more than values between 5 and 10 km, i.e., a ponderation of 1 was applied for the first area and 0.5 for the second area. The total SIC per trip was the mean of these values. This method is not referenced in the literature, but sea ice conditions may vary very quickly, and penguins can respond and adapt their behaviour quickly to these changes (Barreau et al., 2019; Rodary et al., 2000). We have therefore the nearly instant sea ice conditions all along the trip, and on a rather narrow area that may include the changes of positions of the bird underwater. Indeed, GPS locations are only available when birds are at the surface, and the simple speed-based linear interpolation does not take into account the exact movement of the individual.

Chlorophyll-a and marine primary production

Chlorophyll-a (Chla) concentration was estimated around the study area during the study period using monthly satellite imagery from MODIS-AQUA Level-3 Standard Mapped Images of Chla concentration from the NASA Goddard Space Flight Center from the "Ocean Color" Program, directed by the National Aeronautics and Space Administration (NASA) (https://oceancolor.gsfc.nasa.gov/), representing the Chla concentration from coloration of the water surface.

Mean Chla concentration was extracted with R for the area in the D'Urville Sea (ranging from 135 to 145W, and 66N) for 8-days periods with a 4-km spatial resolution. For each trip of each bird, the mean Chla concentration value corresponding to the time of the trip was considered, following the same buffer zone method as for calculating the mean sea ice concentration.

As the primary production is strongly correlated with the Chla concentration (Dierssen et al., 2000; Smith et al., 2001), the krill biomass is expected to follow in a short time-scale, thus a lag of 2 weeks was applied, corresponding approximately to the time between the recorded Chla and the primary production bloom (Ross et al., 2000).

Diet determination

Stable Isotope Analysis

The isotopic ratios of Carbon ($^{13}C/^{12}C$) and Nitrogen ($^{15}N/^{14}N$) are widely used in ecological and diet studies, Carbon isotopic ratio giving a spatial approximation of the water masses where animals feed, and Nitrogen isotopic ratio being related to the trophic level (Cherel et al., 2007).

The C:N ratio permitted to check the delipidation of samples: C:N ratio should not be greater than 3.8. Samples whose C:N ratio was greater than 3.8 were delipidated once more, if possible (Cherel et al, 2006).

Even if the signature of each feather was expected to be relatively homogeneous, a pool of three feathers powdered together was used for each bird, to reduce a potential inter-feather variability (see Appendix 2 for detailed protocol).

Bulk Isotopic Analysis of feathers and plasma

Stable Carbon and Nitrogen isotope analysis was performed in the Oceanographic Laboratory of Villefranche (06). Samples are combusted at 920°C in an elemental analyser (Elementar Vario Pyrocube), and resultant gases were analysed using a continuous-flow isotope ratio mass spectrometer (CF-IRMS) (Isoprime 100), using isotopically certified standard Caffeine IAEA-600 and laboratory standard for bracketing (Acetanilide, Merck, CAS 103-84-4) to check for temporal deviance.

Results are expressed in ‰ (per mil) as the deviation from standards, according to equation 1:

$$\delta X = \left[\left(R_{spl} \,/\, R_{std}\right) - 1\right] \times 1.000 \qquad (1)$$

where X is the studied element (C or N in our case), and R the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard (std) is a reference gas (CO_2 or N_2) calibrated with Caffeine IAEA-600, according to the PeeDee Belemnite (PDB) for Carbon, and atmospheric N_2 for Nitrogen.

A single point correction was performed using the measured value for certified standard, according to equation 2, following Paul and colleagues, (2007):

$$\delta_{spl}^{T} = \left[\frac{(\delta_{spl}^{M}+1000)(\delta_{std}^{T}+1000)}{(\delta_{std}^{M}+1000)}\right] - 1000 \qquad (2)$$

where δ_{spl}^{T} is the calculated isotopic ratio of the sample, δ_{spl}^{M}, the mean isotopic ratio of all samples, $\delta_{std}^{T}$the calculated isotopic ratio of standard and δ_{std}^{M}, the mean isotopic ratio of standards.

$\delta^{13}C$ results were plotted against $\delta^{15}N$ for feather and plasma samples to determine eventual trends in repartition between groups of age or sexes. For plasma samples, $\delta^{13}C$ and $\delta^{15}N$ values were plotted per individual to see the variation between breeding stages and seasons.

Isotopic niche determination

The isotopic niche of individuals was estimated using the *SIBER* package in R (Stable Isotope Bayesian Ellipse in R, Jackson et al., 2011): using a Bayesian recursion with 4,000 iterations, the area of the isotopic niches was calculated with the measured $\delta^{13}C$ and $\delta^{15}N$ values, in order to statistically compare the given niches width of bird groups. This permitted to determine if individuals had the same isotopic niche between breeding seasons and/or breeding stages, or if they could change it, and if birds of different age-classes and/or sexes had different isotopic niches as well, and compare isotopic niches with the previously calculated MCP foraging range areas. Areas were compared with ANOVA and post-hoc Tukey test, between sexes and age-classes, both years pooled in a first time, and year by year in a second time.

Statistical analyses

A multiple analysis of variance (MANOVA) was used to test for differences between breeding seasons, breeding stages, sexes and age-classes, after controlling for the assumptions of normality and homoscedasticity (Shapiro and Fisher t-tests, respectively). For non-normal distributions, comparison of distributions was carried out with a Kolmogorov-Smirnov test.

Throughout this study, statistical significance of results was set at p-values < 0.05.

Most of those parameters were calculated using R, except some brut variables extracted directly from MT-Dive.

Foraging efficiency analysis

The foraging efficiency (FE) is a complex notion, and it had to be approximate with a proxy, like the Catch Per Unit Effort (CPUE) or the Attempting Catch Per Unit Effort (ACPUE) (Le Guen et al., 2018). ACPUE was calculated as the total number of wiggles per trip divided by the total trip bottom duration.

Influence of diving parameters on foraging efficiency (FE) was analysed using a Generalised Linear Model (GLM) run with ACPUE as response variable. Explanatory variables were defined as following: proportion of foraging dives in a trip (forage_prop), mean dive duration (hereafter mean_dive_dur), number of diving bouts (nb_bouts) and of dives (nb_dives) during a trip, total bottom phase duration that is the sum of all durations of bottom phase in a trip (tot_bot_dur), maximum distance to the colony (max_dist), mean Chla along the trip (mean_Chla), mean and maximum SIC along the trip (mean_SIC and max_SIC), as described before. As a lot of these explanatory variables were correlated, a Principal Component Analysis (PCA) was first performed, after imputing missing values with the imputePCA from the missMDA package in R (Josse and Husson, 2016), to obtain two new non-correlated variables (PCA1 and PCA2) corresponding to linear combinations of explanatory variables, using the PCA function from FactoMineR package in R. Individuals were computed as a random effect, enabling to account for repeated measures, as birds were tracked over multiple trips. Breeding season, breeding stage, sex and age-class were set as fixed factors. The most appropriate model was automatically selected after running a descending stepwise selection, using the function *step* in R, that removed one by one unnecessary variables until obtaining the lowest Akaike Information Criterion (AIC), which is a way to choose between different models by penalizing models that have a lot of variables, according to the principle of parsimony.

Results

Diving and foraging analyses

In 2018, dive depth ranged from 1 to 141 m (average 18.3 m), with duration ranging from 2 to 220 s (average 59 s); and in 2019, dive depth ranged from 1 to 132 m (average 18.2 m), with duration ranging from 2 to 221 s (average 60 s). Trip total distance ranged from 2 km to 2,668 km (average 210.4 km). Altogether, foraging dives during a trip represented 48.5 % of the total dives. In 2018, birds performed 41.3 % of foraging dives *versus* 40.9 % in 2019, the difference was significant (ANOVA, $F = 4.67$, $p = 0.03$). Older birds tended to perform more foraging dives than younger birds: in average 51.4 % of foraging dives compared to 48.1 % for the latter, however, the difference was not significant (ANOVA, $F = 2.63$, $p = 0.10$). The difference was particularly significant between breeding seasons, as birds performed in average 46.7 % of foraging dives during the brooding period *versus* 38.6 % during crèching period (ANOVA, $F = 33.28$, $p < 0.001$). The foraging behaviour assessed through the proportion of foraging dives in a trip and the ratio of foraging/travelling dives (f/t ratio) was significantly different between breeding seasons, breeding stages and age-classes, with more foraging dives performed in 2018 than 2019 in a trip, and, during brooding than during crèching and age classes (See Appendix 3). Sex appeared to have no effect.

Foraging trips occurred over a maximum distance of 275 km away from the colony in 2018 and 196 km in 2019, with a mean total trip distance of 166 ± 114 km in 2018 (n = 133) and 128 ± 87 km in 2019 (n = 179) (Table 3, Figure 3). Foraging trips last in average 2.41 ± 1.74 days in 2018 and 1.57 ± 1.19 in 2019. Trip duration was significantly different between breeding seasons (ANOVA, $F = 27.77$, $p < 0.001$) with longer trips in 2018 than 2019, breeding stages (ANOVA, $F = 11.83$, $p < 0.001$), with longer trips during crèching than during brooding, and between males and females (ANOVA, $F = 15.46$, $p < 0.001$), females performing longer trips than males. Maximum distance – i.e. maximum distance away from the colony was significantly greater in 2018 than 2019 (ANOVA, $F = 27.94$, $p < 0.001$) and significantly greater during crèching than during brooding (ANOVA, $F = 79.68$, $p < 0.001$), as well as total distance traveled (ANOVA, $F = 12.82$, $p < 0.001$) between breeding seasons and (ANOVA, $F = 36.08$, $p < 0.001$) between breeding stages. Neither sex nor age seem to have an influence on the distance traveled (Table 4).

Globally, the analysis of variances performed on diving parameters showed that breeding season and breeding stage were the most important factors of variation for 8 of the 14 studied variables (trip duration, number of dives and number of diving bouts per trip, ratio foraging/travelling dives, proportion of foraging dives in a trip, total dive duration, total bottom duration and ACPUE per trip). Sex appeared to be a significant factor of variation for trip duration, number of dives and number of diving bouts per trip, and total bottom duration, females tended to perform longer trips ($p < 0.001$). Females performed more diving bouts and more dives ($p < 0.001$ and 0.007, respectively) cumulating a longer total bottom duration per trip ($p < 0.001$). Maximum depth was principally influenced by individual characteristics: age-class ($p < 0.001$ and 0.008), and sex ($p = 0.003$), while bottom depth only by age-class ($p < 0.001$). Age influenced also the mean dive duration and the proportion of foraging dives, as well as the ratio foraging/travelling (f/t ratio): older individuals performed more foraging dives than younger ones (proportion of foraging dives: $p < 0.001$; f/t ratio: $p = 0.007$), and especially during the brooding stage. Older individuals tended also to dive in average longer, i.e., they spent less time surfacing ($p < 0.001$). Maximum distance only slightly differed between breeding stages ($p = 0.006$) when both breeding season were pooled. However, in 2018, maximum distance was significantly higher during crèching period than during brooding one ($p < 0.001$). In 2018 and 2019, diving parameters were differently impacted by environmental individual characteristics variables, however breeding stage stayed mostly the primary factor of variation (Table 4).

Finally, we found that the great majority of trips performed by the birds had a North-Western bearing (85.4 %). The ones that did not start in this direction (25.7 %) departed in the North-East or North direction, however 11.9 % turned in the North-West direction afterwards, so that only 8.2 % of trips were North-East from the colony. Regarding the repartition of the foraging bouts, birds foraged mostly during the two first thirds of the trip, with diving bouts concentrated at the furthest part of the trip (Figure 5).

Environmental parameter analyses

Sea ice conditions

There was significantly more sea ice in 2018 than 2019 throughout the breeding season (Kolmogorov-Smirnov test), except in October (Table 5, Figure 4). There was a significant difference in mean SIC per trip between breeding seasons (ANOVA, $F = 114.91$, $p < 0.001$) and between breeding stages (ANOVA, $F = 19.14$, $p < 0.001$). There was also a significant difference in mean SIC in 2018 between breeding stages (ANOVA, $F = 25.06$, $p < 0.01$) and between sexes (ANOVA, $F = 11.33$, $p < 0.001$). In 2019, there was no significant difference in mean SIC during trip of individuals, neither between breeding stages, nor age-classes nor sexes.

Chlorophyll-a concentration

Chlorophyll-a concentration (Chla) per trip was not significantly different between age-classes nor sexes; however, highly significant difference was observed between breeding stages (ANOVA, $F = 154.66$, $p < 0.001$), Chla being higher during crèching stage (0.254 ± 0.194 mg.m^{-3}) than during brooding (0.073 ± 0.100 mg.m^{-3}).

Diet determination

Stable Isotope Analysis

The Carbon isotopic ratios ($\delta^{13}C$) from feathers ranged from -21.59 to -25.82 ‰ in 2018, and from - 22.02 to -25.47 ‰ in 2019. The Nitrogen isotopic ratios ($\delta^{15}N$) from feathers ranged from 8.28 to 9.93 ‰ in 2018 and from 8.26 to 10.08 ‰ in 2019. The $\delta^{13}C$ values from plasma ranged from -23.24 to -25.69 ‰ in 2018, and from - 21.37 to -25.37 ‰ in 2019. The $\delta^{15}N$ values ranged from 7.60 to 12.26 ‰ in 2018, and from 8.46 to 14.36 ‰ in 2019.

There were no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values of feathers between breeding seasons, nor sexes or age-classes. There was no significant difference in plasma $\delta^{13}C$ values between breeding seasons, nor breeding stages, sexes and age-classes. $\delta^{15}N$ values tended to differ between breeding stages (ANOVA, $F = 21.74$, $p < 0.001$). Values showed a broader range in Carbon in 2019 than 2018, though non-significant. Younger individuals tended to have a higher variability in Carbon than older individuals, particularly for males in 2018 (Figure 6).

Globally, and especially in 2019, there was a positive trend between $\delta^{13}C$ and $\delta^{15}N$ values, individuals with less negative $\delta^{13}C$ having higher $\delta^{15}N$ values.

Estimations of isotopic niche areas after Bayesian recursion showed that during post-breeding period (feather analysis), when both breeding seasons were pooled, isotopic niches (two-dimensional approximation of the ecologic niche, were dimensions are formed by $\delta^{13}C$ and $\delta^{15}N$) were significantly different between all groups sex-age, but with great overlapping, with old males having the smallest niche, and young females the greatest one (Appendix 4). In 2018, young females tended to have a smaller isotopic niche than the other groups, and in 2019, the isotopic niche was significantly different for all groups sex-age but old males and old females. During the breeding period (plasma analysis), there were significant difference between all sex-age groups but females, as old and young females had a similar isotopic niche. In 2018, all groups had a similar isotopic niche except young males that had the smallest one. In 2019, all sex-age groups had distinct isotopic niches but old and young females (Figure 7 and Appendix 4).

A slight positive correlation could be observed between δ13C and δ15N values (black line on the Figure 7). This relationship was particularly strong on plasma values in breeding season 2019 ($R^2 = 0.73$), and very low in other cases: < 0.2 for feathers values both in breeding season 2018 and 2019, and < 0.1 for plasma values in breeding season 2019.

Foraging efficiency analysis

The two first axes of the Principal Component Analysis explained 69 % of the variance. The first axis was principally composed by trip variables (number of diving bouts and of dives, total diving duration, total bottom duration and trip duration), contributing at 81 % to the axis; proportion of foraging dives and ratio foraging/travelling dives contributed most to the second axis (24 and 22 %, respectively) plus mean dive duration, contributing at 23 %. The third axis was the spatial axis, represented mostly by total travelled distance and total distance from colony (88 %). However, this axis explained only 10.5 % of the variance, it was then not retained.

The Generalised Linear Model (GLM) gives evidence for a strong positive effect of breeding season on foraging efficiency (FE), assessed through ACPUE per trip ($t = 10.308$, $p < 0.001$). Sea ice concentration (SIC) had significant positive effect on FE, as well as on diving parameters of the PCA2-axis, that corresponds mostly to foraging/travelling structure of the trip ($t = 4.749$ and 18.570, respectively, $p < 0.001$), while diving parameters of the PCA1-axis had a significant negative effect on FE ($t = -7.584$, $p < 0.001$). Male gender and breeding stage had a lower significant negative effect on FE ($t = -3.249$ $p = 0.001$ and -2.599, 0.010, respectively). In both breeding seasons, the same factors were retained in the best model, although they not affected FE in the same way. In 2018, diving parameters (PCA2 and PCA1-axes) had respectively a significant positive and negative effect on FE ($t = 12.541$ and -7.711, respectively, $p < 0.001$), while male gender and breeding stage had only a slight effect ($t = - 2.90$ and -2.14, $p = 0.004$ and 0.034). In 2019, diving parameters of the PCA2-axis had the greatest positive effect, with breeding stage ($t = 12.911$ and 5.122, resp., $p < 0.001$), while diving parameters from PCA1-axis and young age-class had a negative effect ($t = -3.737$ and -3.427, respectively, $p < 0.001$) (see Appendix 5).

Discussion

Effect of environmental variables on Adélie penguin foraging efficiency

Our study showed that the sea ice concentration (SIC) was a major factor influencing foraging behaviour of Adélie penguins on the breeding-season- and breeding-stage-scales, due to its annual cycle, while the chlorophyll-a concentration (Chla), due to its seasonal cycle, mostly influenced foraging behaviour on the breeding-stage-scale.

Sea Ice Concentration

Sea Ice Concentration (SIC) in the D'Urville Sea, in front of Pointe Géologie Archipelago greatly differed between the two breeding seasons of the study, except in October. As season progressed, the natural variations/cycle of sea ice showed a decrease of SIC, being at its minima during the crèching period of the Adélie penguin breeding cycle. The inter-annual variability of SIC is likely to have an impact on their foraging behaviour, as it has already been shown, for example, by Yoda and Ropert-Coudert (2007).

Between our two study breeding seasons, we found that longer and further trips occurred in 2018, when sea ice was more extensive. Indeed, because of extensive sea ice, penguins have to travel further by sliding or walking on ice to find open water. Moreover, during years of extensive sea ice, as Adélie penguins have to travel on fast ice before reaching open water, they will then perform less foraging dives than in years of lower SIC (Watanuki et al., 1993). Lescroël and colleagues (2014) found that high SIC reduced the flexibility and constrained the foraging behaviour of Adélie penguins in the Ross Sea, with a quadratic effect on the foraging efficiency (FE, being maximal around 6 to 12 % of SIC), while Le Guen and colleagues (2018) found that breeding success, related to FE, was maximal around 20 % of SIC in Dumont d'Urville, which corroborates our findings. Their SIC values were yet calculated at the colony scale and averaged within an area comprising the maximum distance trips of breeding Adélie penguins from Dumont d'Urville colony, while our SIC values reflected the nearly-instant conditions at spatial and temporal penguins' trip-scale. Our values are then likely to be more variable but also more precise. Watanabe and colleague (2020) also found that an ice-free environment was favourable to the chick body condition and growth of Adélie penguins in East-Antarctica through better availability of open water, less commuting time (i.e., more hunting time), and higher krill density, which corroborates our findings.

Our results are coherent with those of Fraser and Hofmann (2003), who found that Adélie penguins breeding close to Palmer station, West Antarctica, performed shorter trips when sea ice was lower. They explained it by the fact that prey availability was positively related to pluri-annual sea ice cycles, showing low krill recruitment during years of low sea ice concentration.

Our results showed that mean SIC per trip strongly differed between breeding seasons and breeding stages, and the mean SIC during trips had a significant effect on the FE of our penguins when both breeding seasons were pooled. Interestingly, when analysed separately, we did not find a significant effect of SIC on FE within a breeding season, while we observed a significant effect of the FE between breeding seasons. These results confirmed that inter-annual variability in sea ice conditions is a major factor of influence of the FE, and that penguins may conduct different foraging tactics between breeding seasons. Moreover, this result might also highlight the fact that a tactic is set at the beginning of the breeding season and does not differ as season progresses.

Chlorophyll-a concentration

During our study, we observed the higher values of Chlorophyll-a concentration (Chla) during the crèching period. These Chla peaks are explained by the natural cycle of phytoplankton that blooms in spring, when sea ice decreases and light become more available (Dierssen et al., 2000; Smith et al., 2001). Chla is strongly related to oceanic primary productivity, and affects the food resource availability for meso- and upper predators (Atkinson et al., 2019; Dierssen et al., 2000; Loeb et al., 1997). Therefore, Chla is likely to seasonally influence the availability of prey, and indirectly the feeding status performance of the individuals. Indeed, Pütz and colleagues (2014) found for example that juvenile king penguins foraged preferentially in high Chla areas of the open waters of the Southern Ocean. We found as well that the trip distances were positively correlated with Chla, supposing that penguins target high productivity areas to forage. Chla is also of great importance in foraging habitat selection for King penguins (Le Bohec et al. 2008, Pistorius et al., 2017). Here, we did not find any significant effect of Chla on FE of our study Adélie penguins. We suggest that SIC, especially during years of high extent, might either blur the estimation of Chla and/or make this proxy of food resources availability not usable for the Adélie penguin, so that they have to rely on other clues such as social facilitation for example, directing towards places where other penguins are visible, indicating that food is available there (Shealer, 2001).

Chla is an important environmental factor (Ainley et al., 2005), and even if Adélie penguins do not use it as clue in their foraging behaviour, it might indirectly (i.e., through prey availability and abundance) affect other aspects of their biology. Agnew et al., (2015) found for example that Chla positively influenced the survival and the breeding success of breeding little penguins (*Eudyptula minor*) through higher prey abundance.

Lack of precise knowledge in krill biology and ecology in D'Urville Sea and its complex relationship with Adélie penguins may have made the two-weeks temporal lag used to determine Chla along trip of birds uncertain. It would therefore be interesting to investigate prey distribution related to Chla, and deeper research could be performed to determine the availability of food resources for Adélie penguins according to Chla.

Other environmental factors

We expected that Adélie penguins travelled all in the same direction in order to use the currents to come back faster after foraging. The repartition of foraging activities along the trip confirmed this hypothesis, as penguins mostly foraged at the beginning of the trip and came back straight to the colony. This behavioural pattern might also be a way to avoid competition with other colonies westwards from Pétrels' Island. Thiebot et al. (2019) also found that most Adélie penguins from Pétrels' Island travelled westwards during all their annual cycle. It has been proposed by Pütz et al. (2014) and Pistorius et al. (2017) for king penguins travelling against the current from their colony, that they target precise areas of very high productivity, and that the use of current flows would increase the rate of passage to prey resource and decrease the energetic demand.

Effect of individual characteristics on Adélie penguin foraging efficiency

Sex

In both breeding seasons, we found that sex had only a limited effect on FE of Adélie penguins. While our results showed that sex had no general effect on FE during the brooding nor during the crèching periods, they nevertheless highlighted its effects on various diving parameters, such as trip duration, number of diving bouts and of dives, allowing a longer effective hunting/foraging duration. Moreover, females of our study birds tended to perform longer trips, although a larger sample size may be needed to confirm this trend. This sexual segregation was yet found by Clarke and colleagues (1998) and Chappell and colleagues (1993a), and linked to the difference in energetic requirements between males and females Adélie penguins along the breeding season. Indeed, female have higher energetic needs just after egg laying, and tend to put more reproductive effort in chick rearing, while males who fast longer tend to put more energy during the crèching period (Chappell et al., 1993a).

Our results have shown that even if females perform longer trips with more diving bouts and more foraging dives, they did not have a significantly higher foraging efficiency than males. These different patterns of foraging behaviour between males and females might then be a way to limit or avoid intraspecific and particularly inter-sexes competition (Beaulieu et al., 2009).

The latter also found that females adapt their foraging behaviour according to the sex of their offspring and that they tended to catch different kind of prey, travelling further northwards and catching more fish (*Pleurogramma antarcticum*) when they reared female chicks.

Age

Our results revealed that age had an effect on the FE of Adélie penguins. Yet, this age effect was only detectable in breeding season 2019, and we found no effect of age on FE between breeding stages.

Moreover, our study showed that age had an effect on various diving parameters, such as depth or proportion of foraging dives *versus* travelling dives. Older individuals performed more foraging dives and dove in average deeper and longer, compared to younger Adélie penguins. This finding highlights that old individuals may have higher physiological conditions and also more experience, i.e., they may better know how and where to find/catch prey, better know their environment than less-experienced individuals, as they loss less time surfacing. Moreover, given the conditions of extensive sea ice in 2018 resulting in restrained foraging area and potential scarcer access to food resource, we expect higher competition during this breeding season. The condition of older birds give them better chance to catch food before younger individuals, resulting in higher foraging efficiency.

Jaeger and colleagues (2014) highlighted a strong effect of age on male Wandering Albatrosses (*Diomeda exulans*), that progressively shift their foraging area to the colder Sub-antarctic waters and explained this sexual- and age-segregation by potential competitive exclusion. However, they did not know precisely the age of the individuals and only had bimodal age-classes, while Zimmer and colleagues (2011) studied the foraging behaviour on little penguins with three age-classes. They could show by this method that middle-aged little penguins were the most efficient amongst the three age-classes. They explained this result as a trade-off between gain of experience as individuals grow, and senescence, with decreasing body condition. In our study, the old age-class comprises old as well as middle-aged individuals, and this trade-off could not be demonstrated. However, when conditions are favourable, effect of senescence seems to be neglectable in our study birds as they still had a higher foraging efficiency than young, less-experienced individuals.

Foraging behaviour

Diet and isotopic niches

The Carbon isotopic ratios ($\delta^{13}C$) in feathers and plasma of our study birds did not significantly differ between breeding seasons nor breeding stages, while the Nitrogen isotopic ratios ($\delta^{15}N$) tended to be slightly greater in plasma (breeding period/summer) compared to feathers (post-breeding period/fall); although a larger sample size may be needed to confirm this result. Moreover, we found that $\delta^{15}N$ in plasma had a greater variability than in feathers. This suggests that diet during breeding season might be more diversified at least at the population scale, than during the post-breeding season. Since Adélie penguins are visual predators and need sufficient light to forage efficiently (Ballard et al., 2010), we suggest that during breeding period, Adélie penguins might forage deeper within the water column, benefiting from higher diversity of prey thanks to the higher level of light of the summer months.

Interestingly, our results also revealed that Adélie penguins with high $\delta^{13}C$ values tended to have higher $\delta^{15}N$ values. These findings suggest that diet of the individuals that travelled further northward had a slightly higher proportion of fish in their diet than individuals foraging closer to the colony, as fish have a higher trophic-level than krill (Hobson and Welch, 1993). However, Clarke and colleagues (1998) showed that female Adélie penguins from different colonies which travel further from the colony, as mentioned earlier, consumed more krill than males that performed foraging trips closer to the colony, but consumed more fish than females. As sea ice and related krill stocks follow a pluri-annual cycle, the difference may come in the proportion of krill and fish available during the two years of our study, that may be different from the one obtained during the previous cited study.

Higher δ^{15}N values may reflect a greater proportion of fish in the diet (Hobson and Welch, 1993) or could also be due to an onshore to offshore gradient in δ^{15}N values of krill. Indeed, krill feed on different types of resources according to their habitat, off-shelf krill occasionally feeding on higher trophic level prey than off-shelf krill; (Kokubun et al., 2015). Consequently, Adélie penguins foraging further offshore may present a slightly different signature in δ^{15}N as well as δ^{13}C than penguins foraging near the ice shelf. Our results tend to support this explanation, particularly in 2019, where individuals with lower δ^{13}C (foraging in northern latitudes) having lower δ^{15}N than individuals with higher δ^{13}C.

The differences between δ^{13}C and δ^{15}N values were not significant, whatever the group of sex or age, nor between breeding seasons, and this high homogeneity of isotopic values refute the hypothesis of inter-individual specialization of diet but not of foraging area.

We found that younger Adélie penguins tended to have a larger and broader isotopic niche, especially on δ13C. Younger individuals may dive further northwards to avoid direct competition with older birds, or because older birds get access to the most productive areas prior to younger ones, regarding their higher foraging efficiency and greater experience, as explained above. This segregation has been shown in female Adélie penguins, which performed longer and further trips, although this partitioning was coupled with difference in diet (Clarke et al., 1998). A study in king penguins showed that a vertical segregation, with old females performing shorter and deeper trips than males and young individuals of both sexes (Le Vaillant et al., 2013).

We also found that isotopic niches tended to be slightly smaller during breeding season 2018, though not significantly different from 2019. This result might reflect the lower diversity of prey caught by Adélie penguins when their foraging area was restrained.

The stable isotope analysis is a commonly used technique, well recognised to compare different species or populations from different locations (Cherel et al., 2006; Jaeger et al., 2010), however, its wide spatial accuracy makes it difficult to use within the same population, with birds feeding in the same water masses, since the spatial accuracy (10s to 100s of km) might be not fine enough to assess small differences at this scale (Cherel et al., 2007). The tendency showed by females and young Adélie penguins in the D'Urville Sea in their diet could be further investigated through the blood fatty acids profile, permitting a finer description of the consumed prey (e.g., Couturier et al., 2013).

Foraging tactics

Foraging tactics performed by the birds were more homogeneous during the breeding season 2018 than during the breeding season 2019. This may be explained by the extensive sea ice conditions in 2018, which restrained the available foraging zone. Indeed, as explained earlier, during years of extensive sea ice, the foraging areas of breeding Adélie penguins are restrained: they have to travel on fast ice before reaching open-water and, thus, they have to travel further to find food resources and reduce their foraging time to come back to the colony and ensure that their chicks do not starve. They may have less time to forage and thus may perform less foraging dives than in years of less sea ice (Watanuki et al., 1993). We also suggest that, in these reduced foraging areas, prey availability may be restrained as well. The smaller isotopic niches observed during the breeding season 2018 suggest indeed a lower variability of prey, as explained before. As all penguins might target the same places to go hunting (i.e., cracks in ice), the prey depletion during years higher sea ice extent might be even higher than in years with less extensive sea ice (Watanabe et al., 2020).

Relying on the same kind of prey, birds may therefore perform foraging behaviours that are more homogeneous, which, in turn, lead to higher competition between individuals at the population-scale (Cottin et al., 2012), favouring older birds that have a higher FE thanks to their greater experience (Lescroël et al., 2019). The local prey depletion may then force the birds to go further to find food, or adapt their foraging area (Clarke et al., 2006).

Lescroël and colleagues (2010) found that trip duration was increasing as the season progresses, which is consistent with our results. They concluded for evidence in prey depletion or an alteration of availability along the breeding season (Ainley et al., 2004; Balance et al., 2009).

Our results showed that the foraging behaviour of Adélie penguins differed mostly by the f/t ratio dives. This ratio appeared to be the most important of the diving parameters that determine the foraging tactics. When more foraging dives (i.e., long and deep dives, with a long bottom phase) are performed, it allows birds to have a longer effective hunting time (Halsey et al., 2007; Ropert-Coudert et al., 2001). Older individuals, which showed a higher f/t ratio than younger ones, were then more likely to perform more efficient trips. Indeed, thanks to their experience, older individuals may perform more 'targeted' foraging behaviours: they may forage in specific areas as they learned how and where to find their prey, and they may have learned and developed diving skills, increasing their FE (Grecian et al., 2018). By targeting a specific and possibly known-area, they likely loss less time travelling and searching for food compared to younger individuals, as demonstrated previously. Orgeret and colleagues, (2019) found the same kind of patterns in king penguins from from Crozet archipelago, where younger individuals foraged in a significantly broader area than older ones.

As Adélie penguins are central place foragers (Ford et al., 2015), trip duration (and, hence, distance between the foraging grounds and the breeding colony) is of great importance as it determines the survival or not of the chicks (Davoren and Montevecchi, 2003), through insufficient food allocation. For example, Ballard and colleagues (2010), found that parents performed further trips when prey availability was lower, which had negative consequences on the food loads brought to chicks. Longer at-sea foraging trips imply opportunity to perform more dives, increasing the FE. However, too long trips during the brooding stage threaten the survival of chicks (Ballard et al., 2010). An efficient foraging tactic in terms of distance only, may thus not always be the most optimal one, on an ecological point of view. On the other hand, such long-duration and long-distance trips may be performed by individuals whose reproduction has failed and have no more chicks-rearing duties.

The next step would be to deepen the classification of foraging tactics by assigning each trip individually to one of the classified tactics, in order to determine if some patterns are linked to the breeding status (success *versus* failure), breeding stage, sex and/or age-specific.

Conclusion

In the harsh conditions of the Antarctic environment, Adélie penguins rely on the access they have to along the breeding seasons to reliable food supplies, close enough to the colony, and display different foraging behaviours, driven by various factors that might be intrinsic (sex, age) as well as extrinsic (environmental). Given the current context of rapid global changes, there is increasing interest in studying the consistency of foraging behaviour in seabirds. We aimed in this study to determine the effects of breeding season, breeding stage, sex and age on the foraging tactics displayed by Adélie penguins breeding at Pétrels' Island, in the D'Urville Sea. We found that the diving parameters, as components of the foraging behaviour, differed between birds of different age classes, sexes, and among breeding stages and breeding seasons, although birds might show some degree of consistency within and/or between breeding seasons. The effect of high sea ice concentration is not neglectable, as it directly impacts the foraging area, leading to prey depletion and/or lower diversity, which, in turn, favours intraspecific competition. The foraging efficiency, resulting from the chosen tactic, differed as well according to environmental and individual factors, although there was evidence for a higher efficiency of older, more experienced individuals. We then aimed to classify foraging tactics according to their consequent foraging efficiency. In both breeding seasons, higher-efficiency tactics were featured by a high ratio of foraging *versus* travelling dives, whiles lower-efficiency tactics were characterised rather by short and close-to-colony trips. The isotopic niche was expected to allow the characterisation of the diet of our birds; however, a finer-scale method might be more accurate and appropriate. Our study brings a new insight on the foraging ecology of breeding Adélie penguins, and how their foraging activity is driven by environmental conditions as well as sex and age. Age-related behaviours imply a process of learning, and these mechanisms are still very largely unknown. The study of the learning mechanisms displayed by juvenile Adélie penguins when they leave the colony for the first time will help to broaden our knowledge on seabirds' foraging ecology.

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Figure 1: Dumont d'Urville French polar station, Pétrels Island, Pointe Géologie Archipelago, Adélie Land, (66°39'46"S; 140°00'07"E).

Figure 2: Overview of the trips performed by Adélie penguins from Antavia colony (Pétrels Island, Pointe Géologie archipelago, Antarctica).

Figure 3: sea ice concentration extraction for the trip of an Adélie penguin breeding on Pétrels Island, D'Urville sea, Pointe Géologie archipelago.

Figure 3: trends of sea ice concentration (SIC) in front of Pointe Géologie Archipelago (Adélie Land, Antarctica), in the D'Urville Sea.

Figure 4: repartition of the foraging bouts along the foraging trip of an Adélie penguin breeding on Pétrels Island (D'Urville sea, Pointe Géologie Archipelago).

Figure 5: isotopic ratio values of feathers and plasma of Adélie penguins from Antavia colony of Pétrels Island (Pointe Géologie archipelago, Adélie Land, Antarctica)

Figure 6: isotopic niches of Adélie penguins from Antavia colony of Pétrels Island (Pointe Géologie archipelago, Adélie Land, Antarctica) during season 2018 and 2019.

Table 1: equipped Adélie penguins from the Antavia colony of Pétrels Island (Pointe Géologie archipelago, Adélie Land, Antarctica).

Breeding seasons	**Total individuals**	**Available data**	**Young individuals**	**Old individuals**	**Males**	**Females**
2017-2018	76	60	28	32	24	24
2018-2019	60	56	28	28	36	32
Total	*136*	*116*	*56*	*60*	*60*	*56*

Table 2: diving and environmental parameters used in the study and corresponding units, abbreviations and definition.

Diving variables per trip	Abbreviation	Definition
Trip duration (d)	trip_dur	
Number of dives per trip	nb_dive	Sum (all dives of trip)
Standardised number of dives (1/d)	std_nb_dive	Total number of dives / trip duration
Number of diving bouts per trip	nb_bout	Sum (all bouts of trip)
Standardised number of bouts (1/d)	std_nb_bout	Number of bouts / trip duration
Mean dive duration (s)	mean_dive_dur	Mean (duration of all dives of trip)
Mean max depth (m)	max_dep	Mean of maximum depth of all dives of a trip
Mean bout duration (s)	mean_bout_dur	Mean (duration of all bouts of trip)
Mean bottom depth (s)	bot_dep	Total bottom depth of all dives of trip / total bottom duration of all dives of trip
Mean bottom duration (s)	bot_dur	Mean (bottom duration of all dives of trip)
Total distance of trip (km)	totdist	Cumulative distance of the trip
Standardised total distance (km/d)	std_totdist	Trip total distance / trip duration
Max distance to colony (km)	max_dist	
Ratio foraging / travelling dives	ratio_ft	Number of foraging dives / number of travelling dives
Proportion of foraging dives (%)	prop_forag	Total number of foraging dives / total number of dives per trip
Total diving duration (min)	tot_div_dur	Sum (all dives duration)
Total bottom duration (min)	tot_bot_dur	Sum (all bottom duration)
Attempting Catch Per Unit Effort (ACPUE) per trip	acpue_trip	Total number of wiggles per trip / total trip bottom duration

Environmental variables per trip	Abbreviation	Definition
Mean Sea Ice Concentration (SIC) per trip (%)	mean_SIC_trip	SIC / trip area (fraction of ice covered by minimum 15% of sea ice on a 5-km area around each trip)
Mean Chla per trip (%)	mean_chla_trip	Chla / trip area (Chlorophyll-a concentration on a 5-km area around each trip)

Table 3: trip duration and distance among breeding seasons, breeding stages, sex and age classes (mean ± sd)

Trip duration (days)	2018				2019			
	2.41 ± 1.74				1.57 ± 1.19			
	Brooding		Crèching		Brooding		Crèching	
	2.04 ± 1.69		2.64 ± 1.74		1.35 ± 1.33		1.87 ± 0.89	
	Males	Females	Males	Females	Males	Females	Males	Females
	1.13 ± 0.59	2.93 ± 1.93	2.71 ± 1.73	2.59 ± 1.76	0.96 ± 0.34	1.80 ± 1.82	1.73 ± 0.85	2.04 ± 0.93
	Old	Young	Old	Young	Old	Young	Old	Young
	1.93 ± 1.74	2.14 ± 1.67	2.96 ± 1.90	2.41 ± 1.59	1.26 ± 1.34	1.49 ± 1.32	1.89 ± 0.81	1.83 ± 1.07
Total distance (kms)	2018				2019			
	166.20 ± 114.46				127.52 ± 87.35			
	Brooding		Crèching		Brooding		Crèching	
	140.03 ± 107.83		182.48 ± 116.08		92.76 ± 50.81		174.62 ± 103.39	
	Males	Females	Males	Females	Males	Females	Males	Females
	77.18 ± 54.93	200.47 ± 112.28	204.59 ± 122.79	163.38 ± 107.72	81.89 ± 36.12	105.22 ± 61.70	168.59 ± 117.77	182.07 ± 83.43
	Old	Young	Old	Young	Old	Young	Old	Young
	124.07 ± 103.27	154.22 ± 111.72	219.68 ± 123.18	154.78 ± 103.32	83.71 ± 47.32	105.40 ± 53.32	175.17 ± 109.70	173.43 ± 90.41
Maximum distance (kms)	2018				2019			
	78.30 ± 52.39				55.01 ± 3465			
	Brooding		Crèching		Brooding		Crèching	
	54.42 ± 43.20		93.15 ± 52.34		37.91 ± 18.67		37.81 ± 78.18	
	Males	Females	Males	Females	Males	Females	Males	Females
	29.12 ± 20.39	78.75 ± 45.59	102.84 ± 54.03	84.78 ± 49.94	35.67 ± 16.12	40.48 ± 21.10	75.53 ± 36.72	81.46 ± 39.42
	Old	Young	Old	Young	Old	Young	Old	Young
	45.31 ± 35.46	62.52 ± 48.30	112.84 ± 53.16	78.49 ± 47.12	33.61 ± 16.21	43.91 ± 20.34	75.02 ± 39.48	85.02 ± 33.66

Table 4: summary table of variance analysis (ANOVA) between breeding seasons, breeding stages, sexes and age-classes of diving parameters of Adélie penguins breeding at Pétrels Island, Pointe Géologie Archipelago, Adélie Land. Given value is the p-value.
BSeason: breeding season; BStage: breeding stage; ACPUE: Attempting Catch Per Unit Effort

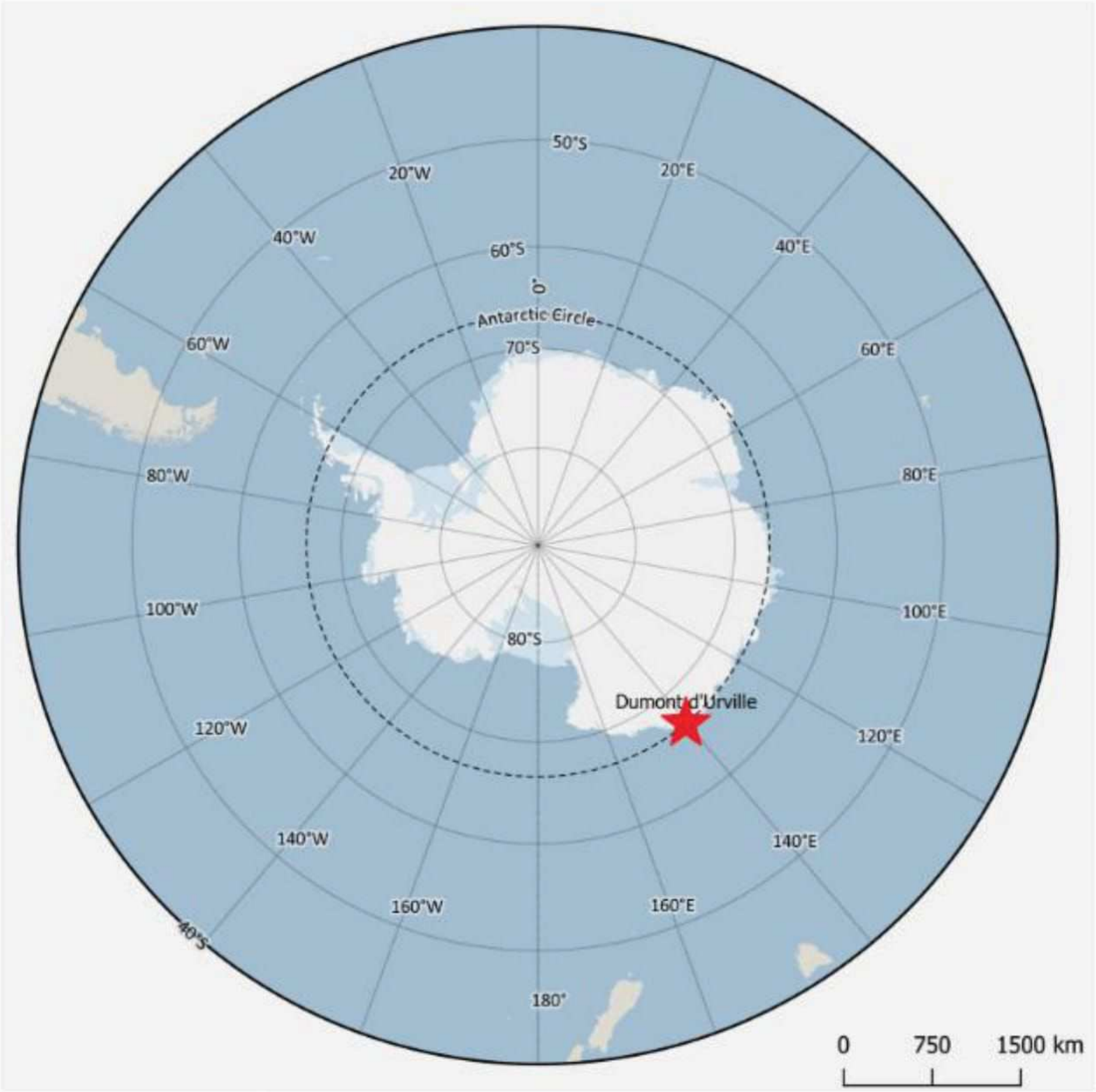
	Trip duration	Number of diving bouts	Number of dives	Maximum distance	Total distance	Max dive depth	Mean dive duration
BSeason	< 0.001	< 0.001	< 0.001	0.281	0.016	0.189	0.673
BStage	< 0.001	0.0013	< 0.001	0.007	0.027	< 0.001	< 0.001
Sex	< 0.001	< 0.001	0.007	0.475	0.233	0.003	0.022
Age	0.473	0.715	0.557	0.070	0.225	0.008	< 0.001

	Ratio F/T	Proportion foraging dives	Total diving duration	Bottom depth	Total bottom duration	Mean dive ACPUE	Trip ACPUE
BSeason	0.002	0.001	< 0.001	0.910	< 0.001	0.277	< 0.001
BStage	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Sex	0.217	0.207	0.012	0.018	0.005	0.168	0.387
Age	0.007	0.001	0.589	< 0.001	0.678	0.069	0.172

Table 5: comparison of monthly sea ice concentration, in % in D'Urville Sea, Pointe Géologie archipelago (Adélie Land, Antarctica), area enclosed in a 350-km radius from the colony, including all trips of studied penguins, between October 2017 and February 2018 and between October 2018 and February 2019. Statistical comparison performed with Kolmogorov-Smirnov test.

	2017-18					**2018-19**					**KS test**	
	mean	**stdev**	**variance**	**min**	**max**	**mean**	**stdev**	**variance**	**min**	**max**	**D**	**p**
Oct	79.63	10.69	114.182	25	93	79.29	11.79	139.05	33	94	0.04	0.34
Nov	71.21	12.50	156.194	28	90	45.33	39.62	1569.77	0	98	0.51	< 0.001
Dec	28.36	32.76	1073.283	0	96	21.65	32.91	1082.81	0	96	0.11	< 0.001
Jan	14.03	29.09	846.231	0	97	6.74	22.36	499.82	0	98	0.18	< 0.001
Feb	10.10	27.31	745.703	0	98	2.76	13.83	191.17	0	94	0.27	< 0.001

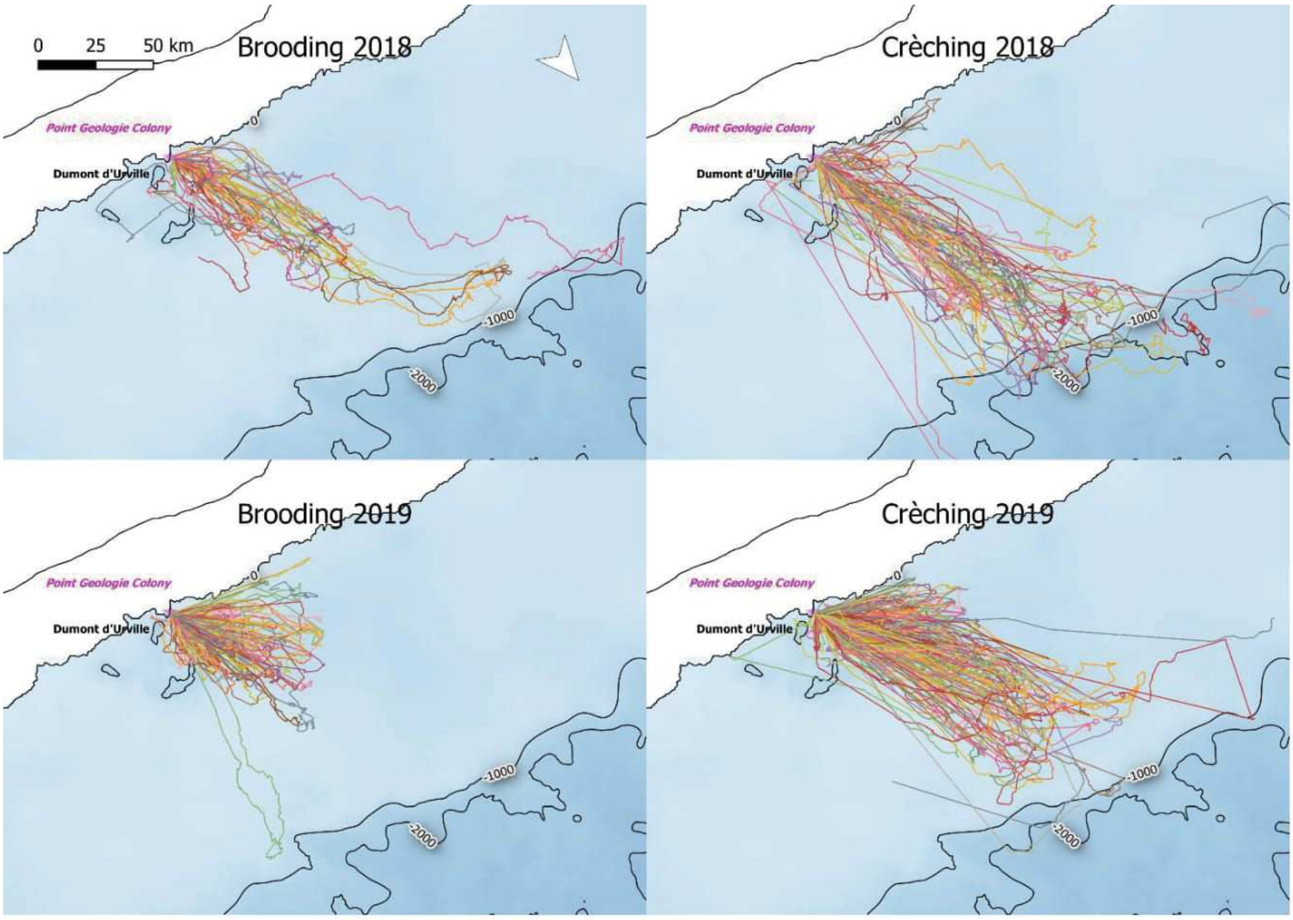
Figure 1



Dumont D'Urville French polar research station is located on Pétrels Island, on Pointe Géologie archipelago, East Antarctica.

Source: Quantarctica, developed by the Norvegian Polar Institute; EPSG 3031; QGIS 3.4.4

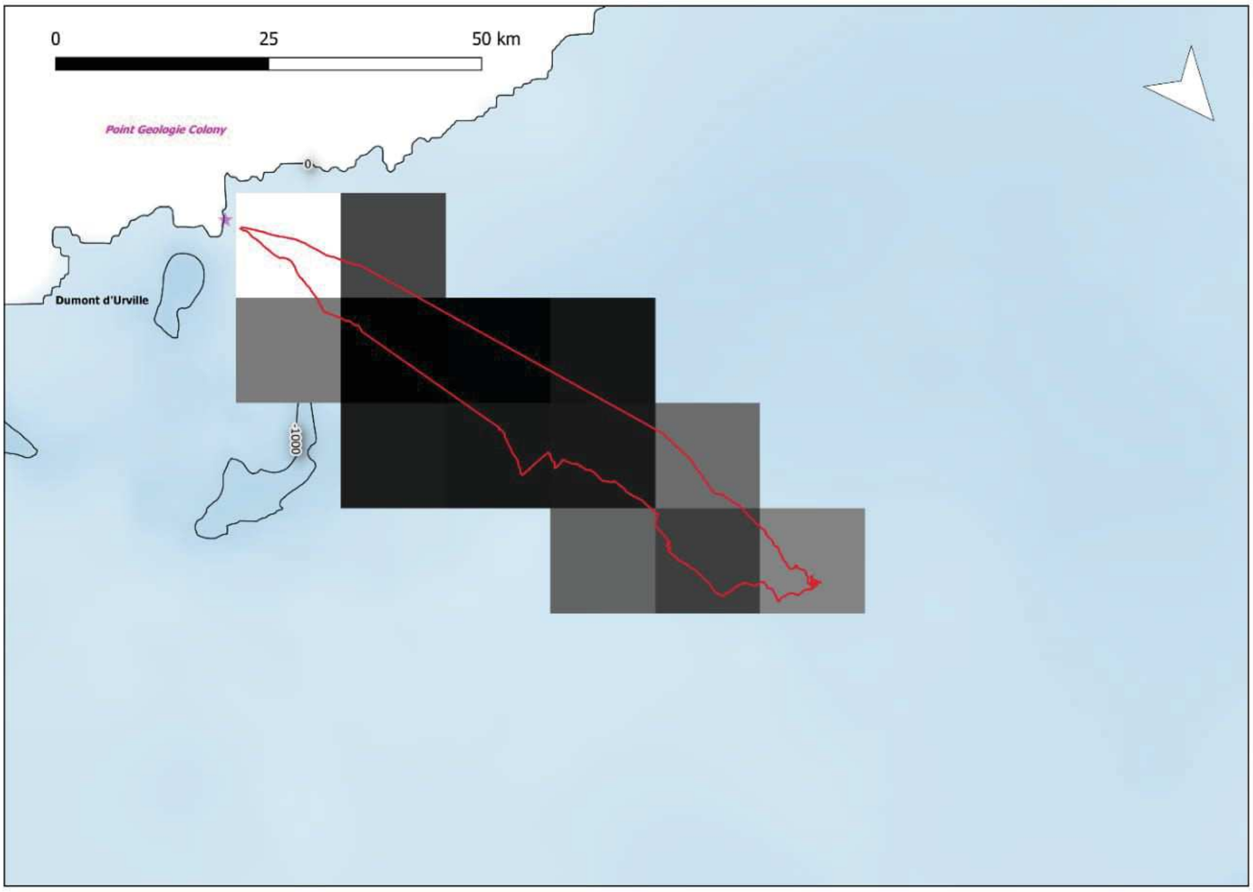
Figure 2



Overview of the trips performed by Adélie penguins from Antavia colony (Pétrels Island, Pointe Géologie archipelago, Antarctica), during brooding and crèching stages (left and right, respectively) in breeding seasons 2018 and 2019(top and bottom, respectively), all sexes and age-classes together

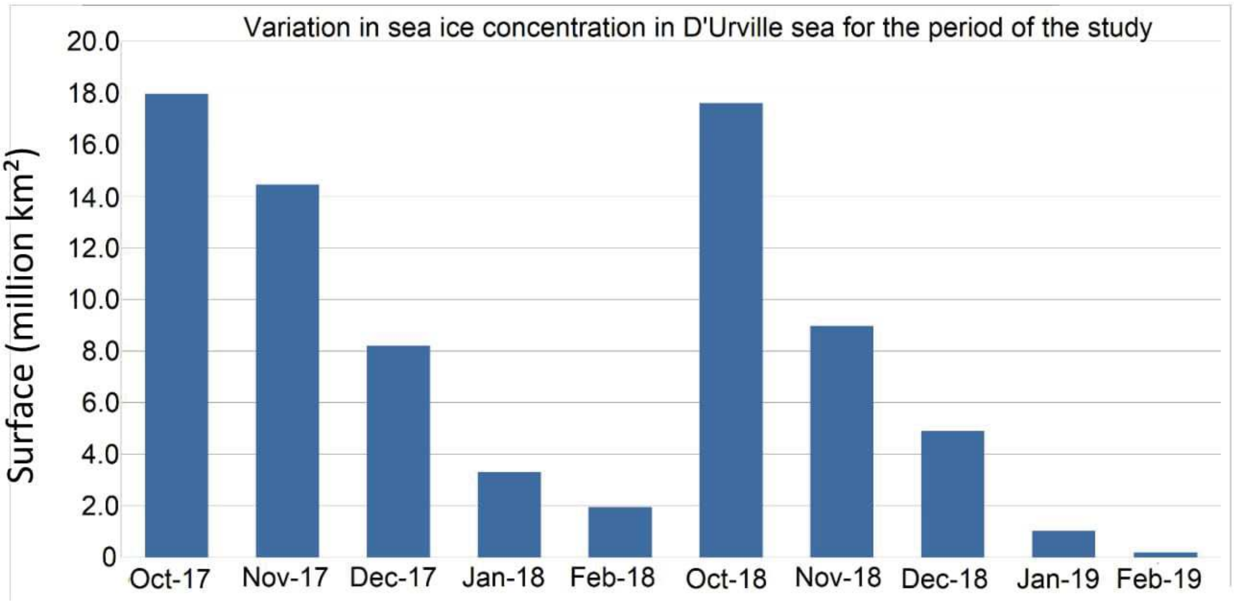
QGIS® 3.4.4

Figure 3



Trip of bird 20171231_6067008, old female, during the brooding stage in breeding season 2018. Trip trajectory (red line) linearly interpolated from GPS coordinates, weekly sea ice concentration raster layer obtained from the IFREMER for the period of the trip (resolution 12.5 km x 12.5 km), extracted (function '*extraction*' in raster treatment tools) on a 10-km buffer zone around the trip trajectory (function '*buffer*' in vector treatment tools).
QGIS ® 3.4.4

Figure 4



Monthly averaged sea ice concentration on an area enclosed in a 350-km radius from the colony including all trips of studied penguins, between October 2017 and February 2018 and October 2018 and February 2019.

Figure 5

Typical example of a trip, here performed by bird 20171231_6067008, old female, during the brooding stage in breeding season 2018.
Black line representing the linearly interpolated trajectory, and black dots the beginning of each diving bout. The blue line represents the direction of the start of the trip.
X-axis: latitude, *y*-axis: longitude

Figure 6 a

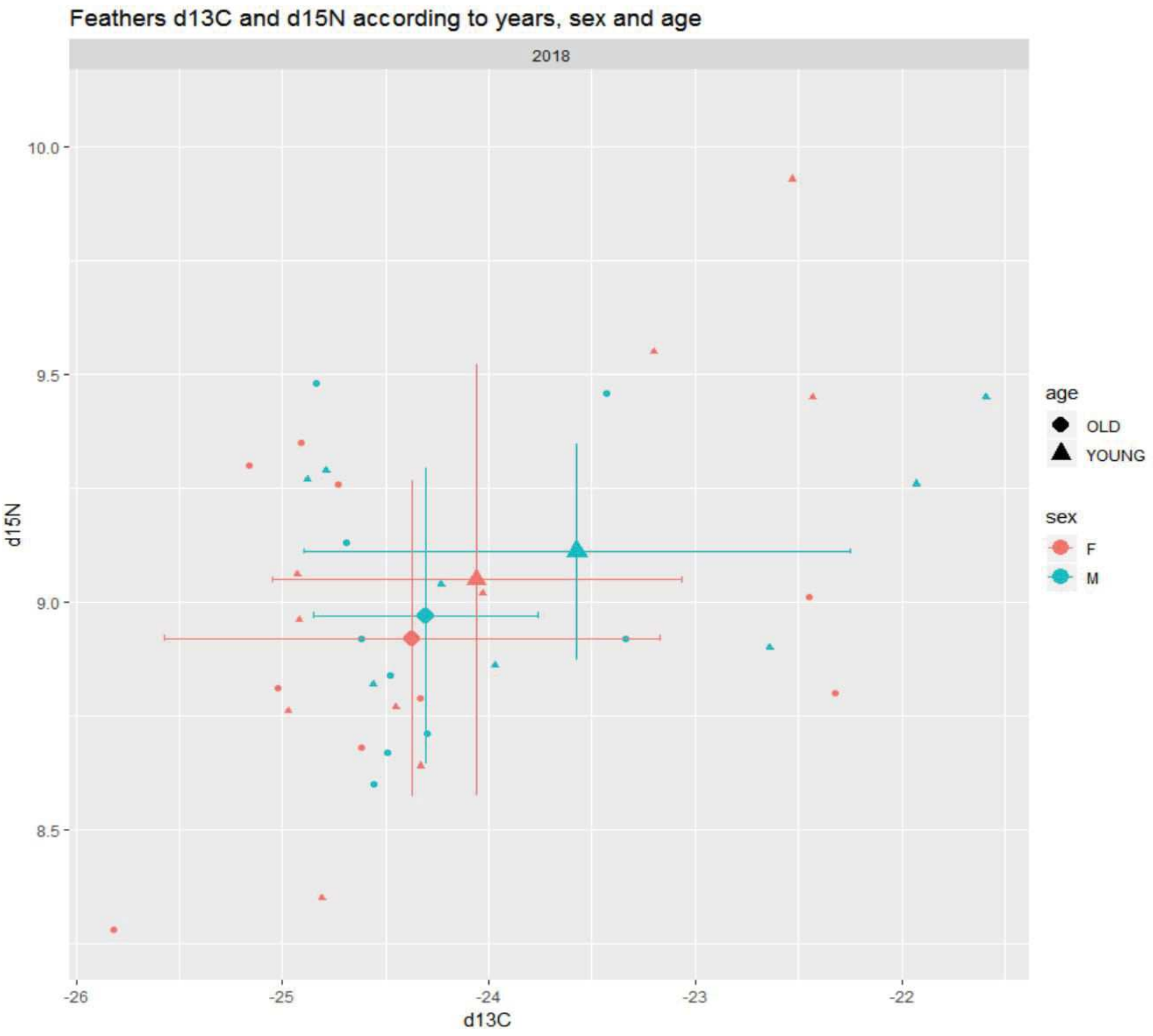

Feathers d13C and d15N according to years, sex and age
2018
d15N
10.0
9.5
9.0
8.5
d13C
-26
-25
-24
-23
-22
age
OLD
YOUNG
sex
F
M

Figure 6 b

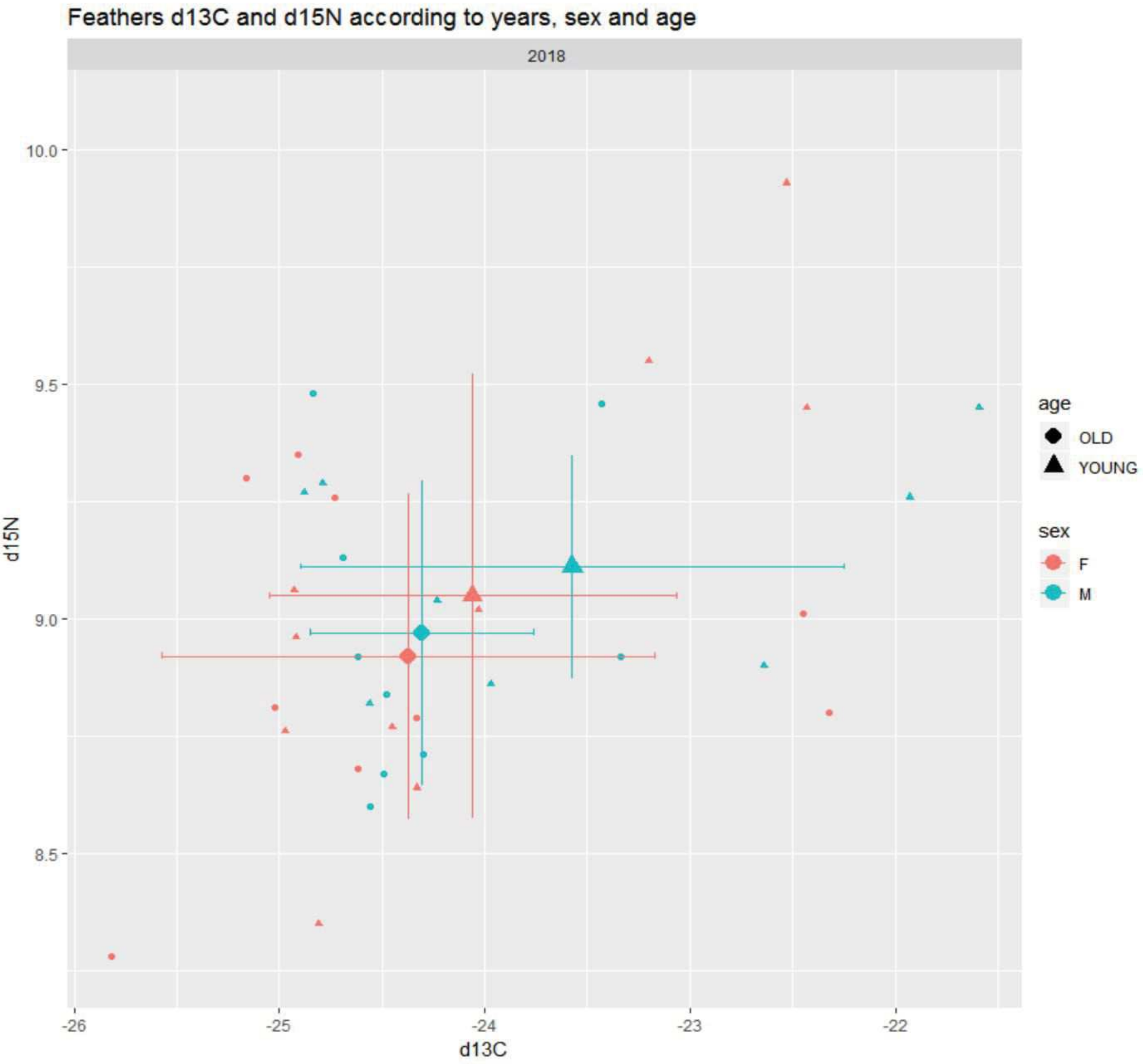
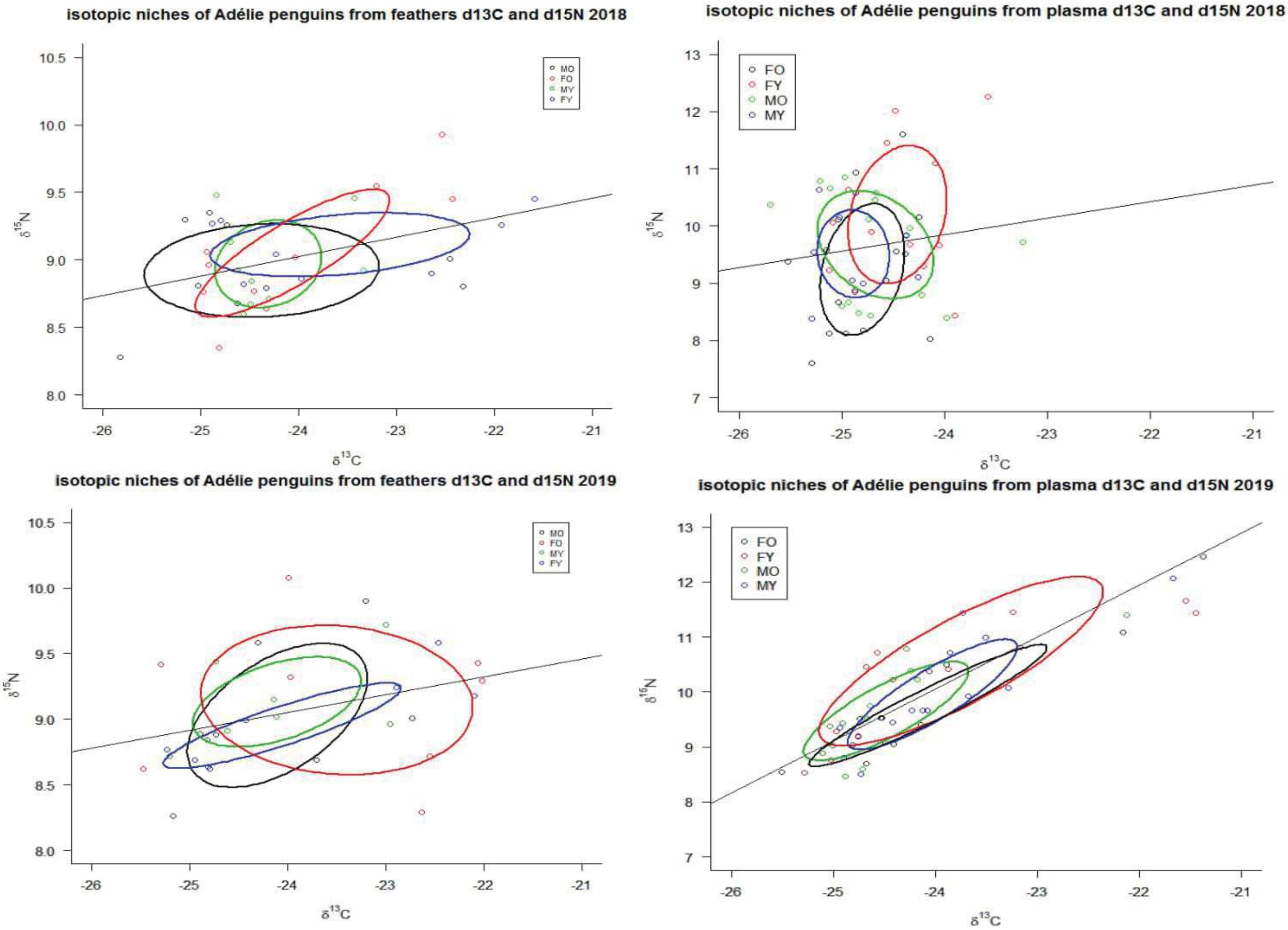

Feathers d13C and d15N according to years, sex and age
2018
10.0
9.5
9.0
8.5
d15N
-26
-25
-24
-23
-22
d13C
age
OLD
YOUNG
sex
F
M

Figure 7



Isotopic niches of Adélie penguins from Antavia colony of Pétrels Island (Pointe Géologie archipelago, Adélie Land, Antarctica) during season 2018 (top) and 2019 (bottom), assessed through isotopic ratios on Carbon (*x*-axis) and Nitrogen (*y*-axis) from feathers (left) and plasma (right).

Note the change of scale in *y*-axis for plasma values.

Supplementary material

Appendix 1: representation of a dive

Appendix 2: detailed protocol for preparation of Stable Isotope Analysis samples on feathers and blood

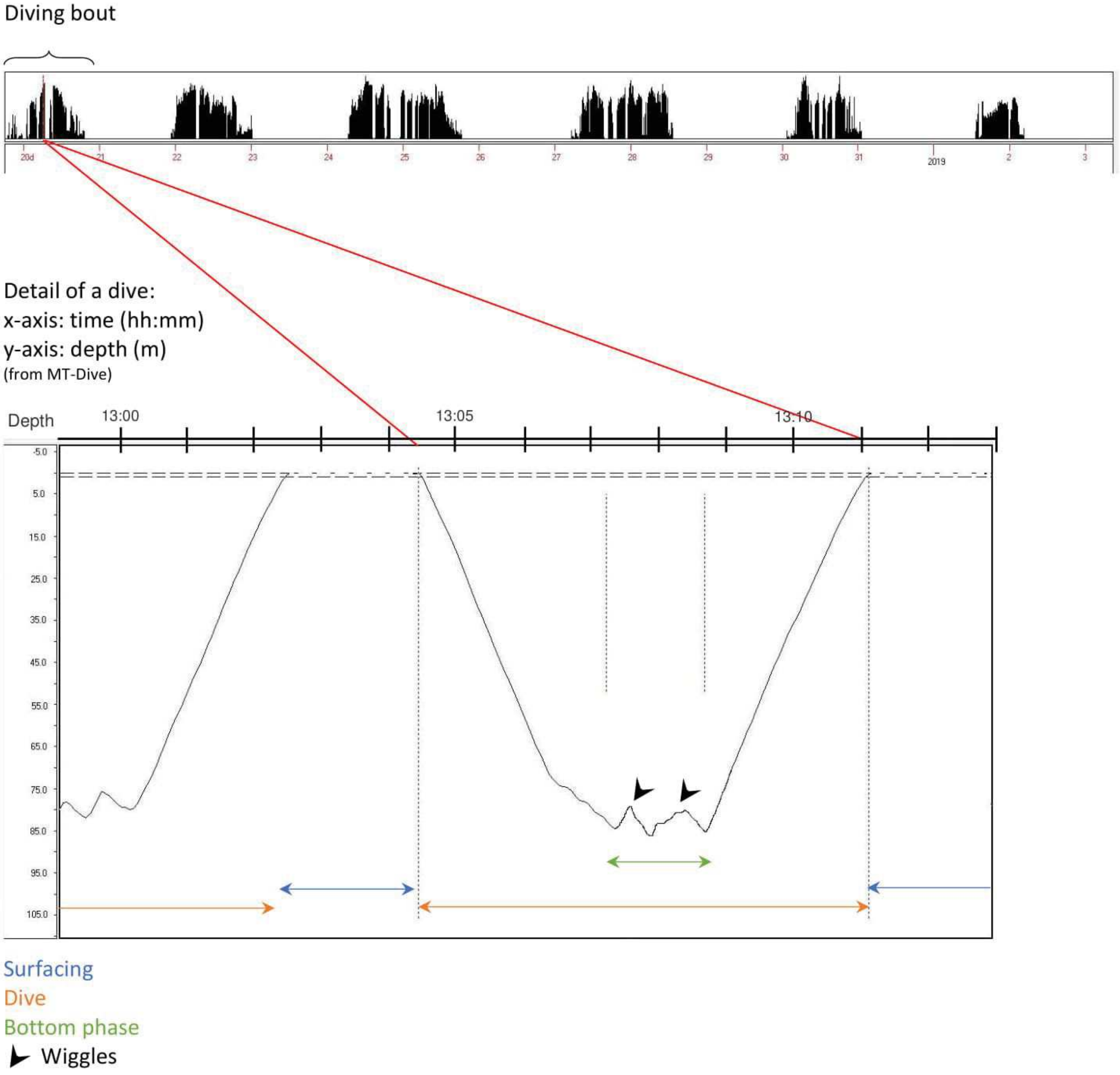
Appendix 3: summary table of major studied parameters

Appendix 4: estimation of isotopic niche areas from feather and plasma $\delta^{13}C$ and $\delta^{15}N$ in Adélie penguins

Appendix 5: results of the Generalised Linear Model

Appendix 1: representation of a dive

Trip overview (from MT-Dive):



Detail of a dive:
x-axis: time (hh:mm)
y-axis: depth (m)
(from MT-Dive)

Figure S.1: Adélie penguins foraging dives can be mostly separated into 3 phases: a rapid, constant descending phase to a particular depth, at or near which they remain for a substantial fraction of the dive (bottom phase), performing (or not) undulations up to 2 m of amplitude (wiggles), and which is the effective hunting phase (Rodary et al., 2000; Ropert-Coudert et al., 2007), and a rapid and steadily ascending phase to the surface, where they can rest for a while before the next dive. Chappell et al. (1993) found that post-dive surfacing rest duration averaged *ca*. 50 % of the diving duration.

Appendix 2: detailed protocol for preparation of SIA samples on feathers and blood

Feathers

1) Cleaning: 3 minutes in a 2:1 chloroform:methanol solution (Hobson, Atwell and Wassenaar (1999) and Wassenaar & Hobson (2000b), Bontempo et al. (2014)), in an ultrasonic bath
2) 3 successive methanol rinses
3) Put the feathers in aluminum foil, close the foil and dry them at 50 degrees for 48h
4) Powdering by hand with surgical scissors in glass tubes
5) Sub-samples preparation (weight, encapsulate). Optimal weigh*t* = 400 µg
6) Analysis

C:N mass ratio control: if C:N > 3.5 (Post et al., 2007) but redo manipulation if > 3.8 (Cherel et al., 2005)

Blood

1) Freeze-drying plasma samples for 24 hours, to evaporate water
2) Plasma delipidation with chloroform:methanol solution (2:1)
   Pour 4mL of the solvent solution for a 10-15 mg sub-sample in a glass tube
   10 min agitation
   5 min centrifugation at 4500 t/min
   Carefully pour the solvent containing the lipidic phase into glass tubes
   Repeat 3 times until solvent is colorless
3) Let dry in oven 45°C for minimum 24 hours
4) Sub-samples preparation (weight, encapsulate). 400 µg per tin capsule
5) Analysis

Appendix 3: summary table of major studied parameters

Table S.1: summary table of mean and standard deviation values for studied diving parameters. Framed bold cells: significant difference (ANOVA, $p < 5\%$).
Parameters: trip duration, number of diving bouts and dives per trip mean sea ice concentration (SIC) and chlorophyll-a (Chla) concentration during a trip, total travelled distance, maximum distance from colony, mean dive duration, ratio number of foraging dives/number of travelling dives during a trip, proportion of foraging dives, total diving duration (i.e., when individuals are not resting at the surface), depth at the bottom phase (see Appendix 2), total bottom duration (sum of all bottom phases of dives of a trip), Attempting Catch per Unit Effort (ACPUE) calculated as number of wiggles divided by bottom duration, calculated per trip (acpue trip) and average of dive ACPUE per trip (mean dive acpue). Brooding and crèching are two breeding stages, the former during which parent alternate between staying at the colony to keep the chicks safe and warm, while the other feed at sea. During crèching, both parents feed at sea and come every few days to feed their chicks, which stay together in 'crèches'.

	Trip duration (day)	nb_bout	nb_dive	SIC (%)	Chla (mg/m3)	Total distance (km)	Mean dive duration (s)
2018	**2.44 ± 1.77**	**22.35 ± 12.60**	**1703.71 ± 1173.67**	**38.92 ± 23.31**	0.15 ± 0.16	297.04 ± 337.80	62.73 ± 13.60
2019	**1.59 ± 1.02**	**12.42 ± 8.30**	**1203.05 ± 699.94**	**17.77 ± 19.59**	0.19 ± 0.19	209.96 ± 399.21	62.26 ± 11.50
Brooding	**1.41 ± 1.24**	**14.17 ± 11.04**	**931.84 ± 636.45**	**20.33 ± 22.02**	**0.07 ± 0.10**	197.90 ± 389.87	**65.76 ± 13.60**
Crèching	**2.36 ± 1.42**	**17.98 ± 11.13**	**1793.67 ± 979.73**	**30.63 ± 23.63**	**0.25 ± 0.19**	282.41 ± 365.44	**59.58 ± 10.33**
Males	**1.71 ± 1.24**	**14.46 ± 9.32**	**1297.39 ± 888.54**	24.50 ± 22.70	0.17 ± 0.18	223.97 ± 358.69	**63.60 ± 12.32**
Females	**2.18 ± 1.57**	**18.38 ± 12.92**	**1514.47 ± 992.28**	27.54 ± 24.28	0.17 ± 0.18	267.08 ± 402.02	**61.01 ± 12.24**
Old	1.88 ± 1.43	15.94 ± 10.45	1373.90 ± 952.97	25.51 ± 22.61	0.18 ± 0.18	262.11 ± 429.26	**64.50 ± 12.11**
Young	1.97 ± 1.41	16.54 ± 12.12	1419.26 ± 929.54	26.28 ± 24.45	0.16 ± 0.18	220.86 ± 307.93	**59.99 ± 12.17**
2018 Brooding	**1.80 ± 1.54**	20.84 ± 11.14	**1073.13 ± 856.76**	**28.96 ± 20.26**	**0.07 ± 0.09**	220.74 ± 281.45	**69.58 ± 15.58**
2018 Crèching	**2.89 ± 1.79**	23.39 ± 13.46	**2140.27 ± 1167.93**	**45.81 ± 22.87**	**0.20 ± 0.18**	349.86 ± 363.84	**57.99 ± 9.57**
2018 Males	2.20 ± 1.64	20.32 ± 11.25	1574.36 ± 1157.60	**33.45 ± 22.76**	0.13 ± 0.15	251.22 ± 266.76	65.3 ± 14.33
2018 Females	2.75 ± 1.89	24.85 ± 13.74	1862.54 ± 1181.07	**45.63 ± 22.33**	0.17 ± 0.17	353.30 ± 403.25	59.58 ± 12.00
2018 Old	2.53 ± 1.84	22.71 ± 11.99	1789.49 ± 1218.59	37.11 ± 20.18	0.17 ± 0.16	310.64 ± 348.78	64.38 ± 14.51
2018 Young	2.35 ± 1.70	21.95 ± 13.29	1609.77 ± 1122.14	40.89 ± 26.30	0.12 ± 0.16	282.15 ± 326.78	60.93 ± 12.37
2019 Brooding	**1.22 ± 1.00**	**10.77 ± 9.32**	**859.70 ± 475**	15.92 ± 21.64	0.07 ± 0.10	186.24 ± 435.42	63.80 ± 12.06
2019 Crèching	**1.97 ± 0.90**	**14.04 ± 6.79**	**1541.59 ± 722.13**	19.59 ± 17.21	0.29 ± 0.20	233.36 ± 359.97	60.74 ± 10.74
2019 Males	**1.40 ± 0.78**	**10.85 ± 5.34**	**1126.27 ± 615.30**	18.98 ± 20.89	0.19 ± 0.19	207.14 ± 405.11	62.54 ± 10.80
2019 Females	**1.83 ± 1.22**	**14.35 ± 10.60**	**1297.96 ± 784.36**	16.29 ± 17.81	0.17 ± 0.19	213.46 ± 393.36	61.90 ± 12.34

	Trip duration (day)	nb_bout	nb_dive	SIC (%)	Chla (mg/m3)	Total distance (km)	Mean dive duration (s)
2019 Old	1.49 ± 0.93	12.00 ± 6.90	1131.91 ± 647.67	18.75 ± 21.21	0.18 ± 0.19	233.86 ± 468.56	**64.57 ± 10.52**
2019 Young	1.72 ± 1.11	12.94 ± 9.78	1292.26 ± 753.60	16.54 ± 17.35	0.19 ± 0.20	180.00 ± 288.83	**59.36 ± 12.05**

	ratio_ft	foraging dives (%)	Total dive duration (min)	Bottom depth (m)	Total bottom duration (min)	Mean dive acpue	Acpue trip
2018	**1.25 ± 0.75**	**0.52 ± 0.11**	**1646.16 ± 1072.15**	18.44 ± 7.55	**549.30 ± 360.62**	**0.02 ± 0.01**	**0.04 ± 0.02**
2019	**1.06 ± 0.60**	**0.49 ± 0.11**	**1187.21 ± 656.93**	18.51 ± 6.95	**340.57 ± 184.95**	**0.02 ± 0.01**	**0.05 ± 0.01**
Brooding	**1.31 ± 0.72**	**0.53 ± 0.12**	**976.86 ± 650.90**	20.19 ± 8.17	**298.00 ± 215.80**	**0.03 ± 0.01**	**0.05 ± 0.02**
Crèching	**0.98 ± 0.58**	**0.47 ± 0.09**	**1695.63 ± 895.51**	17.01 ± 5.82	**526.01 ± 294.64**	**0.02 ± 0.001**	**0.04 ± 0.01**
Males	1.17 ± 0.67	0.51 ± 0.11	1278.07 ± 829.42	19.19 ± 7.81	**390.51 ± 271.02**	0.02 ± 0.01	0.04 ± 0.02
Females	1.09 ± 0.67	0.49 ± 0.10	1467.30 ± 905.43	17.61 ± 6.22	**457.32 ± 297.00**	0.02 ± 0.01	0.04 ± 0.02
Old	**1.20 ± 0.66**	**0.51 ± 0.11**	**1046.16 ± 881.48**	**19.49 ± 7.74**	423.46 ± 288.10	0.02 ± 0.01	0.04 ± 0.02
Young	**1.05 ± 0.67**	**0.48 ± 0.11**	**1342.95 ± 854.35**	**17.28 ± 6.26**	416.82 ± 281.00	0.02 ± 0.01	0.04 ± 0.01
2018 Brooding	**1.65 ± 0.91**	**0.58 ± 0.12**	**1179673.12 ± 877.47**	**21.43 ± 8.90**	**383.95 ± 293.65**	**0.03 ± 0.01**	**0.05 ± 0.02**
2018 Crèching	**0.98 ± 0.44**	**0.48 ± 0.08**	**1969.11 ± 1079.30**	**16.37 ± 5.62**	**663.77 ± 359.41**	**0.02 ± 0.00**	**0.03 ± 0.01**
2018 Males	1.35 ± 0.82	0.54 ± 0.12	1539.85 ± 1075.52	19.75 ± 8.40	508.46 ± 361.13	0.02 ± 0.01	0.04 ± 0.02
2018 Females	1.13 ± 0.64	0.50 ± 0.10	1776.69 ± 1059.17	16.83 ± 6.02	1099.45 ± 355.87	0.02 ± 0.01	0.04 ± 0.01
2018 Old	1.34 ± 0.82	0.53 ± 0.11	1735.35 ± 1119.26	18.92 ± 8.27	578.08 ± 371.84	0.02 ± 0.01	0.04 ± 0.02
2018 Young	1.16 ± 0.65	0.51 ± 0.11	1548.47 ± 1015.73	17.91 ± 6.69	517.78 ± 347.40	0.02 ± 0.01	0.04 ± 0.01
2019 Brooding	1.14 ± 0.53	**0.51 ± 0.11**	**873.30 ± 468.10**	19.55 ± 7.73	**254.10 ± 145.08**	**0.03 ± 0.01**	**0.05 ± 0.02**
2019 Crèching	0.98 ± 0.66	**0.47 ± 0.10**	**1496.74 ± 670.60**	17.49 ± 5.94	**425.82 ± 180.79**	**0.02 ± 0.01**	**0.04 ± 0.01**
2019 Males	1.06 ± 0.53	0.49 ± 0.11	1116.33 ± 577.76	18.84 ± 7.43	**317.63 ± 157.70**	0.02 ± 0.01	0.05 ± 0.02
2019 Females	1.07 ± 0.69	0.49 ± 0.10	1274.84 ± 736.20	18.10 ± 6.32	**368.92 ± 211.13**	0.02 ± 0.01	0.05 ± 0.01
2019 Old	1.12 ± 0.54	**0.50 ± 0.11**	1172.29 ± 623.54	**19.82 ± 7.42**	333.43 ± 171.26	**0.02 ± 0.01**	0.05 ± 0.01
2019 Young	0.99 ± 0.67	**0.47 ± 0.10**	1205.93 ± 698.62	**16.87 ± 5.95**	349.51 ± 201.16	**0.02 ± 0.01**	0.05 ± 0.01

Appendix 4: estimation of isotopic niche areas from feather and plasma $\delta^{13}C$ and $\delta^{15}N$ in Adélie penguins

Table S.2: statistical comparison of estimated isotopic niche areas from feather and plasma isotopic values of Adélie penguins from Antavia colony, Pétrels Island (Pointe Géologie archipelago, Adélie Land). FPR: False Positive Risk (Colquhoun, 2019).
MO: Males Old, MY: Males Young, FO: Females Old, FY: Females Young; n=4000 for each group (Bayesian estimations). P-values from R,

FEATHERS **Groups**	**2018 + 2019** **p**	**2018** **p**	**2019** **p**
MO – MY	< 0.001	< 0.001	< 0.001
FO – FY	< 0.001	< 0.001	< 0.001
MO – FO	< 0.001	< 0.001	< 0.001
MY – FY	< 0.001	< 0.001	< 0.001
MO – FY	< 0.001	< 0.001	< 0.001
MY – FO	< 0.001	< 0.001	< 0.001

PLASMA **Groups**	**2018 + 2019** **p**	**2018** **p**	**2019** **p**
MO – MY	< 0.001	< 0.001	< 0.001
FO – FY	< 0.001	< 0.001	< 0.001
MO – FO	< 0.001	< 0.001	< 0.001
MY – FY	< 0.001	< 0.001	< 0.001
MO – FY	< 0.001	0,173	< 0.001
MY – FO	< 0.001	< 0.001	< 0.001

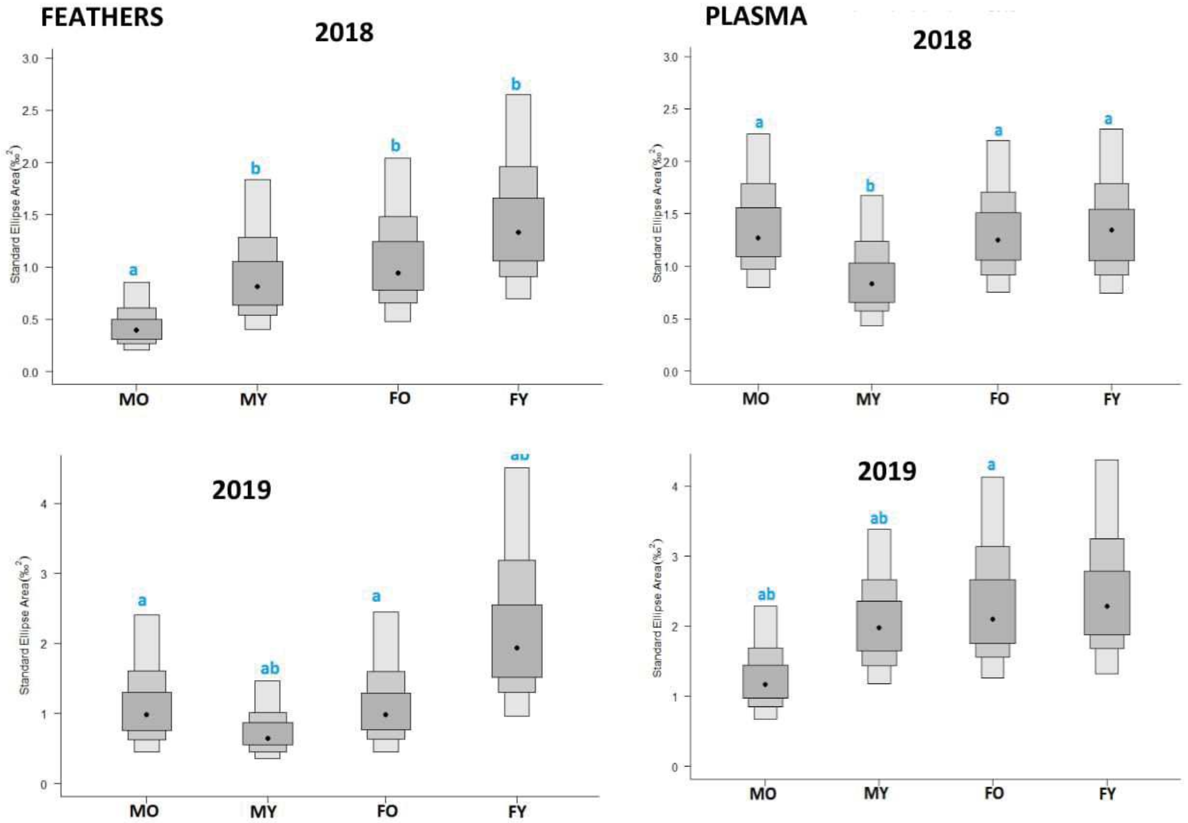


Figure S.1: estimation of isotopic niche areas (in ‰^{2}) from feather (left) and plasma (right) isotopic ratios (each expressed in ‰), after Bayesian iterations, for both years pooled and separately. *x-axis*: δ^{13}C, *y-axis*: δ^{13}C.
MO: males old, MY: males young, FO: females old, FY: females young.

Table S.3: statistical comparison of estimated isotopic niche areas from feather and plasma isotopic values of Adélie penguins from Antavia colony, Pétrels Island (Pointe Géologie archipelago, Adélie Land).
MO: Males Old, MY: Males Young, FO: Females Old, FY: Females Young; n=4000 for each group (Bayesian estimations). P-values from R.

	FEATHERS 2018+2019	**FEATHERS 2018**	**FEATHERS 2019**
	p adj	**p adj**	**p adj**
MO-MY	2.15e-08	2.15e-08	2,15e-08
FO-FY	2.15e-08	2.15e-08	2,15e-08
MO-FO	2.15e-08	2.15e-08	2,15e-08
MY-FY	2.15e-08	1.02e-07	0,99
MO-FY	2.15e-08	2.16e-08	2,15e-08
MY-FO	2.15e-08	0.56	2,15e-08

	PLASMA 2018+2019	**PLASMA 2018**	**PLSAMA 2019**
	p adj	**p adj**	**p adj**
MO-MY	2,15e-08	2,15e-08	2,15e-08
FO-FY	2,15e-08	2,15e-08	2,15e-08
MO-FO	2,15e-08	2,15e-08	2,15e-08
MY-FY	2,15e-08	2,16e-08	2,15e-08
MO-FY	2,15e-08	2,16e-08	2,15e-08
MY-FO	2,15e-08	1	2,16e-08

Appendix 5: results of the Generalised Linear Model

Table S.4: summary of final models after descending-stepwise method. Best combination of variables among a model selected as the one having the lowest Akaike Information Criterion (AIC). Response variable is foraging efficiency (FE), assessed through Attempting Catch Per Unit Effort per trip (acpue_trip), initially included variables are breeding season (Bseason), breeding stage (Bstage), sex, age-class, Sea Ice Concentration (SIC), Chlorophyll-a concentration (Chla) and diving parameters (PCA1 to PCA2).

	Estimate	Std. Error	*t*	P (>|t|)
2018 + 2019 pooled				
FE ~ year + Bstage + sex + age + mean_SIC_trip + mean_chla_trip + PCA1 + PCA2				
Bseason	1.176e-02	1.141e-03	10.308	< 0.001
PCA2	5.059e-03	2.724e-04	18.573	< 0.001
PCA1	-2.084e-03	2.748e-04	-7.584	< 0.001
mean_SIC_trip	1.087e-04	2.288e-05	4.749	< 0.001
sex	-3.105e-03	9.558e-04	-3.249	0.001
Bstage	-2.960e-03	1.139e-03	-2.599	0.010
mean_chla_trip	-6.900e-03	3.448e-03	-2.001	0.046
2018				
FE ~ Bstage + sex + age + PCA1 + PCA2				
PCA2	0.005	4.139e-04	12.541	< 0.001
PCA1	-0.002	3.066e-04	-7.711	< 0.001
sex	-0.004	1.505e-03	-2.903	0.004
Bstage	-0.004	1.736e-03	-2.141	0.034
2019				
FE ~ Bstage + sex + age + PCA1 + PCA2				
PCA2	4.710e-03	3.648e-04	12.911	< 0.001
Bstage	1.596e-04	3.117e-05	5.122	< 0.001
PCA1	-1.583e-03	4.235e-04	-3.737	< 0.001
Age-class	-1.312e-02	3.830e-03	-3.427	< 0.001
sex	-2.912e-03	1.231e-03	-2.366	0.019

Annex D. Foraging tactics and breeding constraints predict contaminant accumulation in fasting Adélie penguins

Foraging tactics and breeding constraints predict contaminant accumulation in fasting Adélie penguins

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Abstract

In seabird species with sex-specific life-history tactics, vulnerability and susceptibility to contaminants might differ between sexes. Contrasting breeding constraints and foraging tactics between females and males in the Adélie penguin (*Pygoscelis adeliæ*), could potentially result in sex-specific accumulation of and stress response to contaminants. To investigate this, we measured the concentrations of polychlorinated biphenyls (PCBs), organochlorine pesticides (OC pesticides), polybrominated flame-retardants (PBDEs), perfluorinated compounds (PFASs) and mercury (Hg) in the blood of Adélie penguins at the end of their incubation fasting period. Their breeding history was determined and their physiological condition was assessed based on their oxidative stress levels, weight loss, body condition and telomere length. Adélie penguins presented relatively low concentrations of legacy and emerging contaminants compared to migratory seabirds breeding in Antarctica, highlighting the low exposure scenario within the Antarctic region. Adélie penguin males had ~ 60% higher blood concentration of Hg than females, while females had ~ 40% higher concentrations of PCBs than males, however we found no sex differences in OC pesticides or PFASs. Cluster profiling showed a primary split between females and males (by dissimilarities in PCBs), and a secondary split within males (by dissimilarities in PFUnA). There were also an overlap between males and females in their contaminant profiles: females with combinations of male-like behavioural tactics had male-like contaminant profiles and vice versa. The three-cluster repartition was best discriminated by individual combinations of foraging ground and fasting length, and the detected sex-differences in contamination thus relied on sex-specific timing of incubation shift and individual behavioural tactics in foraging and fasting, but appeared unrelated to sex-determined physiology. We found no relationships among telomeres, stress and contaminants, although females tended to have higher antioxidant capacities compared to males, which is likely due to different choice in prey.

Keywords: *Antarctica, contaminants, fasting, foraging, oxidative stress, seabirds, sex, telomeres*

1. Introduction

Long-lived species interact with a range of environmental contaminants in their habitat over time (Rowe 2008). Accumulation of contaminants differ between species because of species-specific foraging range, feeding ecology and physiology, that shape encounters with different environmental levels, exposure through food and capacities to store, biotransform and eliminate contaminants (Burger & Gochfeld 2002). Yet, species with similar accumulation rates can experience different health impacts of contaminants due to intrinsic and extrinsic factors that influence the likelihood of toxic effects (Bourgeon et al. 2012, Bustnes et al. 2015). There is also considerable individual variation in contamination within species, due to sex- and life stage-specific feeding ecology, geographical movement patterns, metabolic capacities and elimination (Burger et al. 2007, Robinson et al. 2012, Colabuono et al. 2012, Pichegru et al. 2013). Thus, species, populations and individuals vary in likelihood of accumulation (*vulnerability*) and likelihood of sub-lethal effects (*susceptibility)* (Burger & Gochfeld 2002). More specifically, vulnerability and susceptibility to contaminants may be expected to differ between sexes in species where males and females have contrasting foraging tactics and energetic constraints.

Polar seabirds are long-lived and forage high in the food web on lipid rich prey with species-specific energy management strategies that may increase the risk of contaminant-induced health impairments (Bengtson Nash et al. 2013). Penguins and other seabird groups with fasting strategies during food deprivation, experience elevated accumulation of contaminants through re-mobilisation of stored lipophilic contaminants, weight loss and bioamplification, during already energetically costly life history events (Daley et al. 2014). Although seabirds display low sexual dimorphism in general compared to other birds, females and males are known to exploit different foraging grounds and prey, resulting in sex-specific dietary exposure. One of the striking sexual differences in seabirds, however, is their contrasting breeding cycles. As a result, females and males may invest differently in reproduction (*e.g.* Weimerskirch et al. 2009) and experience different costs (*e.g.* Young et al. 2013); both resulting in inter-individual variation in weight loss and body condition (*e.g.* Velando & Alonso-Alvarez 2003). Age and experience could also influence breeding constraints and circulating concentrations of contaminants, as older and more experienced birds typically experience lower stress levels and higher breeding success (until a certain age) (Angelier et al. 2007).

Our study focuses on the Adélie penguin (*Pygoscelis adeliæ*), a seabird with contrasting foraging tactics and breeding constraints between females and males. As like other penguin species, Adélie penguins alternate between foraging at sea and fasting on land during their breeding cycle. During the austral summer, Adélie penguin females forage in pelagic-offshore systems and rely heavily more on krill (*e.g. Euphausia superba*) than fish species (*e.g. Pleuragramma antarctica*) compared to males, that feed equally on krill and fish but in more coastal-benthic systems (Clarke et al. 1998, Ballard et al. 2010, Widman et al. 2015). While females take on the reproductive cost by undergoing both egg production and two shorter fasting periods, the males fast twice as long as the females (Chappell et al. 1993). Despite the fact that the highly synchronised breeding cycle of Adélie penguins makes the sex-ratio of a random sample highly dependent on the time of sampling, sex-related differences in contaminant accumulation and associated health effects have been mostly overlooked (*e.g.* van den Brink et al. 1998).

The most common approach to investigate sexual differences in contaminant accumulation considers sexes to be pre-set categories, according to which differences in dependent variables are investigated. This complete discretisation of sexual categories has one principal drawback: it does not consider the fact that depending on the traits of interest, sexual dimorphism may range from a clearly bimodal distribution, to more blurred gradients. Therefore, specific traits may show a clear sexual dimorphism as far as distributions are concerned, while the sorting of individuals according to that trait may be much less clear. This is classically the case with body size in humans (Ruff et al. 2000); while males are significantly larger than females, this is not true of *any* randomly chosen pair. In this study, in addition to comparing sexes as *a priori* discrete groups, we also describe data-informed *typical* female-like and male-like behavioural patterns in relation to contaminants as descriptors (relative abundance of contaminant compounds - also referred to as *contaminant profiles*) using a novel approach.

We hypothesise that foraging tactics and breeding constraints influence the vulnerability (likelihood of accumulation) and susceptibility to contaminants (likelihood of sublethal effects) in Adélie penguins. To investigate this, we examine how fasting and diet influence individual circulating concentrations of polychlorinated biphenyls (PCBs), organochlorinated pesticides (OC pesticides), polybrominated flame retardants (PBDEs), perfluorinated compounds (PFASs) and mercury (Hg), and their putative associated physiological stress responses (through oxidative stress and telomere attrition) in known-age Adélie penguins. Furthermore, we predict that it is precisely the distribution of particular traits across sexes, and not the sexual identity itself, that determines differences in interaction with contaminants: the magnitude and patterns of contaminant accumulation are directly influenced by *a*) individual foraging tactics, which in turn is largely determined by sex, *b*) fasting state, which in turn is determined by fasting length and possibly sexually dimorphic individual characteristics, and *c*) circulating contaminants cause a physiological stress response, either in a strictly dose-dependent (possibly sex-specific) way, or through the mediation of (non sex-specific) individual characteristics.

2. Materials and methods

2.1 Fieldwork and data collection

During the austral summer of 2015/16, we collected blood samples from and monitored the annual breeding cycles of 30 known-age Adélie penguins breeding in Pointe Géologie archipelago (Terre Adélie), East Antarctica (66°39′46″S 140°00′07″E). We captured 15 males at the end of their 1st incubation shift when they were relieved by their partners and on their way to the ocean (male 1st departure; ~late November/early December). 15 females were captured at the end of their 2nd incubation shift when they were relieved by their partners and on their way to the ocean (female 2nd departure; ~mid-December) – see Suppl. Fig 1 for schematic overview. Birds were blood sampled (~ 5 mL) from interdigital vein of the feet using a heparinized syringe. The blood samples were centrifuged within the hour and frozen as red blood cells and plasma at -80°C (oxidative stress, telomere length) and -20°C (contaminants and stable isotopes). Birds were also biometrically measured (*i.e.* beak, flippers) and weighted. All individuals were implanted with Passive Integrated Transponder (PIT, < 0.8 g) tags as chicks between 2007 and 2009 and monitored with an automatic identification and weighing system (Le Bohec et al. *in prep.),* which allowed us to determine their breeding cycles and behaviour since their first arrival back in the colony as breeders.

2.2 Contaminant extraction, quantification and data treatment

We targeted quantification of polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDTs) and its metabolites/degradation compounds (DDE and DDD), hexachlorocyclohexane (α-, β-, γ-HCH), hexachlorobenzene (HCB), *trans* and *cis*-chlordanes, polybrominated diphenyl ethers (PBDEs), perfluorinated compounds (PFAS) in plasma (~1 mL), while mercury (Hg) was measured in red blood cells (~ 0.5 mL) (see detailed compound list in Suppl. Table 1). Matrix extractions and quantification of chemical compounds were conducted at the Norwegian Institute for Air Research (NILU) using well-established protocols previously described in Eckbo and colleagues (2019) for POPs, Blévin and colleagues (2016) for PFASs, and NILU in-house protocols for Hg. The limit of detection (LOD) for contaminants was set as the average blank level plus three times the standard deviation of the blanks. In order to avoid overestimating the contaminant concentrations, reporting false non-detects or imputation bias, we followed the methodology in Baccarelli and colleagues (2005) and performed 'a multiple distribution-based imputation with statistical inference'. Further details about chemical analyses and LOD treatment procedures are given in Supplementary information.

2.3 Molecular sex determination

Sex determination of each individual was based on DNA extraction of red blood cells using Nucleospin Blood QuickPure Kit (Macherey-Nagel, Düren Germany) and a subsequent polymerase chain amplification of the CHD1 gene: females display a Z-specific fragment and a W-specific fragment, whereas in males the W fragment is absent (method described and adapted from Sambrook and colleagues (1989).

2.4 Dietary signatures

We measured carbon and nitrogen stable isotopes in red blood cells (~ 0.2 mL) and calculated the ratio between the light and heavy isotope (*i.e.* $\delta^{15}N$ and $\delta^{13}C$) as described by Fisk and colleagues (2001). This is a well-established method for assessing carbon source (*e.g.* pelagic versus benthic) using $\delta^{13}C$, and relative position in the food web (*i.e.* high or low trophic level) using $\delta^{15}N$ (Hobson et al. 1995). The turn-over for stable isotopes in red blood cells is approximately one month (Hobson & Clark 1993), hence the isotopic signal should integrate and reflect the diet before 1st arrival at the colony for males and before 2nd arrival for females.

2.5 Individual characteristics, breeding constraints and body condition

Individual characteristics included age at blood sampling, age at 1st breeding attempt, and past breeding effort. Past breeding effort corresponds to a time-integrated index from breeding cycles from the first appearance in the colony up until the current 2015/16 breeding season (*i.e.* sum of days allocated to breeding).

Fasting state was used as a proxy for breeding constraints and estimated using four descriptors: fasting length, lipid metabolic profile, relative weight loss and body condition after fasting. Fasting length was estimated as the number of days between the 1st arrival and the 1st departure for males, and the 2nd arrival and the 2nd departure for females. A commonly used method for characterising lipid metabolic profiles of animals (high-low lipid content) is the ratio between carbon and nitrogen (C:N) due to the high amount of carbon in lipids (Post et al. 2007, González-Medina et al. 2018). The body mass (BM) of the micro-tagged penguins has been automatically recorded at every arrival and departure; this together with observational information on the length of fasting allowed us to calculate weight loss during the 2015/2016 breeding cycle. Weight loss was divided by the mass at arrival to obtain a relative weight loss that describes the percentage of loss (equation 1 & 2):

$$Relative\ weight\ loss_{male} = (BM_{1st\ departure} - BM_{1st\ arrival})/BM_{1st\ arrival} \qquad (eqn.\ 1)$$

$$Relative\ weight\ loss_{female} = (BM_{2nd\ departure} - BM_{2nd\ arrival})/BM_{2nd\ arrival} \qquad (eqn.\ 2)$$

To account for allometric relationships between body mass and volume when estimating body condition, we calculated a Scaled Mass Index (SMI) for each sex, scaling for the highest correlating length measure where *coef* is the correlation coefficient of body mass ~ flipper length (see Peig & Green 2009, equation 3):

$$SMI_{individual} = body\ mass_{individual}\ x\ (flipper_{mean}/flipper_{individual})\ \hat{}\ coef_{body\ mass\ \sim\ flipper}) \qquad (eqn.\ 3)$$

2.6 Physiological condition and stress responses

We estimated physiological stress response using a snapshot (*i.e.* oxidative stress levels, body condition) and time-integrated approach (*i.e.* telomere length). Oxidative stress result from an imbalance between the production of reactive oxygen species (ROS) and antioxidant defense (*e.g.* Harman 1956), resulting in oxidative damage (Halliwell & Poulsen 2006). Elevated levels of oxidative stress can further lead to increased shortening of telomeres that protect genetic material during cell division to avoid cell senescence (Kotrschal et al. 2007, Epel et al. 2009). Hence, telomere length has been proposed to integrate life-time stress and reflect longevity (*e.g.* Monaghan & Haussmann 2006, Reichert & Stier 2017). We estimated levels of oxidative stress using well-established methods on derivatives of reactive oxygen metabolites (d-ROM) in plasma and total plasma antioxidant capacity (OXY) described by Schull and colleagues (2016). DNA was extracted using Nucleospin Blood QuickPure Kit (Macherey-Nagel, Düren Germany). We estimated the relative length of telomeres by PCR protocol as described by Stier and colleagues (2014).

2.7 Statistical analyses

Statistical analyses were conducted in R 3.4.2 (R Development Core Team 2018).

2.7.1 Sex differences in contaminant concentrations and profiles

We first performed parametric tests (*i.e.* Student t-test, alpha = 0.05) to test for sex differences in mean and distribution of contaminant concentrations and calculated the effect size using Cohen's D. We defined contaminant profiles (profiles of concentrations) as multidimensional descriptors, under the assumption that profiles mirror small and large differences in individual tactics and physiology, which are further used to calculate dissimilarities/distances (*i.e.* chi-square distance) among individuals. Hg was not included in the contaminant matrix because of its relative extreme abundance that could not be corrected by scaling procedures.

We used two different matrices of ecological and physiological variables to describe the dissimilarities among individuals: i) the eco-physiological matrix (body condition, $\partial^{13}C$, $\partial^{15}N$, relative weight loss, lipid-protein ratio), and ii) physiological stress response matrix (relative telomere length, oxidative stress, anti-oxidant capacity, body condition). All variables were scaled before calculating Euclidean distances between individuals. We performed a cluster analysis using a hierarchical ordering (*i.e.* Ward D) in combination with correspondence analysis (CA) (Greenacre & Primicero, 2013). Optimal configuration of clusters is defined as an outcome of all possible combinations of groupings that presents the set of the most "meaningful" associations and was selected based on the squared error sum (*e.g.* Jung et al. 2003).

2.7.2 Vulnerability to contaminants

We calculated a contaminant index (CON) for total concentrations (pg/g) per individual by summing all detected compounds to assess vulnerability. We tested for sex-specific vulnerability to contaminants using a ′cluster profiling' approach and compared it to general linear models (GLMs) as a 'baseline' using sex categories. In the cluster profiling approach, we tested the prediction power of foraging tactics and breeding constraints on contaminant profiles without pre-set sex categories. Using supervised clustering with linear discrimination analysis (LDA, Duda & Hart 1973), we imposed contaminant clusters on the eco-physiological matrix. We performed a Mantel correlation test among matrices and tested how well the model obtained from LDA was to predict contaminant profiles by using a confusion matrix.

In the GLM approach, we tested whether females and males differ in mean response and variance of the response (CON) depending on dietary signatures and breeding constraints (fasting state). To select the most appropriate fasting state variable among the four descriptors, we first followed a forward model selection procedure using Akaike's Information Criterion adjusted for small sample size (AICc). We then run a model of chosen fasting state variable and foraging tactics (dietary signatures) with sex as a fixed effect on the slope of regression and intercept (equation 4):

$$CON \sim sex * foraging\ tactics + sex * fasting\ state \qquad (eqn.\ 4)$$

2.6.3 Susceptibility to contaminants

We calculated individual relative contaminant status (iCON) by summing total contaminant concentrations (pg/g) per individual relative to the sample population (equation 5):

$$iCON = \sum (individual\ concentration\ /\ mean\ of\ population\ concentration) \qquad (eqn.\ 5)$$

To test how iCON and individual characteristics may predict physiological condition, we also used the two-way approach as mentioned above: In the cluster profiling approach, we calculated Euclidean distances between individuals based on a correlation-matrix of physiological variables (body condition, stress levels, relative telomere length). The obtained clusters were imposed on a matrix of contaminants and past breeding experience corrected for age using LDA. In the GLM approach, we tested the following model (equation 6):

$$Physiological\ condition \sim iCON * sex \qquad (eqn.\ 6)$$

3. Results

3.1 Contaminant concentrations in fasting Adélie penguins

In the 15 females, we detected 5/11 OC pesticides (PeCB, HCB, *trans*-nonachlor, *p,p´*-DDE and Mirex), 6/11 PCBs (PCB 28, -66, -118, -138, -153, -180), and 1/20 PFAS (PFUnA), while in the 15 males, we detected 6/11 OC pesticides (PeCB, HCB, *trans*-nonachlor, *cis*-nonachlor, *p,p´*-DDE and Mirex), 5/11 PCBs (PCB 66, -118, -138, -153, -180), no PBDEs, and 1/20 PFAS (PFUnA) (Suppl. Table 1). For comparison between females and males, only compounds that were detected in both sexes were included in further analysis. Both female and male Adélie penguins displayed higher concentrations of OC pesticides (F: 2892.8±956.9, M: 2998±1028.5 pg.g^{-1} wet wt) compared to PCBs (F: 693.9±267.2, M: 238.4±135.7 pg.g^{-1} wet wt) and PFUnA (F: 82.8±3.4, M: 207.6±2.0 pg.g^{-1} wet wt) (see Table 1). Mercury was detected in every individual (F: 0.13±0.04, M: 0.20±0.08 µg.g^{-1} dry wt).

3.2 Sex differences in contaminants, breeding constraints and dietary signatures

Males had 63% higher Hg concentrations (p = 0.003, Cohen´s D = 1.2) compared to females, while females had 38% higher concentrations of $\sum$PCBs compared to males (p < 0.001, Cohen's D = 1.8). There were no sex differences in concentrations of PFUnA or $\sum$OC pesticides (Fig. 1 and Suppl. Table 2).

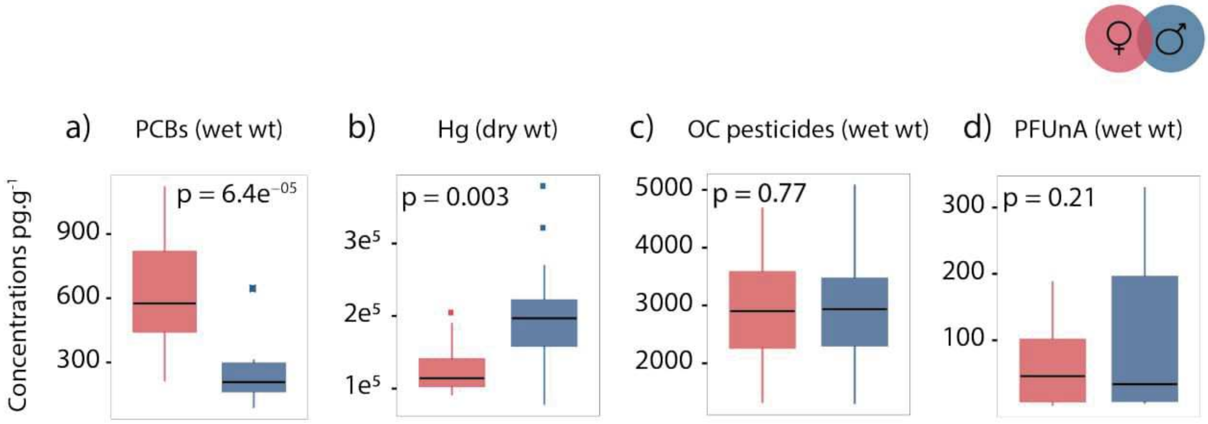

Figure 1. Boxplots showing **(a)** higher concentrations of $\sum$PCBs in females (red) than males (blue), **(b)** higher concentrations of Hg in males than females, but no differences between females and males in **(c)** OC pesticides and **(d)** PFUnA.

Males fasted from 28 to 41 days and lost between 0.10 - 0.50 kg, while females fasted from 5 to 17 days and lost between 0.04 - 0.32 kg. On average, males fasted longer than females ($p < 0.001$, Cohen's D = 7.7), displayed higher relative weight loss ($p = 0.003$, Cohen's D = 1.6) and higher lipid-protein ratio ($p = 0.002$, Cohen's D = 1.3) compared to females, but no sex differences in body condition ($p = 0.310$). We found no sex differences in ∂^{13}C ($p = 0.83$), although males were enriched in ∂^{15}N compared to females ($p < 0.001$, Cohen's D = 3.0) (Fig. 2 and Suppl. Table 2).

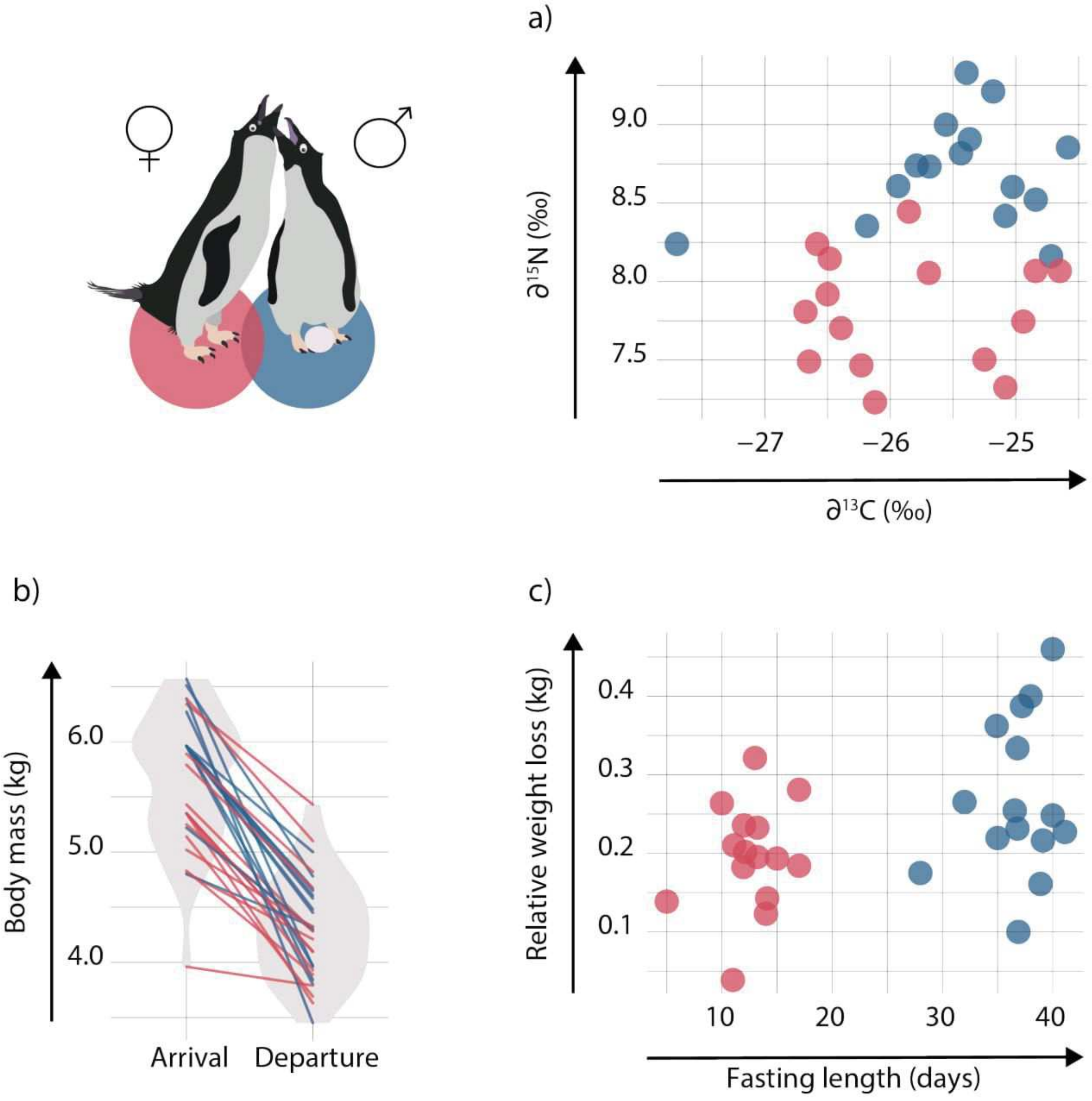

Figure 2. a) Scatterplot of isoscapes (∂^{15}N and ∂^{13}C) showing a higher trophic position in males compared to females but overlapping carbon source. **b)** Violin plot of individual body mass loss (kg) before and after incubation fast showing a higher body mass at arrival in males compared to females but no sex difference at departure. **c)** Scatterplot of breeding constraints showing individual overlap in relative weight loss (kg) and longer fasting length (days) in males compared to females.

3.3 Cluster profiling of contaminants, ecophysiology and stress responses

Cluster profiling of individual contaminants compounds found two primary levels of clusters with a primary split between females and males, and a third level of clusters with a secondary split between males (Fig. 3). There was also an overlap of females and males between clusters.

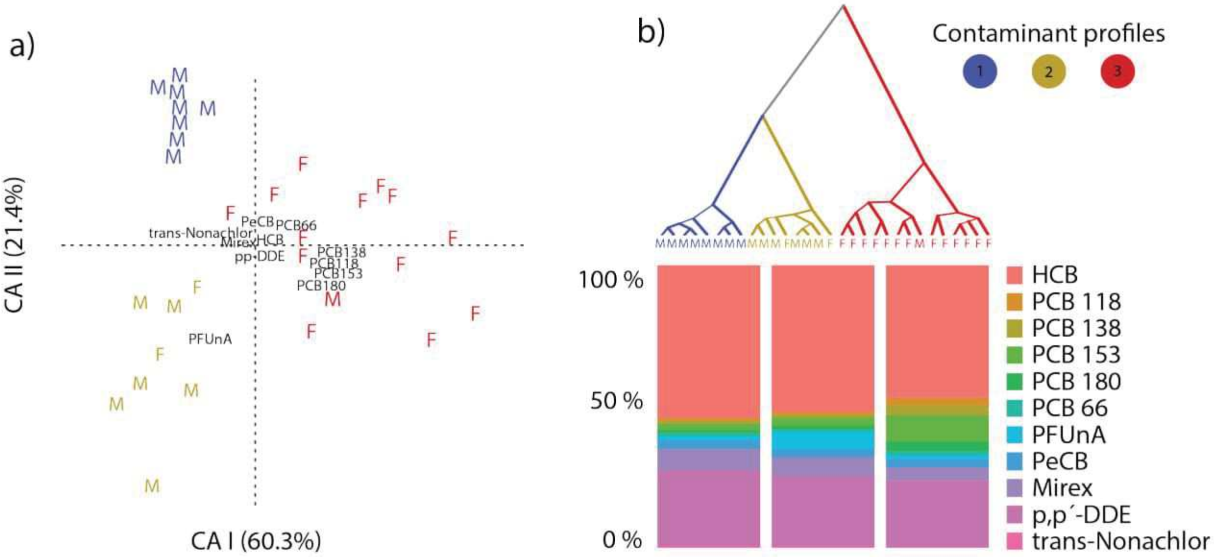

Figure 3. a) Correspondence Analysis (CA)-biplot of contaminant ratio data (individual compounds of detected organochlorine pesticides, PCBs and PFASs) splitting females (F) and males (M) into two groups along CA I driven by dissimilarities in PCBs, and males into two groups along (blue and yellow) CA II driven by dissimilarities in PFUnA. **(b)** Dendrogram of hierarchical clustering showing three clusters (blue, yellow, red) with their respective centroid means of contaminant profiles with a higher abundance of PCBs in cluster 3 (red) compared to the other two clusters and higher abundance of PFUnA in cluster 2 (yellow).

Cluster profiling of ecophysiological variables presented a primary split between females and males driven mainly by dissimilarities in fasting length and $\partial^{15}N$, and a secondary split between males driven mainly by dissimilarities in $\partial^{13}C$ and relative weight loss (Suppl. Fig. 2 & 3). Cluster profiling of physiological stress variables presented a primary split, independent of sex, between individuals driven by dissimilarities in body condition and antioxidant capacity, while a second split individuals by dissimilarities in relative telomere length and oxidative damage (Suppl. Fig. 4).

3.4 The influence of breeding constraints and foraging tactics on contaminant vulnerability

Cluster profiling approach. Carbon source had the highest discriminant coefficient for LD I (98.6%), while body condition had the highest discriminant coefficient for LD II (1.4%) (Fig. 4). The six males (and females) in ecophysiological cluster 2 displayed a coastal diet signature (less negative $\partial^{13}C$) unlike any of the other individuals and had intermediate trophic position between the other clusters of females and males. These six males appear to be extreme fasters and in worse condition compared to the other males (Suppl. Fig. 2 & Suppl. Fig. 3). The supervised clustering using LDA showed a prediction accuracy of 73% (Suppl. Table 3 - see further details on number of clusters in Suppl. Fig. 5 & Suppl. Table 4). We found a significant correlation between Euclidean distances on ecophysiological variables and chi-square distances on contaminant profiles (Mantell's correlation test, $p = 0.005$ – see Suppl. Table 5).

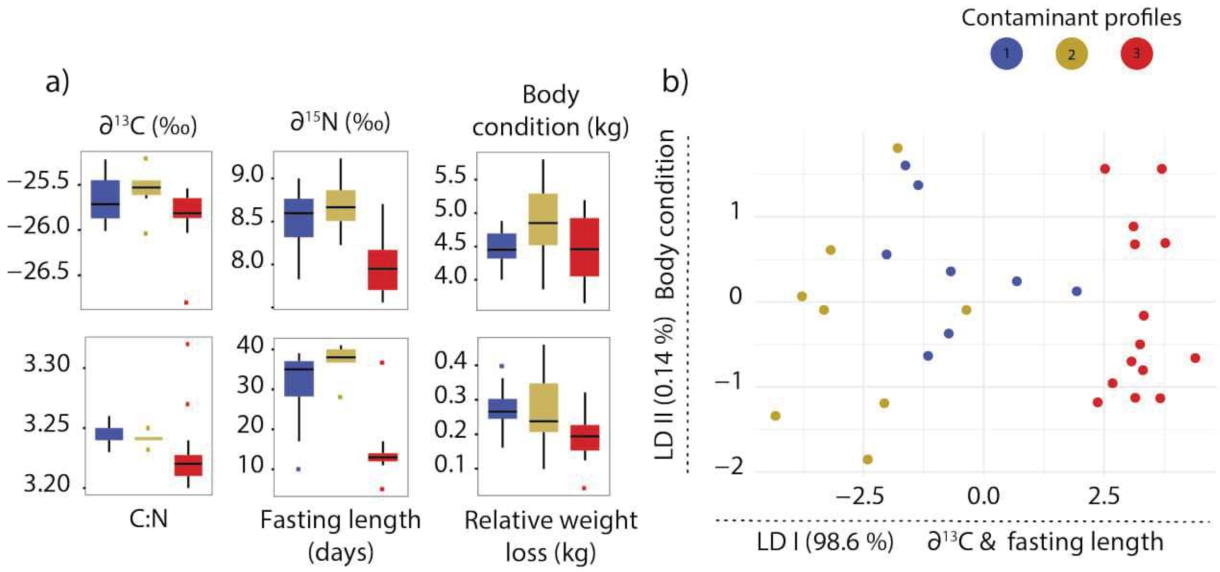

Figure 4. a) Boxplots of ecophysiological variables grouped by contaminant profile clusters showing males in contaminant cluster 2 in better condition and similar relative weight loss despite longer fasting period compared to males in cluster 1. **b)** Linear Discriminant Analysis-plot showing ∂^{13}C and fasting length as the two most important discriminants of the three contaminant profile clusters contributing to linear discriminant I, and body condition as the most contributing variable to linear discriminant II.

General linear approach. Compared to other fasting state proxies, total contaminant concentrations (CON) was best explained by body condition with sex as an interaction (see AICc results from variable selection in Suppl. Table 6) and was thus included in further analysis. Fasting state and foraging tactics did not explain the inter-individual variation in contaminants, and sex had no effect on the intercept or the slope of regression (see model results in Suppl. Table 7).

3.5 The influence of breeding constraints and efforts on contaminant susceptibility

We found no sex differences in antioxidant capacity (OXY, Students' t-test $p = 0.9$) or relative telomere length (RTL, $p = 0.4$), although females tended to have higher levels of oxidative stress than males (OXY, $p = 0.06$) (see Suppl. Table 2).

Cluster profiling approach. iPCBs had the highest coefficient loadings on LD I (64%), while past breeding/fasting experience had the highest coefficient loading on LD II (36%) (Suppl. Fig. 6). Prediction accuracy of the LDA model was estimated to 63.4% (Suppl. Table 8). We found no correlations between Euclidean distances on physiological condition variables and Euclidean distances on contaminant status and past breeding/fasting experience ($p = 0.2$, Suppl. Table 9).

General linear approach. We found no relationships between total contaminant status (iCON) and variables of physiological stress responses (OXY, d-ROM, RTL) using general linear models. Sex had no effect on the intercept or the slope of regressions on any of the covariates (see model results in Suppl. Table 10).

4. Discussion

4.1. The influence of breeding constraints and foraging tactics on contaminant vulnerability

Adélie penguin males displayed ~ 60% higher blood concentrations of Hg and ~ 40% lower blood concentrations of PCBs compared to females, however we found no sex differences in OC pesticides and PFUnA during the incubation period. A common physiological explanation for why female seabirds and mammals often display lower concentrations of contaminants is maternal transfer during reproduction (Drouillard & Norstrom 2001). However, this explanation is not consistent across all seabird species (Robinson et al. 2012) and the magnitude of transfer differs between species (Bargar et al. 2001, Drouillard & Norstrom 2001). A recent meta-study argued that sex-differences in seabird contamination is driven by maternal transfer depending on energy allocation strategies and reproductive investments (Hitchcock et al. 2019). However, by using the contamination ratio between females and males as a proxy for maternal transfer across species, males are simplified as non-breeding females, without taking into account how the interplay between species-specific sexual differences in dietary exposure and species-specific magnitude of maternal transfer, shape sexual differences (see Eng et al. 2013). In contrast to other animal groups, such as fish species in which maternal transfer is a process of passive partitioning (*e.g.* Russell et al. 1999), maternal transfer in birds seems to be a process of saturation due to active transportation of chemical compounds by particle-binding and independent of the mother's body burden (MacLachlan et al. 1994, Eng et al. 2013). The females of Adélie penguin are in the lower range of maternal transfer of lipophilic compounds: 2% of their own body burden (Tanabe et al. 1986). Hence, it seems unlikely that the ~ 60% lower levels of Hg in females versus males can be explained by maternal transfer. This point is further emphasised by the lack of sexual differences in OC pesticides and PFUnA, and reversed sexual differences in PCBs.

The behavioural explanations behind sexual differences in contamination are i) sex-specific dietary exposure due to differences in foraging grounds, different choice of prey and diet compositions (Tavares et al. 2013, Bustamante et al. 2016) and ii) sex-specific breeding constraints through the expected remobilisation of stored contaminants in fat reserves and process of bioamplification that occurs during weight loss (Bustnes et al. 2012, Daley et al. 2014). While we found no influence of dietary signatures or breeding constraints on sex-specific vulnerability to contaminants, we observed different accumulation patterns related to individual foraging tactics and breeding constraints: individuals (both males and females) foraging more in coastal areas and in better condition after fasting had higher abundance of OC pesticides and PFUnA, while individuals in poorer condition and foraging more offshore-pelagic had higher abundance of PCBs. Thus, the combination of individual foraging tactics and breeding constraints, not necessarily significantly different on average (*e.g.* per sex-category or cluster), is of importance since our results indicate that males with a specific combination of a more offshore food source and higher breeding constraints can experience more female-like contaminant profiles than other males, and vice-versa.

4.1.1 Differences in contaminant accumulation through breeding constraints

Prolonged fasting during moult and breeding includes three distinct phases in seabirds (*e.g.* Cherel et al. 1988, Bertile et al. 2016). *Phase I* is short and includes a switch to lipids as main energy source. *Phase II* is a long period of economy (up to several weeks for penguins) during which birds conserve their proteins and lipids reserves are re-mobilised into the bloodstream. After a critical body mass threshold (3.5 kg) in fasting state, birds enter *Phase III* during which proteins are used as main energy source and body mass loss drastically increases (Groscolas & Robin 2001, Cockrem et al. 2006).

Weight loss is known to amplify contaminant concentrations within tissues (Daley et al. 2014), which could explain the observed sex-specific differences in contaminants. Being only mildly larger than females (beak and flipper size, Ainley & Emison 1972; also observed in our study), the Adélie penguin males lost weight at the same or higher rate as females but fasted on average twice as long (M: 36.7 *vs* F: 12.6 days), yet this weight loss was compensated for by being heavier than females at first arrival (also observed in Vleck & Vleck 2002). Subsequently, at the end of the fasting period, we found no sex differences in body condition. Compared to females, males displayed higher C:N, indicating a higher mobilisation of fat reserves. However, individuals with elevated C:N in the blood did not have a higher occurrence of elevated contaminant concentrations. Yet, the split between cluster 1 and 2 indicate that individuals in poorer condition tended to have different contaminant profiles than individuals in better condition; hence, contaminant accumulation patterns were only partially explained by individual abilities to withstand physiological constraints.

4.1.2 Dietary exposure differences through sex-specific timing of incubation shift

During the breeding season, Adélie penguin males forage on a mixed diet of krill and fish in coastal-benthic areas; while females consume mostly krill in more offshore-pelagic areas (Clarke et al. 1998, Colominas-Ciuro et al. 2018). This is in accordance with males displaying a higher trophic position than females. Interestingly, coastal Antarctic fish species (*i.e. Lepidonotothen squamifroms)* are more contaminated by Hg and certain POPs compared to krill and mesopelagic fish (*e.g.* Polito et al. 2016, van den Brink 2011), which explains why males have higher Hg levels compared to females. However, the observed limited sex differences of OC pesticides and reversed sex differences of PCBs, indicate more complex accumulation patterns than dietary exposure as main driving factor, including differences in compound repartition, environmental conditions over the breeding season, biotransformation, etc, that require further research investigations.

If we focus on Hg, previous studies on Hg in feathers and blood of several penguin species, including Adélie penguins, show that females and males experience similar exposure to Hg outside the breeding season and early breeding period (Polito et al. 2016). In contrast to other studies, we found no sex difference in ∂^{13}C, which indicates that males and females on average utilise similar foraging grounds before their differently timed fasting periods (Brasso et al. 2015). The timing of incubation is of importance: isoscapes in red blood cells reflect dietary choices of last month (Hobson & Clark 1993), and these time-frames differ among the individuals based on sex-specific breeding patterns. The higher overall contaminant concentrations in males compared to females is probably due to higher dietary exposure through higher trophic prey before the males' 1st incubation fast (winter diet) *versus* the females' 2nd incubation fast (summer diet).

More specifically, males returning to the colony to breed may have foraged in similar areas offshore as females during their foraging trips after egg laying, but consumed different amounts of fish and krill with different levels of Hg and PCBs. In fact, the individuals of cluster 2 (females and males), that fed more coastal and were in better condition after fast despite fasting the longest, may have simply encountered similar prey closer to the colony before arrival. Thus, the sex-specific timing of incubation shift, that influences the individual dietary exposure before fast, appears to be of higher importance for the circulating concentrations of contaminants during incubation compared to physiological sexual differences *per se*.

4.2 The influence of breeding constraints and experience on contaminant susceptibility

Our results indicate that females and males of Adélie penguins experience different accumulation of contaminants during a crucial life history event already associated with increased antioxidant defense and elevated stress levels (Angelier et al. 2015). In contrast to our predictions and other studies (Constantini et al. 2014), we did not find sex differences in oxidative stress levels, although females tended to have higher antioxidant capacity compared to males. Adélie penguins are known to increase their antioxidant capacities during incubation and through exogenous antioxidants (*i.e.* astaxanthin in krill) (Corsolini et al. 2001, Beaulieu et al. 2009, 2010); possibly explaining the tendency of higher antioxidant capacities in females with a higher consumption of krill compared to males. Females and males seem to cumulate similar total breeding efforts over the season, supported by the lack of sex differences in telomere length (Chappell et al. 1993, this study). Since individuals react differently to the same environmental constraints both by their personalities (Cockrem et al. 2007 & 2013) and inter-individual physiological abilities (Depledge 1990), sub-lethal effects to contaminants are likely to vary there-after.

The presence of contaminants can increase overall stress during crucial life history events (Constantini et al. 2014), however, we found no relationships between contaminant status (iCON) and stress levels, and iCON and past breeding effort were poor discriminators for physiological clusters as indicated by the low prediction accuracy. The lack of relationships between contaminant exposure and physiological condition can be interpreted in several ways: i) the contaminants exposure experienced by Adélie penguins during incubation was too low to induce any stress responses, ii) Adélie penguins may exhibit species-specific resilience to oxidative stress response as extreme divers and fasters (*e.g.* Zenteno-Sávin et al. 2012, Schull et al. 2016), so that iii) our descriptors for physiological condition and study design were unable to detect physiological costs related to the measured contaminants.

Polar seabirds with higher levels of Hg, such as the Arctic Black-legged kittiwake (*Rissa tridactyla*) and the Antarctic Snow petrel (*Pagodroma nivea*), are prone to increased stress response and disrupted breeding behaviour (Tartu et al. 2014 & 2015). Black-legged kittiwakes with higher concentrations of PFASs also present higher levels of oxidative stress (Constantini et al. 2019). In comparison, the Adélie penguins in this study displayed almost ten times lower Hg concentrations compared to snow petrels, and almost a hundred times lower levels of PFASs compared to black-legged kittiwakes (Tartu et al. 2014 & 2015, Constantini et al. 2019). The relative low contamination of Adélie penguins may thus not impair their health. However, it should be noted that our individuals are young breeders (four to nine years old for a life expectancy of 15-20 years, Ainley 2002). Hence, our results may not be applicable to age groups beyond those studied here, as older individuals will experience chronic exposure over time (Rowe 2008).

Sub-lethal effects of contaminants are also conditioned by environmental conditions such as food availability, local weather, ice conditions (Bustnes et al. 2015), that have direct effects on breeding behaviour and success in Adélie penguins (Ainley & Lereche 1973, Chappell et al. 1990). The studied year showed high breeding success and high food availability (Ropert-Coudert et al. 2018), thus our results cannot be extrapolated to breeding seasons with higher environmental constraints (*e.g.* Bustnes et al. 2015), nor does plasma concentrations necessarily reflect contaminant exposure outside the breeding season. For instance, moult period is another energetic costly event for penguins, characterised by prolonged fasting (loosing up to 50% of protein reserves) and elevated stress levels (*e.g.* Adam & Brown 1990, Mazzaro et al. 2013) that may render Adélie penguins more susceptible to toxic effects from re-mobilisation of protein-associated contaminants such as Hg and PFASs.

Authors contribution statements

N.E., C.L.B., and K.B. conceived the ideas and designed the methodology. C.L.B., C.C. and N.E. collected the data. N.E., N.A.W., D.H., S.Z. and Q.S. conducted biological and chemical analyses. N.E., V.P.B., A.H. and N.C. analysed the data. N.E. led writing of manuscript. All authors contributed scientifically to the manuscript and gave final approval for publication.

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Data accessibility

All data are made accessible through FigShare [doi available during the review process].

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Supplementary information

1. Chemical analyses of POPs, PFASs and Hg

We extracted POPs via liquid-liquid extraction in a biphasic mixture of ethanol saturated with ammonium sulphate and hexane. The sample mixture was vortexed briefly followed by the collection of the hexane phase after phase separation. Additional hexane was added vortexed once more followed by phase separation, where the hexane phases were combined from the two extraction steps and evaporated to dryness for lipid determination. The sample was reconstituted in 0.2 ml of hexane and underwent further clean-up using 1 gram of activated Florisil® (450°C) using automated solid phase extraction (SPE). Extracts collected from SPE clean-up were evaporated to approximately 50 µL and ^{13}C-PCB 159 was added as a recovery standard was added to each sample and contaminants quantified by gas chromatography mass spectrometry (GC-MS). All samples were spiked with mass labelled (^{13}C) internal standards prior to extraction to correct for losses during processing. Each sample extraction batch included three blanks for the determination of limits of detection (LOD) and quantification (LOQ).

For PFAS, a sample (between 0.2 and 0.4 mL) spiked with internal standards was extracted in methanol (1 mL) by repeated sonication and vortexing. The supernatant was cleaned-up using ENVI-Carb graphitized carbon absorbent and glacial acetic acid. Extracts were analyzed by UPLC/MS/MS. For Hg, aliquots of 0.20-0.35 g of red blood cells were added 5 mL concentrated supra pure HNO_3 and 3 mL deionized water (MilliQ) and digested at 250°C for 15 minutes, using UltraClave (Milestone, Italy). Blank samples and certified reference material (CRM) were digested in the same run as the blood samples. After digestion, samples, blank samples and CRM were diluted to 50 mL. From the extracts, subsamples of 25 mL were further diluted to 50 mL before 5 ml BrCl were added. Determination of Hg was performed using CV-AFS from Tekran, Canada according to method US-EPA-1631. See Suppl. Table 1 for results on compound level.

Supplementary Table 1. Concentrations of contaminants (given as pg.g^{-1} wet wt for halogenated organic compounds, ng.g^{-1} dry wt for mercury) measured in females and males of Adélie penguins.

		♀			♂		
Chemical group	Compounds	Detection frequency	Mean (median)	SD (min-max)	Detection frequency	Mean (median)	SD (min-max)
Heavy metals	Mercury (Hg)	15/15	127.5 (114.3)	35.6 (90.5-204.9)	15/15	202.3 (196.9)	77.1 (77.3-379.2)
OCs	PeCB	15/15	103.1 (109.0)	21.684 (71.0-139.0)	15/15	92.2 (92.0)	19.724 (54.0-122.0)
	a-HCH	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	b-HCH	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	g-HCH	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	HCB	15/15	1733 (1844)	565.262 (790-2653)	15/15	1752 (1649)	567.907 (767-2932)
	p,p´-DDT	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	o,p´-DDT	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	p,p´-DDE	15/15	884.5 (879)	323.5 (385-1624)	15/15	876.5 (866)	330.9 (372-1541)
	o,p´-DDE	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	p,p´-DDD	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	o,p´-DDD	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	Oxychlordane	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	trans-chlordane	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	cis-chlordane	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	trans-nonachlor	15/15	23.8 (22.0)	11.264 (9.0-57.0)	14/15	27.71 (28.00)	(15.00-42.00)
	cis-nonachlor	1/15	<LOD	<LOD	9/15	10.78 (10.00)	(10.00-13.00)
	mirex	15/15	171.9 (183.0)	68.284 (73.0-276.0)	15/15	251.5 (236.0)	120.601 (91.0-495.0)
PCBs	PCB 28	8/15	57.62 (58.00)	2.463 (43.00-75.00)	0/15	<LOD	<LOD
	PCB 47	0/15	<LOD	<LOD	0/15	<LOD	<LOD

	PCB 52	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PCB 66	13/15	55.08 (53.00)	3.543 (33.00-78.00)	14/15	28.50 (24.00)	(16.00-51.00)
	PCB 71	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PCB 99	1/15	<LOD	<LOD	1/15	<LOD	<LOD
	PCB 101	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PCB 118	8/15	110.0 (111.5)	2.898 (59.00-160.00)	11/15	37.36 (35.00)	(19.00-62.00)
	PCB 138	13/15	120.8 (119.0)	4.367 (30.0-208.0)	14/15	43.57 (35.00)	(13.00-140.00)
	PCB 153	14/15	285.9 (297.5)	4.472 (82.0-511.0)	14/15	103.29 (95.00)	(27.00-298.00)
	PCB 180	8/15	142.6 (157.0)	2.898 (34.0-237.0)	10/15	55.50 (42.00)	(27.00-158.00)
PBDEs	PBDE 28	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 49	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 71	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 47	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 66	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 100	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 99	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 154	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 153	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 183	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PBDE 209	0/15	<LOD	<LOD	0/15	<LOD	<LOD
PFAS	PFOSA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFBS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFPS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFHxS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFHpS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	brPFOS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFOS	0/15	<LOD	<LOD	0/15	<LOD	<LOD

	PFNS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFDcS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFHxA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFHpA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFOA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFNA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFDcA	0/15	<LOD	<LOD	1/15	<LOD	<LOD
	PFUnA	11/15	82.82 (87.00)	3.357 (13.00-189.00)	7/15	207.6 (204.0)	2.503 (77.0-331.0)
	PFDoA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFTriA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	PFTeA	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	6:2FTS	0/15	<LOD	<LOD	0/15	<LOD	<LOD
	8:2 FTS	0/15	<LOD	<LOD	0/15	<LOD	<LOD

2. Treatment of left-censored data (contaminant data < LOD)

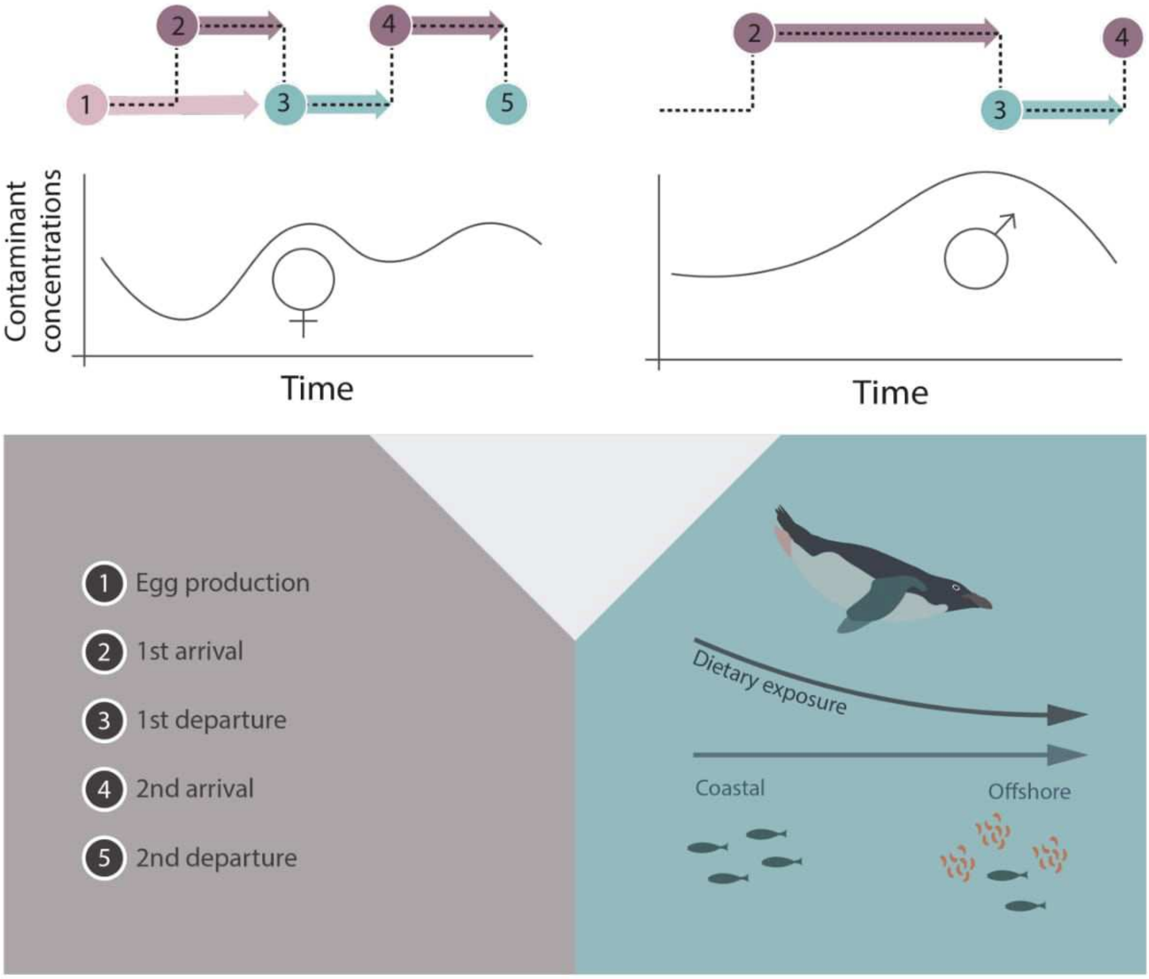
First, we set a threshold of ≥ 6 missing values through simulation of what was necessary to create a lognormal distribution. Contaminants that were not detected in any individuals of any of the two groups (females and males) were considered as absent and discarded from further analyses. For contaminants with more than 6 non-detects in one of the two groups but not in the other, we used the fitted lognormal distribution of the group to infer group comparison statistics. Obviously, these contaminant compounds were excluded from further analyses, but the comparison allowed us to extract valuable information still: if the trial distributions of females (with imputed trial values) was not significantly different from the distribution of group B, the two groups were assumed not to be different in concentrations levels, or vice versa - we could assume that group A and B had different contaminant concentrations.

Secondly, for contaminants with 6 or less non-detects, we used the fitted lognormal distribution of the detected concentrations (*i.e.* concentrations above LOD) to impute a set of trial concentrations for non-detects, with LOD as a maximum. This new distribution was then used to impute new trial values for non-detects, until the mean and distribution of any new distribution stabilised – or until we reached the distribution with highest probability given available information (*i.e.* both detects and non-detects).

Trans-Nonachlor, cis-Nonachlor, PCB28, 66, 99, 118, 138, 153 and 180, and PFUnA were not detected in any of the females, and trans-Nonachlor, cis-Nonachlor, PCB 66, 99, 118, 138, 153 and 180, PFDcA and PFUnA were not detected in any of the males. Thus, only 13 contaminant compounds were detected in one or more females and/or males. Total imputations were 30 data points for females and 27 data points for males, for eight contaminants: 18.8% and 16.3% of total female and male data sets, respectively. Three contaminants (cis-Nonachlor, PCB 28 and 99) were excluded from further analyses (> threshold for number of non-detects) in either females of males. Of the excluded contaminants (cis-nonachlor, PCB 28 and 99) we found that: i) PCB 99 had too many non-detects in both females and males to make any sensible comparison, ii) the distribution of Cis-nonachlor in males was not found to have a significant likelihood of being different from the females (p-value = 0.859), and iii) the distribution of PCB 28 differed between the sexes by significant likelihood (p-value = 0.05). Thus, we can assume that PCB 99 was not present in either sexes, and that females had similar concentrations of cis-nonachlor but higher concentrations of PCB 28 compared to males.

3. Breeding cycle of Adélie penguins

Every austral summer, Adélie penguins return to their breeding site where, after a courtship period of ~12 days, the females will lay one to three, most commonly two, eggs. Afterwards, female and male will divide the incubation period in two shifts; the male takes the 1st incubation shift while the female replenish herself after courtship and egg production. A male's 1st departure is typically 40-45 days after his return to the breeding site when the female will return to switch with her partner (female 2nd arrival) and resume 2nd incubation shift of typically ~12 days, until hatching. Both sexes go through prolonged fasting that results in a 40% loss of body weight depending on fasting length, individual physiological conditions and environmental conditions. See Suppl. Fig. 1 for schematic overview of expected fluctuations of contaminant concentrations during breeding.



Supplementary Figure 1. Schematic overview of breeding cycle during the austral summer for female and male Adélie penguin, and the expected fluctuations in blood-based contaminants and the expected differences in dietary exposure between coastal and offshore feeding areas.

4. Treatment of lipids

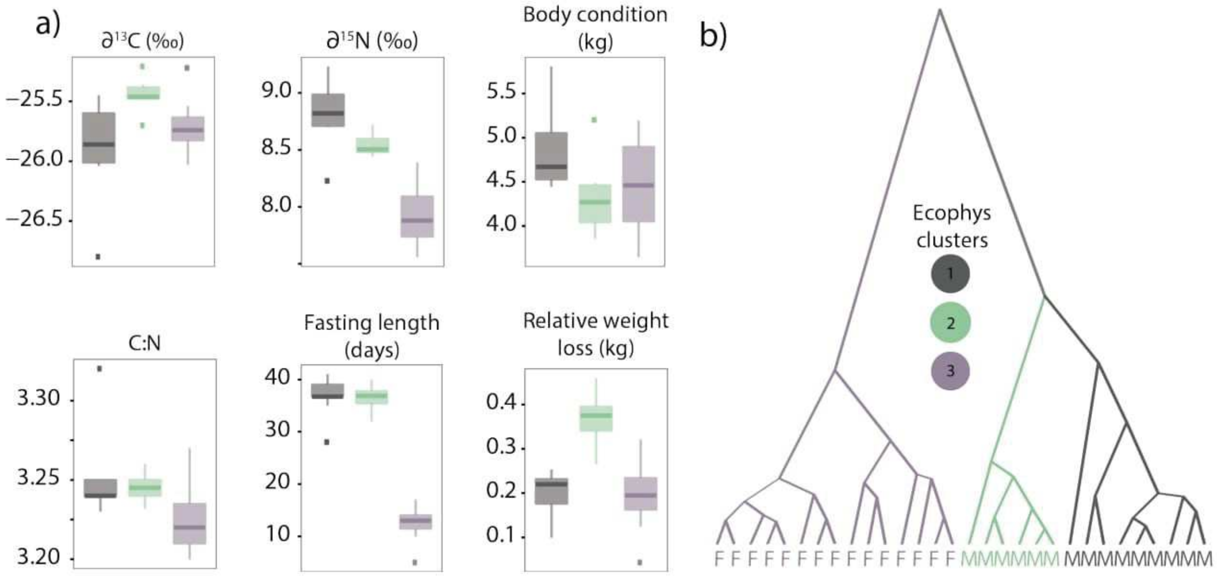
Concentrations of lipophilic contaminants, such as PCBs and OC pesticides, are known to vary with lipid content and lipid composition of the tissue. Lipid are thus often treated as a confounding variable (*i.e.* a variable that influences both the dependent and independent variable resulting in spurious associations) and used to lipid-normalise contaminant data (lipid weight) so to be able to compare absolute concentrations (contaminant burden) between tissues and species of differing lipid contents (Hebert & Keenleyside 1995, Beckmen et al. 1999, Gray 2002). In this study, we are interested in relative circulating concentrations that may reach target toxicity organs, and not absolute contaminant burden in blood. Moreover, the use of total lipid content (*e.g.* dry weight) does not necessarily reflect the heterogeneity of lipid stores that are released during fasting events (*e.g.* Pestana et al. 2014); during seasonal build-up and use of fat resources, adipose tissues may be built from different food source and used in different time frames. Hence, lipid-normalisation of contaminant data is not the most appropriate approach in this context as it may lead to spurious results. Instead, we use total lipids (estimated by lipid metabolic profile; C:N) as a proxy for physiological condition (*i.e.* fasting/feasting condition) and not as an indicator of lipid-associated contaminant release, so that we do not need to explicitly assume homogeneity of lipid sources.

Supplementary Table 2. Sex differences (Students' t-test) in contaminant concentrations (total contaminant load, total contaminant load – Hg, ∑OC Pesticides, ∑PCBs, PFUnA, Hg), foraging tactics (∂^{15}N, ∂^{13}C), fasting state (C:N, relative weight loss, fasting length), mass at arrival and departure, physiological condition (body condition, OXY, d-ROM, RTL) and individual characteristics (age, age at 1st breeding attempt, past breeding effort). Significant p-values (alpha < 0.05) are in bold.

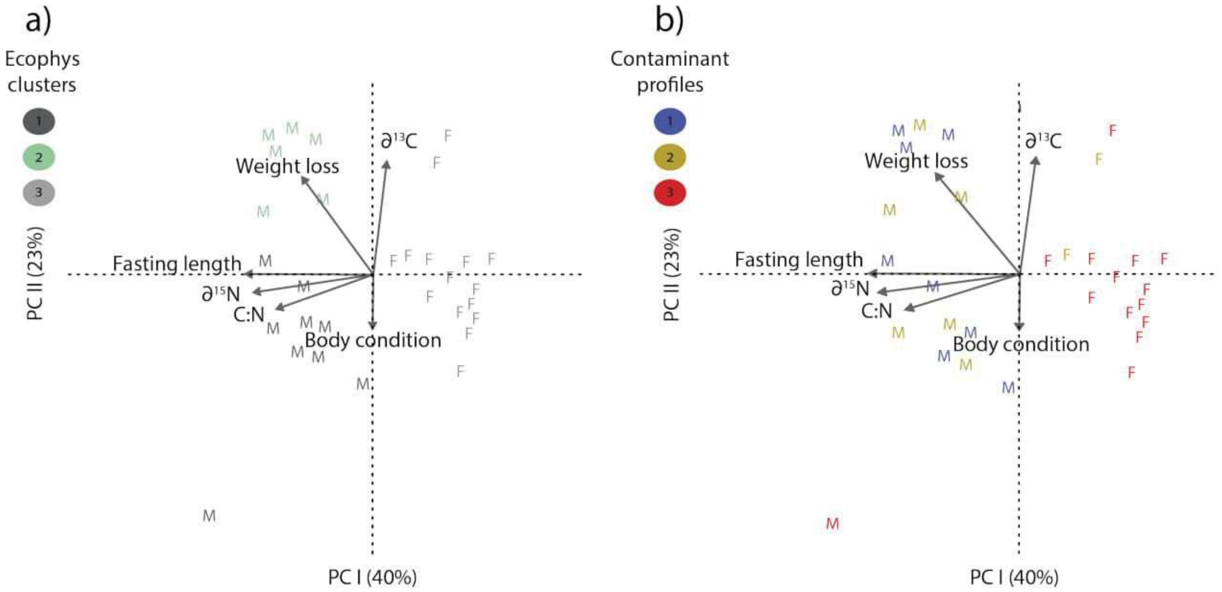
Variable	Females (mean±SD)	Males (mean±SD)	p-value
Total contaminant load (pg.g-1 w.w.)	131117.9±35594.4	205606.4±77549.1	**0.003**
Total contaminant load – Hg (pg.g-1 w.w.)	3577.9±1094.8	3340.4±1124.6	0.563
∑OC Pesticides (pg.g-1 w.w.)	2892.8±956.9	2998.5±1028.5	0.773
∑PCBs (pg.g-1 w.w.)	623.9±267.2	238.4±135.7	**< 0.001**
PFUnA (pg.g-1 w.w.)	61.2±56.4	103.5±113.2	0.210

Hg (pg.g-1 w.w.)	127540±35601.1	202266±77136.9	**0.003**
∂^{15}N (‰)	7.9± 0.3	8.70±0.3	**< 0.001**
∂^{13}C (‰)	-25.7±0.2	-25.7±0.4	0.830
Body condition (kg)	4.5±0.5	4.7±0.5	0.310
C:N ratio	3.22± 0.02	3.25±0.02	**0.002**
Relative weight loss (kg)	0.2± 0.07	0.3±0.10	**0.003**
Fasting length (days)	12.6±2.9	36.7±3.3	**< 0.001**
Mass arrival (kg)	5.4±0.6	6.0±0.5	**0.005**
Mass departure (kg)	4.3±0.5	4.3±0.4	0.815
OXY(uM/OHC neutralised)	219.3±24.1	198.3±34.2	0.062
d-ROM (mg H_2O_2/mL)	36.7±15.2	37.6±237	0.900
RTL (T/S ratio)	1.2±0.4	1.3±0.3	0.400
Age	6.7±1.2	7.1±1.1	0.350
Age at 1st breeding attempt	4.5±1.1	4.4 ±01.0	0.730
Past breeding effort (days)	228.3±78.7	305.4±163.9	0.120

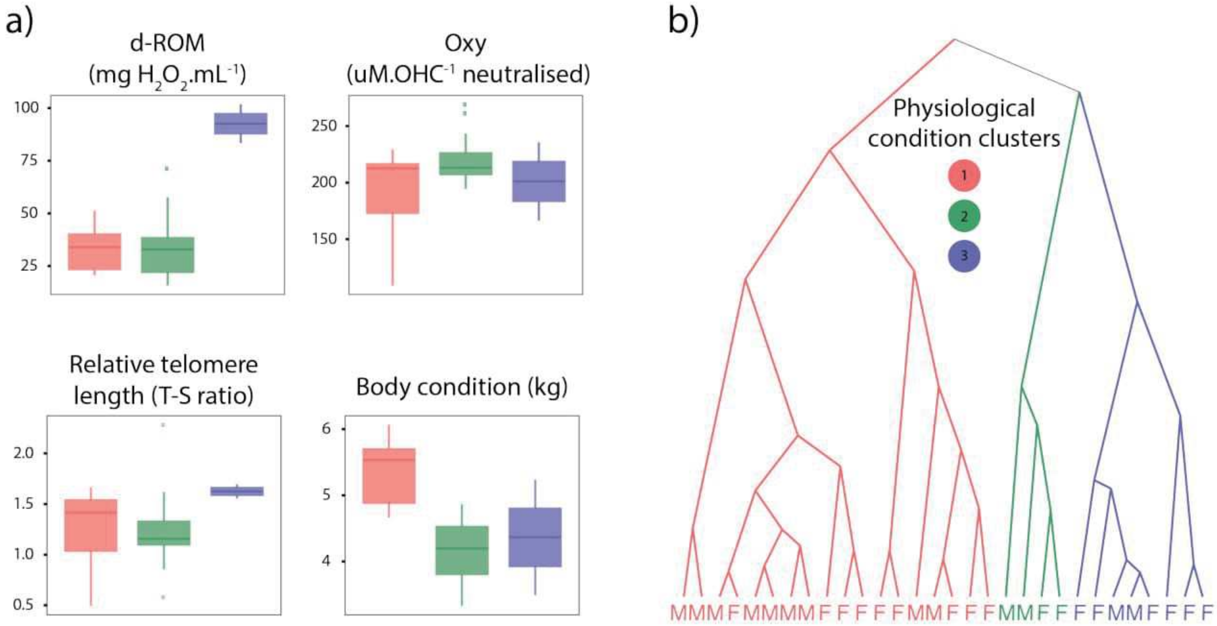
Supplementary Figure 2. **a)** Boxplot of ecophysiological variables (∂^{15}N, ∂^{13}C, body condition, C:N, fasting length and weight loss) grouped by eco-physiological clusters 1 (brown), 2 (green) and 3 (purple). **b)** Dendrogram of hierarchical clustering of eco-physiological variables on Euclidean distances showing the three ecophysiological clusters.



Supplementary Figure 3. Triplot of Principal Component Analysis (PCA) of individuals based on eco-physiological variables, displaying groupings of **a)** ecophysiological clusters and **b)** contaminant profile clusters.



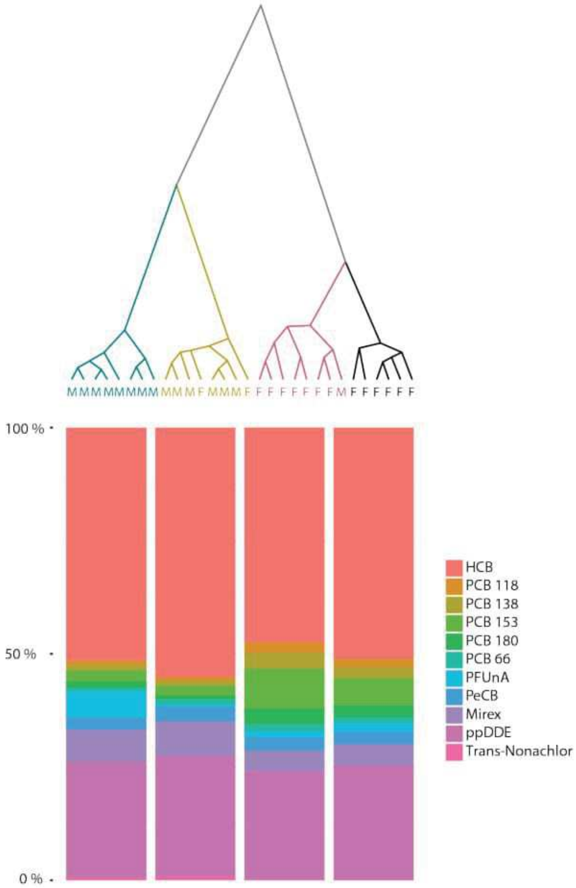
Supplementary Figure 4. a) Boxplots of physiological condition variables (anti-oxidant capacity, oxidative damage, relative telomere length and body condition grouped by physiological condition clusters 1 (red), 2 (green) and 3 (blue). **b)** hierarchical clustering of physiological condition variables on Euclidean distances showing the three physiological condition clusters.



5. Number of clusters

As the primary cluster split was already covered by using pre-set sex groups, including three contaminant clusters allowed us to disentangle which of the eco-physiological descriptors that in combination drove inter-individual variation in contaminant profiles. In addition to the chosen three-cluster repartition, we also found a cluster level 4 that added on a third split within females, driven by dissimilarities in high-chlorinated PCBs (Suppl. Fig. 5). The supervised clustering was thus done for two different levels of contaminant clusters, 3 and 4, and showed a prediction accuracy of 73% and 53%, respectively (Suppl. Table 3 & 4). Thus, the three-cluster repartition of individuals based on contaminant profiles was well predicted by eco-physiological descriptors, better so than a four-cluster repartition. Cluster profiling of physiological stress variables presented unclear optimal levels of clustering beyond two clusters. Since the two-level clusters were already covered in the GLM using pre-set sex categories, we chose to further use cluster level 3.

Supplementary Figure 5. Dendrogram and centroid profiles of contaminant profile cluster level 4.



Supplementary Table 3. Results from linear discriminant analysis of cluster level 3 in contaminant profiling.

Cluster level 3	Coefficient of linear discriminant I	Coefficient of linear discriminant II
$\partial^{13}C$	-1.385	-0.065
$\partial^{15}N$	-1.045	-0.253
C:N	-0.383	0.3424
Fasting length	-1.077	0.211
Body condition	-0.769	-0.738

Relative weight loss	-0.234	0.374

Prior probabilities of groups: 1: 0.33, 2: 0.33, 3: 0.33
Proportion of trace: LD I: 0.986, LD II: 0.014
Prediction error by confusion matrix: 0.267

Supplementary Table 4. Results from linear discriminant analysis of cluster level 4 in contaminant profiling.

Cluster level 4	Coefficient of linear discriminant I	Coefficient of linear discriminant II	Coefficient of linear discriminant III
∂^{13}C	1.291	0.814	-0.007
∂^{15}N	0.959	0.736	-0.196
C:N	0.322	0.592	0.388
Fasting length	1.136	-0.594	0.134
Body condition	0.774	-0.158	-0.755
Relative weight loss	0.331	-0.902	0.279

Prior probabilities of groups: 1: 0.25, 2: 0.25, 3: 0.25, 4: 0.25
Proportion of trace: LD I: 0.950, LD II: 0.040, LD III: 0.009
Prediction error by confusion matrix: 0.467

Supplementary Table 5. Results from Mantell's correlation tests for contaminant profiles versus ecophysiological matrix.

Observation	**Number of replicates**	**Simulated p-value**	**Alternative hypothesis**	**Std.obs.**	**Expectation**	**Variance**
0.219	10000	0.005	Greater	2.901	-0.001	0.006

Supplementary Table 6. Results of general linear models for selecting the most fitting explanatory variable for fasting state (body condition, C:N, relative weight loss and fasting length) in regard to total contaminant concentration (CON).

Model	AICc	Variables	Estimate	SE	t-value	p-value
CON ~ Body condition*Sex	18.8	**Intercept**	12.0	0.7	17.23	**< 0.001**
		Body condition	-0.05	0.2	-0.36	0.724
		Sex	2.14	1.0	2.20	**0.037**
		Body condition*Sex	-0.37	0.2	-1.73	0.095
CON ~ C:N *Sex	27.1	Intercept	14.4	15.0	0.96	0.346
		C:N	-0.8	4.7	-0.18	0.861
		Sex	4.3	20.3	0.21	0.835
		C:N *Sex	-1.2	6.3	-0.19	0.852
CON ~ Relative weight loss*Sex	25.5	**Intercept**	11.6	0.27	43.6	**< 0.001**
		Relative weight loss	0.9	1.27	0.72	0.475
		Sex	0.3	0.37	0.92	0.369
		Relative weight loss*Sex	0.04	1.55	0.03	0.980
CON ~ Fasting length*Sex	27.3	**Intercept**	11.9	0.4	29.8	**< 0.001**
		Fasting length	-0.01	0.03	-0.4	0.723
		Sex	0.34	1.07	0.3	0.755

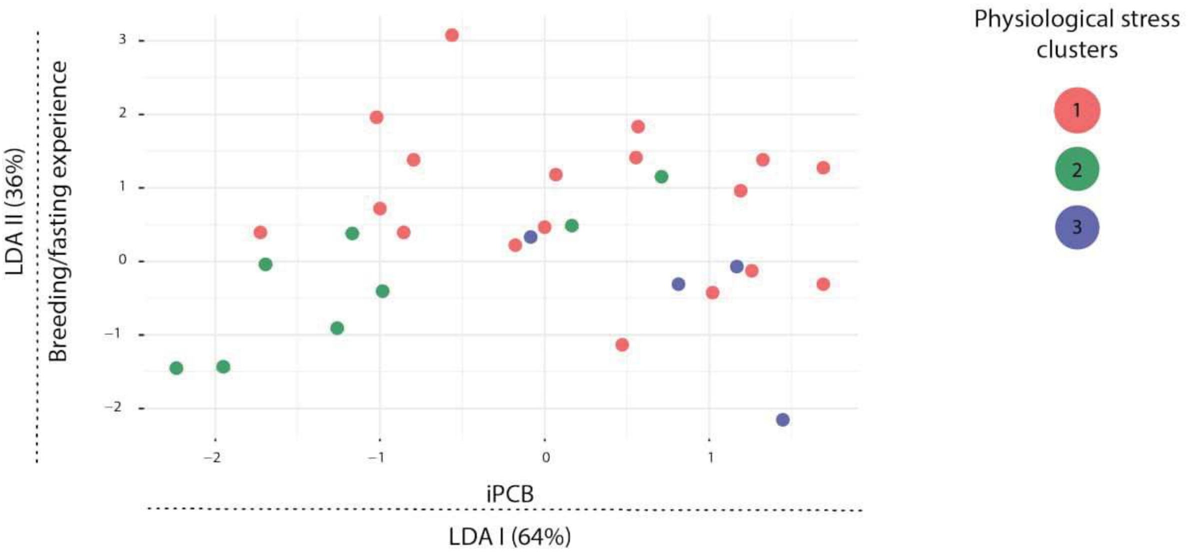
		Fasting length*Sex	0.01	0.04	0.3	0.823

Supplementary Table 7. Results of general linear model for CON explained by fasting state (selected body condition from variable selection) and foraging tactics in interaction with sex category.

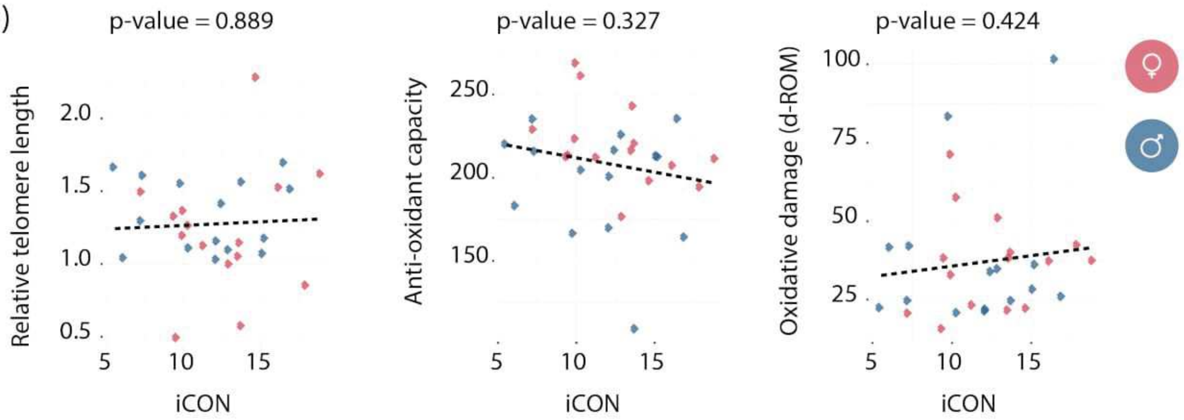
Model	**Variables**	**Estimate**	**SE**	**t-value**	**p-value**
CON ~ Body condition*Sex + ∂^{15}N*Sex + ∂^{13}C*Sex	**Intercept**	3.46	0.9	3.8	**0.001**
	∂^{15}N	-0.02	0.03	-0.5	0.590
	Sex	-0.6	1.02	-0.5	0.603
	∂^{13}C	-0.03	0.04	0.8	0.427
	Body condition	0.006	0.02	-0.4	0.730
	∂^{15}N *Sex	0.03	0.04	0.6	0.570
	∂^{13}C *Sex	-0.02	0.04	-0.5	0.658
	Body condition *Sex	-0.03	0.02	-1.4	0.185

Supplementary Figure 6. (a) Linear Discriminant Analysis-plot with contaminant status (iOCs, iPCB, iPFUnA, iHg) and breeding/fasting experience as discriminants of physiological clusters showing iPCB as the most important discriminator along the first linear discriminant (LD I) and breeding/fasting experience contributing most to the second linear discriminant (LD II). **(b)** Scatterplot plot of the relationship among contaminant status (iCON) and relative telomere length, iCON and antioxidant capacity (Oxy) and iCON and oxidative damage (d-ROM) showing no statistical significance ($p > 0.05$).

a)



b)



Supplementary Table 8. Results of linear discriminant analysis for physiological condition clusters (3) discriminated by contaminant status (iPCB, iPesticides, iPFUnA, iHg) and breeding/fasting experience.

Cluster level 3	Coefficient of linear discriminant I	Coefficient of linear discriminant II
iPesticides	-0.461	-0.364
iPCB	-1.109	-0.501

iPFUnA	0.256	-0.171
iHg	0.138	-0.504
Experience	-0.398	0.968

Prior probabilities of groups: 1: 0.33, 2: 0.33, 3: 0.33
Proportion of trace: LD I: 0.640, LD II: 0.361
Prediction error by confusion matrix: 0.367

Supplementary Table 9. Results from Mantell's correlation tests for matrix of contaminant status and breeding/fasting experience versus physiological condition matrix.

Observation	**Number of replicates**	**Simulated p-value**	**Alternative hypothesis**	**Std.obs.**	**Expectation**	**Variance**
0.074	10000	0.244	Greater	0.669	-0.001	0.013

Supplementary Table 10. General linear model results of physiological condition variables (anti-oxidant capacity (Oxy), oxidative damage (d-ROM) and relative telomere length (RTL) as response explained by total contaminant status (iCON) in interaction with pre-set sex category (female and male).

Model	AICc	Variables	Estimate	SE	t-value	p-value
OXY ~ iCON*Sex	-17.0	**Intercept**	1.72	0.03	55.6	**<0.001**
		Sex	-0.03	0.04	-0.84	0.409
		iCON	-0.002	0.002	-1.11	0.277
		iCON*Sex	0.0008	0.003	0.27	0.787
d-ROM ~ iCON*Sex	273.3	**Intercept**	3.52	0.56	6.13	**< 0.001**
		Sex	-0.27	0.77	-0.35	0.728
		iCON	0.006	0.04	0.15	0.884
		iCON*Sex	0.03	0.06	0.43	0.670
RTL ~ iCON*Sex	32.0	Intercept	-0.003	0.31	-0.009	0.993
		Sex	0.30	0.39	0.78	0.442
		iCON	0.016	0.02	0.69	0.497
		iCON*Sex	-0.02	0.03	-0.57	0.576

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STRASBOURG

Ecologie en mer du manchot Empereur (*Aptenodytes forsteri*)

Stratégies spatio-temporelles de prospection et de recherche alimentaire, et évaluation des outils méthodologiques et de conservation

Résumé

Espèce emblématique régulièrement utilisée pour sensibiliser le public, le manchot empereur est avant tout un prédateur supérieur ainsi qu'une espèce parapluie qui joue un rôle clé au sein des écosystèmes antarctiques. En première ligne face au changement climatique et ses conséquences, il reste cependant beaucoup à apprendre sur la répartition et les activités en mer de cette espèce.

L'utilisation du biologging permet d'affiner la compréhension des interactions existant entre une espèce et les différentes composantes (biotiques et abiotiques) de son environnement dans un souci notamment de gestion, de conservation et d'estimation des potentialités d'adaptation future aux changements globaux.

Dans cette étude, nous développons et partageons de nouvelles méthodes d'équipement qui permettent une durée de suivi accrue et un dérangement réduit des individus équipés.

Grâce à l'analyse spatio-temporelle des données récoltées par le suivi d'individus de différents âges, statuts reproducteurs et issus de différentes colonies autour de l'Antarctique, nous explorons les comportements et stratégies de prospection et de recherche alimentaire présents chez cette espèce, et examinons l'influence des conditions environnementales et de l'habitat sur ces paramètres. Ces informations nous permettent de plus d'évaluer le degré de protection de l'espèce à l'échelle de l'océan Austral et de discuter de plans stratégiques de conservation et gestion globale, telle que la mise en place de réseaux d'Aires Marines Protégées autour du continent Antarctique.

Mots-clés : biologging – conservation – distribution – écologie en mer – Manchot empereur – MPA –océan Austral – raffinement – stratégies d'approvisionnement

Résumé en anglais

Iconic species used to raise public awareness, the Emperor penguin is first and foremost a top predator and umbrella species playing a pivotal role in Antarctic ecosystems. Standing at the forefront of climate upheavals, much remains to be learned about the ecology, distribution, and activities at sea of the species.

Biologging allows to refine our understanding of the interactions between a species and the different components (biotic and abiotic) of its environment, in particular with a view of management, conservation, and assessment of the adaptive capacity of populations to face global change.

In this study, we develop and share new equipment methods that increase equipment and data collection duration, while reducing the disturbance of the equipped individuals.

By carrying out a spatio-temporal analysis of the data collected on individuals of different life-history stages, reproductive status, and from different colonies spanning around Antarctica, we investigate the species' foraging behaviours and strategies and assess the influence of environmental conditions and habitat on these parameters. Such knowledge acquisition allows us to assess the degree of protection of the species at the scale of the Southern Ocean and to discuss strategic plans for conservation and management, such as the establishment of networks of Marine Protected Areas around the Antarctic continent.

Key-words: biologging – conservation – distribution – at-sea ecology – Emperor penguin – MPA – Southern Ocean – refinement – foraging strategies