Corbeau 2020 PhD - Relations entre oiseaux marins et pêcheries

Thesis · October 2020

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LA ROCHELLE UNIVERSITÉ

ÉCOLE DOCTORALE
Euclide

Centre d'Etudes Biologiques de Chizé
UMR 7372 – CNRS / La Rochelle Université

THÈSE
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Soutenue le 08 octobre 2020
pour l'obtention du grade de Docteur de l'Université de La Rochelle
Discipline : Biologie de l'environnement, des Populations, Ecologie

Relations entre oiseaux marins et pêcheries : Albatros sentinelles de l'océan Austral

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A mes grands parents

Préface

Dans ce manuscrit je présente les résultats des études réalisées lors de ma thèse effectuée dans le cadre des programmes européens (ERC) « Earlylife » et « Ocean sentinel » d'Henri Weimerskirch. J'ai eu la chance de mener 3 campagnes de déploiements de balises à Crozet et Kerguelen pendant 7 mois, précédés d'une mission de 4 mois l'été austral 2016/2017, afin de tester de nouveaux prototypes de balises.

Réaliser cette thèse au sein de l'équipe « prédateurs marins » du Centre d'Études Biologiques de Chizé m'a permis d'effectuer de nombreuses collaborations et de continuer à travailler sur des projets entamés lors de mes précédents stages. J'ai également participé à diverses études de terrain menées par différentes équipes du laboratoire et j'ai aussi eu la chance de pouvoir effectuer plusieurs formations et d'encadrer des étudiants sur ce sujet passionnant.

Ce manuscrit remet le sujet dans un contexte plus global des interactions entre les oiseaux et les bateaux dans l'introduction et détaillera les modèles d'études, les balises, les données et les analyses utilisées dans le « matériels et méthodes ». Puis, les résultats sont organisés en trois chapitres composés des trois articles que j'ai rédigés sur le sujet. J'ai souhaité présenter une discussion générale, complémentaire de celles déjà présentées au sein de chaque article, qui ne ciblera donc pas l'intégralité des résultats, mais avant tout les comportements et l'exposition aux bateaux. J'y ai également utilisé les résultats de trois autres articles réalisés en coauteur et pour finir j'évoque nos études actuelles qui donnent lieu à plusieurs articles en préparation ou en cours d'analyse.

Remerciements

Tout d’abord je veux remercier chaleureusement Henri Weimerskirch qui a réussi à me supporter, plus de 8 ans maintenant, depuis mon hivernage aux Kerguelen et notre campagne d’été à Sourcils Noirs. Tu m’as offert de nombreuses opportunités et toujours soutenu, merci !

Je remercie également mes rapporteurs Guy Duhamel et Olivier Duriez ainsi que mes examinateurs Samantha Patrick et Vincent Ridoux pour avoir accepté d’évaluer cette thèse.

Merci à Julien Collet pour ses précieux conseils, sa bonne humeur et les sorties ornithos.

Merci à Florian Orgeret pour ses encouragements et ses réflexions sur Zuur et les données d’Afrique du Sud.

Merci à Adrien Pajot pour les bons moments passés à faire de l’ornitho et à parler de méthodo dans le bureau.

Merci à Rocio pour les longues réflexions que nous avons eues sur les données et sur les projets développés ensemble.

Merci à mes colocs de la maison « Ici C’est Olbreuse » qui a vu passer grand nombre de thésards et d’étudiants et a contribué fortement à la vie de Chizé et aux réflexions existentielles sur la thèse. Merci Julien, Florian, Gaëtan, Meumeu, Tim, William, Jade, Martin, Amélie, Joris, Karine, Bertille, Julie, Juliette. Merci pour les bons moments passés, les séries, les films concepts, les sorties et défis ornithos et les barbecues.

Merci à toute l’équipe de la mission 63 à Kerguelen, ces irréductibles avec qui j’ai énormément partagé : Christophe manchot, Joan, Elsa, Thibault de château, Christophe géophy, Thibaut pop chat, Thomas magic gener, Aymeric, Guillaume pacha, Antoine, Simon, Sophie, Adrien météo et surtout Lauriane.

Mais merci aussi à ceux de la 62 qui sont restés, Maxime et Nathanaël, et à ceux de la 64 qui sont arrivés : Florian (jeune padawan), Élie (inspecteur), Fabrice (hivernator), Frédéric (papy vat), Thomas (l’archer vert) …

Merci au Zornithos 109 de 2013. Nous ne nous sommes plus quittés depuis jusqu’à faire des thèses ensemble : Timothée, Christophe, mon super binôme Joan et Remi, qui est quelque part sur cette planète à manipuler des bestioles.

Merci aux équipes de terrain sans qui tout cela n'aurait pas été possible :

La 54 de Crozet et particulièrement Nicolas (Ragnar), Florent (pour les manips à la cacatière) et Doumé pour son enthousiasme de génie, ses balises toujours pleines de surprises, sa capacité à mettre du stress sur les livraisons de balises jusqu'au tout dernier moment et les très bons moments passés sur la colline et en cabane à Pointe Basse.

La 55 de Crozet : Vincent, Doug, Romain, Roald, puis Célia et Victor pour les indéfectibles maniques tous azimuts…

La 69 de Kerguelen : Julien, Aude et Tobi pour la dernière mission dans mon fief de Kerguelen.

Merci à l'IPEV et aux TAAF pour la logistique dans ces îles perdues du bout du monde. Merci aussi à l'équipage du Marion Dufresne et ses campagnes océano avec qui j'ai passé plus de 100 jours ces dernières années.

Merci à tout le personnel de l'UMR (CNRS et La Rochelle Université) et à son directeur Christophe Guinet, sa directrice adjointe Charline Parenteau et son futur directeur David Grémillet de m'avoir accueilli, parfois logé et souvent nourri (merci Arnaud et Christophe) toutes ces années.

Merci à Dominique, notre maman VAT, pour la gestion de la base de données et son aide précieuse dans toutes les démarches administratives.

Merci à Charly pour les sorties dans la RBI, le suivi des chouettes et tous les bons conseils.

Merci à Olivier qui, sur les conseils de mon super coloc William et de mon ancien collègue du Québec Don Jean, m'a ramassé dans un couloir et m'a emmené faire du terrain au Svalbard. Merci pour ces moments magiques et une fois encore merci Henri d'avoir bien voulu me laisser partir.

Merci à Hervé et Christophe pour les sorties points d'écoute en RBI qui enchantent les printemps.

Merci à toutes les personnes de Chizé avec qui j'ai partagé toutes ces années de travail, d'ultimate, de volley et de tennis et qui n'ont pas vécu à Olbreuse… et il y en a quelques-uns :

Les étudiants, thésards et CDD : Christophe S, Sophie D, Adrien B, Maxime L, Candice M, Erica B, Léa L, Baptiste P, Maxime R, Olivia H, Ryan R, Carine R, Carolina B, Landry B, Émilie D, Pierre Loup J.

Les chercheurs et ITA : Charly B, David P, Akiko K, Yann R, David G, Christophe G, Fred A, Nounours, Karine D, Yves C, Vincent B, Sabrina G, Olivier C, Bruno M, Charline P, Cécile R, Marie P, Simon D, Christian T ; sans oublier l'OFB : Cyril E, Hervé L et Yohan L.

Merci également aux anciens de Chizé que j'ai revu bien des fois (Chizé un jour, Chizé toujours) : Sophie de G, Aurélien P, Paul T, Nory E, Joffrey J, Yves L, Cécile B, Laurie T, Alizée M, Andréas D, Nathan P, Rémi F, Alice C, Rui C, Camille C, Dimitri W et Anthony S.

Mes derniers remerciements vont à ma famille qui m'a toujours soutenu depuis toutes ces années. Merci à mes grands-parents qui connaissent maintenant les TAAF sur le bout des doigts, à mon frère qui commence à son tour une thèse (bon courage à toi) et à ma sœur qui fait maintenant de l'ornitho partout sur la planète. Merci à mes parents, mes plus grands fans. Merci à mon père qui m'apporte, à la toute dernière seconde, à l'aéroport, les balises arrivées en retard et un grand merci à ma mère qui relit avec attention mes lettres et mes manuscrits. Enfin, un immense merci à Lauriane pour son soutien infaillible, même à distance, pour tous les bons moments passés et tous ceux que nous passerons ensemble.

Listes des travaux

Publications en premier auteur sur le sujet de thèse

CHAPITRE 1 :

1. **Corbeau A.**, Collet J., Fontenille M., Weimerskirch H., 2019. How do seabirds modify their search behaviour when encountering fishing boat? ***PLOS ONE***, 14(9): e0222615.

CHAPITRE 2 :

2. **Corbeau A.**, Collet J., Orgeret F., Pistorius P.A., Weimerskirch H., 2021. Fine-scale interactions between boats and large albatrosses indicate variable susceptibility to bycatch risk according to species and populations. ***Animal Conservation*** *(sous presse).*

CHAPITRE 3 :

3. **Corbeau A.**, Collet J., Pajot A., Joo R., Thellier T., Weimerskirch H., 2021. Differences in foraging habitat result in contrasting fisheries interactions in two populations of albatrosses. ***Marine Ecology Progress Series*** *(sous presse).*

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DISCUSSION GENERALE :

4. Weimerskirch H., Collet J., **Corbeau A.**, Pajot A., Hoarau F., Marteau C., Filippi D., Patrick S., 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of non-declared fishing. ***Proceedings of the National Academy of Sciences***, 117(6):3006-3014. **(Annexe 1)**
5. Pajot A., **Corbeau A.**, Weimerskirch H., 2021. Diel at sea activity of two species of great albatrosses: the ontogeny of foraging behaviour. ***Journal of Avian Biology*** *(sous presse).* **(Annexe 2)**
6. Orgeret F., Reisinger R. R, Carpenter-Kling T., Keys D. Z., **Corbeau A.**, Bost C-A., Weirmerskirch H., Pistorius P. A., 2021 Differentiating the effect of intra- and interpopulation competition on spatial segregation in a central place forager. ***Journal of Animal Ecology*** *(en révision).* **(Annexe 3)**

Perspectives :

1. Weimerskirch H., **Corbeau A.**, Collet J., Pajot A., Patrick S. Ontogeny of attraction to boat in albatrosses, personality and conservation implications. *(en préparation).*
2. Joo R., **Corbeau A.**, Basille M., Patrick S., Weimerskirch H. Considerations for machine learning in movement ecology. (*en préparation*).
3. Joo R., **Corbeau A.**, Basille M., Patrick S., Weimerskirch H. Identifying bird-vessel interaction. *(en préparation).*

Autres publications lors de la période de thèse sans rapport direct avec le sujet de thèse

1. **Corbeau A.**, Bost C-A., 2017. A healthy, adult premoulting King Penguin (*Aptenodytes patagonicus*) with a markedly twisted beak. ***Polar record***, 53(6):631-632.
2. **Corbeau A.**, Prudor A., Kato A., Weimerskirch H., 2020. Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. ***Journal of Animal Ecology***, 89(1):20-28.
3. Weimerskirch H., de Grissac S., Ravache A., Prudor A., **Corbeau A.**, Congdon B., McDuie F., Bourgeois K, Dromzée S., Butscher J., Vidal E., Jaeger A., Borsa P., 2020. At-sea movements of wedge-tail shearwaters during and outside the breeding season from four colonies in New Caledonia. ***Marine Ecology Progress Series***, 633:225-238.
4. Collet J., Prudor A., **Corbeau A.**, Mendez L., Weimerskirch H., 2020. First explorations: ontogeny of central-place foraging directions in two tropical seabirds. ***Behavioral ecology***, 31(3):815-825.
5. Patrick S., **Corbeau A.**, Réale D., Weimerskirch H., 2020. Coordination in parental effort decreases with age in a long-lived seabird. ***Oikos***, 129;1763-1772.
6. Wynn J., Collet J., Prudor A., **Corbeau A.**, Padget O., Guilford T., Weimerskirch H., 2020. Evidence for a learnt mechanism of wind-drift compensation in a pelagic seabird. ***Proceeding Royal Society B: Biological Science***, 287(1937):20201970.
7. Patrick S., Martin J., Ummenhofer C., **Corbeau A.**, Weimerskirch H., 2020. Albatrosses respond adaptively to El Nino Southern Oscillation by changing their variance in, but not mean, foraging behaviour. ***Global Change Biology*** *(en révision).*
8. **Corbeau A.**, Pajot A., Pajot M., Peroteau S., Jambon A., 2020. First hybrid White-winged Tern - *Chlidonias leucopterus* X Black Tern - *C. niger* reported in France. ***British Bidrs*** *(soumis).*
9. Collet J., Mendez L., **Corbeau A.**, Prudor A., Weimerskirch H. Different persistence of individual fidelity in two sympatric seabirds in a dynamic environment *(en préparation).*

Formations et communications

1. **Formation :** *Communication écrite*. Pierre Legagneux (CR CNRS) – CEBC, Villers-en-Bois, France – Novembre 2017.
2. **Présentation orale :** *Le programme « Ocean sentinel »*. A bord du Marion Dufresne – Rotation TAAF – Avril 2018.
3. **Présentation orale :** *Le suivi des albatros hurleurs à Crozet, présentation et résultats*. A bord du Marion Dufresne – Campagne Océanographique – Février 2019.
4. **Workshop :** *A Career in Movement Ecology*. Britsh Ecological society : Lucas Börger, Roland Langrock, Justin Travis & Andrea Baier – High Wycombe, Royaume-Unis – Septembre 2018.
5. **Formation :** *Permis bateau option côtière* – Affaires Maritimes – La Rochelle, France – Avril 2019.
6. **Présentation orale :** *Études des comportements de recherche alimentaire des albatros hurleurs en relation avec les pêcheries*. Réunion « Prédateurs marins » – Villers-en-Bois, France – Mai 2019.
7. **Poster :** *How do seabirds modify their search behaviour when encountering fishing boat?* Colloque des deuxièmes années de l'Université de La Rochelle – La Rochelle, France - Juin 2019.
8. **Présentation orale :** *Les grands albatros et leur relation avec les pêcheries*. Colloque des deuxièmes années de l'université de La Rochelle – La Rochelle, France - Juin 2019.
9. **Formation :** *Expérimentation animale sur Faune Sauvage non hébergée*, niveau concepteur. MNHN/CNRS – Paris et Villiers-en-Bois, France - Mars et Septembre 2019.
10. **Présentation orale :** *Relations entre oiseaux marins et pêcheries : Albatros sentinelles de l'océan Austral*. Colloque annuel du Centre d'Études Biologiques de Chizé - Villers-en-Bois, France - Septembre 2019.
11. **Présentation orale :** *Ecologie comportementale par le bio-logging*. Invitation du laboratoire ECOBIO – Rennes, France – Novembre 2019.
12. **Présentation orale :** *Relation entre oiseaux marins et pêcheries : Albatros sentinelles de l'océan austral*. 16èmes journées scientifiques du Comité National Français des Recherches Arctiques et Antarctiques – La Rochelle, France - Septembre 2020.

Lexique

AIS – Automatic Identification System : système d’identification anticollision permettant de connaitre les informations des navires à portée de signal.

ARS – Area Restrict Search : définit un comportement de recherche alimentaire dans une aire restreinte

CCAMLR – Commission for the conservation of Antarctic Marine Living Resources (Commission pour la conservation de la faune et de la flore marines de l’Antarctique)

CEBC – Centre d’Etudes Biologiques de Chizé

CLS – Collecte Localisation Satellites : filiale du Centre national d’études spatiales, d’Ardian et de l’Institut français de recherche pour l’exploitation de la mer. C’est une société internationale, spécialisée dans la fourniture de solutions d’observation et de surveillance de la Terre depuis 1986.

CNRS – Centre National de la Recherche Scientifique

CROSS – Centre Régional Opérationnel de Surveillance et de Sauvetage : ici, l’antenne « sud océan Indien »

ERC – European Research Concil : financeur d’importants programmes de recherche européens

GLMM – Generalized Linear Mixed Model

GLONASS - Global Navigation Satellite System : système de positionnement d’origine soviétique

GPS – Global Position System : système de positionnement d’origine américaine

HMM – Hidden Model Markov : méthode d’identification de comportement à chaque localisation

IOCT – Indian Ocean Tuna Commission

LMM – Linear Mixed Model

SST – Sea Surface Temperature

TAAF – Terres Australes et Antarctiques Françaises : utilisé ici pour les territoires et l’administration française de Crozet, Kerguelen et Saint-Paul Amsterdam

VMS – Vessel Monitoring System

ZEE – Zone Economique Exclusive

Sommaire

Introduction générale

Alexandre CORBEAU

1. Les populations d’oiseaux marins dans le monde et leurs menaces

Les oiseaux marins sont des espèces dépendantes du milieu marin, allant des côtes à la pleine mer en passant par les marais saumâtres, les estuaires et les îles. Il existe 359 espèces d’oiseaux marins qui représentent 3.5% des espèces d’oiseaux dans le monde (Croxall et al. 2012, Paleczny et al. 2015, Dias et al. 2019). Il est estimé que 19% des populations d’oiseaux marins dans le monde sont étudiées, notamment pour leur rôle d’indicateur de l’état de santé du milieu marin dans lequel ils évoluent (Rajpar et al. 2018) car ce sont souvent des prédateurs supérieurs, très sensibles aux changements de leur environnement.

Nous sommes actuellement au milieu d’une crise majeure de perte de biodiversité et dans cette sixième crise d’extinction des espèces due à l’homme, les oiseaux marins ne font pas exception. Il a été mis en évidence que la plupart des populations mondiales d’oiseaux marins étudiées sont en régression (Fig. 1) (Paleczny et al. 2015).

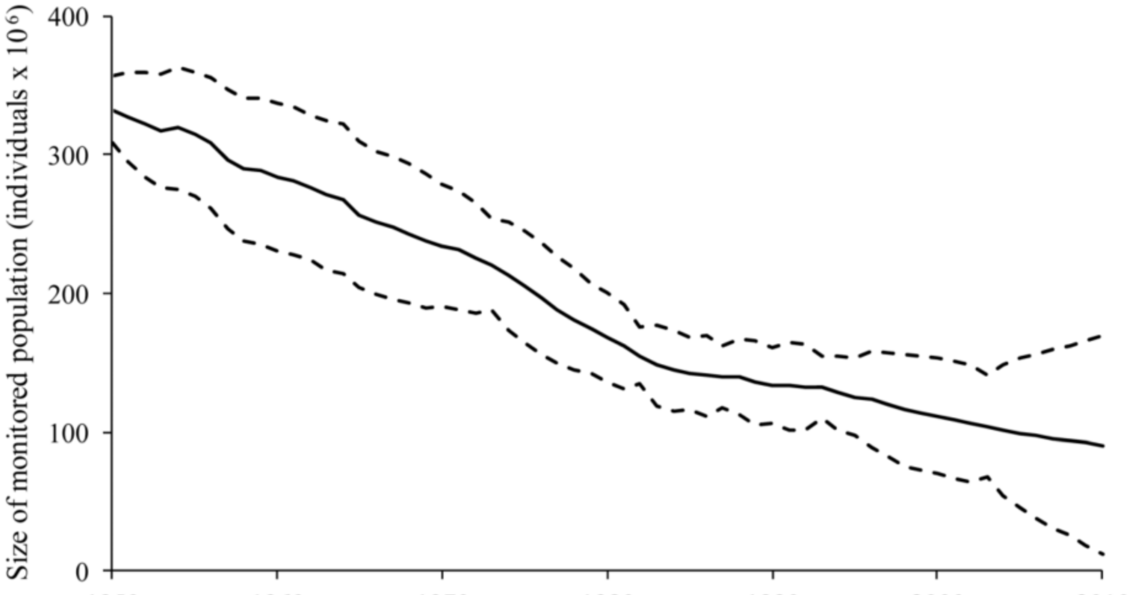


Figure 1 : Chute des populations suivies d’oiseaux marins dans le monde (Paleczny et al. 2015)

Cette diminution à l’échelle du globe s’explique par les risques de plus en plus grands qui pèsent sur ces populations. Ces risques directement ou indirectement liés aux activités humaines touchent toutes les populations et toutes les espèces d’oiseaux marins (Paleczny et al. 2015). Le risque lié aux introductions d’espèces invasives touche le plus grand nombre d’espèces, car de nombreuses espèces d’oiseaux marins nichent sur des îles, milieux très sensibles aux introductions récentes d'espèces prédatrices inconnues jusqu'alors dans ces environnements. Le second risque qui touche le plus d'espèces est celui lié aux captures accidentelles lors des activités humaines de pêche (bycatch), et c'est en moyenne le risque qui a le plus fort impact sur les taux de croissance des populations. Seize autres grands risques sont listés dans les travaux de Paleczny et collaborateurs (2015) tels que la chasse et le piégeage, les changements climatiques, le dérangement, la pollution ou la surpêche (Fig. 2) (Paleczny et al. 2015).

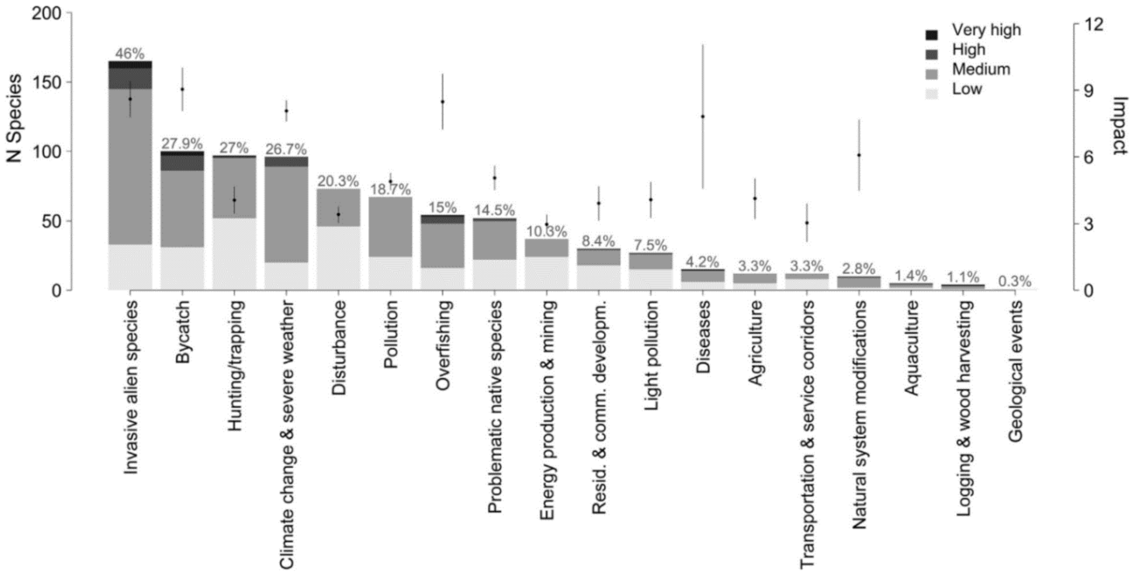


Figure 2 : Risques encourus par les espèces d'oiseaux marins dans le monde (Paleczny et al. 2015)

2. Les activités humaines dans le milieu marin

2.1. Les activités maritimes

La population humaine connait une croissance exponentielle depuis 1950 et atteindra près de 9 à 10 milliards en 2050. Nourrir cette énorme population de façon conventionnelle entraine une emprise toujours plus grande sur le milieu naturel et notamment sur les océans. Recouvrant 70% de la surface du globe, les océans fournissent la majorité des protéines alimentaires à 3 milliards de personnes et font vivre plus de 12% de la population mondiale. L'activité maritime humaine liée à la pêche est considérable (Kroodsma et al. 2018, Watson & Tidd 2018), mais elle l'est d'autant plus si on y ajoute le transport maritime de marchandises ou de personnes. Ainsi, aucune partie des océans n’est totalement à l’écart des activités humaines, seules les régions polaires subissent un impact plus faible (Fig. 3) (Halpern et al. 2008).

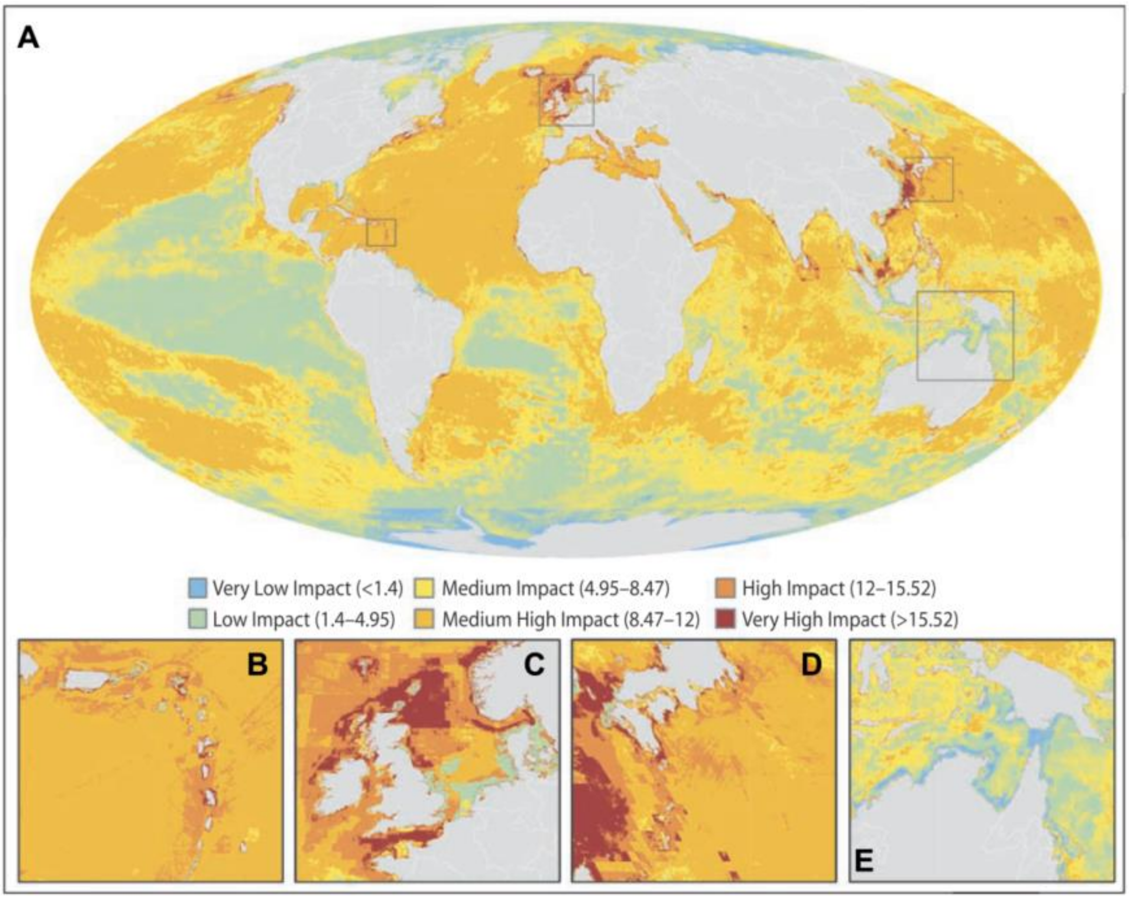


Figure 3 : Impact des activités humaines sur les mers et océans du globe (Halpern et al. 2008)

La densité de bateaux sur le globe est extrêmement forte (Fig. 4) et ne laisse que peu d’espace non occupé entrainant de nombreux contacts entre activités maritimes et faune et tout particulièrement entre bateaux de pêche et oiseaux marins. Ces bateaux de pêche sont responsables des captures accidentelles et de la surpêche, risques dont l’impact sur les populations d’oiseaux marins est très fort et qui affectent respectivement 27.9% et 15% de ces espèces (Paleczny et al. 2015).

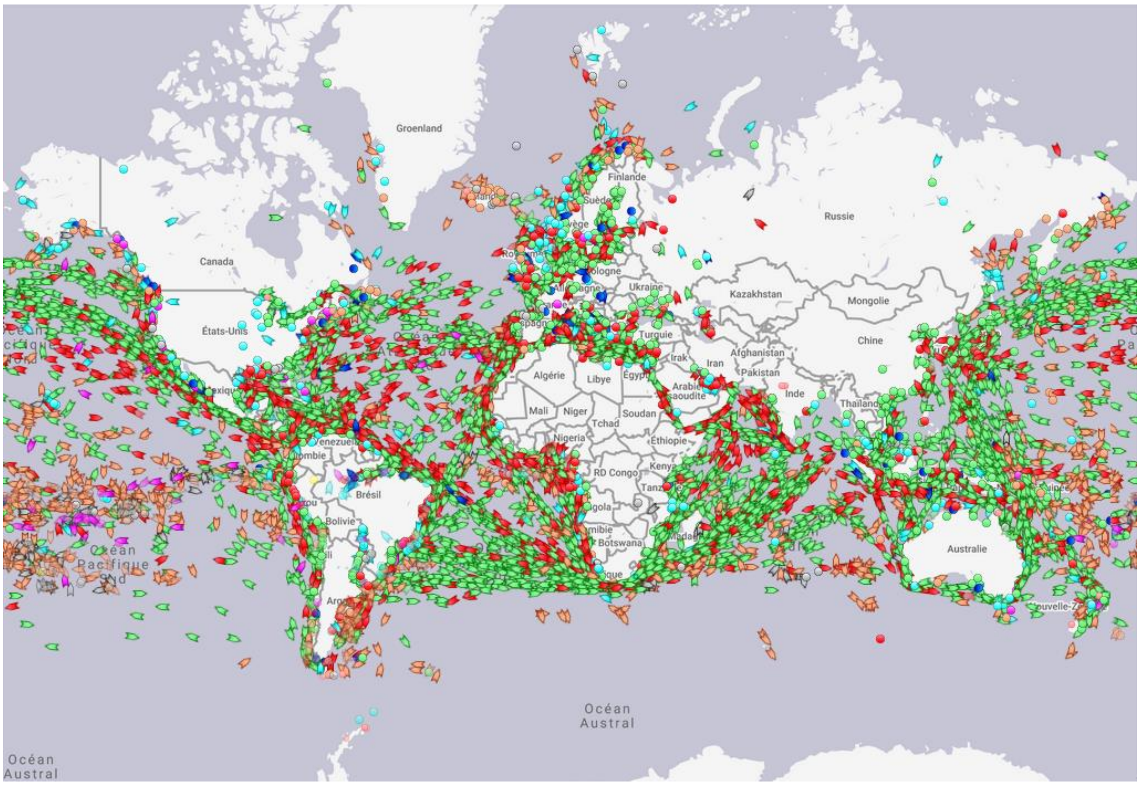


Figure 4 : Trafic maritime mondial (pêche et transport) le 1/08/2020. Marine Traffic ©

2.2. Les pêcheries du sud de l’océan Indien

Notre zone d’étude est localisée au sud de l’océan Indien, entre le sud de Madagascar et le continent antarctique et entre les côtes de l’Afrique du Sud et celles de l’Australie.

Dans cette zone il existe deux grandes techniques de pêche : le chalut et la palangre.

La première est employée le long des côtes du continent africain et au sud de Madagascar et ne représente qu’un danger limité pour l’avifaune (Soriano-Redondo et al. 2016). Dans les Zones Economiques Exclusives (ZEE) des Terres Australes et Antarctiques Françaises (TAAF) le seul bateau de pêche présent autour d’Amsterdam Saint-Paul est un chalutier caseyeur « l’Austral » qui se concentre principalement sur la langouste.

Il existe deux grands types de pêche à la palangre, les palangres pélagiques utilisées dans les pêcheries aux thons et les palangres de fond utilisées pour la pêche à la légine australe. Leurs palangres sont toutes les deux constituées par une ligne mère (câble de pêche pouvant atteindre une centaine de kilomètres de long pour les plus grandes palangres aux thons) à laquelle sont fixées des lignes plus petites (1 à 2 mètres) se terminant par un hameçon.

2.2.1. Les pêcheries aux thons

Les premiers types de pêcheries situées au nord de 40° sud sont des palangriers pêchant le thon, venant majoritairement des pays asiatiques ou d'Espagne et qui pratiquent cette pêche à la fois dans les eaux territoriales et internationales. Cette pêche liée à la mobilité des bancs de thons n'est pas pratiquée sur des zones fixes. Différentes espèces de thon sont visées par ces pêcheries industrielles qui se sont grandement développées depuis 1950 : la bonite (*Katsuwonus pelamis*), le thon jaune (*Thunnus albacares*), le patudo (*Thunnus obesus*) dans les eaux tropicales puis le germon (*Thunnus alalunga*) et le thon rouge du sud (*Thunnus maccoyii*) dans les eaux subtropicales. Les palangres sont pélagiques et déployées entre deux eaux vers 100 à 300 mètres de profondeur selon les espèces visées (Stéquert & Marsac 1986). La ligne mère peut mesurer plus de 100 km de long, avec une ligne secondaire tous les 10 à 100 m. Ces pêcheries mobiles sont très difficiles à surveiller du fait de l'absence de règles notamment dans les eaux internationales. Elles ne sont soumises à aucun contrôle et sont sans contraintes réglementaires de mesures de mitigation. Seules des recommandations de quotas et de bonnes pratiques leur sont fournies et très peu d'observateurs de pêche (personne présente sur le bateau rapportant les faits, mais sans possibilité de verbalisation) sont acceptés à bords.

2.2.2. Les pêcheries à la légine australe

Le second type de pêcherie du sud de l'océan Indien est composé de palangriers pêchant la légine australe (*Dissostichus eleginoides)* en zone subantarctique. Ce poisson, très prisé des marchés asiatiques, représente actuellement la pêche française la plus lucrative. Découvert en 1984 autour de l'archipel des Kerguelen par des chalutiers de l'ex-URSS, cette pêche s'est rapidement développée (dès 1990) par l'utilisation de palangriers plus efficaces. Depuis 1993 c'est 5 000 tonnes de légines qui sont pêchées tous les ans par les palangriers déclarés. Malheureusement entre 1997 et 2004 un véritable pillage des ressources a été effectué par les palangriers illégaux et non déclarés, sans aucune possibilité d'estimation des captures (Lord et al. 2006). Encore maintenant il est très difficile d'estimer les proportions de pêcheries non déclarées.

Cependant, contrairement aux pêcheries de thon, cette pêcherie à la légine se pratique sur des secteurs fixes, aux bords de plateaux océaniques entre 500 et 1 500 mètres de fond. Bien qu'extrêmement étendues, ces aires sont connues, ce qui en facilite leur contrôle.

De plus, la majorité de ces zones se trouve dans des Zones Economiques Exclusive ou bien dans les eaux réglementées de la CCAMLR (Commission pour la conservation de la faune et la flore marine de l'antarctique) ce qui simplifie la surveillance et rend possible l'application des règlementations de la pêche (quota, respect des zones de protections), mais aussi l'application des mesures de mitigations pour limiter les captures accidentelles.

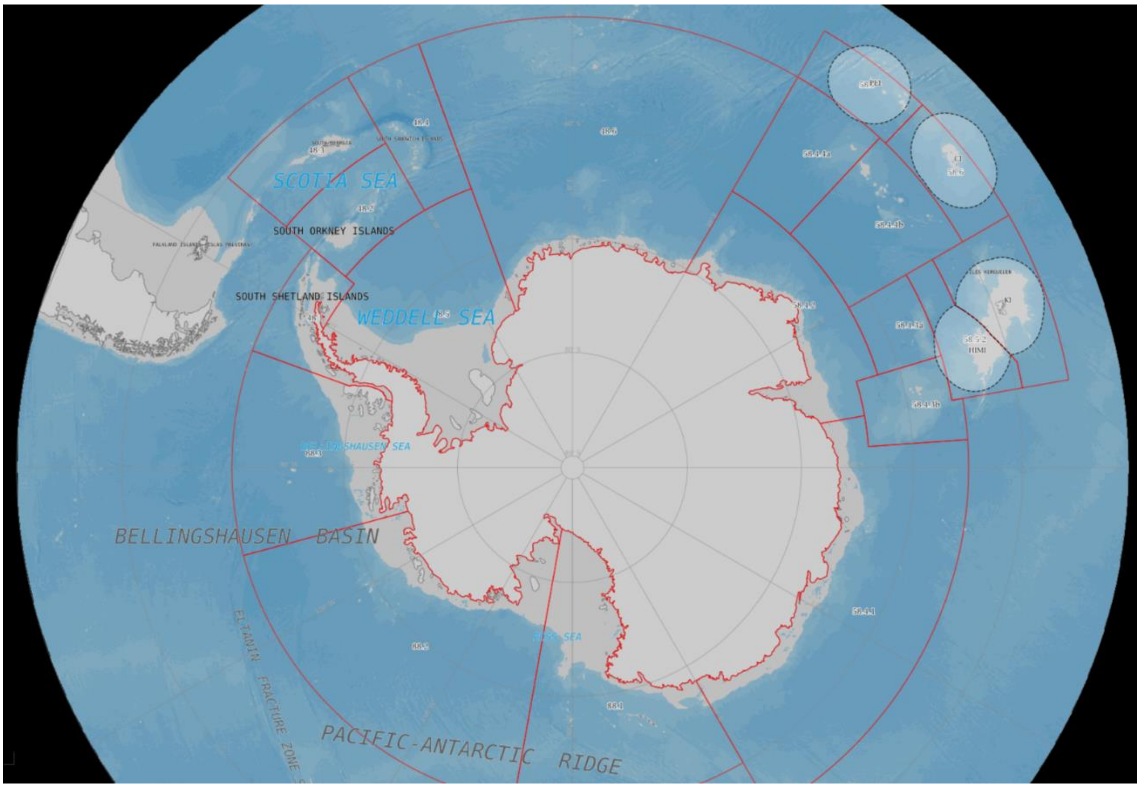


Figure 5 : Carte de l'océan Antarctique (<40° sud). En rouge la zone CCAMLR ; les zones plus claires en pointillés sont les ZEE (de haut en bas) des îles Prince Édouard, des îles Crozet, des îles Kerguelen et de Heard & McDonald (CCAMLR, 2020).

La ligne mère ne mesure que quelques kilomètres de long avec une ligne secondaire tous les quelques mètres. Les quatre pêcheries à la légine de Kerguelen, Heard-McDonald, Crozet et Prince Edward-Marion sont devenues des pêcheries exemplaires dans les gestions des captures accidentelles. En effet, suite aux constatations alarmantes du taux de mortalité d'oiseaux dans les palangres à travers le monde (Croxall et al. 2012) et particulièrement dans cette zone (Delord et al. 2005), des mesures de surveillance de pêche et des mesures de réduction de la mortalité (ou de mitigation) ont été mises en place. Les principales mesures de mitigation mises en place pour réduire la mortalité aviaire sont :

1. Le plombage des lignes afin qu'elles restent émergées et accessibles le moins longtemps possible aux oiseaux.

2. La mise à l'eau des lignes de nuit lorsque la plupart des oiseaux sont moins actifs.
3. La mise en place de banderoles d'effarouchement (bandes de plastique flottant au vent, situées de chaque côté de la palangre empêchant les oiseaux d'avoir accès à la partie émergée de la palangre).
4. L'utilisation de nouveaux modèles de bateau filant les palangres depuis un puits intérieur situé au centre du bateau rendant totalement inaccessibles les lignes aux oiseaux.
5. Le rejet des déchets de pêches en dehors des moments des mises à l'eau et des remontées des lignes qui constituent les principales périodes à risque de captures accidentelles afin de limiter l'attractivité des navires.
6. L'embarquement d'un observateur des pêches, chargé de faire respecter ces règles, ayant la capacité législative de dresser des procès-verbaux, d'obliger les pêcheurs à arrêter l'action de pêche et à changer d'endroit s'il y a constatation d'une surmortalité d'oiseaux (dans la limite de 3 oiseaux morts).

Ces mesures sont obligatoires dans les eaux territoriales françaises des TAAF sur les sept bateaux réunionnais déclarés ainsi que dans les eaux territoriales sud-africaines de l'archipel Prince Édouard (1 bateau déclaré) et il est maintenant totalement interdit de pêcher dans les eaux territoriales australiennes d'Heard & McDonald. Ces mesures sont très fortement recommandées dans la zone CCAMLR par convention signée par 26 pays membres et 10 autres adhérents, sur la protection de ces eaux internationales (Ashford 1998, Waugh et al. 2008).

Pour faire respecter ces règles et lutter contre la pêche illégale, actuellement, seuls trois bateaux patrouilleurs français (2 frégates militaires alternant leur présence sur place et un ancien bateau de pêche) et un Australien surveillent les ZEE françaises et australienne (soit plus de 2 millions de km²).

En conclusion, si cette pêcherie à la légine est effectivement exemplaire sur la gestion du risque de captures accidentelles, ces mesures ne sont évidemment respectées que par les bateaux déclarés dans ces zones réglementées. Qu'en est-il des bateaux déclarés, mais pêchant dans d'autres eaux internationales où ces mesures sont certes recommandées, mais non obligatoires et où aucun contrôle ne peut être effectué ? Qu'en est-il des bateaux pirates ou non déclarés dont la présence et le nombre ne sont même pas connus ? Une étude de 2016 (Pauly & Zeller 2016) a estimé que les données réelles de capture dans le monde étaient 66% supérieures aux données de captures déclarées, notamment en raison de la présence de pêcheries illégales dont l'impact n'est pas réellement connu (Fig. 6).

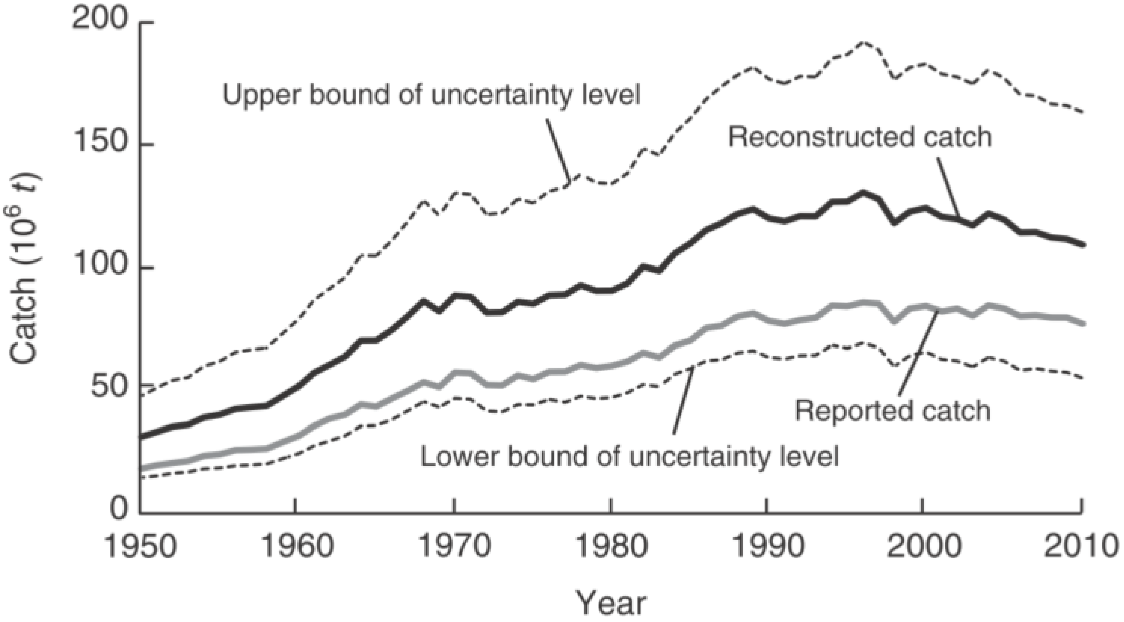


Figure 6 : Estimation des captures de poissons réelles dans le monde (« Reconstructed catch »), vis-à-vis des captures de poissons déclarées par les bateaux de pêche (« Report Catch ») (Pauly & Zeller 2016).

3. Les relations entre les oiseaux marins et les pêcheries

3.1. Ce qui est déjà connu

Les oiseaux marins, présents dans toutes les eaux du globe, sont forcément en contact avec les bateaux qui naviguent eux aussi sur l'ensemble des océans et mers de la planète et de nombreuses études ont fait état des relations bateaux - oiseaux marins.

3.1.1. L'impact des oiseaux marins sur les pêcheries

Dans la littérature, à ma connaissance, il n'y a pas de signalement montrant que les oiseaux marins entraineraient une déprédation importante engendrant des pertes de revenu pour les pêcheurs contrairement aux mammifères marins comme les orques, cachalots ou même les pinnipèdes (Tixier et al., 2010; van den Hoff, Kilpatrick, & Welsford, 2017) qui évoluent pourtant dans des secteurs similaires. Malgré tout, les oiseaux ont un impact financier pour les pêcheurs par le surcoût engendré par la mise en place des mesures de mitigation liées au matériel ou aux conditions de travail plus contraignantes, de nuit notamment (Afán et al. 2018). Dans une moindre mesure, les prises d'appâts sur les hameçons par les oiseaux réduisent les capacités de capture des palangres. Les pêcheurs ont donc intérêt à diminuer autant que possible ces captures accidentelles synonymes de pertes de revenu, même s'il a parfois était observé des captures intentionnelles d'oiseaux marins dans l'ouest de l'Afrique pour la consommation (Gremillet et al. 2015).

3.1.2. La recherche alimentaire

Au cours de leur recherche de nourriture en mer, les oiseaux marins ont de fortes probabilités de rencontrer des bateaux et notamment des bateaux de pêche. Ces éléments du paysage, bien que relativement nouveaux pour les oiseaux marins, car la pêche industrielle n'est utilisée à grande échelle que depuis une centaine d'années, ont entrainé des conséquences notables sur leur recherche alimentaire.

Ces bateaux peuvent être une compétition directe pour les oiseaux. Les pêcheries et les grandes colonies d'oiseaux marins se concentrent inévitablement toutes les deux dans les zones les plus productives en poissons (Fig. 7). La surpêche peut ainsi entrainer une réduction des stocks de leurs proies habituelles et impacte largement les populations d'oiseaux qui vont soit disparaitre, soit devoir s'adapter en changeant de proies qui seront alors moins appropriées (Bertrand et al. 2012a).

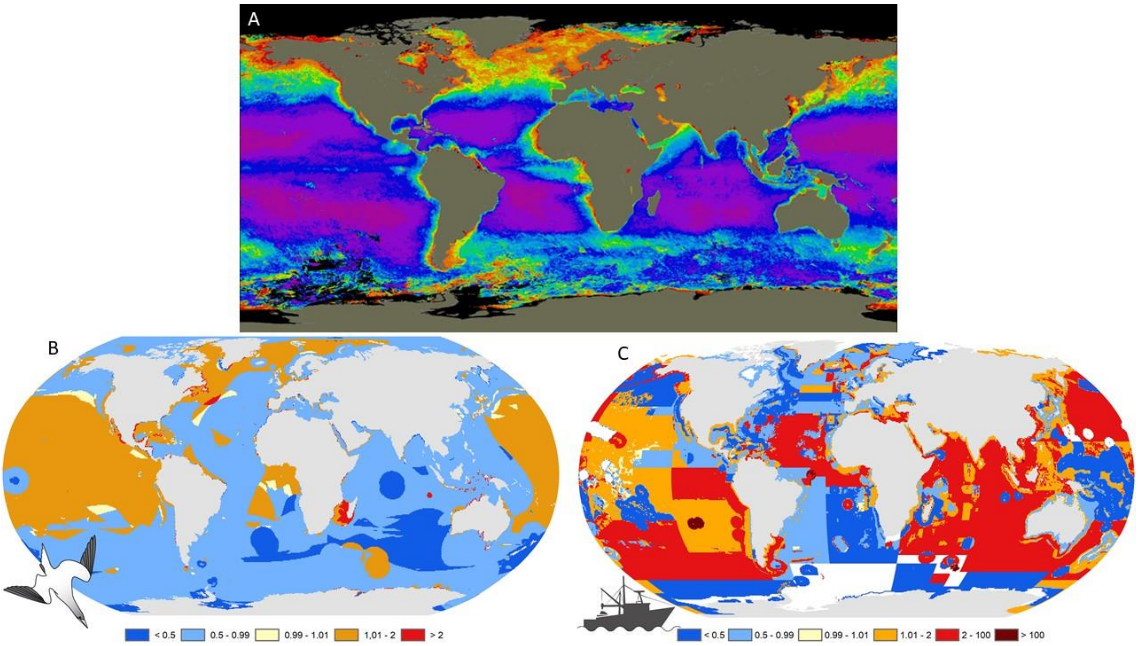


Figure 7 : Carte A : Production primaire de phytoplancton dans le monde (NASA, 1998). Carte B : Densité des oiseaux marins dans le monde (Grémillet et al. 2018). Carte C : Densité des pêcheries dans le monde (Grémillet et al. 2018).

Dans ce premier type de relation, il y a une cooccurrence entre les bateaux de pêche et les oiseaux marins. Ces derniers n'entrent pas volontairement en contact avec les bateaux de pêche, ils subissent leur présence et leur compétition sur leur zone de pêche traditionnelle comme cela a été montré chez les fous du Cap, sur les côtes ouest d'Afrique du Sud par exemple (Okes et al. 2009). Dans un second type de relation existant entre bateaux de pêche et oiseaux marins, il y a une utilisation volontaire par les oiseaux de cette nouvelle source de nourriture (Bugoni et al. 2010). Les bateaux de pêche par leur activité rendent accessible aux oiseaux une nourriture qui ne l'est pas naturellement. Cette nouvelle disponibilité peut être due à quatre facteurs différents. Elle peut être liée au type de pêche pratiquée par la prise de poissons pêchés en profondeur qui n'étaient jusqu'alors pas accessibles aux oiseaux en surface. Elle peut être due aux espèces pêchées avec, par exemple, des viscères et têtes de poissons rejetés sur place qui peuvent être facilement utilisés par les oiseaux alors qu'ils ne se nourriraient jamais sur des thons ou des légines dans d'autres circonstances. Elle peut être la conséquence des moyens de capture utilisés avec des palangres qui permettent l'accès non seulement aux poissons remontés, mais aussi aux appâts mis sur les hameçons au filage des lignes. Elle peut enfin être le résultat de l'absence de sélectivité de la pêche, car une pêche peu sélective entraine une augmentation du nombre de prises non désirées ou accessoires qui sont remises à l'eau, en général mortes ou en mauvais état et qui sont alors aisément accessibles aux oiseaux.

3.1.3. Une nourriture de mauvaise qualité

Un lien direct existe entre la recherche alimentaire des oiseaux marins et la mise à disposition par les bateaux de pêche d'une nourriture qui ne serait naturellement pas disponible sous cette forme. Cette nourriture largement consommée par les oiseaux marins (Bugoni et al. 2010) peut être de moins bonne qualité que leur nourriture naturelle (« *junkfood hypothesis* » - Gremillet et al., 2008; Österblom, Olsson, Blenckner, & Furness, 2008) et pour une même quantité, c'est-à-dire un même estomac rempli, la moindre qualité de cette « junkfood » a des conséquences certaines sur la fitness des individus et des populations entières qui se spécialisent dans ce type de nourriture.

3.1.4. Le risque de captures accidentelles et l'évaluation de ces impacts

La relation entre les oiseaux marins et les pêcheries dont l'impact est le plus étudié est le risque de captures accidentelles (« by-catch »), car c'est la principale cause de mortalité chez les oiseaux marins à travers le monde.

Les oiseaux marins viennent au contact des pêcheries lorsque la nourriture est accessible dans les engins de pêche (sur les hameçons ou prises dans des filets). Ils tentent alors de s'y nourrir et c'est à ce moment-là qu'ils vont être hameçonnés ou emmêlés dans les lignes de pêches et mourir noyés (Fig. 8).

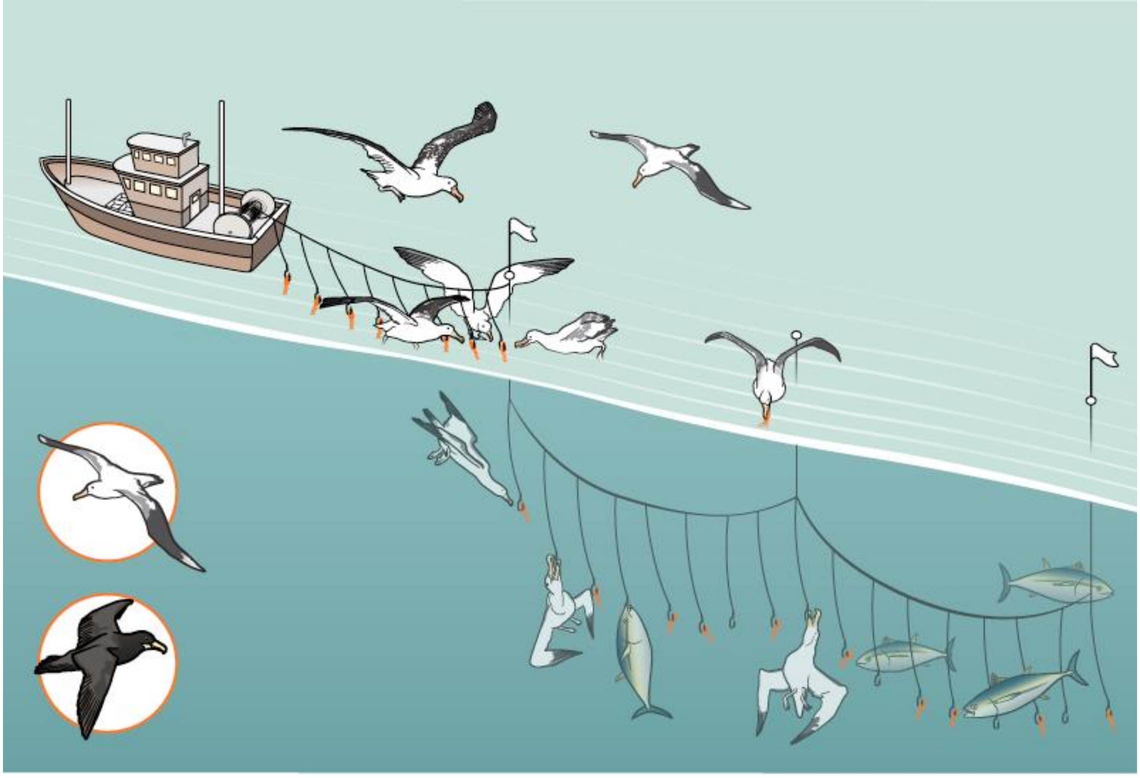


Figure 8 : Schéma de captures accidentelles chez les oiseaux marins dans les pêcheries à la palangre (E. Eng et W. Pipkin smithsonianmag.com, 2016)

Même si les captures accidentelles sont présentes dans la plupart des types de pêcheries, allant des énormes sennes aux petits bateaux de pêche traditionnels (Bærum et al. 2019), c'est bien la pêche à la palangre qui est la plus meurtrière pour les oiseaux marins, mais aussi pour un grand nombre d'autres espèces (requins, dauphins, tortues, raies…) (Jiménez et al. 2019). C'est dans ce type de pêche qu'il est estimé qu'entre 160 000 et 320 000 oiseaux marins sont tués chaque année (Anderson et al. 2011) dont majoritairement des albatros, pétrels et puffins. Cependant depuis 1990 et la mise en place de mesures de mitigations (comme celles évoquées ci-dessus), il a été montré que les captures accidentelles pouvaient être substantiellement diminuées (Jiménez et al. 2020) voire être quasiment nulles dans certaines pêcheries. Dans le même temps, la surveillance des pêches est devenue de plus en plus importante et performante et permet de lutter, ou tout au moins de mettre une certaine pression, sur les pêcheries non déclarées (Anderson et al. 2011).

Ce risque de captures accidentelles existe dès qu'il y a une pêcherie active, mais comment est-il évalué ? Il est très difficile de l'apprécier précisément, car, notamment pour la pêche thonière, il s'agit de plusieurs flottilles avec des bateaux appartenant à de nombreux pays, pas toujours déclarés et navigants dans de vastes océans comprenant de très larges zones d'eaux internationales sans réglementation.

Comme il est impossible de mettre un observateur sur chaque bateau de pêche, ces risques sont classiquement évalués par la superposition des données disponibles de présence des bateaux de pêche avec les aires de répartition des oiseaux issues de la biotélémétrie, et par les rares observations faites sur la mortalité dans le type de pêcherie correspondante. Les données de présence des bateaux peuvent être fournies par chaque pays au sein d'une ZEE, ce sont les données VMS (Vessel Monitoring System). Ces données, très difficiles à obtenir auprès des autorités compétentes, sont souvent dégradées, accessibles avec un délai souvent très long et, dans tous les cas, elles ne correspondent qu'aux bateaux autorisés dans une ZEE. L'autre type de données accessibles est lié à l'effort de pêche issu des données des organisations régionales de pêche et donc dans notre zone d'études l'Indian Ocean Tuna Commission - IOTC et la CCAMLR) avec un nombre d'hameçons des palangriers déclarés par grille 5x5°.

3.2. Le cas des grands albatros dans l'océan Austral

Le groupe des grands albatros est représenté par 6 espèces présentes dans l'océan Austral. Dans cette thèse, je me suis focalisé sur l'albatros hurleur (*Diomedea exulans*) et l'albatros d'Amsterdam (*Diomedea amsterdamensis*). Si peu de choses sont décrites précisément sur le comportement alimentaire de l'albatros d'Amsterdam, nous pouvons vraisemblablement penser que, par similarité morphologique et écologique, son régime alimentaire et ses comportements de recherche alimentaire sont en partie comparables aux albatros hurleurs bien connus.

Les grands albatros sont des prédateurs et charognards opportunistes. Ils pratiquent le vol plané sur d'énormes distances, en moyenne 5 500 km de distance, à 1 300 km autour de leur colonie (Weimerskirch et al. 1993) pendant les trajets d'incubation d'une durée moyenne de 10 jours et s'étendant sur tout l'océan Austral le reste de l'année. La stratégie de ces espèces d'albatros est de parcourir la plus longue distance possible sans effort afin de trouver de la nourriture de façon opportuniste avec environ une capture de proie tous les 100 km (Weimerskirch & Wilson 1992), car ces albatros ne sélectionnent pas de zones spécifiques riches en ressources (Weimerskirch 2007). Les grands albatros lorsqu'ils passent d'un comportement de transit à un comportement de recherche de nourriture actif vont rentrer en ARS (Area Restrict Search) c'est-à-dire adopter un comportement de recherche de proie avec une vitesse qui diminue et une sinuosité qui augmente, et utiliser deux stratégies alimentaires : le nourrissage « en vol opportuniste », ou le nourrissage « posé sur l'eau à attendre » (Weimerskirch et al. 2007). Ils sont principalement charognards et profitent de toutes les sources de nourriture disponibles à la surface de l'océan sachant qu'ils ne se nourrissent jamais à terre. Ils se nourrissent à la surface sans plonger à plus d'un mètre de profondeur et consomment principalement des calmars (Cherel et al. 2017). Une partie de ces calmars sont vraisemblablement des individus morts, qui flottent à la surface après la reproduction (Jackson et al. 2007). C'est pourquoi les pelotes de rejection (où ils régurgitent ce qu'ils n'ont pu digérer) des albatros contiennent quasi systématiquement des becs de calmars, des plumes de manchots ou de gorfous issues certainement des cadavres provenant des nombreuses colonies situées aux abords de leurs sites de reproduction.

Cette capacité à se nourrir d'éléments très divers situés à la surface de l'eau attire inévitablement les albatros vers les bateaux qui rejettent des déchets alimentaires et surtout des déchets de pêches. C'est d'ailleurs ce qui a fondé leur mauvaise réputation dans des temps plus anciens, car lorsqu'un marin passait par-dessus bord dans ces eaux froides et qu'il mourait en moins de dix minutes d'hypothermie, les albatros ne manquaient pas d'utiliser cette nourriture facilement accessible.

Les albatros sont adaptés depuis leur apparition il y a 15 à 20 millions d'années à exploiter des ressources souvent très dispersées et imprévisibles de leur environnement (Weimerskirch 2007). Ils sont connus des grands navigateurs depuis fort longtemps et ont parfois inspiré les poètes (Baudelaire, 1861), mais depuis une cinquantaine d'années les albatros ont vu un nouvel élément entrer dans leur paysage de recherche alimentaire : les bateaux de pêche. Par nature très curieux et opportunistes, les albatros n'ont pas tardé à s'approcher (Collet, Patrick, & Weimerskirch, 2017a, 2017b), parfois dangereusement de ces nouveaux venus.

En 1984, 50% de la population d'albatros hurleurs des Terres Australes et Antarctiques Françaises avait disparu en l'espace de 15 ans à cause de la mortalité induite par la pêche palangrière au thon dans les eaux subtropicales (Weimerskirch & Jouventin 1987, Weimerskirch et al. 1997a). En 6 ans (de 2001 à 2006), c'est près de 40 000 oiseaux qui sont morts dans la nouvelle pêcherie à la légine qui s'est développée dans les eaux françaises, avant la mise en place des mesures de mitigations (Delord et al. 2005, 2010). Il s'agissait principalement de puffins à menton blanc et d'albatros.

Ces albatros sont donc des espèces privilégiées pour étudier les relations entre les oiseaux marins et les pêcheries, non seulement pour les risques certains auxquels ils sont exposés, mais aussi pour leur adaptation comportementale à cette nouvelle présence de bateaux de pêche. Enfin, au sein des populations de l'océan Indien, un exceptionnel suivi long terme permet de connaitre un grand nombre des traits d'histoire de vie de ces espèces (sexe, âge, personnalité, succès reproducteur) et de les comparer aux différents types de bateaux avec lesquels ils sont en contact.

3.3. Ce qui n'est pas encore connu

Même si les grands albatros sont très étudiés et sont considérés comme de bonnes espèces sentinelles des océans (Weimerskirch et al. 2012), de nombreuses zones d'ombre persistent dans leurs relations avec les bateaux de pêche. Nous ne connaissons pas la proportion et l'impact de ces contacts avec les bateaux et s'ils varient d'un individu ou d'une population à l'autre. Nous ne savons pas non plus ce qui influence l'attraction de ces oiseaux pour les bateaux et si cela modifie leur comportement, ou si la rencontre des albatros et des bateaux de pêche n'est que fortuite et le résultat d'une cooccurrence sur un même lieu de pêche. Nous ne savons pas évaluer précisément le risque de captures accidentelles engendré par ces rencontres ainsi que toutes les caractéristiques individuelles des oiseaux et des bateaux qui l'influence. À ce stade nous ignorons également la part prise par la pêche non déclarée dans ces océans très vastes et très difficiles à surveiller.

4. Objectifs et structure de la thèse

4.1. Objectifs, questions et hypothèses de la thèse

Comme nous l'avons vu précédemment peu d'études se concentrent sur les interactions entre les oiseaux marins et les bateaux et de nombreuses questions demeurent. Dans ma thèse je me suis donc intéressé à ces zones d'ombre en prenant le modèle des grands albatros pour répondre aux questions suivantes et émettre un certain nombre d'hypothèses :

- Les comportements de recherche alimentaire des oiseaux marins sont-ils différents entre la recherche de nourriture naturelle et celle associée à un bateau ? (Chapitre 1).
    - ➔ L'attraction au bateau dépend de différents facteurs et notamment de la détection du bateau par les oiseaux et par la présence de congénères. Cela doit conduire à un temps plus important passé derrière les bateaux et une sinuosité plus grande en attendant l'accès à la nourriture. De plus, les différentes pêcheries rencontrées par les albatros ont des pratiques distinctes et donc offrent des accès différents à la nourriture pour les oiseaux marins. Le temps d'attente pourrait être plus grand sur les pêcheries à la légine qui ne travaillent que la nuit et sur de plus petites palangres.
- L'exposition au risque de captures accidentelles est-elle différente d'une population et d'une espèce à l'autre ? (Chapitre 2)
    - ➔ La principale cause de mortalité des grands albatros est liée à leur interaction avec les bateaux. Les différentes espèces et populations de grands albatros de l'ensemble de l'océan Indien ont des comportements et tendances populationnelles différents. Nous nous attendons donc à voir les albatros d'Amsterdam, à très forte croissance populationnelle, être moins exposés que les populations de Marion qui sont en légère hausse ou que les populations de Crozet et de Kerguelen qui sont stables.
- L'estimation du risque de captures accidentelles actuelle est-elle la plus pertinente et la plus fine possible ? (Chapitre 2)
    - ➔ Les données haute résolution des oiseaux, mais aussi des bateaux sont maintenant disponibles, il est donc possible de développer une méthode permettant une estimation à plus fine échelle des interactions entre les oiseaux et les bateaux et ainsi de mieux évaluer le risque de captures accidentelles.
- L'utilisation de l'habitat ne diffère-t-elle pas entre les populations et les individus aux traits d'histoire différents ? Cela ne résulte-t-il pas d'une différence d'exposition au risque de captures accidentelles ? (Chapitre 3)

  - ➔ Nous nous attendons à ce que les traits d'histoire de vie des individus tels que le sexe ou l'âge aient une grande influence sur l'utilisation de l'habitat et l'exposition au risque. Nous prédisons que la population de Kerguelen, qui a un vaste plateau péri insulaire très productif, a un comportement diffèrent de celle de Crozet qui dispose d'un petit plateau. Nous soupçonnons aussi que les femelles, qui se nourrissent plus au nord de leur colonie que les mâles, seront plus exposées au risque de captures accidentelles notamment du fait de leurs rencontres avec des pêcheries aux thons non réglementées.
- Quels sont les éléments qui peuvent influencer l'attraction aux bateaux chez les albatros : l'origine de l'oiseau (Crozet ou Kerguelen) ? Le type de bateau (pêcherie ou cargo / déclaré ou non déclaré) ? La présence de rejets ? (Chapitre 3)
  - ➔ Les oiseaux de Kerguelen sont plus en contact avec des pêcheries déclarées et « peu dangereuses », ils devraient donc être naturellement plus attirés par les bateaux. Les bateaux de pêche fournissent de grandes quantités de nourriture contrairement aux cargos ce qui devrait attirer plus les oiseaux. Enfin l'influence des rejets de pêche sur l'attraction n'a pas été clairement étudiée même si nous supposons qu'ils sont très attractifs.

4.2. Structure de la thèse

Cette thèse a été rendue possible par le développement de nouveaux types de balises visant à évaluer les interactions avec les bateaux et à estimer les proportions de pêcheries non déclarées, ce qui devrait permettre une meilleure évaluation et une connaissance à fine échelle des interactions entre les oiseaux marins et les bateaux et, par là même, leurs risques d'exposition aux captures accidentelles. La thèse repose sur deux lignes directrices : l'acquisition de connaissances fondamentales sur l'écologie comportementale des oiseaux vis-à-vis des bateaux et les applications à la biologie de la conservation liées à l'acquisition de ces connaissances.

Cette thèse est divisée en cinq parties. Après une introduction générale et une première partie détaillant les modèles et sites d'étude, les outils de biotélémétrie utilisés et les métriques calculées sur les données récoltées, trois chapitres se succèdent, composés des articles publiés ou en révision. Chacun des chapitres se compose classiquement d'une introduction de la question, des matériels et méthodes, de la récolte et de l'analyse des données, des résultats et d'une discussion spécifique à la question. Ces articles publiés ou en cours de publication sont restés en anglais et tels qu'ils ont été révisés ou acceptés par des experts indépendants et anonymes.

Le chapitre 1 se concentre sur les changements de comportement de recherche alimentaire des Albatros hurleurs de Crozet dus à la présence de bateaux.

Le chapitre 2 évalue les différences d'exposition des populations et espèces (Albatros hurleur et Albatros d'Amsterdam) de l'océan Indien au risque de captures accidentelles tout en proposant une nouvelle méthode pour affiner cette estimation du risque.

Le chapitre 3 s'intéresse à l'utilisation de l'habitat par l'albatros hurleur qui peut être différent selon les populations ou les sexes et qui entraine une différence de rencontre et de comportement lié au bateau.

Enfin, une discussion générale reprend les questions et hypothèses de départ ainsi que les résultats obtenus afin de les mettre en relation avec les différents travaux réalisés en collaboration sur ce sujet et la littérature pour proposer quelques perspectives et applications concrètes adaptées à la biologie de la conservation.

Matériels et méthodes

Alexandre CORBEAU

1. Les espèces étudiées : l'albatros hurleur et l'albatros d'Amsterdam

1.1. Description

1.1.1. Systématique

L'albatros hurleur - *Dimodea exulans* (Linnaeus, 1758) et l'albatros d'Amsterdam - D*iomedea amsterdamensis* - Roux, Jouventin, Mougin, Stahl & Weimerskirch, 1983 appartiennent à la famille des *Diomedeidae* et à l'ordre des Procellariiformes. Anciennement considéré comme faisant partie de la même super espèce du « grand albatros », c'est en 1983 que l'albatros Amsterdam a été décrit comme une espèce à part entière et que le complexe de super espèce des grands albatros a été séparé en 6 espèces : *Diomedea exulens, amsterdamensis, antipodensis, dabbenena, epomophora, sanfordi.*

1.1.2. Morphologie

Très proche par la taille, l'albatros hurleur, avec un poids oscillant entre 6,5 et 12 kg et une envergure de 2.50 à 3.70 m, est cependant plus grand que l'albatros d'Amsterdam pesant entre 4.8 à 8 kg pour 2.80 à 3.40 m d'envergure (Shirihai & Kirwan 2008, Onley & Scofield 2013). Considérés comme les espèces ayant la plus grande envergure du monde aviaire, ces deux albatros sont parfaitement adaptés aux conditions de la vie marine et aux vents extrêmes qui soufflent en permanence dans leur aire de répartition. Spécialistes du plané dynamique à faible altitude, ils excellent à surfer sur les dépressions créées par les vagues nombreuses et fortes des mers australes.

Les jeunes albatros hurleurs juvéniles sont entièrement brun chocolat sur les parties supérieures du plumage puis ils blanchissent d'année en année tandis que le bout des rémiges et des rectrices devient noir vers l'âge de 6-7 ans (Fig. 9). Des vermicules noires remplacent le brun et disparaissent au profit d'un blanc immaculé en commençant par la tête. Les oiseaux de plus de 30 ans sont complètement blancs à l'exception des extrémités des rémiges primaires qui restent noires (Fig. 9).

Figure 9 : Jeune albatros hurleur d'un an (en haut à gauche). Femelle d'albatros hurleur de 10 à 15 ans et son poussin (en bas à gauche). Mâle d'albatros hurleur de plus de 30 ans (à droite). (A. Corbeau)

Chez l'albatros d'Amsterdam, la teinte générale de l'oiseau reste dans les bruns chocolat toute la vie bien qu'il blanchisse légèrement avec l'âge jusqu'à obtenir un plumage pommelé chez les adultes (Fig. 10). La différenciation du juvénile d'albatros hurleur des albatros d'Amsterdam au plumage peu pommelé (âgé de moins de 20 ans) se fait grâce à un liseré noir situé au niveau de la jointure du bec, allant de la commissure au crochet, présent chez tous les Albatros d'Amsterdam (Fig. 10).

Figure 10 : Albatros d'Amsterdam adulte (A. Corbeau)

1.1.3. Différence mâle-femelle

Les sexes sont facilement différenciables chez les deux espèces lorsque les deux partenaires sont présents l'un à côté de l'autre, car les femelles des deux espèces ont un dimorphisme de taille d'environ 10% inférieur aux mâles (Weimerskirch et al., 2014). La plupart du temps les deux partenaires n'étant pas visibles simultanément, il est possible de différencier les sexes sur les individus « typiques », exception faite des femelles âgées de plus de 25/30 ans très imposantes, grâce à la coloration du plumage et à la forme de la tête et du bec.

Les femelles blanchissent moins vite que les mâles et conservent plus longtemps du noir et des vermicules sur le plumage. Ainsi, lors de leur première reproduction (7-8 ans) (Weimerskirch, Jouventin, & Stahl, 1985) les femelles présentent encore des vermicules sur le haut de la tête alors que les mâles, plus blancs et légèrement plus âgés à leur première reproduction (10-12 ans) (Weimerskirch et al., 1985), ont une tête entièrement blanche (Fig. 11 et 12).

Les différences se remarquent également à la forme de la tête de l'oiseau. Elle est plus « triangulaire » chez la femelle grâce à ses arcades sourcilières plus marquées et convergentes vers le bec, alors que la tête des mâles est plus ronde et plus massive (Fig. 11 et 12). De même, la femelle possède un bec plus fin avec une courbure du culmen plus prononcée. En effet la plupart du temps les mâles ont un crochet très prononcé et un bec massif avec des arêtes supérieures et inférieures quasiment parallèles, alors que chez la femelle la différence plus importante entre l'épaisseur du bec au niveau du crochet et celle du milieu du bec provoque un effet de courbure du culmen (Fig. 11 et 12).

Figure 11 : Femelles d'albatros hurleur de 8 ans (haut) et de 37 ans (bas). (A. Corbeau)

Figure 12 : Mâles d'albatros hurleur de 13 ans (haut) et de 37 ans (bas). (A.Corbeau)

L'ensemble de ces critères est utilisé sur le terrain pour sexer les oiseaux. Le sexe est évalué tous les ans chez tous les individus rencontrés afin qu'il soit confirmé sur plusieurs années et par différents observateurs. Ces critères ne sont toutefois pas utilisables pour le sexage des juvéniles c'est pourquoi celui-ci ne peut se faire qu'à partir de critères biométriques au moment de l'envol des poussins.

1.1.4. Habitat

L’albatros hurleur et l’albatros d’Amsterdam sont tous les deux des oiseaux marins pélagiques qui vivent dans l’hémisphère sud.

L’albatros d’Amsterdam est strictement endémique de l’île d’Amsterdam (Terres Australes et Antarctiques Françaises) située dans le sud de l’océan Indien. Son aire de répartition maritime se situe dans l’océan Indien entre 45° et 30 ° Sud, allant des côtes de l’Afrique du Sud à celles de l’Australie. (Fig. 13)

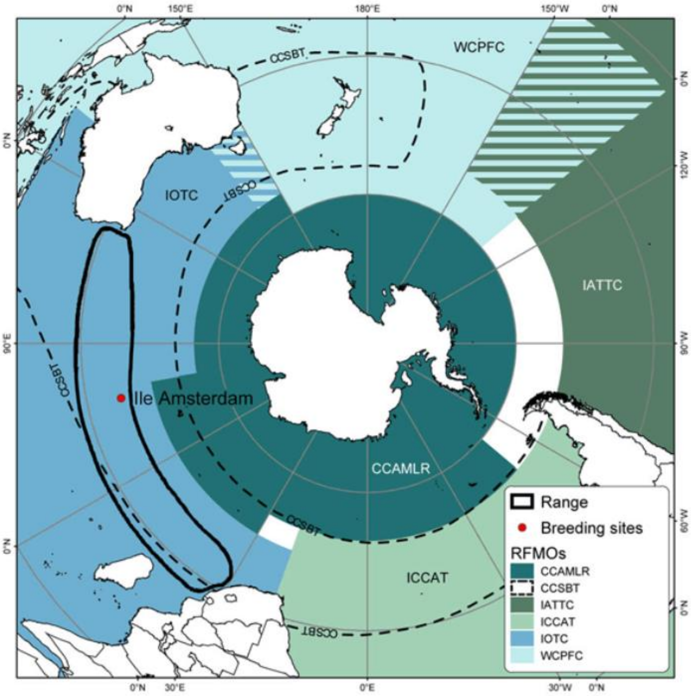


Figure 13 : Localisation de l’unique site de reproduction et limites approximatives de l’aire de distribution de l’albatros d’Amsterdam. Les limites des Organisations Régionales de Gestion des Pêches (ORGP) sont également représentées (Accord sur la conservation des albatros et Pétrel ©)

L’albatros hurleur se reproduit sur la plupart des îles subantarctiques à l’exception des terres continentales. Il utilise l’ensemble des zones de la planète situées entre les latitudes 70° sud (le continent antarctique) et 30° sud (Fig. 14).

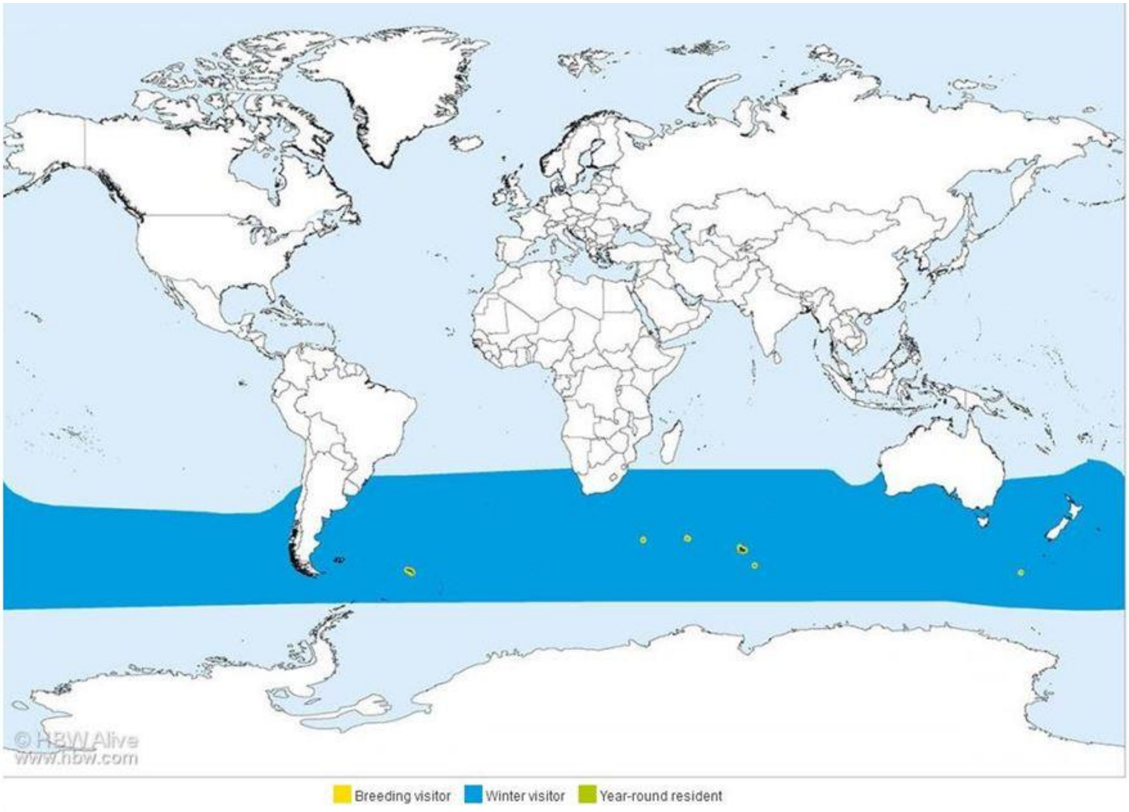


Figure 14 : Carte de répartition de l’albatros hurleur (Del Hoyo et al. 1992)

L’albatros hurleur et celui d’Amsterdam se reproduisent dans les végétations rases communes dans ces îles et sur des zones relativement plates. Contrairement aux « petits albatros » (*Thalassarche*) ils vivent au sein de colonies lâches dont les nids peuvent être éloignés de plus d’un kilomètre les uns des autres. Le nid est construit à partir d’éléments de la végétation environnante le plus souvent indigènes (l’*Acaena adscendens*, le *Poa cookii* ou la *Festuca magellanica*). Le milieu peut être aussi bien sec que très humide. Dans ce dernier cas, les nids des albatros sont alors plus imposants et plus hauts (jusqu’à 40 cm) afin de garder au sec leur progéniture (Fig. 15).

Figure 15 : Nid surélevé pour éviter l’inondation

1.2. Cycle de vie et phénologie

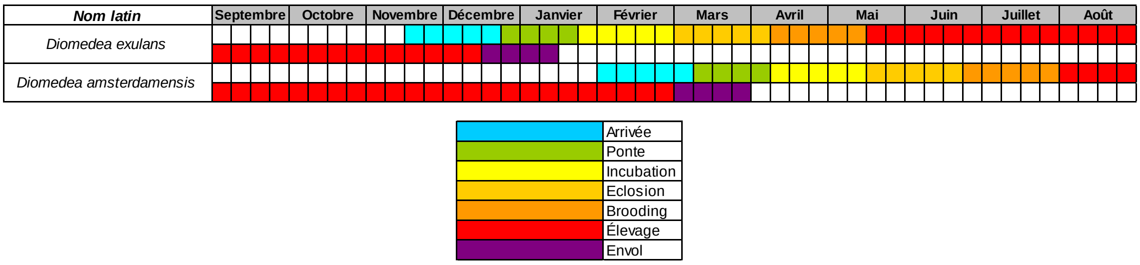
Dès la mi-novembre ce sont les mâles d'albatros hurleur qui arrivent les premiers sur les sites de reproduction afin de préparer les nids qui sont reconstruits chaque année. Une fois les deux membres du couple de retour sur le site, les partenaires entament leurs parades et s'accouplent. La ponte n'est que très peu synchronisée au sein de la colonie et peut s'étaler sur un mois, de fin décembre à fin janvier (Tableau 1). Lors de l'incubation (73 jours), le couple se relaie, l'un couve sur le nid, l'autre part en mer pour des trajets de recherche de nourriture allant de 2 à 51 jours (9 jours de moyenne et de médiane). L'échange des partenaires sur le nid est la plupart du temps très court (entre 10 minutes et 2 heures), mais à ce moment-là, les deux oiseaux se toilettent mutuellement la tête (partie inaccessible à l'oiseau lui-même) et consolident leur nid. Après avoir pondu, la femelle garde l'œuf et le premier voyage en mer est effectué par le mâle. À l'éclosion, les trajets raccourcissent notablement (3 à 5 jours en moyenne). Le couple continue de se relayer jusqu'à ce que le poussin soit autonome thermiquement vers 31-38 jours. À ce moment-là, les deux parents partent en mer chacun de leur côté et reviennent régulièrement le nourrir (tous les 10 à 30 jours) jusqu'en décembre/ janvier de l'année suivante. Vers la fin de cette période de nourrissage par les parents, ceux-ci espacent leurs allers- retours et le poussin, qui est alors plus gros que les adultes et pèse jusqu'à 14.5kg, finit d'acquérir son plumage juvénile. Il va ensuite se muscler, perdre ses réserves de graisse et s'entrainer au vol. Ses parents ne le nourrissant plus, le juvénile va devoir partir en mer seul pour chercher sa propre nourriture. Le jeune albatros ne reviendra qu'exceptionnellement sur la colonie avant ses 5 ans et commencera à s'exercer aux parades entre 6 et 12 ans pour effectuer ses premières reproductions vers 7-8 ans chez les femelles et 10-12 ans chez les mâles (Weimerskirch et al., 1985).

Le cycle de reproduction de ces espèces d'albatros durant plus d'une année entière, après l'envol de leur poussin le couple passe une année « sabbatique » en mer afin de pouvoir revenir pour le cycle de reproduction suivant en bonne condition physique. Cependant, en cas d'échec pendant la couvaison ou très tôt après l'éclosion, les adultes partent plus tôt en mer et très souvent retentent une reproduction dès le cycle suivant (Tableau 1).

Chez les albatros d'Amsterdam, le cycle est identique avec deux mois et demi de retard, car il est moins contraint par les saisons plus froides du subantarctique (Tableau 1).

D’une manière générale ces deux espèces d’albatros sont sympatriques et reviennent se reproduire, la très grande majorité du temps, à l’endroit même où ils sont nés. Les couples sont fidèles au cours de leur vie et s’il devait y avoir un changement de partenaire (suite à un divorce exceptionnel ou une mortalité) un couple se reformera avec un partenaire d’âge et donc d’expérience similaire (Jouventin et al. 1999).

Tableau 1 – Phénologie de reproduction chez l’albatros hurleur (Diomedea exulens) et l’albatros d’Amsterdam (Diomedea amsterdamensis)



1.3. Menaces et tendance populationnelle

Comme nous l’avons vu dans l’introduction, la principale menace qui pèse sur ces espèces d’albatros est la surpêche et les captures accidentelles qui en découlent.

Mais, en plus des dangers en mer, les albatros sont également soumis sur leurs aires de reproduction à des pressions principalement dues aux espèces et pathogènes introduits par l’homme (Phillips et al. 2016).

Les rats et les souris peuvent s’attaquer aux poussins d’albatros comme cela a été constaté à l’île de Gough (Wanless et al. 2007). De même, à Kerguelen, depuis 2013 des chats harets prédatent des poussins. Des projets de régulations et d’extermination de ces prédateurs introduits sont actuellement en cours sur les territoires français.

Sur l’île d’Amsterdam, la présence de pathogènes (choléra aviaire causé par *Pasteurella multocida*) sur les colonies d’albatros de Carter (*Thalassarche carteri*) (Gamble et al. 2019), situées non loin du lieu de reproduction de l’albatros d’Amsterdam, oblige à la plus grande vigilance et à des mesures de décontaminations strictes lors des visites de la colonie pour éviter les transmissions entre oiseaux.

Classée en danger critique d’extinction depuis la description de l’espèce en 1983 où seule une dizaine de couples reproducteurs étaient présents, la population d’albatros d’Amsterdam est en forte croissance. Actuellement, 35 couples reproducteurs sont dénombrés ce qui a permis son déclassement d’espèce « en danger critique d’extinction » à espèce « en danger » par l’Union International pour la Conservation de la Nature en

2019 grâce à sa forte croissance, et ce, malgré le très faible nombre d'individus (plus de 300 au total) (Weimerskirch et al. 2018a) (Fig. 16).

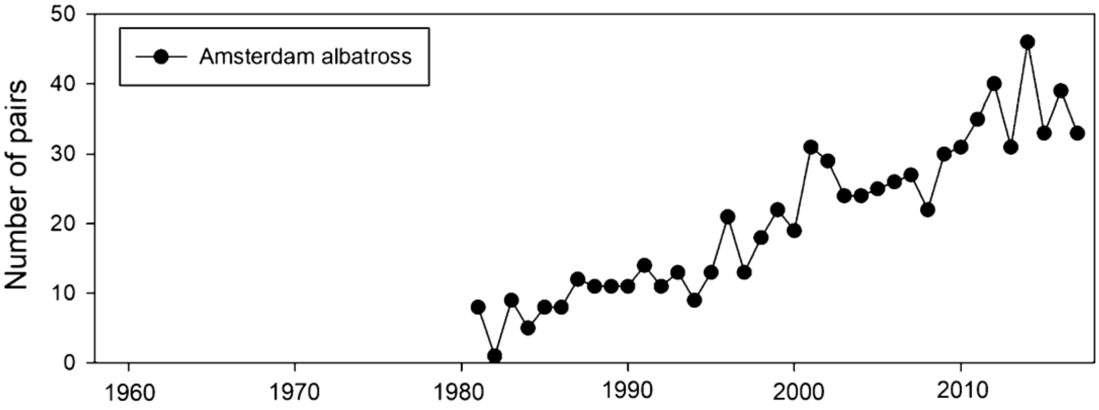


Figure 16 : Tendance du nombre de couples reproducteurs d'Albatros d'Amsterdam (Weimerskirch et al. 2018a)

Pour l'albatros hurleur, le développement de la pèche palangrière au thon dans les années 60 a entraîné la chute drastique des populations des îles françaises jusqu'au milieu des années 1980 (Weimerskirch et al. 1997a). Ces 10 dernières années ont vu une stabilisation du nombre d'oiseaux (Weimerskirch et al. 2018a) (Fig. 17).

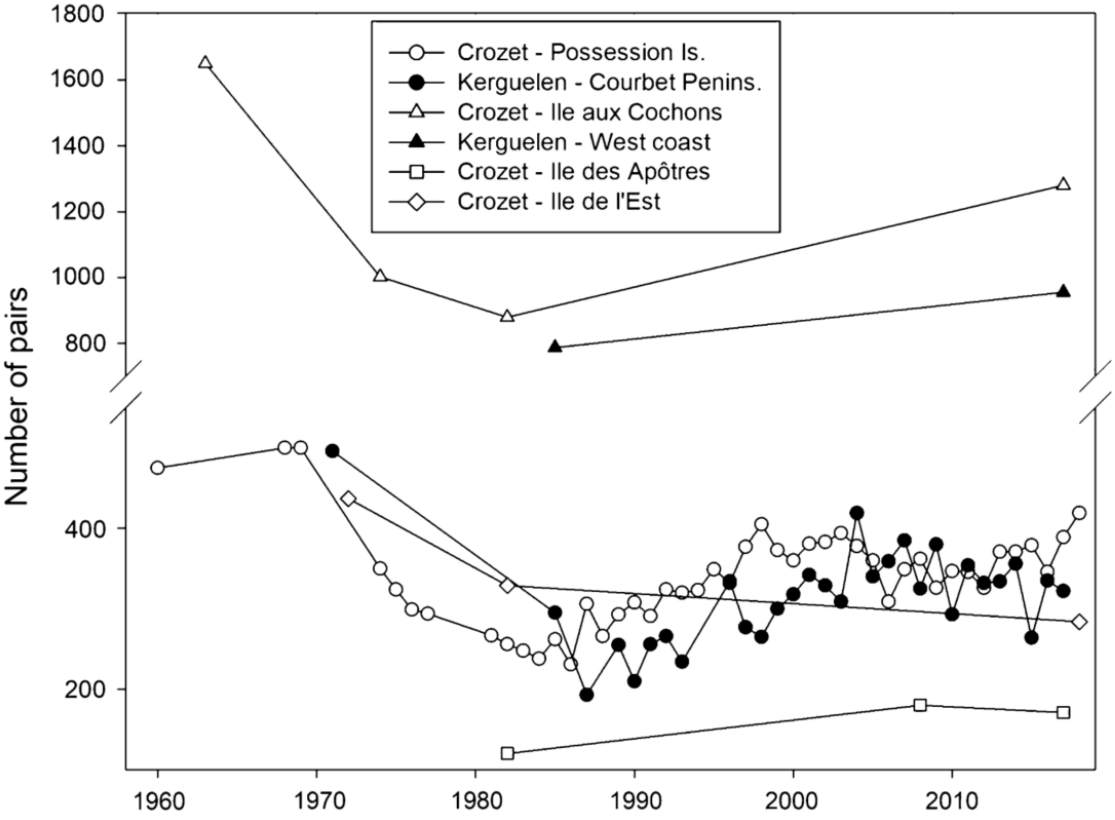


Figure 17 : Tendance du nombre de couples reproducteurs d'Albatros hurleurs sur les îles Crozet et Kerguelen (Weimerskirch et al. 2018a)

2. Les sites d'études

Cette thèse étudie les populations de grands albatros (albatros hurleur et d'Amsterdam) de l'océan Indien. Ces populations sont situées dans la partie sud de l'océan Indien sur les îles subantarctiques de Marion, Crozet et Kerguelen et sur l'île subtropicale d'Amsterdam.

Il faut noter que la profondeur des fonds océaniques de ces zones d'études se situe au-delà des 4000 mètres, mais que les îles elles-mêmes sont localisées sur différents plateaux inférieurs à 2000 mètres de fond. L'archipel de Kerguelen, ainsi que celui d'Heard Mc Donald, est posé sur le plus gros plateau océanique des océans Indien et Austral et le plus productif de cette zone (Dulaiova et al. 2009, Cavagna et al. 2014). Marion et Crozet se trouvent sur de plus petits plateaux océaniques alors qu'Amsterdam n'en a quasiment pas. Le plateau Del Cano situé entre ceux de Marion et de Crozet joue un rôle important dans la recherche alimentaire des oiseaux marins de ces îles (Fig. 16).

Les différences de bathymétrie entre le fond et le plateau sont propices aux « upwellings » c'est-à-dire à des remontées d'eaux froides profondes entrainant une très grande production primaire en surface. De même, Amsterdam est situé non loin au nord du front subtropical, Crozet et Prince Édouard entre le front subtropical et subantarctique et Kerguelen au milieu du front polaire (Fig. 18). Ces fronts sont des zones à fort gradient de température provoquant également une forte production primaire. Ce sont ces conditions particulières qui expliquent la richesse de ces eaux et donc la présence des plus grandes concentrations d'oiseaux et mammifères marins au monde.

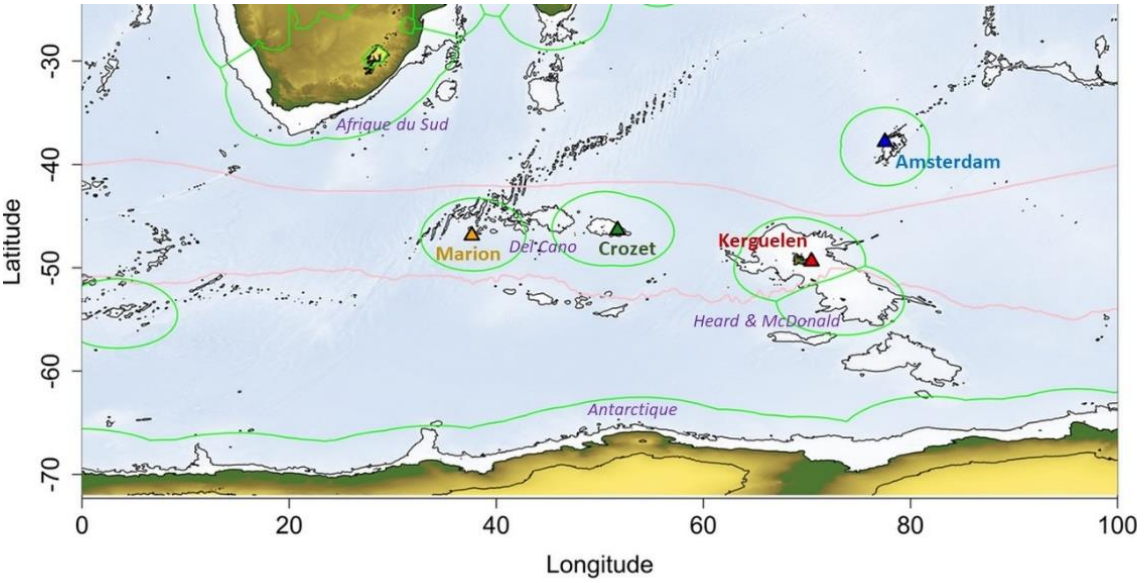


Figure 18 : Carte de la zone d'étude avec les îles et plateaux océaniques (lignes noires bathymétriques à -2000m, 0m et +2000 m). Les lignes vertes : ZEE ; les lignes roses : les fronts subantarctique et polaire.

2.1. L'île d'Amsterdam

2.1.1. Géographie

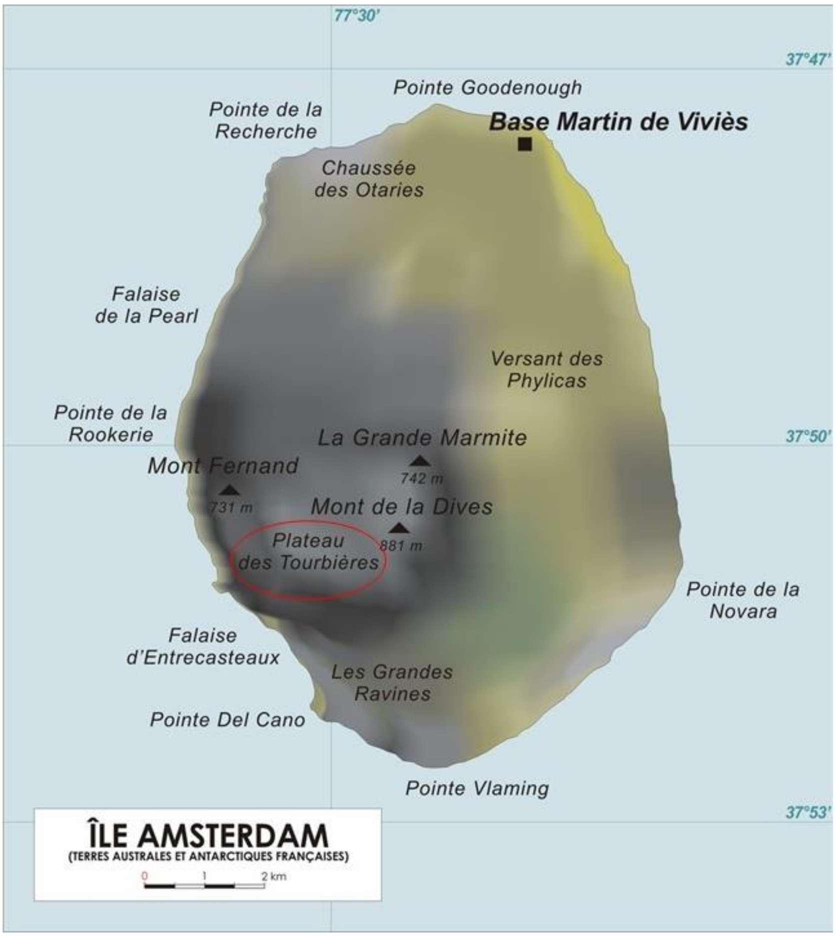


Figure 19 : Carte de l'île d'Amsterdam avec la colonie d'étude du Plateau des Tourbières

L'île d'Amsterdam (38° sud, 77° ouest – Fig. 19), considérée comme la plus éloignée de tous les continents du monde, est une île volcanique d'environ 700 000 ans. Relativement ronde (10x7 km), sa superficie est de 58km². Avec Saint-Paul, elle fait partie des seuls territoires subtropicaux des Terres Australes et Antarctiques Françaises.

C'est uniquement sur le « plateau des tourbières », zone très humide à végétation de graminées rases, que l'albatros d'Amsterdam se reproduit.

2.1.2. Suivis long terme

Amsterdam fait partie des zones de suivis des programmes scientifiques du Centre d'Études Biologiques de Chizé (soutenu par le programme 109 de l'institut polaire français Paul Emile Victor - IPEV) et chaque année un volontaire effectue un suivi complet des albatros : recherche et marquage des nids, contrôle des partenaires au nid et suivi du succès reproducteur. Chaque année le baguage de tous les individus non bagués est réalisé ainsi qu’un sexage visuel afin de corriger d’éventuelles erreurs dans le temps. Un sexage génétique peut être fait lors de campagnes spécifiques.

À Amsterdam le suivi annuel des albatros a commencé en 1982 et est devenu annuel et complet depuis 1985. L’ensemble des individus de cette espèce étant concentré sur la colonie d’études du plateau des Tourbières (Fig. 19), tous les albatros d’Amsterdam sont bagués grâce à ce suivi long terme.

2.2. L’archipel de Crozet

2.2.1. Géographie

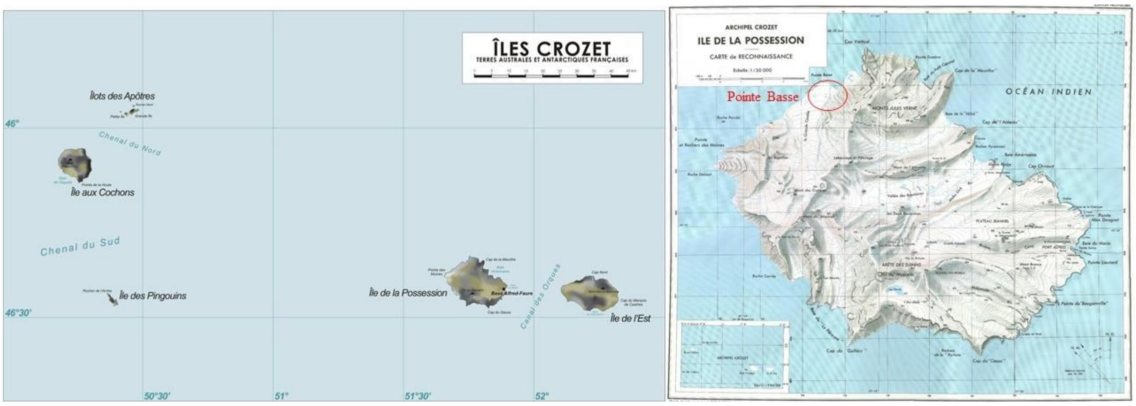


Figure 20 : Carte de l’archipel des îles Crozet (gauche) et carte de l’île de la Possession avec la colonie d’étude de Pointe Basse (droite - IGN).

L’archipel de Crozet (46° sud, 52° ouest – Fig. 20) est composé de cinq îles : l’île de la Possession, l’île de l’Est, l’île aux Cochons, l’île aux Pingouins et les ilots des Apôtres. L’archipel de Crozet est entièrement issu du volcanisme et l’île de la Possession a eu une activité volcanique il y a 9 millions et qui s’est arrêtée il y a environ 100 000 ans. Cette île de 150 km² est très escarpée avec un sommet à 934 mètres et des falaises sur la plupart des pourtours de l’île.

Les albatros hurleurs se localisent dans les zones relativement plates et recouvertes de végétation. La principale colonie est située au nord de l’île sur Pointe Basse, mais de nombreux nids sont également installés à l’Est autour de la Baie du Marin et de la Baie Américaine (Fig. 20).

Le suivi annuel est uniquement réalisé sur l’île de la Possession, où est située la base scientifique.

2.2.2. Suivis long terme

Seule la population de l'île de la Possession est suivie annuellement depuis 1965 par les mêmes protocoles que ceux utilisés dans toutes les îles des TAAF et réalisés par les volontaires du programme 109 envoyés par l'IPEV. Près de 400 nids sont contrôlés annuellement sur l'ensemble de cette île.

Les autres îles ne sont étudiées que lors de très rares expéditions spécifiques ou de comptage par hélicoptère, voire même grâce à des suivis satellites (Weimerskirch et al., 2018).

2.3. L'archipel des Kerguelen

2.3.1. Géographie

Figure 21 : Carte de l'archipel de Kerguelen avec la colonie d'étude de Pointe Morne (IGN)

Kerguelen (49° sud, 69° ouest – Fig. 21) est l'archipel volcanique le plus ancien du monde (35 millions d'années) et le deuxième plus étendu après l'Islande. Situé le plus au sud parmi nos sites d'études, c'est aussi le plus vaste avec une île principale de 6500 km² et de nombreux ilots pour une surface totale de 7200 km². La partie ouest de l'archipel, très escarpée avec un sommet de 1850 mètres, est partiellement recouverte de calottes glaciaires. De nombreuses colonies d'albatros hurleurs se situent dans les vallées glaciaires du sud de l'île. Mais c'est à l'est, sur la péninsule sédimentaire de Courbet, que se situe le plus grand nombre de couples et particulièrement la colonie de Pointe Morne.

En plus d'être sur un important plateau océanique, Kerguelen est traversé par le front polaire situé au nord de l'archipel en hiver et au sud en été. Associé aux éléments dissous issus de l'érosion de l'île tels que le fer, cet archipel constitue une zone de production majeure de l'océan Austral (Cavagna et al. 2014).

2.3.2. Suivis long terme

Suivant les mêmes protocoles du programme 109 (IPEV) que les précédents sites d'études français, un suivi complet est réalisé annuellement sur la colonie de Pointe Morne (Fig. 21). Le reste de la péninsule Courbet est contrôlé deux fois par an lors de comptages spécifiques tandis que les autres colonies de l'archipel ne font l'objet de comptages que lors de campagnes dédiées réalisées tous les 5-6 ans par la réserve naturelle des TAAF.

2.4. L'île Marion

2.4.1. Géographie

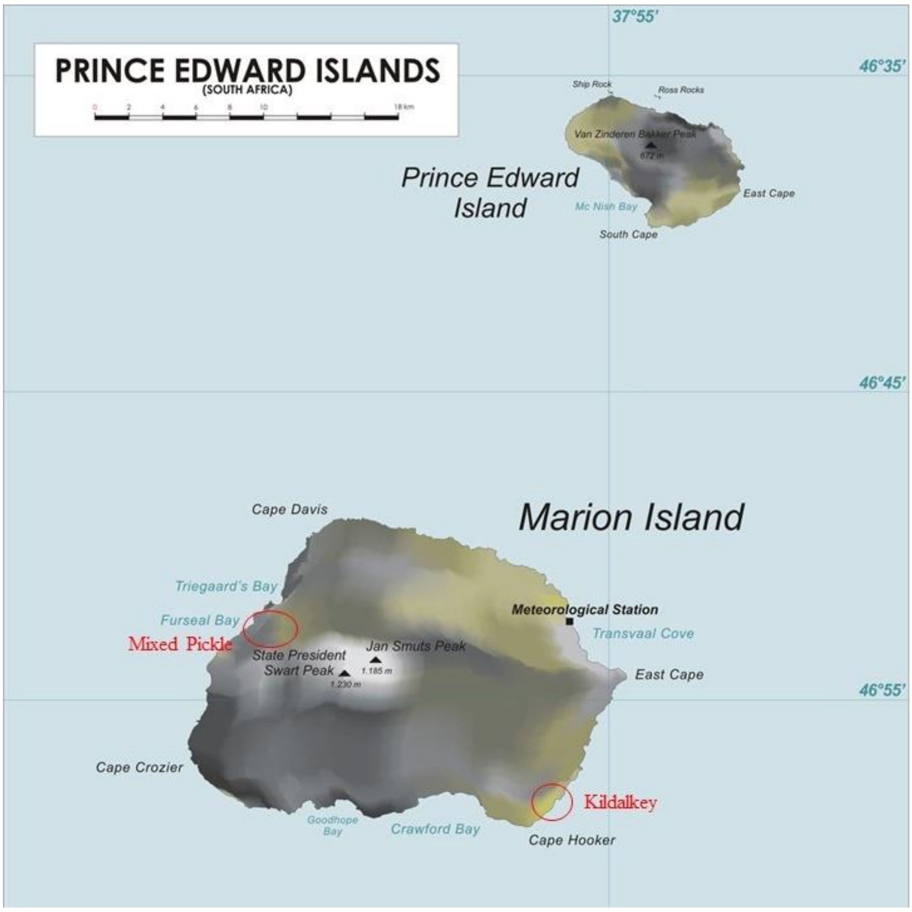


Figure 22 : Carte de l'archipel des iles Prince Edward avec la colonie d'étude de « Mixed Pickle » et « Kildalkey » sur l'île Marion

Marion (47° sud, 38° ouest – Fig. 22) est la plus grande île de l'archipel des îles du Prince-Édouard, avec ses 290 km² (25x16 km). Cet archipel d'îles volcanique (500 000 ans) est sous autorité sud-Africaine. Elle est très similaire à Crozet par sa taille, sa géologie, ses habitats, mais aussi par la diversité de ses d'espèces.

2.4.2. Suivis long terme

Différentes équipes de l'université de Cape Town suivent les albatros de cette île. Les données utilisées dans cette thèse sont issues des suivis réalisés par l'équipe de Pierre Pistorius qui déploie des balises sur les albatros au nord (Mixed-Pickle) et au sud (Kildakey) de l'île depuis 2015 (Fig. 22).

3. Biotélémétrie

3.1. Types de balises utilisées

Les balises utilisées dans cette étude sont les premières au monde possédant un récepteur radar de taille assez petite pour être déployé sur des animaux.

Ces balises ont été développées en collaboration avec Dominique Filippi de Sextant Technology (®Nouvelle-Zélande) dans le cadre du projet européen ERC « Earlylife » d'Henri Weimerskirch. Elles sont constituées essentiellement d'un récepteur radar qui permet de capter les ondes d'un radar de bateau situé à proximité de la balise (Weimerskirch et al. 2018b). Elles possèdent également une antenne de localisation utilisant le système GPS et GLONASS pour de meilleures performances. Cette antenne céramique est plate dans les premiers modèles de balise (XGPS) et devient filaire dans les nouveaux modèles (XSpoutnik, Centurion et XArgos)

Différentes générations se sont succédé, s'améliorant au fur et à mesure des expériences:

Les XGPS : ce sont des circuits imprimés intégrant un récepteur radar et une puce de localisation en céramique carrée montés avec une batterie rechargeable et interchangeable. L'ensemble est scellé avant le déploiement dans une gaine thermorétractable transparente dont la colle est placée côté intérieur (Fig. 23).

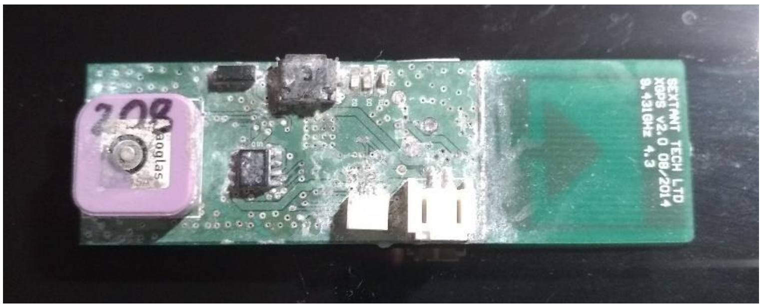


Figure 23 : XGPS

Les XIridium : Ce sont des circuits imprimés de même type que les XGPS auxquels il a été ajouté un panneau solaire et une antenne iridium permettant de transmettre l'information en direct par satellite, le tout coulé dans de la résine. Ces balises ont été développées pour être déployées sur des juvéniles après leur envol et donc posées à perte. Cette antenne iridium de type militaire intégrée à la balise n'a malheureusement pas supporté les conditions particulières liées aux comportements des albatros et a rompu en ne fournissant que très peu de données (Fig. 24).

Figure 24 : XIridium qui a perdu son antenne

Les XSpoutnik : ce sont des XGPS intégrant en plus un accéléromètre, un enregistreur de lumière basique et deux électrodes d'activité permettant de savoir si la balise est dans l'eau ou non. Ces dernières fonctionnalités n'ont pas été utilisées lors de nos déploiements. Dans ce modèle, les circuits imprimés sont scellés avec la batterie dans un boitier étanche imprimé en 3D et l'antenne de localisation en céramique est désormais remplacée par une antenne filaire dépassant du boitier. Cette première génération test n'était pas totalement étanche et la plupart des balises ont pris l'eau sur le long terme. Des solutions ont été apportées par Sextant Technology, mais nous n'en avons pas redéployé lors des missions suivantes (Fig. 25).

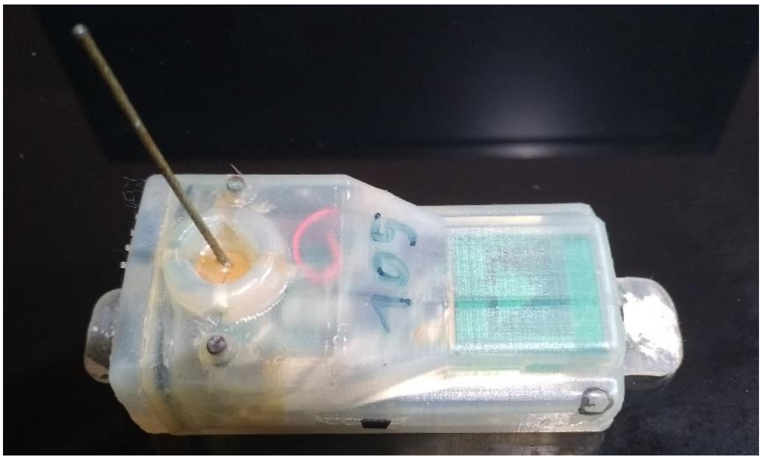


Figure 25 : Première génération des XSpoutnik

Les Centurions : ces balises constituent la nouvelle génération des XIridium dont l'antenne iridium est remplacée par une antenne Argos en câble souple. L'antenne de localisation comme pour les XSpoutnik est une antenne filaire qui sort du boitier imprimé permettant une meilleure réception du signal (hors du plumage). Une deuxième génération de Centurion a été développée en 2018 avec une performance accrue de la batterie dans le temps, une fermeture du boitier facilitée par un pas de vis et des antennes en câble gainées pour éviter la rouille (Fig. 26).

Figure 26 : Première génération (gauche) et deuxième génération (droite) des Centurion posées sur les adultes reproducteurs

Les XArgos : ce sont les versions légères et compactes des Centurions avec une batterie plus légère et donc de capacité plus faible. Déployées à perte sur des juvéniles, des immatures ou des oiseaux en échec de reproduction, ces balises peuvent théoriquement tenir jusqu'à la mue de l'oiseau grâce à leur panneau solaire. Peu de balises ont malheureusement tenu jusque-là à cause de la faible exposition au soleil des balises, de batteries parfois défaillantes (problème lié au fournisseur des batteries) et des potentielles surconsommations des balises non prévues (Fig. 27).

Figure 27 : Première génération (gauche) et deuxième génération (droite) des XArgos posées à perte » sur des individus non reproducteurs.

Ces balises sont donc en perpétuelle évolution et nous avons effectué chaque année des tests et apporté des améliorations à nos modèles. Cela a parfois entrainé des pertes de données, principalement sur les jeunes qui ont une forte contrainte de tenue de la batterie dans le temps. Chez les adultes, les trajets étant plus courts, les résultats ont été plus satisfaisants.

3.2. Déploiements

3.2.1. Technique

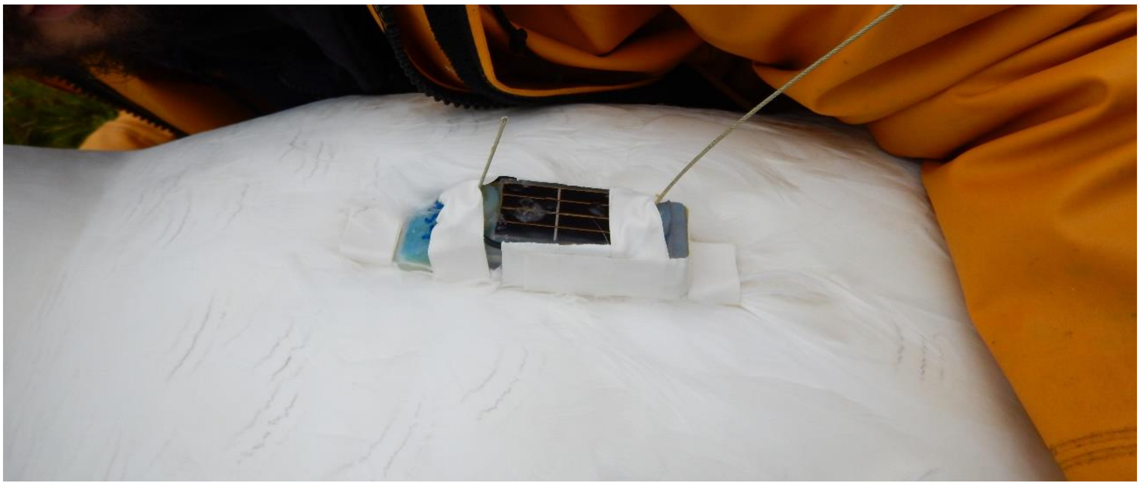


Figure 28 : Centurion posé avec du Tesa sur les plumes du dos d'un adulte reproducteur

La pose des balises se réalise depuis de nombreuses années sur ces espèces (Jouventin & Weimerskirch 1990) et la technique de scotcher la balise sur les plumes a fait ses preuves. Nous fixons les balises sur le dos de l'oiseau exactement sur sa colonne vertébrale et au niveau de son centre de gravité (entre les deux ailes et légèrement sous la bosse située sur son dos). À cet emplacement précis, la gêne pour l'oiseau est la plus faible possible tout en permettant aux antennes et panneaux solaires d'être efficaces (Fig. 28). Notons tout de même qu'un oiseau posé, a très souvent les plumes de ses ailes qui recouvrent la balise ce qui ne gêne pas les récepteurs et les émetteurs, mais affecte la capacité de recharge de la batterie par les panneaux solaires (Fig. 29).

Figure 29 : Juvénile équipé dont les ailes recouvrent la balise

Les balises sont scotchées avec du Tesa (© Berlin, Allemagne) de la couleur du plumage, afin que la balise soit la plus discrète possible et que l'oiseau ne cherche pas à enlever un élément étranger de couleur collé sur son dos. Seuls les antennes (filaires, céramiques et radar) et les panneaux solaires ne sont pas recouverts de Tesa. Pour une meilleure fixation, notamment sur les balises posées « à perte », de la ®Loctite 401 est utilisée pour coller le scotch à la balise et le scotch sur lui-même, mais en aucun cas de la Loctite n'est mise sur le plumage de l'oiseau.

Le fait de fixer les balises aux plumes permet dans le cas des balises posées « à perte » ou dans le cas d'une non-récupération (aucun cas avéré dans cette étude) de ne pas laisser une balise non fonctionnelle sur le dos de l'oiseau pour le restant de sa vie, qui peut par ailleurs être très longue chez ces espèces. Ainsi, quoiqu'il arrive, la balise tombe à la mue suivante et ne laisse aucune séquelle à l'oiseau.

3.2.2. Nombre et période

Les déploiements se sont réalisés sur 5 années de janvier 2016 à avril 2020 (Fig. 30).

Figure 30 : Déploiement test des premières balises Centurion à Crozet (2018)

167 trajets avec les données de détection de bateaux par le radar (donc sans compter les balises de Marion) sont utilisables (sur les 186 déploiements) après les 4 saisons de déploiement sur les adultes reproducteurs (Tableau 2)

Tableau 2 : Nombre de trajets issus des déploiements sur les adultes reproducteurs

Nombre de trajets/balises déployées (Nombre utilisable) Pour les adultes reproducteurs	CROZET				KERGUELEN	AMSTERDAM	MARION	Total
	XGPS	XSpoutnik	Centurion (incubation)	Centurion (élevage)	Centurion (incubation)	Centurion (incubation)	GPS (incubation)	
2015/2016	49 (40)	NA	NA	NA	NA	NA	NA	**49 (40)**
2016/2017	31 (26)	NA	NA	NA	NA	NA	NA	**31 (26)**
2017/2018	19 (17)	10 (1)	28 (27)	7 (7)	NA	NA	NA	**64 (52)**
2018/2019	NA	NA	49 (45)	NA	30 (24)	10 (8)	47 (27)	**89 (76)**

Quant aux oiseaux non reproducteurs qui sont les juvéniles, les immatures, les adultes en échec de reproduction ou les adultes en post-reproduction après le départ de leur poussin ; 101 trajets sont utilisables avec les détections de radar sur les 146 déploiements (Tableau 3).

Tableau 3 : Nombre de trajets issus des déploiements sur les juvéniles, les immatures et les adultes en échec de reproduction ou en post-reproduction (année sabbatique)

Nombre de trajets/balises déployées (Nombre utilisable) Pour les oiseaux non reproducteurs	**CROZET**				**KERGUELEN**			**AMSTERDAM**	**Total**
	XIridium	**XArgos (juv)**	**XArgos (Immature)**	**Centurion (échec et post repro)**	**XArgos (juv)**	**XArgos (Immature)**	**Centurion (échec et post repro)**	**XArgos (juv)**	
2016/2017	10 (0)	NA	NA	NA	NA	NA	NA	NA	**10 (0)**
2017/2018	NA	17 (6)	NA	NA	NA	NA	NA	NA	**17 (6)**
2018/2019	NA	17 (8)	12 (11)	7 (6)	23 (18)	8 (8)	2 (2)	10 (8)	**79 (61)**
2019/2020	NA	15 (13)	NA	NA	15 (15)	NA	NA	10 (6)	**40 (34)**

Aucune mortalité ou échec de reproduction n'a été constaté en lien avec la balise ou sa pose.

4. Les données des bateaux

Trois types de données issues des bateaux présents dans la zone d'étude ont été utilisées dans cette thèse.

Les premières données sont issues du récepteur radar intégré aux balises déployées et permettent de connaitre la présence d'un bateau à moins de 5 km (Weimerskirch et al., 2018).

Les secondes proviennent de la récupération des signaux AIS (Automatic Identification Systeme). À l'origine l'AIS est un système anticollision permettant aux bateaux d'avoir, à longue portée (plusieurs dizaines de kilomètres), des informations sur les bateaux environnants : identifiant, pays d'attache, type de bateau, longueur, activités, géolocalisation, vitesse et cap. Ces informations sont avant tout disponibles pour éviter les collisions et respecter les priorités. Depuis près de 3 ans, ces informations reçues par satellite sont disponibles en temps réel, avec seulement quelques minutes de délai, pour visualisation sur des plateformes telles que « Global fishing watch » ou « Marine traffic ». Il est impossible de les télécharger ou de les enregistrer, mais ces sociétés, ou d'autres spécialisées dans les jeux de données transmis par satellite telle que Collecte Localisation Satellites - CLS par exemple, peuvent les vendre. Pour cette thèse, les données ont été achetées à CLS et les fichiers AIS par minute ont été téléchargés quotidiennement lors des périodes de déploiement. La résolution maximale de ces données AIS est d'une localisation par bateau toutes les six minutes lorsque les signaux sont captés par des antennes terrestres sur les côtes. En pleine mer les données sont en moyenne d'une localisation toutes les 9-10 minutes avec une précision optimale de l'ordre de la dizaine de mètres lorsqu'il n'y a pas de problème de transmission de données.

Le troisième type de données issues des bateaux, utilisées dans le chapitre 3, est composé des données de rejets des bateaux de pêche. La réserve naturelle et l'administration des Terres Australes et Antarctiques Françaises assurant la présence d'un observateur des pêches sur les sept bateaux déclarés des eaux françaises des TAAF, ces observateurs notent les localisations et heures des rejets effectués par les bateaux de pêche.

5. Le projet « Ocean sentinel »

5.1. Un « Proof of Concept »

Extension du programme européen (ERC) « Earlylife » d'Henri Weimerskirch, le principe de ce projet a été de développer de nouveaux types de balises qui, une fois déployées sur des albatros, permettraient de détecter la présence de bateaux et de transmettre cette information quasiment en direct. Le but a été de prouver que ce concept est fonctionnel et qu'il peut être appliqué et utilisé par tous.

5.1. Le principe

L'albatros équipé d'une de nos balises est naturellement attiré par les bateaux lors de ses trajets de recherche alimentaire. Lorsque l'oiseau rencontre un navire, la balise détecte son signal radar. La balise transmet sa géolocalisation au moment du contact avec le bateau par le système de communication satellite d'Argos ®. Une fois reçue en direct (avec un maximum d'une heure de décalage) nous pouvons comparer cette position à l'ensemble des positions de bateaux déclarés (reçues via les AIS). Si aucune correspondance n'est trouvée, le bateau est donc non déclaré. À ce moment, si le bateau non déclaré est dans une ZEE nous distribuons cette information aux autorités partenaires (en France ce sont les Terres Australes et Antarctiques Françaises et le Centre Régional Opérationnel de Surveillance et de Sauvetage sud océan indien) qui travaillent directement avec la marine nationale afin d'envoyer sur place une frégate militaire assignée à la surveillance des pêches et ainsi arraisonner le bateau illégal en flagrant délit (Fig. 31).

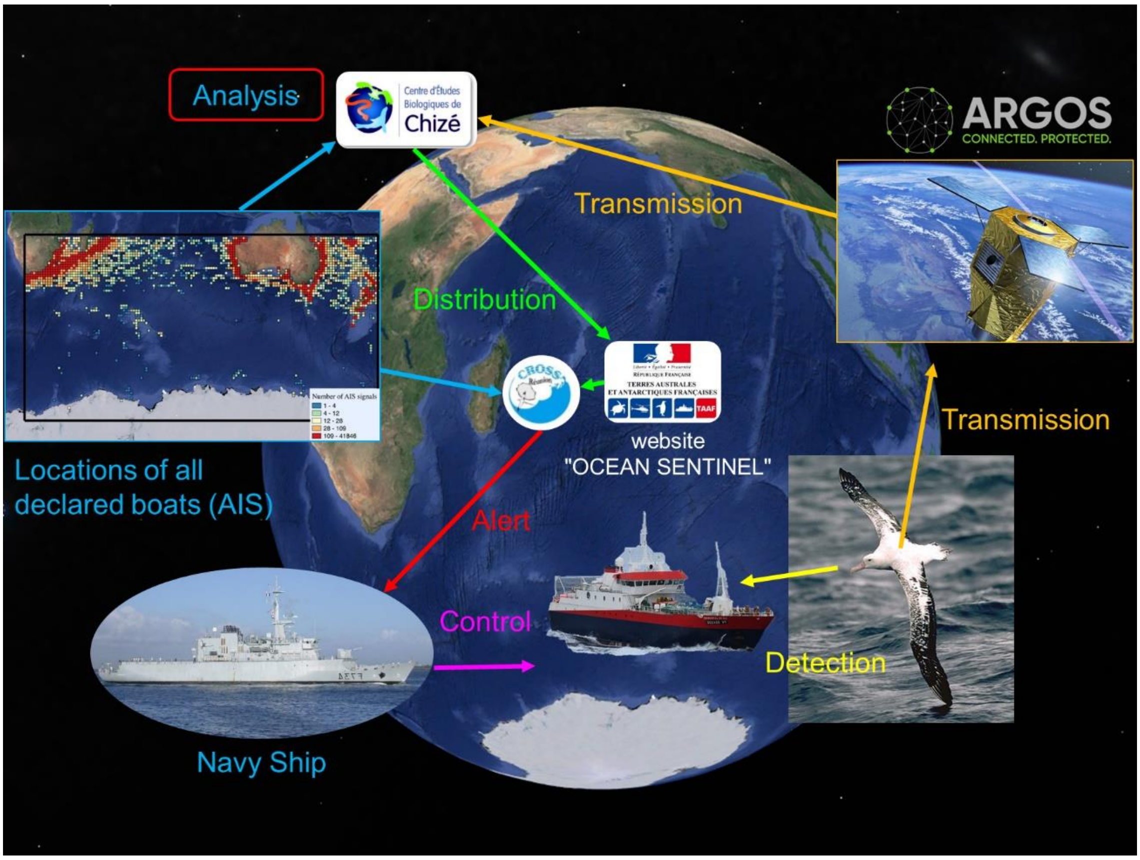


Figure 31 : Schéma explicatif du principe du programme « Ocean sentinel » (Weimerskirch et al. 2020a)

5.2. Les objectifs

5.2.1. La surveillance des pêches

Le premier objectif de ce programme est de fournir une capacité de surveillance des pêches dans des endroits inaccessibles aux bateaux de surveillance. En effet, les albatros couvrent des milliers de kilomètres carrés alors que les 2 ou 3 bateaux dédiés à la surveillance en sont incapables. De plus, les albatros, attirés par les bateaux, vont le plus souvent rentrer en contact avec les bateaux situés à proximité. Cette « surveillance aviaire » permet ainsi de lutter contre la pêche non déclarée qui non seulement constitue la principale cause de mortalité des oiseaux marins par les captures accidentelles, mais aussi pille les ressources des océans.

En cas de non-intervention des autorités en direct due à l'éloignement des zones de contrôle et à la nécessité du flagrant délit, cela permet dans tous les cas, de fournir une estimation de la présence et de la proportion de bateaux non déclarés, totalement inconnues jusqu'alors.

5.2.2. L'étude des relations entre les oiseaux marins et les pêcheries

Dans le cadre du projet « Ocean sentinel » où s'inscrit cette thèse, nous avons pu étudier un certain nombre de questions d'écologie comportementale grâce aux nouveaux types de balises utilisées. La biotélémétrie est un formidable outil de connaissance qui permet d'acquérir des jeux de données énormes, totalement inaccessibles autrement, offrant pour la première fois la possibilité d'étudier à très fine échelle les relations entre les albatros et les bateaux.

6. Paramètres sur les données de biotélémétrie

6.1. Les paramètres des localisations d'oiseaux

Pour chaque donnée de localisation issue des balises, nous obtenons une heure précise, une longitude et une latitude qui nous permettent ensuite d'effectuer de très nombreux calculs et d'établir divers paramètres.

Lorsque les données sont récupérées sur les balises, il est nécessaire dans un premier temps de s'assurer de la fiabilité des localisations et donc de filtrer les données aberrantes ou non réalistes. Pour cela nous calculons entre deux localisations les intervalles de temps puis de distance à l'aide du package « adehabitatLT » permettant de tenir compte de la courbure de la terre. Nous pouvons ensuite calculer une vitesse appelée vitesse au sol, car ne tenant pas compte de l'altitude, négligeable chez les albatros qui ne montent pas en altitude. Cette vitesse nous permet de filtrer les données, car le seuil de 150 km/h en moyenne sur 2 minutes étant considéré comme inatteignable par un albatros (Weimerskirch et al. 2020a) les localisations adhérentes peuvent ainsi être éliminées.

6.2. L'ajout des données de bateaux

Les données de bateaux issues du capteur radar de la balise sont fusionnées temporellement avec les données de géolocalisations. Cette fusion était effectuée manuellement jusqu'en 2018, mais, suite à des améliorations du logiciel d'extraction fourni par Sextant Technology (logiciel Hermes) la fusion est désormais automatique.

Pour les XGPS, les XSpoutnik et les Centurions, nous pouvons donc savoir, à chaque localisation, si l'oiseau équipé est en contact avec un bateau ou non. Sachant toutefois que la période d'écoute du radar (1 minute toutes les 5 minutes) est inférieure à la période entre les localisations (toutes les 2 minutes), il en résulte que sur certaines localisations l'écoute radar est désactivée et considérée comme telle, et non pas comme étant synonyme d'absence de bateau. Cela n'a que peu d'influence sur la détection ou non d'un contact avec un bateau étant donné que celui-ci est détecté à 5 kilomètres et que le détecteur de radar de la balise est en veille au maximum 4 minutes. Or, en 4 minutes à 150 km/h (vitesse maximale), l'albatros peut couvrir au mieux 10 km en ligne droite, ce qui correspond à la distance la plus courte lors d'un contact avec un bateau (détection à 5 km suivie d'un aller-retour jusqu'au bateau, soit 10 km).

Pour les XIridium et les XArgos les informations sont transmises par satellite toutes les heures, avec une géolocalisation par heure et quatre données radar résumant les 4 quarts d'heure d'écoute des balises. L'antenne radar est en écoute 3 minutes toutes les 15 minutes.

Pour les données AIS nous n'avions pas la même base temps entre les localisations de navires et celles de nos oiseaux. Ces données pouvaient donc se retrouver fortement décalées dans le temps. Pour éviter ce problème et compter le nombre de bateaux en contact avec les oiseaux, nous avons premièrement recensé les bateaux environnants, spatialement et temporellement. Nous avons répertorié tous les navires situés à moins de 5, 30 ou 100 km selon l'évènement, avec une heure de localisation des navires inférieure à 66 minutes (seuil choisi pour inclure tous les intervalles de localisations des jeunes albatros - XArgos et XIridium) par rapport à la plus proche heure de localisation des oiseaux. Dans un second temps, nous avons ajouté les bateaux non précédemment comptabilisés, mais qui étaient présents dans le rayon choisi (5, 30 ou 100 km) une fois leurs positions interpolées à l'heure de la localisation de l'oiseau. C'est à dire que pour une localisation à un temps *t* d'un oiseau, nous avons interpolé pour le même temps *t* (même date/heure/minute) la localisation du bateau entre sa précédente position (*t*-1) et sa suivante (*t*+1). Nous avons réalisé cette interpolation en considérant que le bateau se déplaçait à vitesse constante et en ligne droite ce qui est bien plus probable de la part d'un navire que de la part d'un albatros en vol (Fig. 32).

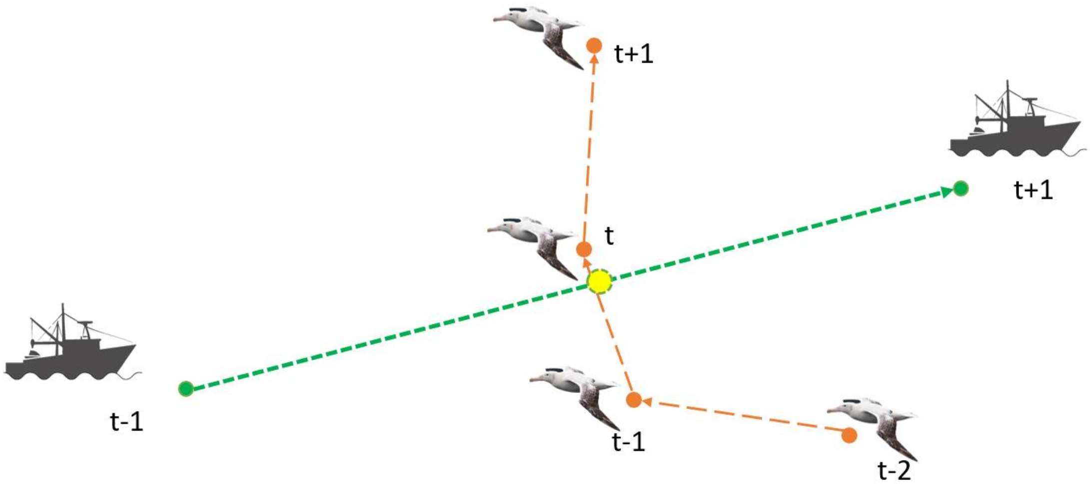


Figure 32 : Principe de l'interpolation des positions de bateaux pour effectuer les correspondances spatio-temporelles entre les données de bateaux et celles des oiseaux

6.3. Définitions des « évènements »

Une fois les correspondances établies entre les données de l'oiseau et celles des bateaux, nous avons identifié différents « évènements » accomplis par les oiseaux.

6.3.1. Les trajets alimentaires

Le premier évènement effectué par l'oiseau et le plus décrit dans la littérature est évidemment le trajet de recherche alimentaire. Nous avons défini un trajet comme un aller-retour en mer d'un oiseau partant et revenant sur la même colonie. Afin de ne pas tenir compte des données de l'oiseau à terre nous avons retiré tous les points situés à 5 km autour de la colonie. En effet, lors des premiers envols ou lors de la relève, il arrive fréquemment que les oiseaux se déplacent autour de leur nid, mais sans commencer réellement leurs trajets alimentaires. Ils se déplacent afin de passer la nuit à l'écart de la colonie, se nettoyer, boire en mer près de la colonie ou effectuer leurs premiers vols tests. Ces comportements spécifiques aux abords de la colonie entrainent des déplacements qui n'excèdent pas 5 km autour du nid, c'est pourquoi les trajets sont définis, début et fin, à partir de 5 km de la localisation du nid de l'oiseau équipé.

6.3.2. Les « évènements » de rencontre

Trois types d'évènements de rencontre entre albatros et bateaux ont été définis à partir des données : des « évènements radar » issus des détections radar des balises, des « évènements *nearby* » issus de la présence de signaux de bateaux AIS situés à moins de

5 km et des « évènements *encounter* » issus de ces mêmes données AIS mais localisés à moins de 30 km de l'oiseau (Fig. 33).

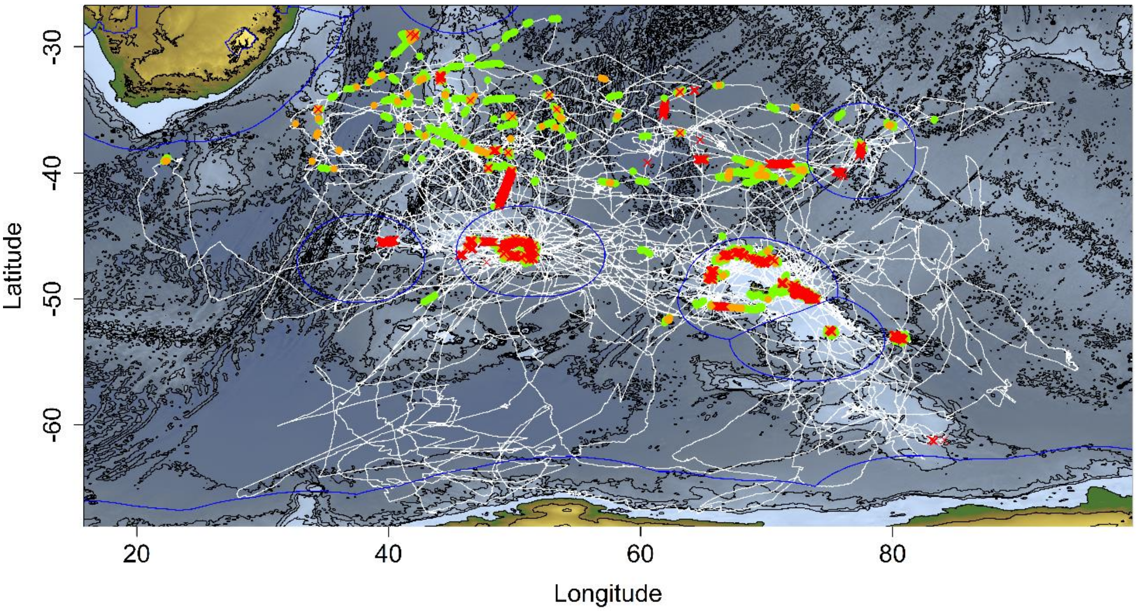


Figure 33 : Carte des trajets des albatros en incubation d'Amsterdam, de Crozet et de Kerguelen en 2018/2019 et les évènements de rencontre avec les bateaux (vert= « encounter » <30 km ; orange = « nearby » <5 km ; croix rouge : « radar »). ZEE en bleu.

Ces évènements sont constitués d'une série de localisations d'oiseau comportant un signal bateau (soit par radar, soit à moins de 5 ou 30 km, avec les données AIS) entre lesquelles il n'y a pas d'absences de ce signal bateau inférieures à deux heures consécutives. Au-delà de deux heures de localisation d'oiseaux sans signal bateau, la prochaine localisation d'oiseau avec une détection de bateau sera considérée comme faisant partie d'un nouvel évènement. Cela nous permet de tenir compte des changements de comportement qui peuvent amener l'albatros à se déplacer ou à attendre posé sur l'eau et sortir ainsi de la zone de détection radar ou de la zone définie des 5 ou 30 km pour un court moment. Ce laps de temps n'est pas synonyme d'un changement d'évènement ou même de bateau, c'est pour cela qu'une marge de deux heures est définie pour ces évènements de rencontre.

Les derniers évènements créés sont des évènements liés à la présence de rejets de la part des bateaux de pêche. De la même manière que pour les précédents évènements nous considérons qu'il existe un évènement de rejet lorsque l'oiseau est situé à moins de 5 km de la localisation du rejet, et ce, durant les 6 heures qui suivent ce rejet. Nous considérons qu'il y a changement « d'évènement rejet » lorsque l'oiseau s'est éloigné pendant plus de 2 heures de ce rejet.

6.4. Les paramètres des « évènements »

Pour chaque évènement divers paramètres sont calculés tels que le temps et les distances parcourues lors d'un évènement ou la distance maximale à la colonie. Des ratios de temps de présence sont également définis : ratios liés à divers évènements s'imbriquant les uns dans les autres (exemple : le temps passé en évènement radar au sein d'un même trajet), des ratios de temps passé dans certains types d'habitats (eaux, ZEE, plateau océanique…) (Fig. 33). Nous avons également calculé des moyennes de données continues telles que les vitesses, la bathymétrie, ou le nombre de bateaux à 5, 30 ou 100 km et leurs différents types.

6.5. Les données environnementales

La caractérisation de l'habitat par les données environnementales est essentielle dans ce projet. Les différents types de grands habitats entrainent différentes productions primaires. Les phénomènes de « upwelling » sont dépendants des forts changements de bathymétrie (entre les fonds et les plateaux océaniques). De même les fronts (polaire, subantarctique ou subtropical) sont des zones de convergence d'eaux à températures différentes. Ces deux phénomènes engendrent une grande production primaire. La température de surface de la mer (Sea Surface Temperature - SST) est également un facteur essentiel à retenir pour suivre des changements d'eaux, de saisons ou même de cycle annuel. Enfin, les comportements des albatros diffèrent entre jour et nuit et la baisse d'activité nocturne très nette doit parfois conduire à étudier séparément les périodes diurnes et nocturnes.

Les données de bathymétrie sont issues des données de la NOAA via le package « marmap » avec une résolution de 1 minute. Elles sont intemporelles, car l'échelle biologique de nos études est beaucoup trop faible pour des changements de bathymétrie majeurs.

La SST est issue des données issues du site de Copernicus qui évalue (via le « Met Office ») par satellite la température de surface de la mer toutes les heures sur des carrés de 0.25x0.25°.

Les fronts polaires étant des zones de changement de température entre les eaux variant au cours des saisons, nous nous sommes basés sur les référencements issus de Moore, Belkin et collaborateurs (1999 & 1996) lors des périodes d'équipement des oiseaux.

Le jour et la nuit ont été déterminés selon leur définition civile qui considère que la nuit est tombée lorsque le soleil est 6° en dessous de l'horizon. Le jour se lève lorsque le soleil est 6° sous l'horizon, car les premières lueurs du jour arrivent avant le lever réel du soleil. Le package « tripEstimation » permet d'avoir les degrés d'inclinaison du soleil selon la géolocalisation ainsi que la date et l'heure de la journée. À chaque localisation enregistrée de l'albatros, nous avons donc pu avoir l'inclinaison du soleil et en déduire si celle-ci était diurne ou nocturne.

Des limites administratives ont été utilisées, telles que les Zones Economiques Exclusives (ZEE) afin de connaitre la nationalité des eaux dans lesquelles naviguent les oiseaux et donc les législations qui en découlent. Ces frontières administratives sont facilement accessibles et reconnues par l'ONU (Organisation des Nations Unies). De même dans le chapitre 2, des grilles de 5x5° ont été utilisées pour faciliter les comparaisons avec des études antérieures. Ces grilles sont définies par l'IOTC (Indian Ocean Tuna Commission - référence : IOTC-2018-TCAC04-DATA04) qui fournit sur son site des couches permettant une universalité de ces grilles.

7. Les analyses statistiques

L'ensemble des analyses statistiques utilisées sont décrites pour chaque chapitre dans la partie « *Material and methods* ». La plupart des comparaisons statistiques réalisées dans cette thèse sont des modèles linéaires (simples ou complexes) à effet mixte. L'effet aléatoire (mixte) est principalement employé afin de ne pas surévaluer le poids des individus lors qu'ils représentent plusieurs unités statistiques (trajets, évènement…). Ces tests ont été réalisés avec les packages « lme4 » ou « glmmTMB ». Les distributions des paramètres puis des résidus ont été testés avec le package « fitdistrplus ».

Deux méthodes ont été utilisées afin de définir les comportements des oiseaux dans les chapitres 1 et 3 :

- La première (chapitre 1), consiste à définir des zones de recherche alimentaire des oiseaux appelée ARS (Area Restricted Search). La méthode du First-passage Time (FPT) a été utilisée dans ce chapitre avec le package R « adehabitatLT ». Elle consiste à évaluer combien de temps passe un animal dans un cercle d'un rayon donné (Fauchald & Tveraa 2003). Le trajet est tout d'abord rééchantillonné en sections de 1km, une valeur de FPT est calculée pour chaque rayon (ici 2, 5, 10, 20, 40, 60, 80, 100 et 150km), puis la méthode de Lavielle (Lavielle 1999, 2005) est appliquée pour segmenter le trajet selon la valeur du FPT. Cela permet de déterminer les ARS qui sont représentées par les segments du trajet plus lent et/ou plus sinueux (valeur de FTP plus élevée) par rapport à la moyenne de la journée (Fig. 34). Pour les petites échelles de 2, 5, et 10 km, les données de nuit ont été retirées pour éviter de détecter des ARS de petites échelles toute la nuit alors que l'oiseau se repose simplement sur l'eau (Weimerskirch et al. 1997).

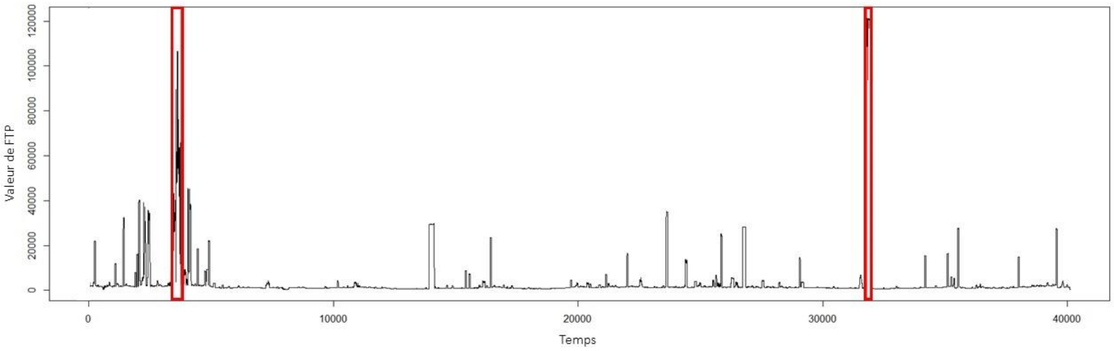


Figure 34 : Choix des ARS (encart rouge) en fonction des valeurs de FTP plus élevée.

- La seconde méthode (chapitre 2) utilise les modèles de Markov caché (HMM) qui consiste à définir des états pour chaque localisation de l'oiseau basés sur les probabilités de changement de ces états selon des paramètres préalablement choisis. Ici nous nous sommes basés sur l'étude de Clay et collaborateurs (2020) qui définit trois états chez les albatros hurleurs selon la vitesse et la sinuosité : les états de « route », de « repos » et de « recherche ». Il faut noter que pour pourvoir réaliser des HMM, le prérequis principal est que les localisations doivent être exactement constantes dans le temps. C'est pour cela que les données reçues ont été extrapolées afin d'obtenir des données exactement toutes les 2 minutes alors que ces intervalles se situaient préalablement entre 55 secondes et 2,20 minutes. Ces interpolations se font en ligne droite entre 2 localisations en tenant compte de la rotondité de la terre grâce au package « tripEstimation ».

Chapitre 1 : les changements de comportements dus à la présence de bateaux

Corbeau A., Collet J., Fontenille M., Weimerskirch H., 2019. How do seabirds modify their search behaviour when encountering fishing boat? ***PLoS ONE***, 14(9): e0222615.

Abstract

Seabirds are well known to be attracted by fishing boats to forage on offal and baits. We used recently developed loggers that record accurate GPS position and detect the presence of boats through their radar emissions to examine how albatrosses use Area Restricted Search (ARS) and if so, have specific ARS behaviours, when attending boats. As much as 78.5% of locations with a radar detection (contact with boat) during a trip occurred within ARS: 36.8% of all large-scale ARS (n=212) and 14.7% of all small-scale ARS (n=1476) were associated with the presence of a boat. During small-scale ARS, birds spent more time and had greater sinuosity during boat-associated ARS compared with other ARS that we considered natural. For, small-scale ARS associated with boats, those performed over shelves were longer in duration, had greater sinuosity, and birds spent more time sitting on water compared with oceanic ARS associated with boats. We also found that the proportion of small-scale ARS tend to be more frequently nested in larger-scale ARS was higher for birds associated with boats and that ARS behaviour differed between oceanic (tuna fisheries) and shelf-edge (mainly Patagonian toothfish fisheries) habitats. We suggest that, in seabird species attracted by boats, a significant amount of ARS behaviours are associated with boats, and that it is important to be able to separate ARS behaviours associated to boats from natural searching behaviours. Our study suggests that studying ARS characteristics should help attribute specific behaviours associated to the presence of boats and understand associated risks between fisheries.

1. Introduction

Foraging behaviour is a central life-history trait because it determines energy acquisition (Stearns 1980). When searching for resources, animals often display Area Restricted Search (ARS) behaviour whereby they increase sinuosity and reduce speed in specific areas (Kareiva & Odell 1987, Hill et al. 2000, Hills 2004). This behaviour is generally assumed to increase the probability of encountering prey that are aggregated, patchy, and often widely dispersed (Benhamou 1992). Various methods have been developed to characterize ARS zones during movements of animals (Bennison et al. 2018). In marine or other environments where data on resource distribution is lacking, the ARS zones of predators have been used as proxies for areas of greater prey resource availability (Weimerskirch et al. 2007, Hamer et al. 2009, Pacheco-Cobos et al. 2019). In the absence of better information on prey resource distribution, ARS zones of predators have also been used to define marine protected areas (Lascelles et al. 2016, Heerah et al. 2019). Seabirds are well-known to be attracted by fishing boats, and often forage behind these boats (Votier et al. 2004, Gremillet et al. 2008, Bicknell et al. 2013). Seabirds can obtain important food resource from fishery offal or baits (Tasker 2000). However, this food resource may be of poor nutritional quality (Gremillet et al. 2008) and fishery equipment such as long-lines and trawls can induce high seabird mortality (Croxall et al. 2012). Today the main threat for several seabird families, such as albatrosses and petrels, is the mortality induced by long-line fisheries (Delord et al. 2005, Anderson et al. 2011).

During recent years, with the development of bio-logging techniques, it has become possible to study seabirds-fisheries interactions by combining tracking systems such as GPS and VMS (Vessel Monitoring System) data (Torres et al. 2011, 2013). When interacting with fishing boats, seabirds often reduce their speed and alter their sinuosity, resulting in ARS behaviour (Torres et al. 2011, Bodey et al. 2014). When ARS zones are identified to determine foraging areas of seabirds, or to help designate marine protected areas, the occurrence of such interactions with fishing boats could lead to important and undesired biases. However, getting access to VMS or Automatic Identification System (AIS) data to quantify this bias is challenging for seabird researchers; access is often restricted for fisheries within national Exclusive Economic Zones (EEZs) and rarely exist or is incomplete for fisheries operating in international oceanic waters. Thus, when examining the movements and foraging behaviour of seabirds, it is difficult to attribute ARS movements to fishery presence or to the active search for natural resources.

Here we used recently developed loggers that record accurate GPS position and detect the presence of boats through their radar emissions (Weimerskirch et al. 2018b) to examine whether albatrosses use ARS and have specific ARS behaviours, when attending boats compared with presumed natural foraging. Wandering albatrosses (*Diomedea exulans*) are strongly-attracted to fishing boats worldwide and are threatened by bycatch risks (Weimerskirch et al. 1997a, Delord et al. 2005). Previous tracking studies showed wandering albatrosses use ARS behaviour extensively at different spatial scales (Weimerskirch et al. 2007). ARS behaviour, however, was not always associated with prey capture and it was not known whether ARS or prey capture were linked with the presence of a boat (Weimerskirch et al. 2007). We hypothesized that 1) albatrosses should modify their ARS behaviour when attending boats, 2) the parameters describing the ARS (duration, sinuosity, and habitats) should be different from natural (not associated with a boat) ARS behaviour. We also examined whether ARS differed between habitats (shelves or oceanic waters) where different fisheries operate, to understand if behaviours and associated risks are influenced by the fishing types.

2. Material and methods

Licences and permissions were granted by the Ethic Committee of Institut Polaire Francais

(IPEV) and by the Préfet of Terres australes et antarctiques francaises (TAAF) after advices from the Comité de l'Environnement Polaire (CEP).

2.1. Field work

The study was carried out on a population of wandering albatrosses from Possession Island, Crozet Islands (46°21’S; 51°42’E) during January–March 2016, 2017, and 2018. All wandering albatrosses Possession have been monitored annually from 1966 (Weimerskirch et al. 1997a) and therefore all individuals are banded, sexed, and aged. The age of birds equipped ranged between 8 and 43 years. A total of 90 loggers (Fig 1.1) were deployed on 48 females and 42 males: 36 in 2016, 22 in 2017 and 32 in 2018.

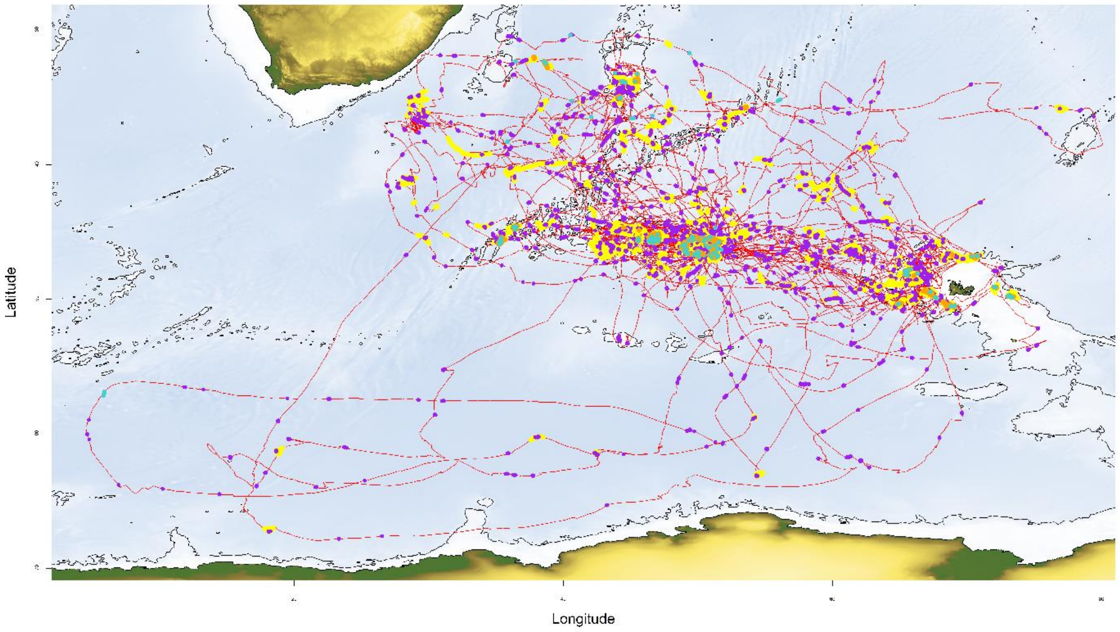


Fig 1.1. Map of all wandering albatross trips (red). ARS: one point per minute: yellow dot = large scales without radar detection and purple dot = small scales without radar detection; orange dot = large scales with radar detection; turquoise dot = small scales with radar detection. Bathymetry: isobaths for shelves (-2200 m deep).

Loggers (XGPS, Sextant technology – New Zealand) recorded GPS positions each minute and scanned for the presence of radar emissions (within 5 km maximum) for one minute each five minutes (Weimerskirch et al. 2018b).

We affixed loggers on the back feathers with tape (Tesa® 4651, Beirersdorff, Germany) during a shift change with their partner, and each bird was weighed before release. When the bird returned to its nest after a foraging trip, the logger was recovered and the bird weighed again to estimate mass-gain during the foraging trip. Bird handling generally lasted less than 10 min, never exceeding 15 min. The mass of the logger was 60–75g (120x40x20mm), i.e. between 0.49% to 1.21% of the total weight of birds, much less than the 3% recommended for flying birds (Phillips et al. 2003).

2.2. Analysis

All data management and statistical analysis were performed under R environment (R Core Team 2017). We filtered data by removing all coordinates with speeds >100 km.h^{-1} (Weimerskirch et al. 2002).

2.2.1. Area Restricted Search

Area-Restricted-Search (ARS) behaviours are performed at various scales (Pinaud 2007), often with a nested structure (fine-scale intensive local search within a larger-scale ARS, Fig 1.2). To detect these ARS structures at multiple scales, we used the First Passage Time (FPT) method (Fauchald & Tveraa 2003, Suryan et al. 2006). For ARS calculation, tracks were resampled with one location every segment of 1 km (Pinaud 2007). Because the standard variance peak procedure to identify putative scales of interest has been debated (Barraquand & Benhamou 2008), we *a priori* fixed a range of 10 radius scales for analyses (kilometres): 2, 5, 10, 20, 30, 40, 60, 80, 100, 125, 150 km used in previous FPT analyses. Visual inspection and preliminary analyses led us to regroup them in three main categories for analyses: small scales (2, 5, 10 km), large scales (20, 40, 60, 80 km) and very-large scales (100, 125, 150 km). Because 83.2% of very-large scales ARS (n=155) had nested, large-scale ARS and because analyses on very-large-scale ARS yielded very similar results to large-scale ARS, we report results only for small- (n=1476) and large-scale ARS (n=212) (Fig 1.1).

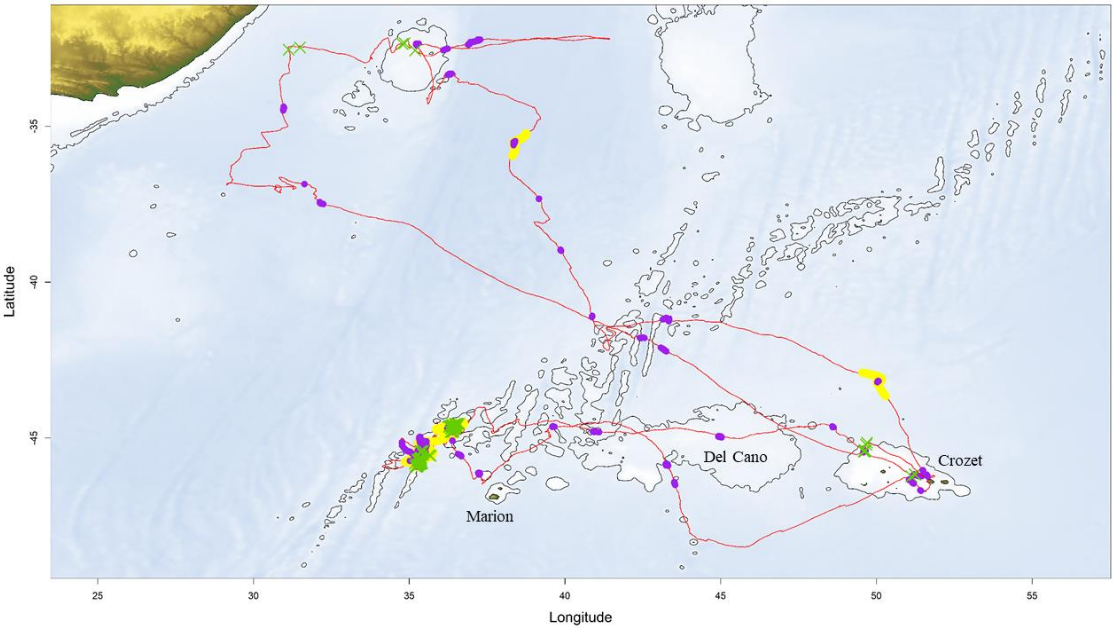


Fig 1.2. Map of two wandering albatross trips (red) with one over the shelf and one in oceanic waters. ARS: one point per minute: yellow dot = large scales; purple dot = small scales. Radar detections: green cross per location with boat detection. Bathymetry: isobaths for shelves (-2200 m deep).

Wandering albatrosses are not active at night when they mainly sit on water to rest or sleep (Weimerskirch, H et al. 1997). This can lead FPT analysis to spuriously identify night-resting areas as ARS (Bennison et al. 2018). We overcame this issue differently for small- and large-scale ARS. For small-scale ARS, we removed locations at night and only worked with daylight locations. For large-scale ARS, this was not possible because focusing our analyses on daytime only created border effects (of a size proportional to the scale of ARS investigated) where FPT cannot be calculated. Moreover, some large-scale ARS can be performed over several consecutive days. Thus, for large-scale ARS, we measured the proportion of the ARS duration that occurred at night, and included this measure in our analyses (see below) to control for its potential effect. Night-time was defined as the period when the sun was six-degree or more below the horizon (civil twilight).

We used R package ‘adehabitatLT’ (Calenge 2006) to calculate FPT values for each radius and then the Lavielle method (Lavielle 1999, 2005) to segment the track based on their FPT values. Each segment was identified as ARS or not when its FPT values were above the average FPT value of the entire trip (large-scale ARS) or the average FPT value for the day (small-scale ARS).

2.2.2. Bathymetry data

We used the R package ‘marmap’ (Pante & Simon-Bouhet 2013) to estimate depth values at each location (data extracted from ‘ETOPO1 Global Relief Model’ from ‘National Oceanic and Atmospheric Administration’). We estimated the average depth of each ARS, and classified ARS as either over oceanic waters (< -2200 m on average) or over shelves (> -2200 m). We also used it to created maps (Figs 1.1 and 1.2).

2.2.3. Descriptive parameters of ARS

For each ARS we calculated the following parameters: duration (h), sinuosity ($1 - \frac{\text{straight−line distance between the first and the last location of the ARS}}{\text{total distance travelled in the ARS}}$), average distance to the colony (km), proportion of ARS during the night (large-scale ARS only), average depth (m), proportion of time spent sitting on water and for large ARS, the proportion of small ARS nested in larger ARS. We also estimated the proportion of time spent on the water during each ARS, by considering that birds were sitting on the water when speeds were <10 km.h^{-1} (Weimerskirch et al. 2002). We considered that birds were associated with boats when at least one radar detection was recorded, knowing that loggers detect radar at a maximum distance of 5km (Weimerskirch et al. 2018b). We also considered an encounter as a series (from 1 to 220) of successive radar detections, with a least 2 hours with no radar detection between two encounters.

2.2.4. Statistical analyses

To analyse differences between natural ARS and boat-associated ARS, we used Generalised Linear Mixed Model (binomial family with individual included as a random factor) and estimated marginal R² and conditional R² following the Nakagawa & Schielzeth method (R package ‘MuMIn’ (Johnson 2014)) (Tables 1.1, 1.2 and 1.3). We analysed separately small- and large-scale ARS. Values are given as means ± one Standard Deviation, otherwise stated.

Table 1.1 - Generalised Linear Mixed Model results for differences between small/large scales of natural ARS and boat-associated ARS.

Significant level: ‘***’ <0.001; ‘**’ <0.01; ‘*’ <0.05.

	Small scales					**Large scales**				
	Natural ARS (n=1259)	Boat associated ARS (n=217) 14.702%	Differences (GLMM) (r^2m=0.398 r^2c=0.607)			Natural ARS (n=134)	Boat associated ARS (n=78) 36.793%	Differences (GLMM) (r^2m=0.777 r^2c=0.906)		
	Mean ±sd	**Mean ±sd**	**Slope**	**Z value**	**Significance**	**Mean ±sd**	**Mean ±sd**	**Slope**	**Z value**	**Significance**
(Intercept)			-4.232	-8.731	***			-7.212	-2.042	*
Duration (h)	2.7 ±2.9	4.6 ±3.2	0.163	4.621	***	23.5 ±24.9	56.2 ±43.9	0.022	1.472	0.141
Sinuosity	0.5 ±0.3	0.7 ±0.2	3.600	7.277	***	0.6 ±0.2	0.9 ±0.1	11.444	2.661	**
Average distance to the colony (km)	772.5 ±656.6	538.2 ±571.1	-0.0005	-1.912	0.056	784.4 ±642.3	514.5 ±542.8	-0.001	-1.397	0.163
Average bathymetry (m)	-2626.3 ±1570.3	-1470.7 ±888.0	0.0006	5.214	***	-3086.3 ±1484.2	-1380.0 ±709.3	0.002	3.288	**
Proportion of time spent on water	0.5 ±0.3	0.6 ±0.2	-0.242	-0.563	0.573	0.5 ±0.2	0.6 ±0.1	3.945	1.659	0.097
Proportion of small ARS nested in larger ARS	0.3 ±0.4	0.7 ±0.5	1.105	4.949	***					
Proportion of night						0.5 ±0.3	0.4 ±0.1	-2.529	-1.314	0.189

Table 1.2 - Generalised Linear Mixed Model results for differences between small scales in ocean waters /over shelf of natural ARS and boat-associated ARS. Significant level: ‘***’ <0.001; ‘**’ <0.01; ‘*’ <0.05.

Small scales	**Oceanic waters**					**Above shelf**				
	Natural ARS (n=666)	Boat associated ARS (n=16) 2.40%	Differences (GLMM) (r^2m=0.010 r^2c=0.860)			Natural ARS (n=593)	Boat associated ARS (n=201) 33.90%	Differences (GLMM) (r^2m=0.355 r^2c=0.573)		
	Mean ±sd	**Mean ±sd**	**Slope**	**Z value**	**Significance**	**Mean ±sd**	**Mean ±sd**	**Slope**	**Z value**	**Significance**
(Intercept)			-6.971	-2.640	**			-5.289	-8.881	***
Duration (h)	2.6 ±2.9	2.8 ±2.6	0.070	0.532	0.595	2.7 ±2.8	4.7 ±3.2	0.194	4.632	***
Sinuosity	0.5 ±0.3	0.5 ±0.2	-0.636	-0.447	0.655	0.6 ±0.2	0.8 ±0.2	4.318	7.388	***
Average distance to the colony (km)	990.8 ±681.1	1458.7 ±753.8	-0.0001	-0.228	0.820	527.2 ±529.9	464.9 ±486.3	-0.001	-3.139	**
Average bathymetry (m)	-3908.8 ±929.7	-3968.7 ±1062.2	0.0002	0.480	0.632	-1185.9 ±583.3	-1271.9 ±477.6	-0.0002	-0.923	0.356
Proportion of time spent on water	0.5 ±0.3	0.5 ±0.3	-0.327	-0.245	0.807	0.5 ±0.3	0.6 ±0.2	-0.394	-0.800	0.424
Proportion of small ARS nested in larger ARS	0.3 ±0.4	0.3 ±0.5	0.654	0.692	0.489	0.4 ±0.5	0.8 ±0.4	1.177	4.569	***

Table 1.3 - Generalised Linear Mixed Model results for differences between small scales ARS with boats detection on shelf or in oceanic waters.

Small scales boat-associated ARS	Oceanic waters (n=16)	Shelf (n=201)	Differences (GLMM)		
	Mean ±sd	**Mean ±sd**	**Slope**	**Z value**	**Significance**
(Intercept)			52.327	15034.100	***
Duration (h)	2.8 ±2.6	4.7 ±3.2	17.886	3132.400	***
Sinuosity	0.5 ±0.2	0.8 ±0.2	-12.547	-1812.900	***
Proportion of time spent on water	0.5 ±0.3	0.6 ±0.2	0.707	100.800	***
Proportion of small ARS nested in larger ARS	0.3 ±0.5	0.8 ±0.4	1.254	359.600	***

Significant level: '***' <0.001; '**' <0.01; '*' <0.05.

3. Results

3.1. Foraging trip characteristics

Foraging trips consisted of rapid, direct movements interspersed with small and large ARS (Figs 1.1 and 1.2). There was no difference between males and females or among years in ARS characteristics (S1.1 Table), therefore we pooled sexes and years for analyses. All birds made small- and large-scale ARS. Of 90 birds tracked, 24 birds (26.7%) had no detection of radar during their trips (13 females and 11 males). On average, 78.5% (median = 96.9% and standard deviation = 33.8%) of locations with a radar detection during a trip (a contact with boats) occurred within an ARS identified with the FPT method ($n_{\text{radar detection in ARS}}$=5386; $n_{\text{all radar detection}}$= 6368). During their trips, birds spent 22.2% ±7.3 of their time in small-scale ARS and 40.9% ±19.9 in large-scale ARS, 36.9% (n=545) of small-scale ARS were nested in larger-scale ARS (Fig 1.3). Birds spent 0.9% ± 1.3% of their total foraging time directly associated (with at least a radar detection) with a boat and had on average 4.3 ± 4.8 boat encounters per trip (maximum = 21). We considered ARS without radar detection to be 'natural' ARS (n=1393), and those with radar detections to be 'boat-associated' ARS (n=295).

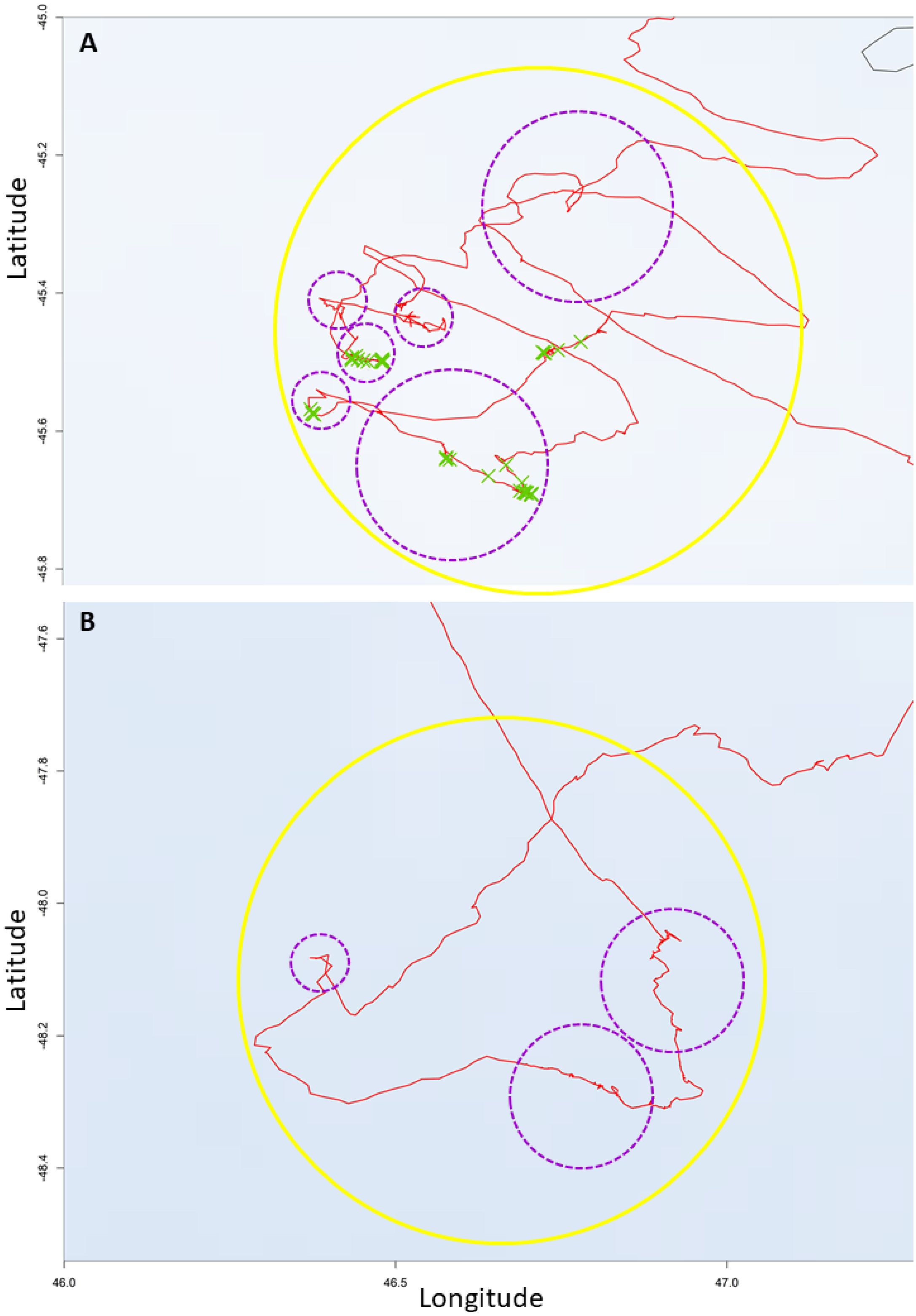


Fig 1.3. Maps of boat-associated ARS (A): 1 large-scale ARS – solid yellow circle + 6 small-scale ARS nested – dotted purple circles) **and natural ARS (B)**: 1 large-scale ARS – solid yellow circle + 3 small-scale ARS nested – dotted purple circles) - Albatross trip

(red line). Radar detections: green cross per location with radar detection. Bathymetry: isobaths for shelves (-2200 m deep).

3.2. Difference between natural ARS and boat-associated ARS

Only 14.7% of small-scale ARS ($n_{\text{all small ARS}}$=1476) and 36.8% of large-scale ARS ($n_{\text{all large ARS}}$=212), 36.8% were associated with the presence of a boat.

For small-scale ARS, birds spent more time and had greater sinuosity during boat-associated ARS compared to natural ARS (Figs 1.3 and 1.4, Table 1.1 – Small-scale ARS, GLMM: marginal R^2=0.398 and conditional R^2=0.607; Y = -4.232 + 0.163 duration of ARS + 3.6 sinuosity of ARS - 0.0005 average distance to the colony of the ARS + 0.0006 average bathymetry of ARS -0.242 proportion of time spent sitting on water in ARS). Small-scale, boat-associated ARS were performed over shallower waters and mostly occurred over shelves (Table 2) and tended to be more frequently nested in larger-scale ARS (Table 1) than natural ARS. There was no significant difference in the proportion of time spent sitting on water and in the average distance to the colony between natural and boat-associated small ARS (Table 1 – Small scales).

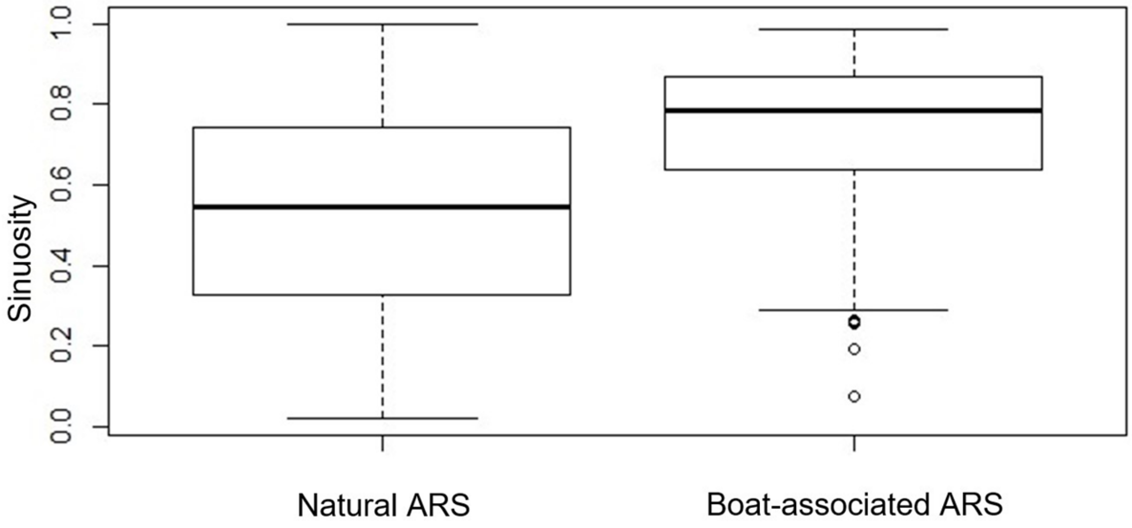


Fig 1.4. Sinuosity boxplot of small scales ARS: natural ARS are significantly different than ARS associated with a boat.

For large-scale ARS, boat-associated ARS were more sinuous than natural ARS (Fig 1.3), but there was no difference in duration, average distance to the colony, and proportion of time spent sitting on water between natural and boat-associated ARS. For large-scale ARS, there was no difference in the proportion of night spent between natural and boat-associated ARS (Table 1 – Large scales).

3.3. Difference between oceanic and shelves small-scale ARS

When comparing small-scale ARS performed over oceanic waters from those over shelves, we found no significant differences in the associated parameters between natural and boat-associated ARS in oceanic waters (Table 2 – Oceanic waters). For small scale ARS over shelves, duration, sinuosity and proportion of small ARS nested in larger ARS were higher for boat-associated ARS compared to natural. ARS with boats were also on average closer to the colony than natural ARS (Table 2 – Shelf).

If we consider only ARS associated with boats, small-scale ARS over shelves were longer in duration, had greater sinuosity, and birds spent more time sitting on water compared with oceanic ARS (Table 3).

4. Discussion

Our study is the first to precisely estimate to what extent ARS behaviours in seabirds are associated with the presence of boats. Previous studies showed that the behaviour of birds associated with boats equipped with VMS had different behaviour from other ARS (Torres et al. 2011, Bodey et al. 2014, Collet et al. 2015), that could be natural or associated with boats without VMS. By using loggers equipped with radar detectors, we have shown that as much as 78% of boat detections occurred in an ARS, and that wandering albatrosses, modified their movements when associating with boats. Albatrosses are attracted by boats and may associate with them for variable durations; they can either have a brief encounter lasting a few minutes while following a cruising boat, or they may attend a fishing boat in operation (Collet et al. 2017b, Weimerskirch et al. 2018b). In the latter case, birds probably entered into an ARS behaviour, whereas for the first cases, they do not probably use ARS. However, our results showed that the majority of ARS were not associated with boats, and thus this searching behaviour can be considered a natural foraging behaviour.

When attending boats, ARS had different characteristics from natural ARS, they were longer in duration, more sinuous, and occurred over shallower waters. Since these ARS probably occurred with fishing boats, birds may have stayed for long periods behind boats to access food, waiting for the release of offal or the setting of long–lines when they try to take baits. Greater sinuosity may be explained by the specific movement of birds whereby they continuously take-off and land using wind to stay close from the boats in operation, but also when they followed a slow-moving fishing boat in operation. At finer temporal scales (<30 min), sinuosity can be lower if albatrosses following fishing boats, and particularly long-liners, may actually display locally very straight paths as a fishing line is set or hauled (Torres et al. 2011), but our results showed that this did not occur during natural or boat-associated ARS.

We also found that a large proportion of small-scale ARS were nested in larger-scale ARS when birds were associated with boats, compared to natural ARS. This could reflect the movements of fishing boats themselves, but most of the duration of large-scale ARS were not associated with fishing boats. We suggest nested ARS structure arises from a common large-scale habitat selection between boats and albatrosses. A large proportion (57%) of larger-scale ARS occurred over shelf-edges or seamounts (e.g. south of Madagascar), where many fishing boats operate. Wandering albatrosses may recognise the boundaries of these areas and increase their search intensity over these shallower waters (Weimerskirch et al. 2014a, de Grissac et al. 2017, Pereira et al. 2018). Indeed it was shown previously that ARS in this species were not necessarily triggered by prey capture (Weimerskirch et al. 2007), but high-foraging efficiency could also be achieved if they were triggered by favourable habitat recognition (Benhamou 1992, Sabarros et al. 2014). Then, when encountering and interacting with fishing boats in these areas, they would display finer-scale, nested ARS behaviour. This would also explain why boat-associated ARS were more likely to be nested when over shelves compared with oceanic waters.

In the southern Indian Ocean, fisheries operate either over shelves (and especially shelf-edges) or over oceanic waters. In oceanic waters, in the range of wandering albatrosses, extensive long-line fisheries operate in sub-tropical and tropical waters where they target various species of tuna and cause high albatross mortality (Brothers 1991 199, Weimerskirch et al. 1997a, Anderson et al. 2011). Over shelf-edges or shelves, Crozet wandering albatrosses encounter predominately long-liners targeting Patagonian toothfish around Crozet and Kerguelen Islands and other shelves in sub-Antarctic waters such as the Del Cano rise (Fig 1.2). These fisheries also caused high mortality historically, but now that they are regulated in EEZs, these fisheries have reduced albatross mortality in EEZs (Delord et al. 2005). In subtropical waters, wandering albatrosses encounter fishing boats over seamounts, especially south of Madagascar (Fig 1.2), but also over oceanic waters. ARS behaviours associated with boats probably occur mostly with fishing boats in operation (Collet et al. 2017b). We found that ARS behaviour differed between oceanic-tuna fisheries and shelf-edge fisheries (mainly Patagonian toothfish). Over shelf edges, small-scale ARS were longer in duration and more sinuous, indicating more intense foraging behaviour compared to oceanic-tuna fisheries. These differences may be due to different operational practices between these fisheries, longer-lines (thus duration of line-setting and hauling), and different baits and offal (Rollinson et al. 2016).

This study showed that a significant proportion (21.2%) of ARS behaviours made by wandering albatrosses occurred in association with boats and that 73% of birds encountered a boat during their foraging trips. Our results demonstrate fisheries can extensively modify the foraging behaviour of seabirds such as albatrosses. Natural ARS behaviour, however, remains by far the majority of the foraging behaviour. Because longline fisheries induce high mortality of albatrosses, it is important to be able to determine whether foraging birds associate with a boat and increase risk. Our study constitutes an important and promising step towards accurate quantitative predictions of vessel association at sea. Developing predictive analyses through unsupervised machine learning approaches (Trost et al. 2014) or by the use of Hidden-Markov-Model (HMM) (Langrock et al. 2012, Joo et al. 2013) should allow scientists to determine the degree to which movement recorded simply by GPS, may be related to the presence of a boat. Having access to this predictive capability could open up interesting perspectives on retrospective studies with tracking data and how the attraction of albatrosses to boats may have ‘evolved’ throughout decades of GPS tracking (Henri Weimerskirch, 2018).

5. Acknowledgements

We thank the *Institut Polaire français Paul Emile Victor (Prog. 109 – Henri Weimerskirch)* for logistical support and the TAAF Administration for allowing us to work on Crozet. We thank the fieldworkers involved in the study on Crozet, and in particular Samantha Patrick, Gaspard Bernard, Nicolas Moulin and Célia Lesage. We thank Dominique Filippi for fieldwork assistance and for the design and construction of these devices. We thank Jean-Yves Barnagaud for statistical advice and Pierre-Loup Jan for advice on GLMM. This study is part of the programs EARLYLIFE, funded by a European Research Council Advanced Grant under the European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 to Henri Weimerskirch).

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7. Supporting information

S1.1 Table – Differences between females and males for trips and ARS parameters.

	Mean	Standard deviation	Mean	Standard deviation	Z value	Significance (P value)
Parameters for trip						
	Female (n=48)		**Male (n=42)**		**Difference**	
Proportion of radar detection who are in ARS	0.732	0.366	0.846	0.265	1.203	0.229
Time spent behind boat (h)	17.368	18.689	17.543	16.190	1.276	0.202
Maximum range (km)	1081.400	718.676	1074.400	795.702	1.104	0.270
Proportion of radar	0.008	0.011	0.010	0.016	-0.695	0.487
Proportion of small ARS	0.204	0.068	0.241	0.074	2.534	*
Proportion of medium ARS	0.408	0.198	0.409	0.203	-0.020	0.984
Proportion of large ARS	0.377	0.217	0.361	0.197	0.591	0.555
Total distance (km)	5373.900	2965.777	4916.800	3454.978	-0.721	0.471
Average speed (km.h-1)	22.540	6.383	21.301	7.034	1.722	0.085
Average bathymetry (m)	-2453.800	960.523	-2332.200	903.936	1.747	0.081
Proportion of time spent on water	0.4243	0.124	0.457	0.101	1.904	0.057
Proportion of small ARS nest in large ARS	0.104	0.079	0.115	0.078	-1.370	0.171
Proportion of medium ARS nest in large ARS	0.120	0.073	0.138	0.096	-0.581	0.561
Proportion of small ARS nest in medium ARS	0.307	0.188	0.281	0.172	-0.644	0.520
Number of boats encounter	4.688	5.684	3.880	3.514	-1.309	0.191
Parameters for ARS						
	Female (n=1030)		**Male (n=813)**		**Difference**	
Duration (h)	12.960	28.748	13.280	25.093	0.249	0.803
Proportion of radar detected	0.057	0.165	0.071	0.189	-0.123	0.902
Total distance (km)	160.430	423.737	133.600	269.563	-0.284	0.777
average speed (km.h-1)	13.920	10.777	13.420	12.083	0.148	0.883
sinuosity	0.594	0.259	0.612	0.254	0.189	0.850
average distance to the colony (km)	710.400	604.480	728.940	690.644	-0.084	0.933
proportion of night	0.098	0.205	0.100	0.201	-0.071	0.944
average bathymetry (m)	-2513.000	1454.600	-2306.000	1598.929	0.361	0.718
proportion of time spent on water	0.512	0.248	0.546	0.239	0.256	0.798
proportion of small ARS nest in large ARS	0.257	0.437	0.246	0.431	-0.168	0.867
proportion of medium ARS nest in large ARS	0.0714	0.254	0.074	0.260	-0.076	0.940
proportion of small ARS nest in medium ARS	0.278	0.447	0.259	0.437	-0.015	0.988
time spent in contact to boat (h)	0.105	0.344	0.150	0.386	0.202	0.840
distance from the beginning to the end of ARS (km)	28.460	54.290	26.148	49.562	0.105	0.916

Significant level: ‘***’ <0.001; ‘**’ <0.01; ‘*’ <0.05.

Chapitre 2 : Différences d'exposition au risque de captures accidentelles entre populations et espèces

Corbeau A., Collet J., Orgeret F., Pistorius P.A., Weimerskirch H., 2021. Fine-scale interactions between boats and large albatrosses indicate variable susceptibility to bycatch risk according to species and populations. ***Animal Conservation*** (*sous press*)

Abstract

Many seabirds are attracted by fishing boats where they exploit foraging opportunities which often involve bycatch-related mortality. Bycatch risk is generally estimated by overlapping seabirds foraging ranges with coarse-scale monthly maps of fishing efforts. A more direct estimation would be the time birds actually spend attending fishing boats.

Here we matched data from Automatic Identification Systems from all declared boats in the Southern Ocean, with 143 simultaneous foraging trips from all populations of large albatrosses (Diomedea amsterdamensis and Diomedea exulans) breeding in the Indian Ocean (Marion, Crozet, Kerguelen, Amsterdam islands). We quantified and compared real-time co-occurrence between boats and albatrosses, at different scales (100, 30 and 5 km). We also examined to what extent co-occurrence at a large-scale (5x5° grid cell) predicted fine-scale attendance (5 km).

Albatrosses on average spent about 3 h per trip attending fishing boats (<5 km) at both Amsterdam and Marion and about 30 h per trip at Kerguelen. In all populations >90% of declared fishing boat attendances occurred within Economic Exclusive Zones (EEZ) where bycatch mitigation measures are enforced. Outside EEZs, birds from all populations to a large extent also attended non-fishing boats. Fishing boat density at a large scale (5x5°, 100 km) was a poor predictor of time spent attending fishing boats (<5 km) across populations.

Our results indicate a large variation in fishing boat densities within the foraging ranges of different populations, and in time birds spent attending boats. We discuss the pros and cons of considering bycatch risk at a large geographic scale and methods that can be implemented to improve estimation of seabird vulnerability to fishing activities when fine-scale data is available particularly for conservation purpose on those highly threatened species.

Key words: albatross populations; biologging; bycatch assessment; ecological trap; fisheries.

1. Introduction

In marine ecosystems, together with climate change, industrial fisheries constitute the main driver of ecological deterioration (Pauly et al. 2002). Fisheries interact with marine predators mainly by competing for resources (Cury et al. 2011, Grémillet et al. 2018) and by inducing mortality through bycatch of non-target species (Lewison et al. 2004). Fisheries can also facilitate access to prey for higher predators along the food chain or provide additional food resources (Oro et al. 2013). As a result, many seabird species and marine mammals are attracted to fishing boats (Votier et al., 2004; Read, 2008; Brothers et al., 2010; Bugoni, McGill, & Furness, 2010) in search of foraging opportunities associated with fishing bait or discards (Votier et al., 2004; Bicknell et al., 2013). However, the associated bycatch is one of the primary threats for seabird populations around the world (Croxall et al. 2012). Moreover, in some seabird populations the poor quality of these food resources negatively affect reproductive success (Gremillet et al. 2008, Le Bot et al. 2018). Another concern is that populations heavily reliant on fishing vessels for food resources may be negatively impacted by changes in fishing policies (Bicknell et al. 2013).

Bycatch is the most important threat for albatrosses and large petrels while at sea with high levels of mortality often induced by longline fisheries (Delord et al. 2005, Anderson et al. 2011, Croxall et al. 2012). In the Southern Ocean, albatrosses overlap extensively with longline fisheries, targeting tuna in oceanic waters, and various species of bottom-dwelling fishes over shelves and shelf-edges, in international waters as well as the Economic Exclusive Zones (EEZ) of the respective countries. The extent of spatio-temporal overlap between different density of fisheries and albatross foraging grounds has been inferred to represent mortality risk for various populations (Bertrand et al. 2012b, Clay et al. 2019, Heerah et al. 2019). However, information on fisheries location is generally available at a large scale, especially in international waters. For example, global fishing efforts provided by Regional Fisheries Management Organisations for tuna and billfishes is only available at a monthly and by 5x5° cell resolution (Clay et al. 2019, Heerah et al. 2019). This approach overlooks the possibility that fisheries and seabirds could co-occur at a large scale without birds interacting with the fishing boats, particularly if they are not attracted by vessels (Clark et al. 2020). To better estimate mortality risk it is therefore necessary to complement these approaches with more direct information on the actual time birds spend attending fishing boats and how this varies spatially (Torres et al. 2013). This has been hampered in the past by difficulties in obtaining fine scale information on fishing vessel movements from fishing operators or authorities. This information can be made available through Vessel Monitoring Systems (VMS) but it is often confidential (Votier et al., 2010) and restricted to confined EEZ territories. Several studies have combined VMS information and fine scale tracking of seabirds to study interactions (Torres et al., 2013; Collet, Patrick, & Weimerskirch, 2017) but these have been restricted to specific small-scale geographic sectors.

In the Indian Ocean, large scale active longline tuna fisheries in open waters and Patagonian toothfish (*Dissostichus eleginoides*) fisheries operating over sub-Antarctic shelf edges and sea mounts overlap with the foraging ranges of the two large albatross species (wandering - *Diomedea exulans* and Amsterdam - *Diomedea amsterdamensis*) breeding in the region (Weimerskirch, Brothers, & Jouventin, 1997; Delord et al., 2005). The past decline of the former species has been attributed to bycatch associated with longline fisheries (Brothers, 1991; Weimerskirch, Brothers, & Jouventin, 1997; Nel et al., 2002). Despite mitigation measures that have been implemented by toothfish longline fisheries within the EEZs, which has resulted in a reduction in bycatch by this fishery (Delord et al., 2005; Weimerskirch et al., 2018), there are still concerns of bycatch risk from longline fisheries targeting tuna in international waters where no mitigation measures are implemented or from illegal or uncontrolled fisheries for toothfish without mitigation measures (Brothers, 1991; Weimerskirch, Brothers, & Jouventin, 1997; Weimerskirch et al., 2020). Moreover, within more regulated EEZ waters it is important to estimate the extent to which albatrosses of different species and populations spend interacting with toothfish longliners, to better quantify potential sub-lethal issues of dependence and possibly poor forage quality (Bicknell et al. 2013, Le Bot et al. 2018).

In this study, we combined a large tracking dataset of foraging albatrosses (Weimerskirch et al., 2020) with the locations and types of all declared boats from Automatic Identification System (AIS) in the southern Indian Ocean. GPS tracking data were collected in 2018/2019 on breeding adults from all four major populations of large albatrosses in the Indian Ocean. We spatio-temporally matched these datasets to estimate the degree of co-occurrence at various scales from seascape (<100 km from the tracked individual), through encounter (<30 km) to attendance (<5 km), following Weimerskirch et al. (2020). We particularly focused on the time spent attending fishing boats (<5 km) as a potential proxy for bycatch and other boat-associated risks. We examined how it differed among individuals and populations, how it differed with different types of fishing and non-fishing boats, and how it differed between EEZs around subantarctic islands and international waters where different fisheries operate with different mitigation measures. Finally, to assess to what extent co-occurrence at a larger-scale reflects co-occurrence at finer-scale and could be used as a proxy for bycatch risk (exposure to bycatch risk), we compared the time spent attending fishing boats (<5 km) to the encounter rate (30 km) and the density of boats in the seascape (<100 km) as well as to the more widely used method of aggregating boat data by Regional Fisheries Management Organisations (RFMO: 5x5° grid). We 1) hypothesized that there is a large variation in the levels of exposure to boats according to albatrosses' foraging zones and range, 2) tested to what extent it resulted in variation in the time spent attending boats and 3) tested whether large scale 5x5° grid methods provide an adequate reflection of the attendance to boats and therefore the exposure to the risk of bycatch. We then discuss implications for bycatch and sub-lethal risks to the different populations.

2. Material and methods

2.1. Field sites

Fieldwork was carried out in French southern territories (Crozet, Kerguelen & Amsterdam) during the course of a large-scale Ocean Sentinel program between January and April 2019, during the breeding season of large albatrosses in the Southern Indian Ocean (Weimerskirch et al., 2020). We deployed loggers on incubating wandering albatrosses at Possession Island (Crozet Islands) and at the Kerguelen Islands, and on Amsterdam albatrosses at Amsterdam Island. During the same season, incubation wandering albatrosses were fitted with GPS loggers at South Africa's Marion Island, Prince Edward Islands.

2.2. Loggers

On Crozet, Kerguelen and Amsterdam, Centurion loggers (65 g) recording GPS location every 2 min were deployed on incubating birds for one or two successive foraging trips (Weimerskirch et al., 2020). On Marion, GPS loggers (IgotU, 60 g) recording locations every 20 min were deployed for several trips during the incubation and brooding period. The loggers were attached to the back feathers with Tesa® Tape (Germany), and represented between 0.5 and 0.85% of large albatross body mass, much less than the maximum 3% recommended for loggers attached on flying seabirds (Phillips et al. 2003).

2.3. GPS data and AIS Dataset

A total of 143 trips on incubating albatrosses was recorded, with 57 trips from 27 individuals on Marion Island, 10 trips from 8 individuals at Amsterdam, 49 trips from 49 individuals at Crozet and 27 trips from 24 individuals at Kerguelen.

After using speed filters (150 km.h-1; Weimerskirch et al., 2020), we divided tracks by trips (removing location on land).

AIS data for all fishing and non-fishing boats (Fig. S2.1) were obtained from French satellite transmission society (*Collecte Localisation Satellites*) for the study period for the sector 10°-180°E, 20°-70°S through the Ocean sentinel program (Weimerskirch et al., 2020), providing a total of 120 million AIS locations. Through the AIS system, in addition to regular GPS locations (mean resolution of 10 min) we obtained continuous data on identification name, nationality, type of boat (fishing or not), and activity for all declared boats in the Southern Indian Ocean. AIS data and bird locations were spatio-temporally matched following Weimerskirch et al. (2020) to produce a dataset where all GPS locations of each bird from each population are associated to the presence/absence, number and types of boats transmitting AIS information within ranges of 100, 30 and 5 km from birds (Fig. 2.1).

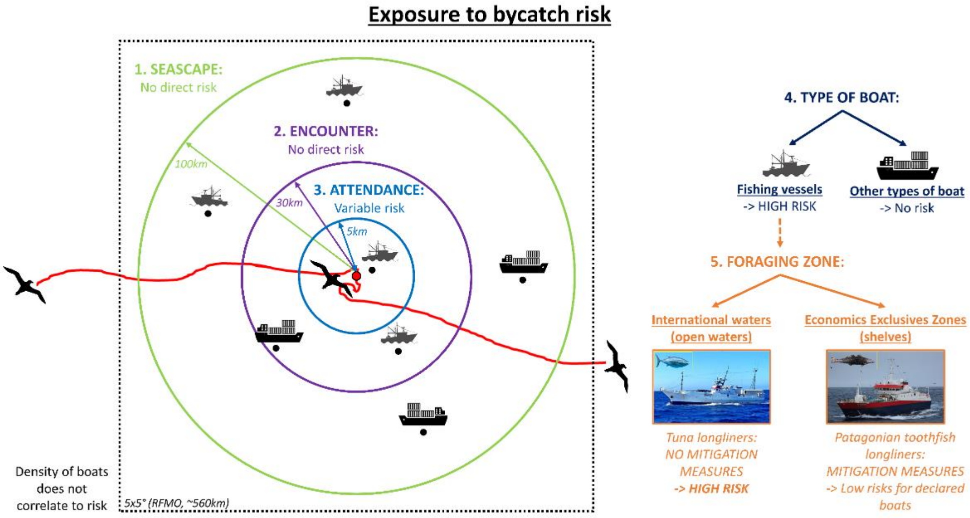

Figure 2.1 – Conceptual model illustrating the five points required to be checked to estimate exposure to bycatch risk applicable by species and populations.

These different radius distances from birds are used to characterize the ‘boat seascape’ (within 100 km around the tracked bird), the ‘boats encountered’ (30 km) and the ‘boats attended’ (5 km). The 30 km distance was used as it is the distance within which an albatross can visually detect a boat (Collet, Patrick, & Weimerskirch, 2015). The 5 km threshold is the approximate distance within which wandering albatrosses are seen to engage in specific foraging behaviours around boats (3 km; Collet et al., 2015) and is used to facilitate comparisons with previous studies that used radar detectors with a range detection of 5 km (Weimerskirch et al., 2017, 2020).

We defined ‘events’ (attendance and encounter events) as periods of consecutive bird locations within the respective distances of at least one boat with time intervals of less than 2 hours. To compare sites, and accommodate the relatively coarse scale GPS sampling at Marion Island, we removed all events (attendance and encounter) lasting less than 20 min. This procedure also limits the effects of uncertainties on “instantaneous” bird-boat distances (Weimerskirch et al., 2020). We also removed the few incomplete trips for presenting trip statistics (Table 2.1).

To compare with other studies using large scale 5x5°of fishing effort provided by RFMOs (Clay et al. 2019, Heerah et al. 2019), we merged all AIS locations present during the study period within grid cells of 5x5° (Fig. S2.1).

2.4. Environmental variables

AIS data do not provide detailed information on the type of fishing gear used nor the mitigation measures employed by fishing boats. We tried to further infer this information from the waters they operated in. We added bathymetry data to each bird location (R package ‘marmap’, Pante and Simon-Bouhet, 2013), which was extracted from ‘ETOPO1 Global Relief Model’ from ‘National Oceanic and Atmospheric). We used it to categorize bird locations as on a shelf or a shelf-edge (above -2000 m), where mainly benthic fish are targeted, or off the shelf, where tunas and billfishes are the main target. We also considered whether locations were within EEZ or not (data from http://www.marineregions.org) and separately considered the time in attendance for specific EEZs with enforced mitigation measures within the range of our populations (Crozet, Kerguelen, Heard, McDonald Saint-Paul and Amsterdam Islands). Finally, from estimates of the locations of the polar front (Moore et al. 1999) and the subtropical front

(Belkin & Gordon 1996) we further categorized bird locations into Antarctic, subantarctic and subtropical waters.

2.5. Analyses

For visualization purposes, we used kernel Utilization Distributions (UDs 50 and 90%), using the R package 'adehabitatHR' (smoothing parameters, h=1 degree).

To compare different parameters (Table 2.1) between each population, we used linear mixed model or generalized linear mixed models (depending on the distribution, using R package "fitdistrPlus"). Negative binomial family were used for over-dispersed count data and binomial family for ratio data (R packages 'lme4' and "lmerTest"). Bird individual identities were used as random factors. We further used post-hoc tests (Tukey tests, R package multicomp) and Holm-Bonferroni correction for P values. We used a Chi² test to compare distributions of the number of trips with or without boat interaction between populations.

To compare density of boat to the exposure to bycatch risk (time birds spent behind boat) per 5x5° grid, we summed AIS locations (for all types of boat and only for fishing boats) per grid cell used by each study population during their respective incubation-period months (April for Amsterdam birds, January and February for Crozet and Kerguelen birds, and February and March for Marion birds). We then used Pearson correlation to examine whether density of boat are related to the time spent by birds in general, with boats in their seascape (<100 km), with boats encountered (<30 km) and with boats attended (<5 km) (exposure to bycatch risk) in the same 5x5° grid cells used by birds.

3. Results

For the 143 trips recorded during incubation, there were no significant differences between populations in the duration of foraging trips. Mean maximum distance from the colony, however, differed between Kerguelen (shortest) and Marion (longest) (Table 2.1).

Birds from Kerguelen spent more time foraging within EEZs (74%±32, Table 2.1) than birds from Crozet (57%±35), Amsterdam (39%±41) and Marion (36%±24). Amsterdam and Marion birds spent less time foraging over shelf waters (20%±29 and 11%±15 respectively) as compared to Crozet (40%±33) and Kerguelen birds (65%±29) (Fig. 2.2) (Table 2.1 and Table S2.1 for test values).

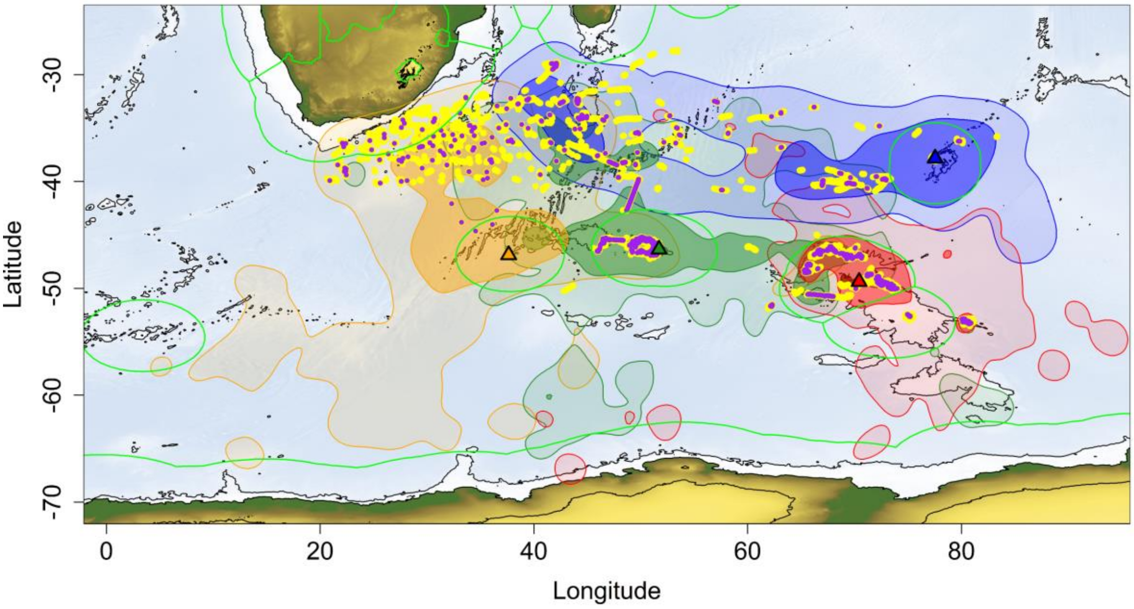

Figure 2.2 - Map of the South Indian Ocean with kernel utilization distribution 50% (darker shade) and 90% (lighter shade) of birds for each site (triangles) (blue = Amsterdam, green = Crozet, red= Kerguelen, orange= Marion); yellow dots represent encounter events and purple dots, attendance events; isobaths: -2000 m (shelf), 0 m and +2000 m; light-green lines represent EEZ.

Table 2.1 – Differences between each site: mean and standard deviation of parameters and significance letters of Tuckey tests (same letter in different site mean no difference and different letters mean significant differences).

	Amsterdam ***(trips: n=10, 10 complete)***			**Crozet** ***(trips: n=49, 48 complete)***			**Kerguelen** ***(trips: n=27, 23 complete)***			**Marion** ***(trips: n=57, 53 complete)***		
	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter
PER TRIP (n=143)												
Maximum distance from the colony (km)	1637.70	1281.10	AB	1177.90	813.90	AB	886.60	711.85	A	1424.70	660.54	B
Trip duration (day)	9.53	3.48	A	11.09	5.60	A	10.60	4.14	A	12.60	4.46	A
Ratio in EEZ	0.39	0.41	AC	0.57	0.35	AB	0.74	0.32	B	0.36	0.24	C
Ratio on shelf	0.20	0.29	AC	0.40	0.33	A	0.65	0.29	B	0.11	0.15	C
Ration in Antarctic waters	0.00	0.00	A	0.07	0.20	A	0.19	0.30	A	0.12	0.26	A
Ration in subantarctic waters	0.03	0.07	A	0.72	0.34	B	0.78	0.30	B	0.57	0.31	B
Ration in subtropical waters	0.97	0.07	A	0.21	0.32	BC	0.02	0.13	B	0.31	0.32	C
Number of encounters	5.10	7.61	A	3.06	2.18	A	2.89	2.65	A	4.23	5.45	A
Time in encounter (h)	19.04	23.28	A	17.08	18.36	A	53.30	62.82	B	11.91	21.96	A
Number of attendances	1.80	2.20	A	1.71	1.57	A	3.59	4.41	A	1.72	2.70	A
Time in attendance (h)	4.31	6.97	A	6.75	11.00	A	31.14	38.22	B	3.21	10.20	A
Time in attendance with fishing vessels (h)	3.16	7.56	A	6.68	11.31	A	30.63	39.27	B	2.64	10.31	A
Time in attendance in EEZ (h)	2.90	6.71	A	5.84	11.14	A	28.37	38.60	B	2.46	10.24	A
Time in attendance out EEZ (h)	1.42	2.40	A	0.91	2.74	A	2.77	11.56	A	0.75	1.58	A
Time in attendance with fishing vessels in EEZ (h)	2.82	6.75	A	5.84	11.14	A	28.36	38.60	B	2.45	10.24	A
Time in attendance with fishing vessels out EEZ (h)	0.11	0.28	A	0.60	2.66	A	0.00	0.00	A	0.14	0.68	A
Ratio of fishing vessels attended (5km)	0.64	0.43	AB	0.76	0.42	AB	0.95	0.23	A	0.22	0.37	B
Ratio of fishing vessels encountered (30km)	0.63	0.36	AB	0.76	0.40	A	0.92	0.28	A	0.17	0.32	B
Ratio of fishing vessels in seascape (100km)	0.43	0.27	A	0.75	0.36	B	0.92	0.23	B	0.16	0.29	A
PER LOCATION (n=619631)												
Number of boats attended (5km)	0.02	0.16	A	0.02	0.15	A	0.11	0.31	B	0.01	0.11	C
Number of boats encountered (30km)	0.19	0.84	A	0.06	0.26	B	0.23	0.43	C	0.05	0.26	B
Number of boats in seascape (100km)	1.99	5.08	A	0.29	0.60	B	0.40	0.60	C	0.35	1.11	D
Number of fishing vessels in seascape (100km)	0.83	1.93	A	0.21	0.51	B	0.39	0.60	C	0.07	0.33	D
Ratio of number of boats 5 km / 100 km	0.04	0.19	A	0.07	0.24	A	0.30	0.45	B	0.04	0.18	A

Amsterdam albatrosses spent most of their time in subtropical waters (97%±07). In contrast, the three wandering albatross populations foraged mainly in subantarctic waters (57%±31 to 78%±30) (Fig. 2.2) (Table 2.1 and Table S2.1 for test values).

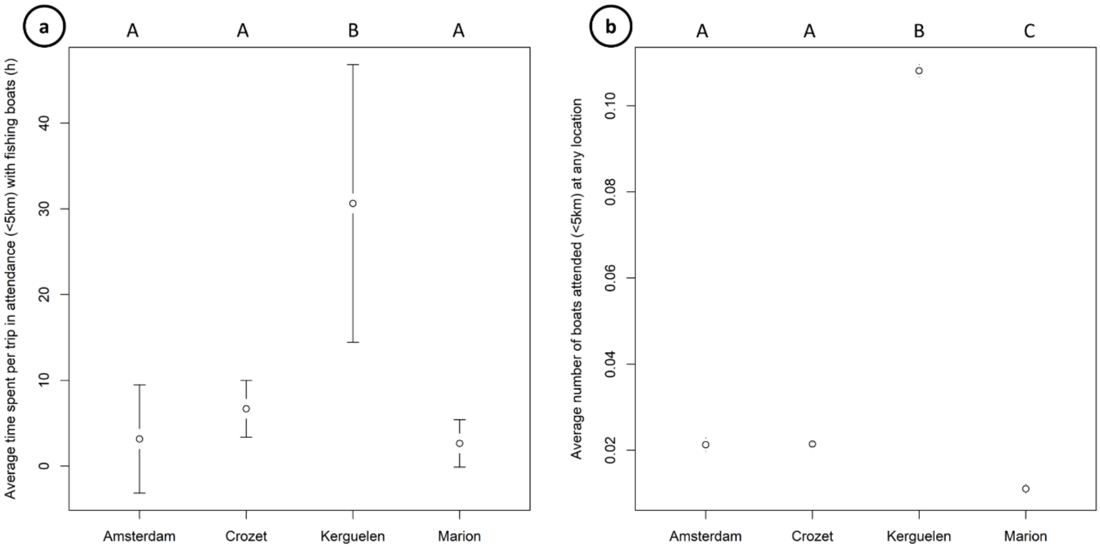

Figure 2.3 – Proxy of bycatch risk as **(a)** time spent per trip in attendance (within 5km) with fishing boats (hours) and **(b)** Number of boat attended (within 5 km) at any location; Mean and confidence interval (95%) of each site. Letters represent significant difference.

Among the 143 trips recorded, the percentages of trips with at least one boat within 100 km (boat seascape), were significantly different between populations, ranging from 68% to 100% (Chi², 3 = 24.9; p value = 1.5e-05) (Table 2.2). The percentage of trips with boats encountered (within 30 km) also varied significantly between sites, from 63 to 85% (Chi², 3 = 9.08; p value = 0.028) (Table 2.2). Finally, the percentage of trips with attendance (within 5 km) of boats were also significantly different between sites, varying from 47 to 73 % (Chi², 3 = 8.01; p value = 0.046) (Table 2.2).

Table 2.2 – Number (and percentage) of trips per site with boats in seascapes (100km), encountered (30km) and attended (5km).

	Amsterdam *(n=10)*	**Crozet *(n=49)***	**Kerguelen *(n=27)***	**Marion *(n=57)***	**TOTAL (n=143)**
With boats in seascape (100km)	9 (90%)	48 (97.96%)	27 (100%)	39 (68.42%)	**123 (86.01%)**
With boats encountered (30km)	8 (80%)	42 (85.71%)	23 (85.19%)	36 (63.16%)	**109 (76.22%)**
With boats attended (5km)	6 (60%)	36 (73.47%)	18 (66.67%)	27 (47.37%)	**87 (60.84%)**

The number of encounters and attendance events per trip, when considering fishing boats and other boats together (transport, tankers, etc.) was broadly similar between populations (Table 2.1 and Table S2.1 for test values). Kerguelen birds nonetheless spent more time on average per trip within 30 km of all types of boats (53 h±62), within 5 km of all type of boats (31 h±38) and within 5 km of fishing boats (30.6 h±39) (Fig. 2.3a) than birds from other populations (Table 2.1 and Table S2.1 for test values). Similarly, Kerguelen birds spent significantly more time attending boats inside EEZs (with mitigation measures) than birds from other populations. However, outside EEZs (where mitigation measures are less controlled) the different populations spent similar time attending AIS-recorded boats of all types, and similar time attending AIS-recorded fishing boats (Table 2.1 and Table S2.1 for test values).

Based on all location, Amsterdam birds on average had the greatest number of boats (1.9±5) and the greatest number of fishing boats (0.83±1.9) in their seascapes (<100 km), at least twice as much as other populations (Table 2.1 and Table S2.1 for test values). However, at Kerguelen, birds on average had the greatest number of boat encounters (<30 km: 0.2±0.4), the highest number of boats attended (<5 km: 0.1±0.3, Fig. 2.3b) and the highest ratio of the number of boats attended relative to the number of boats in the seascape (0.3±0.5), most of the time by a factor of 5-10 fold compared to other populations (Table 2.1 and Table S2.1 for test values).

Marion and Amsterdam birds had a smaller proportion of fishing versus non-fishing boats in their seascapes (<100 km) compared to other populations (Table 2.1 and Table S2.1 for test values). Marion birds had a significantly lower proportion of fishing boats among encountered boats (<30 km) than Crozet and Kerguelen and slightly less than Amsterdam. The proportion of fishing boats among attended boats (<5 km) was not different between Marion, Amsterdam and Crozet birds (0.22±0.4, 0.64±0.4 and 0.76±0.4, respectively), but it was lower for Marion than for Kerguelen birds (0.95±0.2, Table 2.1 and Table S2.1 for test values).

Finally, we found that at all locations, birds attended only a small proportion of the total number of boats in their seascapes: 30%±45 for Kerguelen birds which was significantly higher than for Crozet birds (7%±24) and for Marion and Amsterdam birds (4% ±0.19; Table 2.1 and Table S2.1 for test values).

For all four populations, there were no significant correlations between the time spent by birds per 5x5° grid cell (in general, with boats in their seascape, with boats encountered and with boats attended) and between the density of boat (the number of AIS signals) per 5x5° grid cell used by birds. This applied when considering all types of boats as well as fishing boats only (Table 2.3 and Fig. S2.1).

Table 2.3 – Correlations (with p value of Pearson test) between the number of AIS signals (total and for fishing boats only) per 5x5° grid cells and the time spent by birds in same 5x5° grid cell (for a total time, for time with boats in seascape (<100km), for time with boats in encounter (<30km) and for time with boats in attendance (<5km)) for the active months of the different populations of albatrosses.

ANALYSES FOR 5x5° GRID	Amsterdam (n=37 cells)		Crozet (n=63 cells)		Kerguelen (n=41 cells)		Marion (n=54 cells)	
	Number of AIS signals (April)	Number of AIS fishery signals (April)	Number of AIS signal (January & February)	Number of AIS fishery signals (January & February)	Number of AIS signals (January & February)	Number of AIS fishery signals (January & February)	Number of AIS signals (February & March)	Number of AIS fishery signals (February & March)
Bird time spent in grid cell	-0.113 (p=0.52)	-0.113 (p=0.52)	-0.094 (p=0.48)	-0.094 (p=0.48)	-0.039 (p=0.81)	-0.056 (p=0.73)	-0.012 (p=0.94)	-0.012 (p=0.94)
Bird time spent with boat at 100km	0.062 (p=0.72)	0.062 (p=0.73)	-0.021 (p=0.87)	-0.021 (p=0.88)	0.026 (p=0.87)	0.008 (p=0.96)	0.199 (p=0.18)	0.199 (p=0.19)
Bird time spent in encounter	0.194 (p=0.27)	0.192 (p=0.28)	-0.029 (p=0.83)	-0.029 (p=0.83)	0.025 (p=0.88)	0.007 (p=0.97)	0.164 (p=0.28)	0.165 (p=0.28)
Bird time spent in attendance	-0.050 (p=0.78)	-0.052 (p=0.77)	-0.038 (p=0.78)	-0.037 (p=0.78)	0.018 (p=0.91)	0.002 (p=0.99)	-0.014 (p=0.93)	-0.014 (p=0.93)

4. Discussion

Our study clearly indicates strong differences between populations in the time spent attending boats, with different associated exposure to bycatch risks (Fig. 2.3a). Furthermore, we clearly show that these variations in time spent attending boats are not a simple function of the density of boats in the seascape, as previous methods aimed at assessing bycatch risk have assumed. Indeed, we have shown that using AIS data combined with fine scale GPS tracking of seabirds can provide a considerably more reliable estimate of exposure to bycatch risks, through the documentation of the actual time birds spend interacting at a fine scale with different types of declared boats (Fig. 2.1). Indeed, most previous studies used monthly maps of the number of hooks deployed within aggregated 5x5° cells (around 560x560 km in our region) to estimate risks incurred by foraging birds (Clay et al. 2019, Heerah et al. 2019), but here we show that analyses at this scale do not correlate at all with time spent interacting with boats.

Previous studies investigating fine-scale interactions with boats used VMS signals of fishing boats (Torres et al., 2013; Collet, Patrick, & Weimerskirch, 2017b; Clark et al., 2020), but VMS data are only available for declared boats inside EEZs, and are not always available for each fishing sector or country. Here we studied fine scale seabird – boat interactions over a large oceanic basin covering several EEZs as well as extensive international waters, using AIS rather than VMS data. AIS data also have some limitations such as an unknown proportion of boats not continuously using their AIS (Weimerskirch et al., 2020) as its use is not compulsory in international waters. However, to date AIS data constitute the only source of boat locations at large geographic scales. Although previous studies have used AIS data (e.g. Natale et al., 2015; Winnard et al., 2018; Wong et al., 2018; Burger et al., 2019) to estimate fishing densities, here we provide a standardized comparison of fine scale exposure to bycatch risk (boat by boat for each bird) on the scale of an ocean basin. Overall, we found that all four study populations spent considerably more time attending fisheries boats within EEZs (most boats using bycatch mitigation measures) than in international waters. On average, birds from all populations spent less than 1h per trip attending declared fishing boats outside EEZs where bycatch mitigation measures are not generally adopted potentially leading to high seabird mortality. Although at least 3 out of the 4 study populations are potentially at risk of bycatch from these declared fleets outside EEZs (where no bycatch mitigation measures are required), birds appear to spend limited time attending them. This result could be very different if non-declared boats (without AIS) could also be included. Indeed, illegal, undeclared and unregulated fleets may represent up to 30% of boat encounters for breeding large albatrosses (Weimerskirch et al., 2020). The lack of information on these boats can partly be remedied by using new loggers that can detect radar emission of boats up to 5 km away (Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2017). In sectors where fishing vessels use powerful lights to attract target species, satellite images of illumination could be used as an alternative method (Park et al. 2020). However, AIS data provide additional information on boat characteristics and nationality at a global scale, so that more accurate results could be reached by combining them with other methods such as radar detectors (Weimerskirch et al., 2020).

AIS data revealed that the four populations of large albatrosses breeding within the Indian Ocean foraged in very different boat seascapes. Yet, the time spent interacting with fishing boats within or beyond EEZs could not be predicted by the respective boat densities within the foraging ranges of the different populations. Fishing boats in the area mainly fall within two categories: toothfish longline fisheries operating on the edges of subantarctic shelves and tuna longlining fisheries operating in subtropical waters (Corbeau et al. 2019). In addition, many non-fishing boats (cargo, tankers) transit through subtropical waters between Africa, Asia and Australia. Birds from Marion had the least contact with boats, with a large proportion of trips without boat encounters, yet most attended boats were not fishing boats. This can potentially be explained by the limited extent of shelf waters at the Prince Edward islands and the very small scale of the declared toothfish fishery in the region in comparison to Crozet and Kerguelen (Weimerskirch et al., 2020). Furthermore, birds from Marion spent a relatively low proportion of their foraging time in subtropical waters (in contrast to Amsterdam birds). Conversely, Amsterdam birds were found within the densest boat seascape, both in terms of boat density and in terms of fishing boats density. This is of particular concern for this endangered species with less than 60 pairs breeding annually on Amsterdam Island (Thiebot et al. 2015, Heerah et al. 2019). Yet, birds from Marion and Amsterdam populations eventually spent very similar average amounts of time with declared fishing boats both within or outside EEZs (with different bycatch mitigation measures). In contrast, compared to Marion and Amsterdam populations, Kerguelen birds spent considerably more time with fishing boats and mostly within EEZs with much lower boat densities and Crozet birds appeared to spend more time with fishing boats both outside and within EEZs. The larger productive shelf and EEZ of Kerguelen and the continuous presence of legal boats could explain this specialization of Kerguelen birds for fishing vessels (with mitigations measures and no-mortalities).

Moreover, we have shown that large-scale overlap analyses (5x5°) of AIS data was not related to the proxy of fine-scale bycatch risk (Table 2.3). It is therefore very clear that the density of (fishing) boats within the foraging range does not linearly translate into time spent attending boats. This discrepancy between boat density in the foraging range of seabirds and the actual time birds spent attending fishing boats calls for caution when estimating bycatch risk from large-scale overlap data. AIS data is costly but it may be more easily accessible to researchers than the often confidential and geographically-restricted VMS data (Votier et al., 2010) to allow for fine-scale analyses. However, large-scale overlap analyses will still be needed in particular when bird tracking data is available at lower resolution than that offered by GPS tracking devices (Clay et al., 2019). This may be the case for many studies using GLS devices on non-breeding individuals (juveniles, failed breeders, adults in winter or on sabbatical, etc.) or for small species for which relatively large GPS device deployment could be problematic (Le Corre et al. 2012, Delord et al. 2014). It would thus be useful to understand why a higher boat density does not necessarily translate into more time spent by seabirds attending boats, and under what circumstances this applies, to improve bycatch risk estimation from large-scale data.

Boats may also cause other non-lethal issues beyond bycatch (nutritional and/or dependence issues), especially if they become an important part of birds’ time budgets (Fig. 2.3b) and/or diet. To our knowledge, there are very few studies that have looked at how boats other than fishing boats may impact foraging success and behavior in seabirds. However, it seems that our studied birds spent a low fraction of their foraging time attending them. Of greater concern is the large amount of time Kerguelen birds seem to spend attending the toothfish longline fishery operating around their breeding ground. The nature, quality and amount of food albatrosses can obtain from these toothfish fisheries are unclear considering bycatch mitigation measures that are implemented, especially considering that discards should be released after maceration, and not during fishing operations, limiting the energetic advantage of attending fishing boats (Gremillet et al. 2008). Yet, Kerguelen birds appear to spend considerable time attending fishing boats and to be more dependent on them than the Crozet population.

An important question about bycatch risk is whether the large differences we observe in the time incubating birds spent attending different types of fishing boats across populations may be related to differences in population trends. Amsterdam albatrosses have been increasing since the 1980s at such a high rate suggesting that they suffer limited if any mortality from fisheries (Rivalan, Barbraud, Inchausti, & Weimerskirch, 2010; Weimerskirch et al., 1997). Although they forage in zones with high densities of both fishing and non-fishing boats, birds do not seem to be particularly attracted by fishing boats: the low interaction to boats may explain why this population has been able to increase steadily over the past four years. The three other populations have shown similar trends until about 15 years ago, with a steep decline in the 1970s and early 1980 followed by a partial recovery (Nel et al., 2002; Weimerskirch et al., 1997). Since then, the population on Marion has been increasing, whereas Kerguelen and Crozet populations are stable (Ryan, Jones, Dyer, Upfold, & Crawford, 2009; Weimerskirch et al., 2018). This difference in population dynamics of the wandering albatross populations could be mainly related to the lower encounter and attendance rates of Marion birds compared to Crozet and Kerguelen birds.

Seabirds are one of the animal groups with the largest proportion of threatened species and there has been much effort globally to better understand causative mechanisms behind declining populations for conservation purposes. In this paper, we proposed a simple method for estimating fine scale interactions between seabirds and boats with AIS (Fig. 2.1). This method is easily implemented through the combination of seabirds GPS tracks, now routinely collected globally (Burger & Shaffer, 2008; Le Corre et al., 2012), and AIS data, which is readily available (International Maritime Organisation).

Combining AIS and fine scale tracking data we provided a more direct and comprehensive assessment to date of bycatch risk for large albatrosses breeding in the Indian Ocean, including for one of the most threatened bird species. We illustrated the pros and cons of using AIS data for such estimations, compared to other existing methods (large-scale overlap analyses and/or use of bird-borne radar detectors). Importantly we showed that fishing boat density may not be a good proxy to predict time spent attending boats and bycatch risk for specific populations. Our results revealed extensive variations in the time and proportion of foraging time populations spent attending various types of boats, which may cause other non-lethal issues beyond bycatch risks, especially in the Kerguelen population. In particular, we provided evidence that the endangered

Amsterdam albatross may not be at a high risk of bycatch despite its overlap with fisheries at a large scale. Thus, future studies investigating bycatch risks should favor when possible the use of fine scale tracking and fisheries data to be able to provide robust estimates.

5. Acknowledgements

The study is a contribution to the Program EARLYLIFE funded by a European Research Council Advanced Grant under the European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 to Henri Weimerskirch) and to the Program Ocean Sentinel funded by the ERC under European Community's H2020 Program (Grant Agreement ERC-2017-PoC_780058 to HW). The fieldwork was funded by program IPEV n° 109. South Africa's Department of Environmental Affairs provided logistical support for fieldwork on Marion Island, which was funded through the South African National Research Foundation (grant SNA93071 to Pierre Pistorius).

Field procedures on Crozet, Kerguelen and Amsterdam were authorised by the 'Préfet of Terres Australes et Antarctiques Françaises'. We thank the Reserve Nationale des TAAF for funding loggers deployed on Amsterdam Island. We thank the fieldworkers involved in the study on four sites, in particular Florent Lacoste, Tobie Getti, Aude Schreiber, Jérémy Dechartre, Yusuke Goto, Yoshi Yonehara, Danielle and Stephan Keys. We thank Adrien Pajot, for the help with AIS data. We thank the house 'Ici c'est Olbreuse' for providing accommodation and fruitful discussions to half of the authors.

6. Data accessibility

Data are available in figshare at doi: 10.6084/m9.figshare.10289096 (Weimerskirch et al. 2019)

7. Authors’ contribution

HW conceived the project, AC, JC, FO, HW and PP contributed data and/or did field work and prepared the data, JC merged AIS data to tracking data, AC performed all the other analyses, AC and HW wrote the original paper and all authors commented on earlier drafts.

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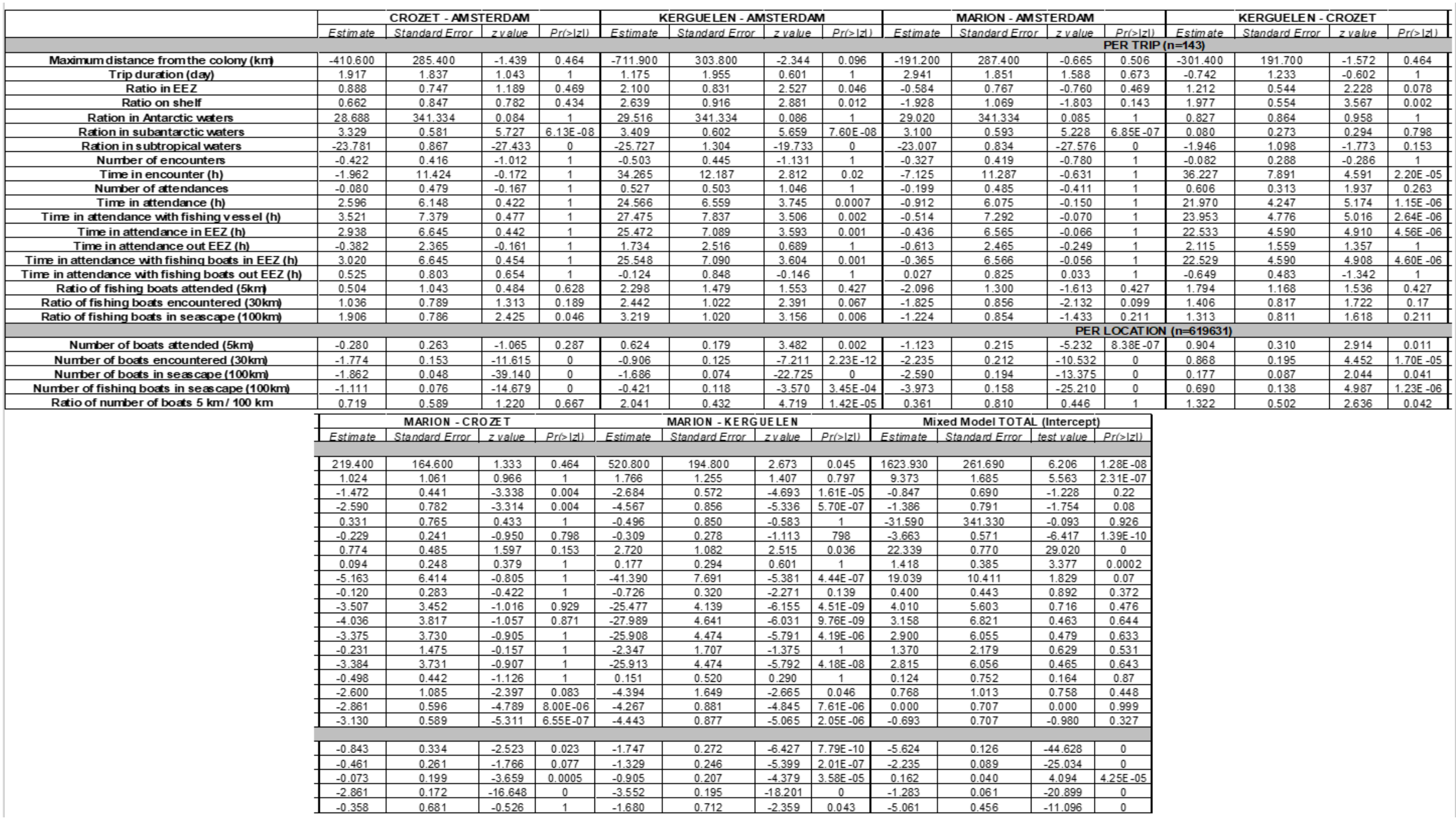
9. Supporting information

Table S2.1 – Results of LMM and GLMM (mixed models) for each parameters and for Tukey test between the four sites



	CROZET - AMSTERDAM				KERGUELEN - AMSTERDAM				MARION - AMSTERDAM				KERGUELEN - CROZET			
	Estimate	*Standard Error*	*z value*	*Pr(>|z|)*	*Estimate*	*Standard Error*	*z value*	*Pr(>|z|)*	*Estimate*	*Standard Error*	*z value*	*Pr(>|z|)*	*Estimate*	*Standard Error*	*z value*	*Pr(>|z|)*
PER TRIP (n=143)																
Maximum distance from the colony (km)	-410.600	285.400	-1.439	0.464	-711.900	303.800	-2.344	0.096	-191.200	287.400	-0.665	0.506	-301.400	191.700	-1.572	0.464
Trip duration (day)	1.917	1.837	1.043	1	1.175	1.955	0.601	1	2.941	1.851	1.588	0.673	-0.742	1.233	-0.602	1
Ratio in EEZ	0.888	0.747	1.189	0.469	2.100	0.831	2.527	0.046	-0.584	0.767	-0.760	0.469	1.212	0.544	2.228	0.078
Ratio on shelf	0.662	0.847	0.782	0.434	2.639	0.916	2.881	0.012	-1.928	1.069	-1.803	0.143	1.977	0.554	3.567	0.002
Ration in Antarctic waters	28.688	341.334	0.084	1	29.516	341.334	0.086	1	29.020	341.334	0.085	1	0.827	0.864	0.958	1
Ration in subantarctic waters	3.329	0.581	5.727	6.13E-08	3.409	0.602	5.659	7.60E-08	3.100	0.593	5.228	6.85E-07	0.080	0.273	0.294	0.798
Ration in subtropical waters	-23.781	0.867	-27.433	0	-25.727	1.304	-19.733	0	-23.007	0.834	-27.576	0	-1.946	1.098	-1.773	0.153
Number of encounters	-0.422	0.416	-1.012	1	-0.503	0.445	-1.131	1	-0.327	0.419	-0.780	1	-0.082	0.288	-0.286	1
Time in encounter (h)	-1.962	11.424	-0.172	1	34.265	12.187	2.812	0.02	-7.125	11.287	-0.631	1	36.227	7.891	4.591	2.20E-05
Number of attendances	-0.080	0.479	-0.167	1	0.527	0.503	1.046	1	-0.199	0.485	-0.411	1	0.606	0.313	1.937	0.263
Time in attendance (h)	2.596	6.148	0.422	1	24.566	6.559	3.745	0.0007	-0.912	6.075	-0.150	1	21.970	4.247	5.174	1.15E-06
Time in attendance with fishing vessel (h)	3.521	7.379	0.477	1	27.475	7.837	3.506	0.002	-0.514	7.292	-0.070	1	23.953	4.776	5.016	2.64E-06
Time in attendance in EEZ (h)	2.938	6.645	0.442	1	25.472	7.089	3.593	0.001	-0.436	6.565	-0.066	1	22.533	4.590	4.910	4.56E-06
Time in attendance out EEZ (h)	-0.382	2.365	-0.161	1	1.734	2.516	0.689	1	-0.613	2.465	-0.249	1	2.115	1.559	1.357	1
Time in attendance with fishing boats in EEZ (h)	3.020	6.645	0.454	1	25.548	7.090	3.604	0.001	-0.365	6.566	-0.056	1	22.529	4.590	4.908	4.60E-06
Time in attendance with fishing boats out EEZ (h)	0.525	0.803	0.654	1	-0.124	0.848	-0.146	1	0.027	0.825	0.033	1	-0.649	0.483	-1.342	1
Ratio of fishing boats attended (5km)	0.504	1.043	0.484	0.628	2.298	1.479	1.553	0.427	-2.096	1.300	-1.613	0.427	1.794	1.168	1.536	0.427
Ratio of fishing boats encountered (30km)	1.036	0.789	1.313	0.189	2.442	1.022	2.391	0.067	-1.825	0.856	-2.132	0.099	1.406	0.817	1.722	0.17
Ratio of fishing boats in seascape (100km)	1.906	0.786	2.425	0.046	3.219	1.020	3.156	0.006	-1.224	0.854	-1.433	0.211	1.313	0.811	1.618	0.211
PER LOCATION (n=619631)																
Number of boats attended (5km)	-0.280	0.263	-1.065	0.287	0.624	0.179	3.482	0.002	-1.123	0.215	-5.232	8.38E-07	0.904	0.310	2.914	0.011
Number of boats encountered (30km)	-1.774	0.153	-11.615	0	-0.906	0.125	-7.211	2.23E-12	-2.235	0.212	-10.532	0	0.868	0.195	4.452	1.70E-05
Number of boats in seascape (100km)	-1.862	0.048	-39.140	0	-1.686	0.074	-22.725	0	-2.590	0.194	-13.375	0	0.177	0.087	2.044	0.041
Number of fishing boats in seascape (100km)	-1.111	0.076	-14.679	0	-0.421	0.118	-3.570	3.45E-04	-3.973	0.158	-25.210	0	0.690	0.138	4.987	1.23E-06
Ratio of number of boats 5 km / 100 km	0.719	0.589	1.220	0.667	2.041	0.432	4.719	1.42E-05	0.361	0.810	0.446	1	1.322	0.502	2.636	0.042

MARION - CROZET				MARION - KERGUELEN				Mixed Model TOTAL (Intercept)			
Estimate	*Standard Error*	*z value*	*Pr(>|z|)*	*Estimate*	*Standard Error*	*z value*	*Pr(>|z|)*	*Estimate*	*Standard Error*	*test value*	*Pr(>|z|)*
219.400	164.600	1.333	0.464	520.800	194.800	2.673	0.045	1623.930	261.690	6.206	1.28E-08
1.024	1.061	0.966	1	1.766	1.255	1.407	0.797	9.373	1.685	5.563	2.31E-07
-1.472	0.441	-3.338	0.004	-2.684	0.572	-4.693	1.61E-05	-0.847	0.690	-1.228	0.22
-2.590	0.782	-3.314	0.004	-4.567	0.856	-5.336	5.70E-07	-1.386	0.791	-1.754	0.08
0.331	0.765	0.433	1	-0.496	0.850	-0.583	1	-31.590	341.330	-0.093	0.926
-0.229	0.241	-0.950	0.798	-0.309	0.278	-1.113	798	-3.663	0.571	-6.417	1.39E-10
0.774	0.485	1.597	0.153	2.720	1.082	2.515	0.036	22.339	0.770	29.020	0
0.094	0.248	0.379	1	0.177	0.294	0.601	1	1.418	0.385	3.377	0.0002
-5.163	6.414	-0.805	1	-41.390	7.691	-5.381	4.44E-07	19.039	10.411	1.829	0.07
-0.120	0.283	-0.422	1	-0.726	0.320	-2.271	0.139	0.400	0.443	0.892	0.372
-3.507	3.452	-1.016	0.929	-25.477	4.139	-6.155	4.51E-09	4.010	5.603	0.716	0.476
-4.036	3.817	-1.057	0.871	-27.989	4.641	-6.031	9.76E-09	3.158	6.821	0.463	0.644
-3.375	3.730	-0.905	1	-25.908	4.474	-5.791	4.19E-06	2.900	6.055	0.479	0.633
-0.231	1.475	-0.157	1	-2.347	1.707	-1.375	1	1.370	2.179	0.629	0.531
-3.384	3.731	-0.907	1	-25.913	4.474	-5.792	4.18E-08	2.815	6.056	0.465	0.643
-0.498	0.442	-1.126	1	0.151	0.520	0.290	1	0.124	0.752	0.164	0.87
-2.600	1.085	-2.397	0.083	-4.394	1.649	-2.665	0.046	0.768	1.013	0.758	0.448
-2.861	0.596	-4.789	8.00E-06	-4.267	0.881	-4.845	7.61E-06	0.000	0.707	0.000	0.999
-3.130	0.589	-5.311	6.55E-07	-4.443	0.877	-5.065	2.05E-06	-0.693	0.707	-0.980	0.327
-0.843	0.334	-2.523	0.023	-1.747	0.272	-6.427	7.79E-10	-5.624	0.126	-44.628	0
-0.461	0.261	-1.766	0.077	-1.329	0.246	-5.399	2.01E-07	-2.235	0.089	-25.034	0
-0.073	0.199	-3.659	0.0005	-0.905	0.207	-4.379	3.58E-05	0.162	0.040	4.094	4.25E-05
-2.861	0.172	-16.648	0	-3.552	0.195	-18.201	0	-1.283	0.061	-20.899	0
-0.358	0.681	-0.526	1	-1.680	0.712	-2.359	0.043	-5.061	0.456	-11.096	0

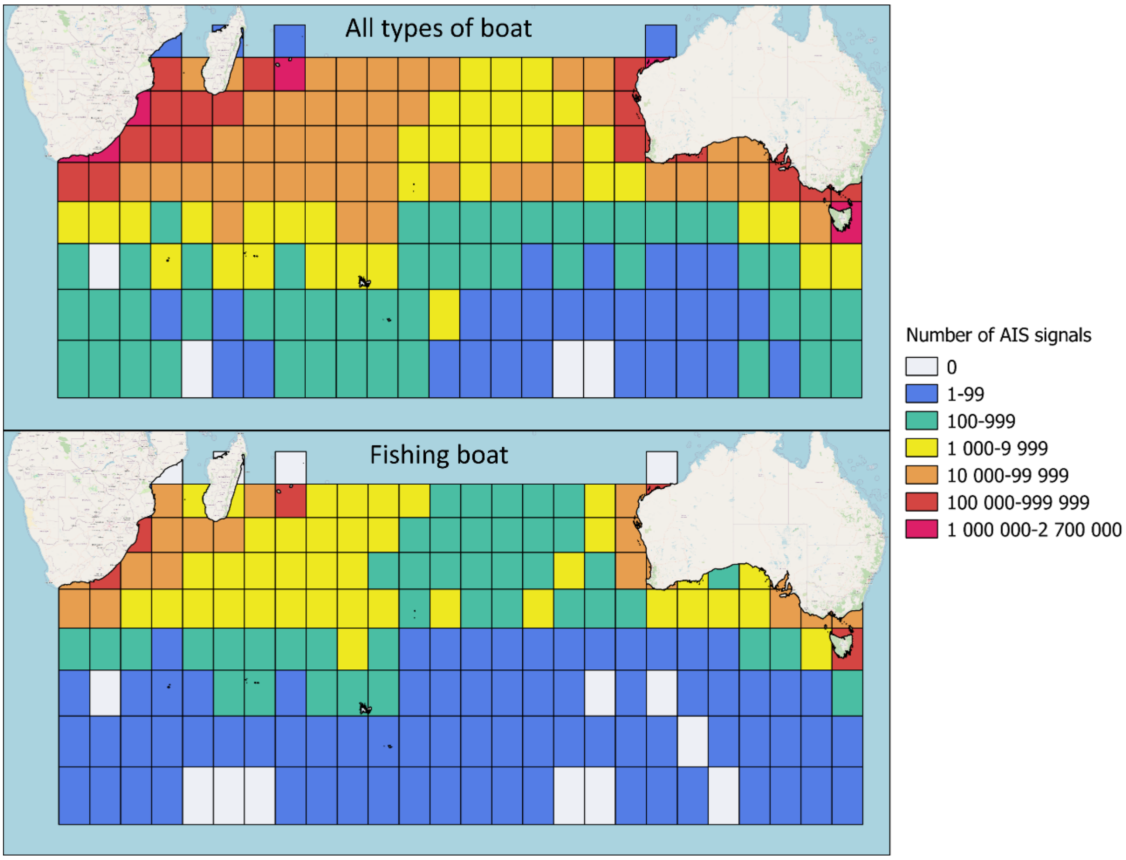


Figure S2.1 - Distribution of AIS locations per 5x5° grid (for all types of boats and for fishing boats only) in the study sector recorded in January, February, March and April 2019.

Chapitre 3 : différentes stratégies d’utilisation de l’habitat entrainent différents niveaux d’interaction avec les bateaux

Corbeau A., Collet J., Pajot A., Joo R., Thellier T., Weimerskirch H., 2021. Differences in foraging habitat result in contrasting fisheries interactions in two populations of albatrosses. ***Marine Ecology Progress Series*** *(sous presse*).

Abstract

Albatrosses attend fishing boats to feed on fishing discards but are often at risk of accidental bycatch. To examine whether populations (same specie) and sexes differ in their overlap with fisheries due to differences in habitat use, we combined the use of recently developed loggers equipped with GPS and boat radar detectors with Automatic-Identification-System (AIS) data.

Our study indicates that incubating wandering albatrosses (*Diomedea exulans*) from Crozet and Kerguelen foraged in different habitats although the duration of trips was similar. Both female and male Kerguelen birds took advantage of the large and productive surrounding shelf, whereas Crozet birds used the small shelf around the islands in a smaller extent. In Crozet, there was segregation between males and females, the latter favouring deeper and warmer waters.

The two strategies of habitat use led to different overlap and attraction to boats, with Kerguelen birds encountering and attending boats for longer and at closer proximity to the colony than Crozet birds. Crozet females encountered boats at greater distances from the colony than males. Because of different habitat use, foraging outside EEZ and further to colony, Crozet birds attended more non-declared boats (without AIS) than Kerguelen birds.

Albatrosses were more attracted by fisheries than cargo vessels and were especially attracted by fishing discards that led them to attend vessels for longer periods for both sexes and populations. The differences found between populations and individuals in terms of habitat specialization and encounter rate of fisheries should be considered for future assessments of risk of bycatch.

1. Introduction

Fisheries are operating over the world oceans, affecting the long term sustainability of many fish stocks (Pauly et al. 2002). Non declared and illegal fisheries have a significant impact on marine ecosystems which is difficult to estimate (Weimerskirch et al. 2020). In addition to the impact on fish stocks, legal and illegal fisheries impact marine ecosystems through the bycatch of non-target species such as sharks, sea turtles or seabirds (Finkbeiner et al. 2011, Croxall et al. 2012, Worm et al. 2013, Lewison et al. 2014, Gianuca et al. 2017). Among seabirds, albatrosses are one of the most threatened group mainly because of bycatch in longline fisheries (Votier et al. 2004, Delord et al. 2005, Anderson et al. 2011, Croxall et al. 2012, Phillips et al. 2016). Albatrosses have been attracted to boats for centuries, and over the last decades they have attended fishing boats in large numbers to feed on fishing discards, but also on baits of longlines where they can be drowned (Weimerskirch et al. 1997c, Delord et al. 2005, Anderson et al. 2011). This accidental mortality due to fisheries is considered to be the major cause of decline for many albatross populations (Paleczny et al. 2015, Weimerskirch et al. 2018a).

The difference in demographic trends observed between species (Weimerskirch et al. 2018a) and populations of the same species (e.g. between the Indian and Atlantic Oceans ; Ryan et al. 2009, Pardo et al. 2017), could be due to a difference in susceptibility to bycatch. The latter could be explained either by differences in overlap between fisheries and the natural foraging habitat of albatrosses (Clay et al. 2019, Heerah et al. 2019) or by differences in the level of attraction to boats (Collet et al. 2017), or both. It is therefore important to consider the potential variations in the foraging habitats used by different populations, and their overlap with fisheries to better assess their susceptibility to bycatch. For 25 years, measures to reduce incidental mortality of albatrosses and petrels (e.g. night setting of line, line weighing, bird scaring devices) have been progressively implemented in the demersal fisheries in the EEZ of the sub Antarctic Islands, leading to reduce mortality (Weimerskirch et al. 2018a). In addition to reduced bycatch risk, for 20 years it has been recommended in the subantarctic zone that fishing discards are not released during longline setting (Waugh et al. 2008). Instead, they are meant to be kept onboard and only later released between fishing operations. Very little is known on the role of such fishing discard practices on the attraction of albatrosses to fishing boats. Although it is likely that the greatest factor is the fishing practices and mitigation measures employed by the fisheries, differences in attendance and attraction between populations and species could be an important factor explaining risks of bycatch.

Wandering albatrosses are large seabirds, with a strong sexual dimorphism, that are attracted in large numbers by fishing vessels (Weimerskirch et al. 2020). In the Indian Ocean they favour shelf edge habitats and seamounts (Louzao et al. 2011) and in a lesser extent oceanic waters. They are potentially in contact with two types of fisheries that can put them at risk of bycatch. Pelagic long-line fisheries for tuna operate in subtropical international oceanic waters, and do not use mitigation measures. Demersal long-line fisheries for Patagonia toothfish (*Dissostichus eleginoides*) operate over shelf edges in subantarctic waters, mainly within the Economic Exclusive Zone (EEZ) around sub-Antarctic islands, where mitigation measures are compulsory for licensed vessels (Waugh et al. 2008).

Populations breeding on two archipelagos of the Indian Ocean, Crozet and Kerguelen (separated from each other by 1300 km) have contrasting surrounding habitats. Kerguelen islands are surrounded by a vast shelf (1 310 000 km²), whereas Crozet islands sit within a small-sized shelf (37 000 km²).

The two populations, although genetically very close (Milot et al. 2007), have contrasted spatial distributions and strategies during migration: Kerguelen birds migrate to distant shelf areas in the Pacific, whereas Crozet birds stay in oceanic waters in the Indian Ocean (Weimerskirch et al. 2015). Little is known on the foraging movements of Kerguelen birds during the breeding season, in contrast with the better-studied Crozet birds (Weimerskirch et al. 2015). In Crozet, breeding birds forage over a mix of oceanic and shelf waters (Weimerskirch et al. 2014b). Crozet birds overlap with fisheries over shelf areas as well as over oceanic waters (Weimerskirch et al. 2018b, Corbeau et al. 2019) and they are strongly attracted by Patagonian toothfish longliners operating over shelf edges (Collet et al. 2017c). Until very recently, no studies were performed on those behaviour among Kerguelen birds.

Here the aims of the study were (1) to compare the foraging habitats of the two populations during the breeding season, (2) to compare the overlap with fisheries between the two populations and their attraction to boats -especially fishing boats - including non-declared-illegal boats, and (3) to estimate the role of fishing discards on the attractiveness of birds to fishing boats and if we found some benefits in those attraction in terms of breeding success. We used loggers with a GPS and a boat radar detector (Weimerskirch et al. 2018b) along with Automatic Identification System (AIS) data from all declared boats in the studied area (Weimerskirch et al. 2020). In addition, we used data on fishing discards release from 7 French declared longliners operating around the Crozet and Kerguelen archipelagos during the study period. In our analyses, we further controlled for suspected factors of attraction to boats such as competition due to sexual size dimorphism (Weimerskirch et al. 2014b), fishing practices (Collet et al. 2017c), or fishing discards presence (Cherel et al. 1996), and how they could vary between the two populations.

Wandering albatrosses have significant sexual dimorphism with noticeably larger body size among males and coincides with different uses of habitats (Weimerskirch et al. 2014b, Pereira et al. 2018). These differences in space use might also translated into differences in overlap with fisheries. However, a previous study showed no differences in the attraction to longline boats on the shelf around the breeding grounds between males and females in the Crozet population (Collet et al. 2017c).

In this study, we compare the foraging movements and overlap with fishing boats (declared and non-declared or illegal) of breeding Kerguelen and Crozet wandering albatrosses. Those two populations follow the same demographic trend (Weimerskirch et al. 2018a) although the colonies are surrounded by very different habitats. To compare the habitat use, foraging strategies and interactions with boats between these two populations, we tested whether differences in interactions with boats were attributable to differences in foraging habitats and/or to differences in behavioural responses to boats: either differences in attraction of birds to boats and/or in time spent with boats encountered once attracted. We further controlled for suspected factors of attraction to boats such as competition due to sexual size dimorphism (Weimerskirch et al. 2014b), fishing practices (Collet et al. 2017c), or fishing discards presence (Cherel et al. 1996) and how they could vary between the two populations. To reduce bycatch risk, it is recommended in the subantarctic zone that fishing discards are not released during longline setting (Waugh et al. 2008). Instead, they are meant to be kept onboard and only later released between fishing operations. Very little is known on the role of such fishing discards practices on the attraction of albatrosses to fishing boats.

To complete those aims and study the overlap between albatrosses and fisheries, including non-declared fisheries, we combined the use of recently developed loggers equipped with a GPS and boat radar detectors (Weimerskirch et al. 2018b) with Automatic Identification System (AIS) data from all declared boats in the study area (Weimerskirch et al. 2020). In addition, we used original data of release fishing discards from 7 French declared longliners operating around the Crozet and Kerguelen Islands during the study period.

2. Material and methods

We performed all analyses in the R software and environment (v 3.5.2; R core team 2020).

2.1. Filedwork

Fieldwork was carried out in Crozet and Kerguelen archipelagos, Southern Indian Ocean, between January and April 2019 (see details of the program in Weimerskirch et al., 2020). Wandering albatrosses have been studied for 60 and 25 years at Crozet and Kerguelen, respectively. The sex and breeding success (defined as flight of the chick during the breeding cycle in 2019) of individuals have been derived from these long-term studies (Weimerskirch et al. 2018a).

2.2. Loggers

Centurion loggers (65g) recorded GPS locations every ~2 min and, every 5 min, recorded radar emissions of every boat at less than 5 km during 1 min (all loggers details are in Weimerskirch et al. 2020). Loggers were deployed on incubating birds for one or two successive foraging trips. The loggers were attached to the back feathers with Tesa® Tape (Germany), and represented between 0.5 - 0.85% of the body mass of wandering albatrosses, much less than the maximum 3% recommended for loggers attached on flying seabirds (Phillips et al. 2003). The deployment procedures and logger sizes are similar to those employed in previous studies that showed no negative effects on trip duration or breeding success (Weimerskirch et al. 1995, Barbraud & Weimerskirch 2012).

2.3. Albatross and boat dataset

We deployed loggers on 69 incubating wandering albatrosses: 45 at Crozet (24 females and 21 males) and 24 at Kerguelen (10 females and 14 males). We obtained 71 complete trips (48 trips from 44 individuals at Crozet and 23 trips from 21 individuals at Kerguelen; 1 logger failed to record trips, and 3 incomplete trips, due to battery issues, were removed; Table 3.1).

All the data were speed filtered (150 km.h-1) and tracks were divided by trips (removing locations on land). In order to link boat presence and individual GPS tracks, we followed the procedure in Weimerskirch et al. (2020) using (1) the radar detection recorded on the centurion logger and (2) cross-matching it with AIS. AIS data provides the identification, name, nationality, type of boat (fishery or cargo mainly), location and activity for all declared fishing and non-fishing boats in the Southern Indian Ocean. AIS data were spatio-temporally matched with bird-borne GPS and radar detection data to produce a dataset where all GPS locations of each bird from each population are associated to the presence/absence, number and types of boats transmitting AIS information within ranges of 30 and 5 km from birds. The presence/absence of declared or undeclared boats within a range of 5 km was determined from the radar detectors (Weimerskirch et al. 2018b), a boat is considered undeclared (and illegal inside EEZ where AIS is required) when radar detector receives a signal without AIS within 5 km.

These different radius distances from birds were used to characterise the ‘boat encountered’ (bird tracked within 30 km from a boat with AIS), the ‘boats attended’ (bird within 5 km from a boat with AIS) and the ‘radar events’ (boats detected by radar detector). The 30 km threshold chosen for encounters was the distance within which an albatross can visually detect a boat (Collet et al. 2015, Pirotta et al. 2018). The 5 km threshold is close to the distance at which albatrosses have been seen to engage in specific foraging behaviour associated with vessels (Collet et al. 2015) and is used to facilitate comparisons with studies using embarked radar detectors (included in the loggers) with a detection range of 5 km (Weimerskirch et al. 2018b, 2020, Corbeau et al. 2019). We defined ‘events’ (encounter, attendance and radar events) as periods of consecutive bird locations (with time gaps of less than 2 hours) within the respective distances of at least one boat.

2.4. Discards data

Discards data for the studied period were obtained from fisheries observers onboard the 7 French legal longliners operating in the Economic Exclusive Zone (EEZ) around Crozet and Kerguelen. The time and location of each discard release considered as ‘discard events', were matched to the seabird tracking data. We considered a 'discard event" in the following 6 hours within a range of 5 km to location of a discard released.

2.5. Environmental variables

The bathymetry, water masses, sea surface temperature and presence or not in an EEZ corresponding to each bird location were added to the dataset. Bathymetry was extracted from the 'ETOPO1 Global Relief Model' from the 'National Oceanic and Atmospheric Administration' using the R package 'marmap' (Pante & Simon-Bouhet 2013). We considered bird locations to be over a shelf (shelf and shelf break) for depth above -2000 m or over oceanic waters (deeper than 2000 m). From estimations of the locations of the Polar Front (Moore et al. 1999) and the Subtropical Front (Belkin & Gordon 1996) we further categorized bird locations into water masses, either Antarctic (south of Polar Front), subantarctic (between Polar and Subtropical Fronts) and subtropical waters (North of Subtropical Front). Finally, we added hourly Sea Surface Temperature (SST) for each bird location, extracted from Copernicus data (https://www.copernicus.eu). We also considered whether locations were within all EEZs or not (data from http://www.marineregions.org).

2.6. Analyses

The behaviours along their trips were inferred with hidden Markov models (HMMs), the tracking data were linearly interpolated to obtain strictly regular two-minute time steps. We then computed step length and turning angles, to identify the hidden behavioural modes that could be revealed through these two observed variables. As in Clay et al. (2020), who analysed the tracking data from the same species, we expected to find three types of behaviour in albatross foraging trips: travel (or directed flight, with high speeds and shallow turning angles), search (with moderate speeds and turning angles, considered as foraging behaviour), and rest (with low speeds and shallower turning angles). Thus, a three-state HMM (Morales et al. 2004) was fitted to the interpolated tracks. Gamma and von Mises distributions were used to model the conditional distributions of step lengths and angles (the observed variables) to the states. The initial values for the parameters of the HMM are shown in Table S3.1 – S3.2 – S3.3 and Figure S3.1 – S3.2. The state sequences were reconstructed via the Viterbi algorithm (Rabiner 1989). This analysis was performed using the R package 'momentuHMM' (McClintock & Michelot 2018). The results were validated through expert judgement: based on the biological knowledge of the foraging behaviour of the species, the main author validated visual representations of the tracks with the inferred sequences (see more details in Fig. S3.3).

To compare different variables between populations of Crozet and Kerguelen, and between sexes of the two populations, we used linear mixed models (t test) and generalised linear mixed models (Z test) (R package ‘lme4’, ‘lmerTest’ and ‘glmmTMB’) (Table S3.4). The negative binomial distribution was used for over-dispersed count data, the binomial distribution for ratio data, and the Gaussian distribution for all others. We used the R package ‘fitdistrPlus’ for residual diagnostics (Table S3.4). For each variable (Table 3.1 and Table S3.4 for test values) we made a model to compare the two populations, then another model to compare sexes for Crozet birds and another for Kerguelen birds. In each model, bird ID was used as a random factor.

First, we compared the SST and Bathymetry at each fixed and interpolated bird location, and then only Bathymetry identified as “search” via HMMs (Table 3.1 and Table S3.4 for test values).Second, we used each complete trip to compare their range, duration, proportion of time (ratio) on shelf, proportion of time in different waters, proportion of time in EEZ, proportion of time in the three different HMM states (and within those states, we considered three conditions: in general, above shelf or in oceanic waters). Then, we used the radar detector as the most reliable measure of contact with boats, for comparisons of trip ratio in contact with boats (general, declared and undeclared) and for radar event comparison of distance to the nest and duration of this “event” (in general, for declared and for undeclared boats) (Table 3.1 and Table S3.4 for test values).Third, we used AIS data and encounter events to define the encounter duration and the ‘attraction’ to boat as the time spent in attendance (<5 km from boats) and sitting in the water (speed <10 km.h^{-1}; Weimerskirch et al. 2002) divided by the time within encounter range (<30 km from boats). Then, we compared for each encounter, the distance to the nest, the attraction and the duration. For the models, attraction and encounter duration, on discard data we only used data (encounter events) of the 7 declared French fishing boats, the only ones with recorded fishing discards (Table 3.1 and Table S3.4 for test values).

Table 3.1 – Differences between sexes for each population: mean and standard deviation of variable and slope value (estimate of LMM or GLMM) and p value (t or Z test). Differences between populations: p value. Significativity: ***(p <0.001); ** (0.01 <p <0.001); *(0.05 <p <0.01).

	CROZET			KERGUELEN			Difference between Crozet and Kerguelen
	Female (n=24)	Male (n=21)	Pr	Female (n=10)	Male (n=14)	Pr	Pr
	Mean (±Standard deviation)	Mean (Standard deviation)		Mean (Standard deviation)	Mean (Standard deviation)		
per location (n= 537522)							
Bathymetry (m)	-3218.3 (±1413.01)	-2754.91 (±1703.37)	0.08.	-1942.14 (±1483.74)	-2152.22 (±1540.73)	0.67	0.001**
Bathymetry in "search" (m)	-3032.12 (±1490.88)	-2367.46 (±1831.37)	0.001**	-1546.60 (±1429.72)	-1552.13 (±1525.28)	0.91	0.002**
SST (°C)	13.35 (±6.69)	7.61 (±3.96)	0.002**	6.18 (±4.26)	4.98 (±3.61)	0.39	6.0e-05***
per trip (n=71)							
Range (m)	1496784.04 (±744155.70)	825029.54 (±750857.18)	0.002**	871555.91 (±722680.07)	998357.58 (±784426.58)	0.72	0.31
Duration (h)	300.19 (±130.32)	232.1 (±133.42)	0.11	255.74 (±117.98)	253.15 (±133.09)	0.96	0.64
Ratio on shelf	0.3 (±0.27)	0.51 (±0.36)	0.02*	0.71 (±0.32)	0.56 (±0.29)	0.41	0.002**
Ratio in antarctic waters	0.06 (±0.17)	0.09 (±0.24)	0.67	0.13 (±0.25)	0.22 (±0.34)	0.33	0.41
Ratio in subantarctic waters	0.60 (±0.34)	0.86 (±0.26)	0.02*	0.82 (±0.27)	0.74 (±0.34)	0.69	0.51
Ratio in subtropical waters	0.34 (±0.36)	0.05 (±0.13)	0.03*	0.05 (±0.17)	0.04 (±0.13)	0.84	0.13
Ratio in EEZ	0.44 (±0.31)	0.72 (±0.31)	0.01*	0.74 (±0.36)	0.69 (±0.30)	0.54	0.04*
Ratio in "travel"	0.44 (±0.1)	0.27 (±0.14)	7.4e-05***	0.38 (±0.14)	0.36 (±0.11)	0.82	0.90
Ratio in "travel" on shelf	0.11 (±0.08)	0.1 (±0.07)	0.82	0.22 (±0.12)	0.19 (±0.13)	0.49	6.3e-05***
Ratio in "travel" on ocean	0.33 (±0.15)	0.18 (±0.15)	0.001**	0.15 (±0.16)	0.18 (±0.12)	0.69	0.02*
Ratio in "search"	0.24 (±0.06)	0.28 (±0.08)	0.99	0.34 (±0.14)	0.29 (±0.12)	0.95	0.23
Ratio in "search" on shelf	0.1 (±0.11)	0.17 (±0.14)	0.05.	0.27 (±0.20)	0.2 (±0.16)	0.33	0.006**
Ratio in "search" on ocean	0.14 (±0.06)	0.11 (±0.09)	0.33	0.07 (±0.07)	0.09 (±0.06)	0.47	0.01*
Ratio in "rest"	0.33 (±0.07)	0.44 (±0.11)	2.2e-04***	0.28 (±0.10)	0.35 (±0.11)	0.20	0.04*
Ratio in "rest" on shelf	0.10 (±0.09)	0.24 (±0.22)	0.007**	0.21 (±0.14)	0.17 (±0.11)	0.51	0.36
Ratio in "rest" on ocean	0.22 (±0.1)	0.2 (±0.15)	0.63	0.07 (±0.09)	0.17 (±0.14)	0.09	0.007**
Ratio in contact with boat	0.03 (±0.07)	0.04 (±0.06)	0.92	0.11 (±0.14)	0.04 (±0.05)	0.51	0.51
Ratio in contact with declared boat	0.03 (±0.05)	0.05 (±0.07)	0.77	0.11 (±0.14)	0.06 (±0.05)	0.75	0.47
Ratio in contact with undeclared boat	0.03 (±0.07)	0.01 (±0.01)	0.64	0.00 (±0.00)	0.01 (±0.02)	0.81	0.74
per encounter (n=248)							
Distance from the nest (m)	1094907.41 (±711969.48)	316393.09 (±424445.4)	0.004**	387662.43 (±432637.75)	197838.16 (±192929.04)	0.06	0.03*
Attraction	0.12 (±0.24)	0.16 (±0.20)	0.49	0.30 (±0.28)	0.21 (±0.32)	0.32	0.02*
Duration (min)	200.19 (±251.65)	489.45 (±558.3)	2.1e-05***	1130.74 (±1435.45)	752.41 (±1670.65)	0.17	2.0e-04***
Attraction in French EEZ	0.17 (±0.19)	0.17 (±0.20)	0.63	0.31 (±0.28)	0.22 (±0.32)	0.51	0.03 *
Duration encounter in French EEZ (min)	468.58 (±506.28)	484.04 (±526.94)	0.02 *	1207.44 (±1527.13)	753.56 (±1711.05)	0.12	0.04 *
Attraction Fisheries	0.16 (±0.21)	0.18 (±0.20)	0.281	0.31 (±0.28)	0.23 (±0.33)	0.68	0.02*
Duration encounter Fisheries (min)	326.68 (±344.77)	533.84 (±576.28)	0.006**	1166.49 (±1501.31)	747.77 (±1743.73)	0.12	0.03*
Attraction with fishing discard	0.27 (±0.21)	0.32 (±0.22)	0.60	0.42 (±0.26)	0.46 (±0.43)	0.79	0.11
Duration encounter with fishing discard (min)	683.8 (±557.38)	881.05 (±806.11)	0.45	2107.69 (±1777.83)	1237.36 (±3142.28)	0.23	0.19
Attraction without fishing discard	0.12 (±0.18)	0.11 (±0.15)	0.89	0.27 (±0.28)	0.19 (±0.25)	0.55	0.03*
Duration encounter without fishing discard (min)	287.22 (±278.87)	352.64 (±266.22)	0.19	429.05 (±456.05)	630.61 (±643.2)	0.35	0.03*
per radar events (n=193)							
Distance from the nest (m)	788763.53 (±688158.86)	244832.17 (±307186.42)	0.01 *	259313.67 (±134639.16)	220825.69 (±186285.07)	0.743	0.90
Duration (min)	181.81 (±212.09)	192.32 (±190.65)	0.80	271.11 (±279.3)	173.69 (±185.97)	0.14	0.47
Duration for declared boat (min)	120.87 (±150.57)	187.29 (±191.56)	0.11	287.04 (±275.00)	178.92 (±193.84)	0.12	0.18
Duration for undeclared boat (min)	251.9 (±252.02)	234.6 (±198.35)	0.89	198.72 (±300.74)	124.00 (±74.98)	0.42	0.32

3. Results

3.1. Trip description

Foraging trip ranges and duration were similar between Crozet and Kerguelen. At Crozet (Fig. 3.1), females travelled further but with similar duration as males. In Kerguelen (Fig. 3.2), females and males had similar foraging ranges and duration (Table 3.1 and Table S3.4 for test values).

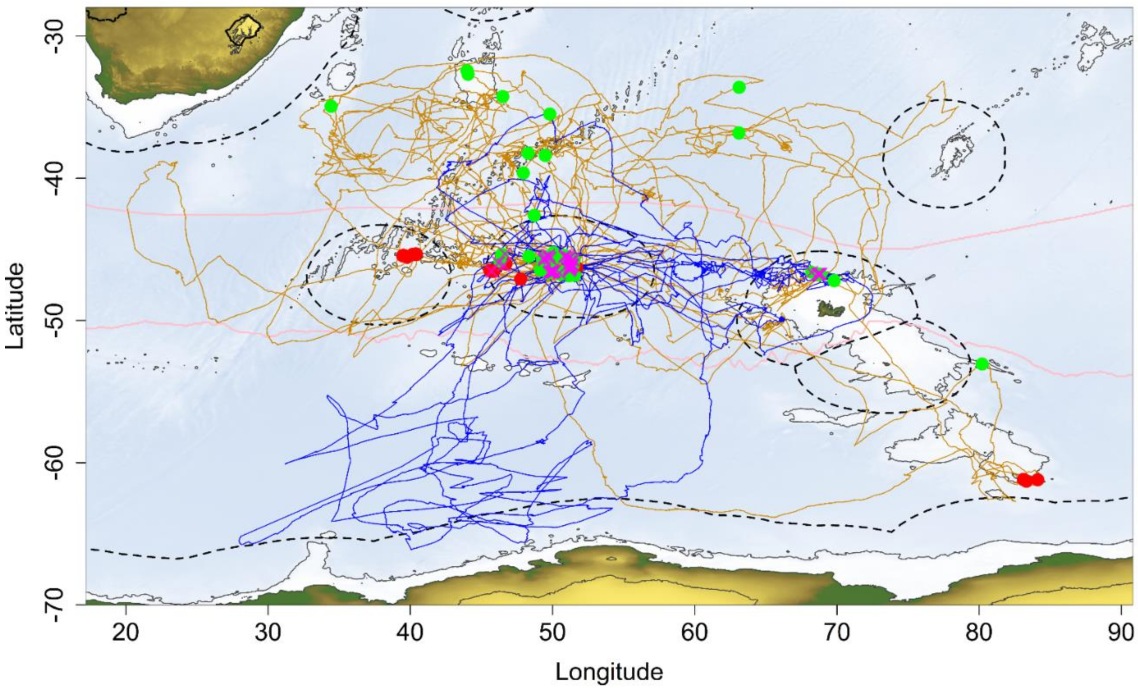


Figure 3.1 - Map of the South Indian Ocean with tracks of **Crozet** birds (blue for males and orange for females); red dots represent undeclared boat contact and green dots declared boat contact; purple cross represent release discarded of seven French longliners; isobaths: -2000 m (shelf), 0 m and +2000 m; pink lines represent Subantarctic and Polar Fronts; dashed black lines represent EEZ.

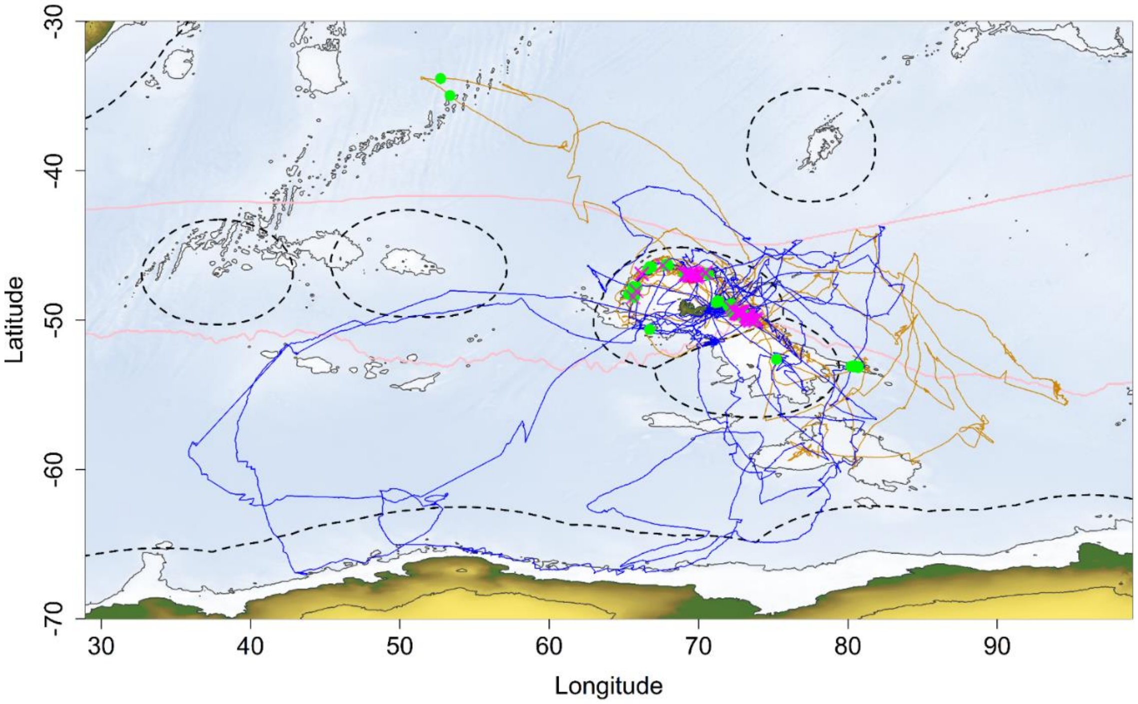


Figure 3.2 - Map of the South Indian Ocean with tracks of **Kerguelen** birds (blue for males and orange for females); red dots represent undeclared boat contact and green dots declared boat contact; purple cross represent release discarded of seven French longliners; isobaths: -2000 m (shelf), 0 m and +2000 m; pink lines represent Subantarctic and Polar Fronts; dashed black lines represent EEZ.

The proportion of time spent in 'search' mode per trip was not significantly different between Crozet and Kerguelen and between sexes for Crozet. The proportion of time spent in 'travel' mode was similar between Crozet and Kerguelen, and between sexes at Kerguelen, but at Crozet females spent more time travelling than males. Crozet birds spent more time resting than Kerguelen birds, and Crozet males spent more time resting than Crozet females (Fig. 3.3 – first column; Table 3.1; Table S3.4 for test values).

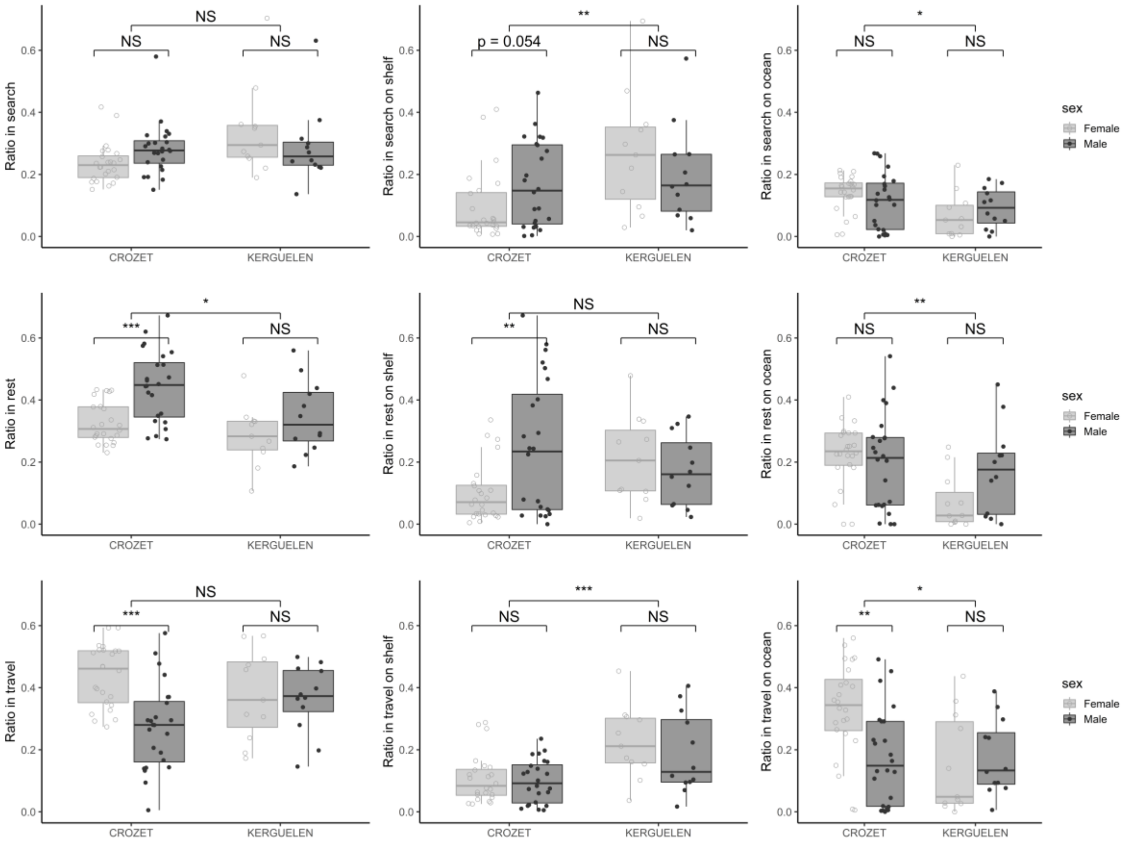


Figure 3.3 – Boxplots of proportion of time spent in each of the three behaviours: search (first row), rest (second row), and travel (third row), for each population and sex. First column: in general; second column: on the shelf; third column: over the ocean. Significativity: NS (No Significant); ***(p <0.001); ** (0.01 <p <0.001); *(0.05 <p <0.01).

3.2. Habitat use

Kerguelen birds used colder waters than Crozet birds. Males and females from Kerguelen foraged in similar water temperatures, females from Crozet foraged in warmer waters than males (Table 3.1; Table S3.4 for test values). Crozet albatrosses foraged over deeper waters than Kerguelen birds which spent more time over shelf edges. Crozet females foraged over deeper waters than males whereas there were no differences between sexes at Kerguelen (Table 3.1, Table S3.4 for test values). Therefore, Kerguelen birds spent more time in ‘search’ and ‘travel’ modes over shelves than Crozet birds, with females from Crozet travelling more and resting less over oceanic waters than males (Fig. 3.3; Table S3.4 for test values).

We also found that Kerguelen and Crozet birds foraged over Antarctic, subantarctic and subtropical waters in similar proportions. Crozet females foraged in a larger proportion over subtropical waters than males that favoured subantarctic waters (Fig. 3.1) (Table 3.1; Table S3.4 for test values). Finally, Kerguelen birds spent more time in EEZs and over shelves than Crozet birds, with no significant differences between sexes at Kerguelen, whereas Crozet males spent more time in EEZs and over shelves than females (Fig. 3.1 & 3.2) (Table 3.1; Table S3.4 for test values). Some Crozet birds foraged over the Kerguelen Shelf (Fig. 3.1 & 3.2)

3.3. Interactions with boats (from radar data)

The analysis of radar detector data showed that Crozet birds contacted more (27.78%: n=25/90) undeclared boats than Kerguelen birds (14.56%: n=15/103) (chi^2=4.3, df=1, p value=0.02) but spent the same proportion of time per trip in contact with boats (declared and non-declared) and there was no difference between sexes (Table 3.1; Table S3.4 for test values).

When considering all boats from radar detectors data and separating declared boats from non-declared (no AIS) boats, we found no differences between Crozet and Kerguelen and between sexes within each population. Equally, we found no differences between populations and sexes in the durations of the radar events, for declared and non-declared boats. We found that Crozet females encountered boats further from the colony than males (Table 3.1; Table S3.4 for test values). The duration of the contacts (defined by radar detection) with declared boats (n=153, mean duration=207.82min±sd224) and non-declared boats (n=40, mean duration=222.33min±245) was similar ($slope_{GLMM\ estimate}$=-0.20±0.24, Z value=-0.83, p value=0.408).

3.4. Behaviour associated with boats (from AIS data)

We found that Crozet birds encountered boats with AIS (<30 km from boats with AIS) at a greater distance from the colony than Kerguelen birds, Crozet females encountering boats further than males and Kerguelen females slightly further than males (Table 3.1; Table S3.4 for test values). Moreover, Crozet birds were less attracted by boats and spent less time behind boats than Kerguelen birds inside and outside French EEZ. In Crozet, males spent more time within 30 km of boats than females. (Table 3.1; Table S3.4 for test values; Table S3.5). However, birds from Crozet and Kerguelen spent the same proportion of time per trip behind boats (declared and non-declared) and there was no difference between sexes (Table 3.1; Table S3.4 for test values).

Attraction and duration of encounters were higher and longer, respectively, for fishing boats (n=174, mean attraction=0.22±0.26 (41% of encounter without attendance); mean duration=686.81min±1188) than for cargo vessels (n=55, mean attraction=0.09±0.25 (84% of encounter without attendance); mean duration=105.82min±81; attraction: slope=1.06±0.51, Z value =2.07, p value = 0.038; encounter duration: slope = 1.49±0.27, Z value = 5.42, p value = 6.12e-08) (Fig. S3.4). When considering only fishing boats, attraction and duration were higher and longer for Kerguelen birds than Crozet birds. There was no difference between sexes in attraction and duration in Kerguelen, whereas for Crozet, male birds had similar attraction rates but stayed within encounter range of fishing boats for longer periods of time than females (Table 3.1; Table S3.4 for test values; Table S3.5).

We found no evidence that the attraction rate or the duration of encounter affected the breeding success during the breeding season (successful breeders: n=152, mean attraction=0.19±0.27 (51% of encounter without attendance); mean duration=564.91min±1104; failed breeders : n=33, mean attraction=0.11±0.16 (55% of encounter without attendance); mean duration=446.64min±511 - attraction: slope=1.72±1.03, Z value =1.66, p value = 0.096; encounter duration: slope=-0.26±0.40, Z value =-0.65, p value = 0.515). We also found no difference in the breeding success of Crozet (0.75; successful breeders: n=410; failed breeders: n=102) and Kerguelen (0.80; successful breeders: n=60; failed breeders: n=12) populations (chi^2=0.04, df=1, p value=0.84).

3.5. Fishing discards of French longliners

Attraction and duration of boat encounters (<30 km from AIS, for the 7 French longliners) were higher and longer when fishing discards were released (within 5 km) (with fishing discards: n=52, mean attraction=0.38±0.29 (13% of encounter without attendance); mean duration=1314.89min±1856; without fishing discards: n=98, mean attraction=0.16±0.22 (49% of encounter without attendance); mean duration=404.71min±415) (attraction: slope=1.18±0.40, Z value=2.95, p value=0. 0032; encounter duration: slope=1.12±0.20, Z value=5.48, p value=4.14e-08).

The attraction and the duration of encounters were not different between populations and sexes in the presence of discards. In the absence of discards attraction and duration of encounters (for the 7 French longliners) were higherfor Kerguelen birds compared to Crozet birds, with no sex differences (Table 3.1; Table S3.4 for test values; Table S3.5).

4. Discussion

4.1. Differences in habitat use between populations and sexes

Our study indicates that, although the duration of foraging trips was similar, incubating wandering albatrosses from these two populations foraged in different habitats. Kerguelen birds took advantage of the large and productive surrounding shelf (Dulaiova et al. 2009, Cavagna et al. 2014), whereas Crozet birds used the small shelf of Crozet to a lesser extent, but travelled to other shelves such as the Del Cano Rise or the Kerguelen Shelf. These results are also confirmed by the analysis of behaviours inferred by the Hidden Markov Model showing that Kerguelen birds travel and search more over the shelf whereas Crozet birds travel, search and rest more in oceanic waters (Fig. 3.3). In particular, Crozet females foraged over deep waters, in the subtropical waters. Kerguelen wandering albatrosses hence appeared to be highly specialized in foraging over shelf areas during the breeding season, as well as outside the breeding season when they migrated to spend their sabbatical year over shelves off Chile and New Zealand (Weimerskirch et al. 2015). In contrast, Crozet birds foraged more over deeper waters during and outside the breeding season. A possible explanation is that Crozet is farther north, making it more viable for females to travel to subtropical waters.

Wandering albatrosses have similar population sizes in Crozet and Kerguelen (2200 pairs) (Weimerskirch et al. 2018a). In Kerguelen we found no differences in foraging parameters and habitats between males and females whereas for Crozet we confirmed the segregation between males and females (Weimerskirch et al. 1993, 1997b, 2014b), females favouring deeper and warmer waters than males. This difference between sites may be explained by the presence of the large productive shelf around Kerguelen that could reduce competition between sexes, whereas the smaller shelf around Crozet may force the smaller females to forage at greater distances in less productive waters. Indeed, the Kerguelen Shelf is not only larger but also more productive than the small Crozet Shelf (Dulaiova et al. 2009, Cavagna et al. 2014).

4.2. Overlap and attraction to boats

The strong differences in foraging habitats between the two populations and sexes have consequences on their overlap with fishing boats (exhaustive from radar detector) and on their behaviour behind boats (from AIS data). In this study, we estimated attractiveness as the time spent in attendance (<5 km) and sitting on the water behind boat divided by the time within encounter range (<30 km, when bird can see boats), quantifying the extent to which being within potential perceptual distance of a boat led to higher interactions. Overall, wandering albatross from both populations and both sexes, were equivalent in time spent per trip in contact with all types of boat (from radar detector), declared and non-declared. We found no differences in the duration of contact with boats (estimated from radar detector) between populations and sexes. However, in Crozet, more than 25% of contacts with boats were associated with non-declared boats, whereas in Kerguelen, this happened less than 15% of the time.

However, the two strategies of habitat use led to different overlap and attraction to boats, with Kerguelen birds encountering more boats than Crozet birds. Kerguelen birds encountered and attended boats for longer periods and closer to the colony, with no sex specific differences. Conversely, Crozet females encountered boats at greater distances from the colony than males, because of their propensity to forage in subtropical waters. On the other hand, since old males from Crozet foraged in Antarctic waters where there was a reduced boat traffic and fishing activity (Weimerskirch et al. 2014b), the average number of males attending boats was reduced. We found the same result when we considered boats encounters inside French EEZ, which reinforces our suggestion that even if the birds are in the presence of the same boats (exactly the same 7 French longliners for the EEZs of Crozet and Kerguelen and a small fraction of non-declared boats (Weimerskirch et al. 2020)), the birds of Kerguelen are still more attracted and forage for longer periods behind boats than Crozet birds. For Crozet birds, although attraction is similar between males and females, we found that males encounter boats closer to the colony and for longer durations. Females foraging in subtropical waters were more likely to encounter tuna longliners in oceanic waters (leading to shorter interactions or Area Restricted Search, ARS), and male foraging more over shelves encounter toothfish longliner, closer to colony, characterized by longer interactions and ARS (Corbeau et al. 2019).

Although we found important differences between populations and individuals in terms of encounters of fishing boats, we found no consequences in terms of breeding success. The contact rate of individuals did not affect the individual breeding success, and the breeding success of the Crozet and Kerguelen populations were similar. On the long term, the differences in attractiveness and time spent in encounter between populations did not affect the trends in population size that are similar between the two populations (Weimerskirch et al. 2018a).

A couple of studies have assumed that seabirds are attracted by fishing boats (Wahl & Heinemann 1979, Skov & Durinck 2001), and a recent study showed that seabirds can also be attracted by other types of boats (Weimerskirch et al. 2020). Here we demonstrate for the first time that albatrosses are more attracted and forage for longer periods associated with fishing boats compared to cargo vessels.

4.3. Role of fishery discards

Fishery discards are a source of food for many seabird populations (Votier et al. 2004) although in some cases they might be of lower food quality than “natural” food (Gremillet et al. 2008). Our study suggests that the release of fishing discards clearly attracted wandering albatrosses and led them to stay longer within sight of boats, compared to boats that were not releasing discards. Both sexes from the two populations were more attracted by boats when discards were released. Fishing discards appear as a significant source of food for scavenging birds and especially albatrosses (Bugoni et al. 2010) and it is suggested that release of fishing discards should be controlled to decrease bycatch risk (Waugh et al. 2008). Indeed, a new study, in North Atlantic, shows that the banishment of fishing discards led Gannets (*Morus bassanus*) to be no longer attracted by boats (Clark et al. 2020). Nowadays, in the EEZ around Crozet and Kerguelen, French authorities require fishers not to release discards during line setting to avoid bycatch. However, the disappearance of this source of food may have a significant impact (Bicknell et al. 2013) on those populations that have adapted to this new food source. In order to assess this impact, future studies should focus on quantifying the proportion of the total food intake that fishing discard represent compared to natural food.

In conclusion, our study shows that for the same species, populations and even sexes, can differ extensively in their foraging habitat and such differences have important implications for their overlap with fisheries and consequently for their susceptibility to bycatch risks. Future studies on risk assessments should take into account this additional complexity.

5. Acknowledgements

The study is a contribution to the Program EARLYLIFE funded by a European Research Council Advanced Grant under the European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 to Henri Weimerskirch) and to the Program Ocean Sentinel funded by the ERC under European Community's H2020 Program (Grant Agreement ERC-2017-PoC_780058 to HW). The fieldwork was also funded by program IPEV n ° 109.

Rocío Joo is funded by a Human Frontier Research Program Young Investigator Grant (SeabirdSound—RGY0072/2017).

Field procedures were supported by the 'Terres Australes et Antarctiques Françaises'. We thank the fieldworkers involved in the study on sites, Florent Lacoste, Tobie Getti, Aude Schreiber, Yusuke Goto, Yoshi Yonehara. We thank the 'French southern lands nature reserve' for providing fishing discards data, especially Adrien Chaigne, Samuel Peroteau and all the fisheries observer on board of the longliners.

Data are available in figshare at DOI: 10.6084/m9.figshare.10289096 (Weimerskirch, Collet, Corbeau, Pajot, Hoarau, Marteau, Filippi, Patrick, et al., 2019).

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7. Supporting information

Table S3.1 - Initial values of parameters of the distributions of observed variables for the Hidden Markov Model. The choice was based on results in (Clay et al. 2020), but modified in order to consider the difference in time scale respect to that study.

Observed variable	**Parameter**	**State 1 (« travel »)**	**State 2 (« search »)**	**State 3 (« rest »)**
Step length	Shape	1.3	0.58	0.04
	Scale	0.65	1.21	0.1
	Inflation	10^{-5}	10^{-5}	10^{-3}
Angle	Location	$-7x10^{-4}$	$6.5x10^{-3}$	$3x10^{-3}$
	Concentration	9.81	0.69	1.14

Table S3.2 - HMM estimates for step length and angle

Observed variable	**Parameter**	**State 1 (« travel »)**	**State 2 (« search »)**	**State 3 (« rest »)**
Step length	Shape	1.63	0.23	0.05
	Scale	0.58	0.34	0.03
	Inflation	1.9×10^{-5}	4×10^{-5}	3.6×10^{-4}
Angle	Location	$2.3x10^{-4}$	$1.5x10^{-3}$	$3.7x10^{-3}$
	Concentration	1.54	0.30	7.06

Table S3.3 - Transition probabilities between HMM states.

	State 1 (« travel »)	**State 2 (« search »)**	**State 3 (« rest »)**
State 1 (« travel »)	0.95	0.05	5.4×10^{-5}
State 2 (« search »)	0.07	0.85	0.08
State 3 (« rest »)	5.8×10^{-16}	0.07	0.93

Table S3.4 – Results of LMM (t test) and GLMM (Z test) (mixed models) for each variable between populations and between sexes inside each population. Significativity: ***(p <0.001); ** (0.01 <p <0.001); *(0.05 <p <0.01).

	CROZET (Male vs Female)				KERGUELEN (Male vs Female)				KERGUELEN vs CROZET				Distribution
	Estimate	Standard error	test value	p value	Estimate	standard error	test value	p value	Estimate	standard error	test value	p value	
per location (n= 537522)													
Bathymetry (m)	-551.37	303.73	-1.815	0.0764.	169.20	392.2	0.431	0.67	871.68	254.15	3.43	0.00104**	Gaussian
Bathymetry in "search" (m)	-1175.00	365.5	-3.215	0.0013**	46.06	422.83	0.109	0.914	915.24	277.07	3.303	0.00154**	Gaussian
SST (°C)	4.38	1.3157	3.326	0.00181**	1.03	1.1826	0.869	0.394	-4.65	1.0847	-4.286	5.96e-05***	Gaussian
per trip (n=71)													
Range (m)	-0.82	0.2678	-3.07	0.00215**	0.12	0.3375	0.36	0.723	-0.21	0.2100	-1.02	0.309	Negative binomial
Duration (h)	-64.67	39.18	-1.651	0.106	-2.59	52.646	-0.049	0.961	-15.97	34.06	-0.469	0.641	Gaussian
Ratio on shelf	1.61	0.6831	2.356	0.0185*	-0.81	0.9930	-0.817	0.4142	1.74	0.5650	3.070	0.00214**	Binomial
Ratio in antarctic waters	0.85	1.9839	0.427	0.66917	1.20	1.243	0.969	0.3327	0.59	0.7252	0.819	0.413	Binomial
Ratio in subantarctic waters	1.78	0.7408	2.401	0.0163*	-0.41	1.0274	-0.395	0.6931	0.39	0.5970	0.659	0.5097	Binomial
Ratio in subtropical waters	-2.31	1.0391	-2.218	0.0266*	-0.40	2.0405	-0.198	0.8432	-1.64	1.0736	-1.532	0.126	Binomial
Ratio in EEZ	1.58	0.6238	2.533	0.0113*	0.63	1.0288	0.611	0.541	1.20	0.5823	2.057	0.0397*	Binomial
Ratio in "travel"	-0.16	0.03547	-4.387	7.38e-05***	-0.01	0.05314	-0.235	0.816	0.005	0.035963	0.133	0.895	Gaussian
Ratio in "travel" on shelf	-0.005	0.021640	-0.228	0.82	-0.04	0.05165	-0.697	0.494	0.10	0.02398	4.289	6.31e-05***	Gaussian
Ratio in "travel" on ocean	-0.15	0.04396	-3.421	0.0014**	0.02	0.05896	0.398	0.69428	-0.10	0.04149	-2.423	0.0182*	Gaussian
Ratio in "search"	33.92	1831.79	0.019	0.985	-0.10	1.48016	-0.064	0.9486	1.50	1.253	1.197	0.231477	Binomial
Ratio in "search" on shelf	0.07	0.03555	1.985	0.05363.	-0.07	0.07348	-0.992	0.333	0.11	0.03775	2.821	0.00635**	Gaussian
Ratio in "search" on ocean	-0.02	0.02198	-0.987	0.329	0.02	0.02895	0.755	0.4702	-0.05	0.01901	-2.631	0.0107*	Gaussian
Ratio in "rest"	0.11	0.02744	4.037	0.00022***	0.07	0.04903	1.328	0.2	-0.06	0.02849	-2.138	0.0364*	Gaussian
Ratio in "rest" on shelf	0.13	0.04723	2.703	0.00687**	-0.04	0.05675	-0.661	0.508	0.59	0.6367	0.924	0.355387	Gaussian
Ratio in "rest" on ocean	-0.02	0.03760	-0.491	0.626	0.10	0.05336	1.833	0.0851.	-0.09	0.03341	-2.772	0.00729**	Gaussian
Ratio in contact with boat	0.16	1.5475	0.103	0.91771	-1.18	1.8039	-0.655	0.5123	0.73	1.1143	0.657	0.511	Binomial
Ratio in contact with declared boat	0.58	1.9509	0.299	0.7649	-0.62	1.9414	-0.319	0.7501	0.90	1.2345	0.727	0.467218	Binomial
Ratio in contact with undeclared boat	-1.77	3.778	-0.468	0.6400	2.55	10.832	0.235	0.814	-1.25	3.715	-0.338	0.73572	Binomial
per encounter (n=248)													
Distance from the nest (m)	-1.16	0.4001	-2.91	0.00367**	-0.98	0.5190	-1.89	0.0586.	-0.80	0.3704	-2.15	0.0318*	Negative binomial
Attraction	0.33	0.4665	0.696	0.486	-0.48	0.4859	-0.996	0.31934	0.80	0.3333	2.396	0.0166*	Binomial
Duration (min)	0.98	0.2315	4.25	2.13e-05***	-0.66	0.4763	-1.385	0.166	0.99	0.2661	3.724	0.000196***	Negative binomial
Attraction in French EEZ	0.3072	0.6361	0.483	0.629169	-0.3524	0.5383	-0.655	0.51274	1.0013	0.4583	2.185	0.0289 *	Binomial
Duration encounter in French EEZ (min)	0.6007	0.2644	2.272	0.0231 *	-0.8401	0.5413	-1.552	0.121	0.5753	0.2927	1.965	0.0494 *	Negative binomial
Attraction Fisheries	0.90	0.8315	1.078	0.281	-0.2231	0.5381	-0.415	0.67836	1.0088	0.4411	2.287	0.0222*	Binomial
Duration encounter Fisheries (min)	0.68	0.2508	2.725	0.00642**	-0.8003	0.5192	-1.541	0.123	0.5986	0.2772	2.16	0.0308*	Negative binomial
Attraction with fishing discard	0.06	0.10805	0.523	0.60128	0.03487	0.12828	0.272	0.786	0.12387	0.07685	1.612	0.107	Gaussian
Duration encounter with fishing discard (min)	0.36	0.4728	0.757	0.449	-1.0115	0.8470	-1.194	0.232	0.6216	0.4778	1.301	0.193	Negative binomial
Attraction without fishing discard	-0.12	0.8477	-0.144	0.88537	-0.4611	0.7800	-0.591	0.5544	1.8301	0.8317	2.201	0.0278*	Binomial
Duration encounter without fishing discard (min)	0.35	0.2627	1.313	0.189	0.3851	0.4096	0.94	0.347	0.4674	0.2089	2.24	0.0252*	Negative binomial
per radar events (n=193)													
Distance from the nest (m)	-1.13	0.4559	-2.47	0.0136 *	-0.08571	0.26149	-0.33	0.743	0.0400	0.3222	0.12	0.901	Negative binomial
Duration (min)	0.06	0.22448	0.25	0.802	-0.4109	0.2783	-1.476	0.14	0.1389	0.1939	0.72	0.474	Negative binomial
Duration for declared boat (min)	0.44	0.2733	1.602	0.109	-0.4517	0.2939	-1.537	0.124	0.2978	0.2238	1.33	0.183	Negative binomial
Duration for undeclared boat (min)	-0.07	0.50177	-0.142	0.887	-0.4717	0.5882	-0.802	0.423	-0.3289	0.3301	-0.996	0.319	Negative binomial

Table S3.5 – Number of encounters (and percentage of those encounters without any attendance) used for models with attraction.

	CROZET		KERGUELEN	
	Female	**Male**	**Female**	**Male**
Attraction	93 (65.6%)	64 (42.2%)	47 (31.9%)	44 (56.8%)
Attraction Fisheries	80 (65.0%)	57 (42.1%)	40 (32.5%)	40 (57.5%)
Attraction with fishing discard	5 (20.0%)	20 (10.0%)	13 (30.8%)	6 (33.3%)
Attraction without fishing discard	23 (52.2%)	36 (47.2%)	24 (20.8%)	23 (47.8%)
Attraction in French EEZ	29 (44.8%)	54 (33.3%)	39 (28.2%)	41 (56.1%)

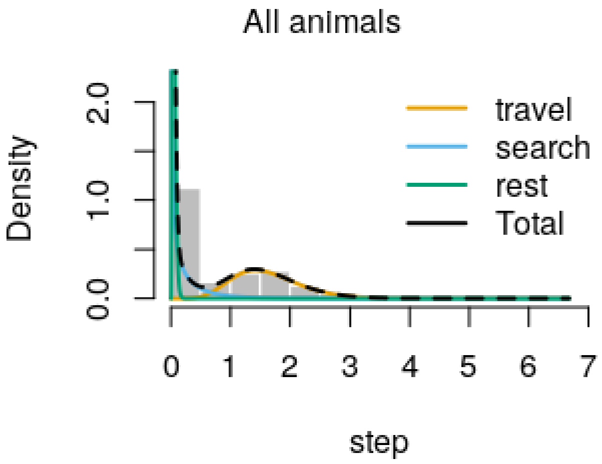

Figure S3.1 - Step length distribution for the three HMM states.

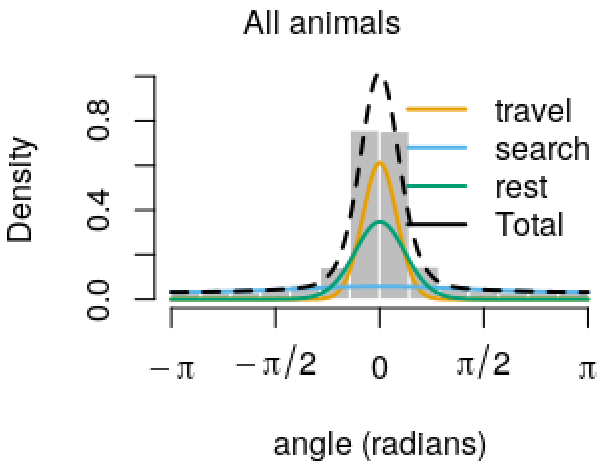

Figure S3.2 - Turning angle distribution for the three HMM states.

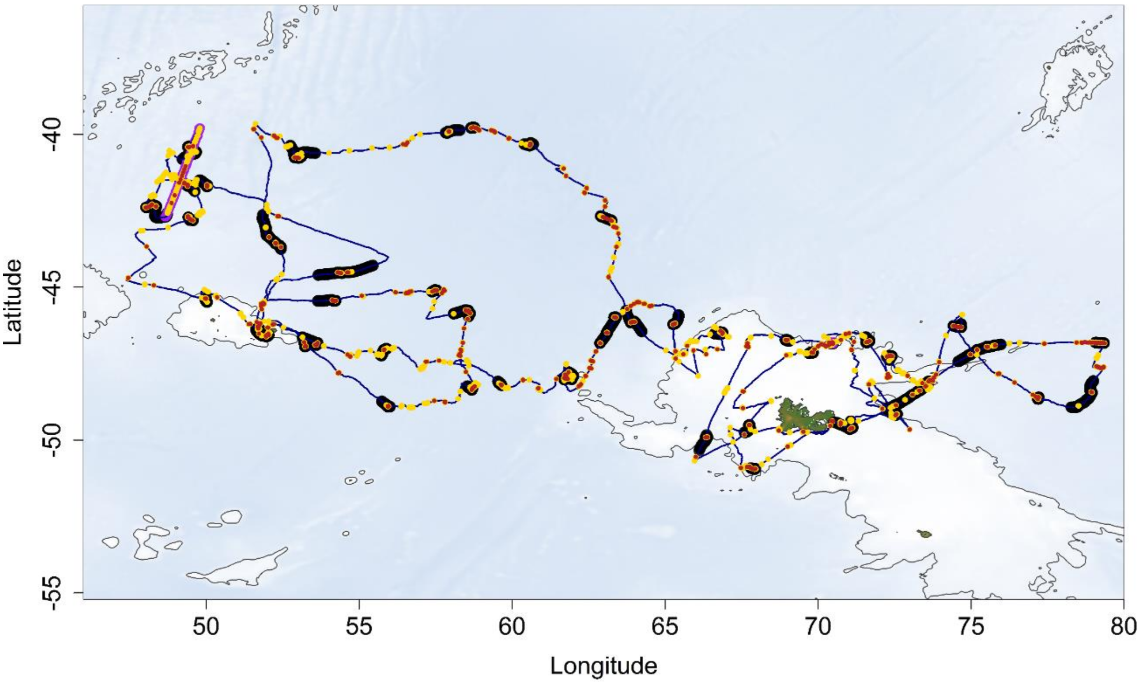

Figure S3 – Illustration of HMM behavioural states (following methods from Clay et al. 2020) of 5 randomly selected foraging trips (3 from Crozet birds and 2 from Kerguelen birds) : "travel" (in blue line), "rest" (red dots), "search" (yellow dots). Note that, to keep the model simple, the HMM was fitted without covariates such as boat attendance (purple), night periods (thick black lines) or bathymetry (blue shades in the map and 2000m isobath line).

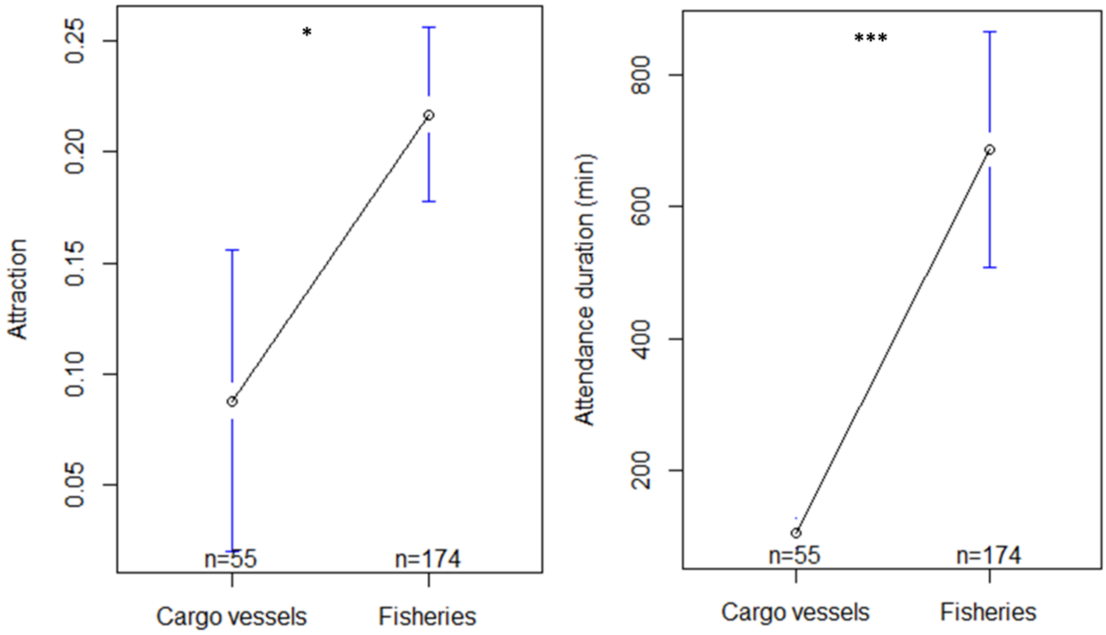

Figure S4 – Differences in attraction (left plot) and attendance duration (right plot) for Cargo and fishing vessels (mean ± one standard error).

Discussion générale

Alexandre CORBEAU

Cette thèse sur les interactions entre albatros et bateaux de pêche est en grande partie basée sur l'utilisation de nouvelles balises développées au cours des 5 dernières années au laboratoire de Chizé dans le cadre de deux programmes ERC. Diverses méthodes existent pour évaluer les interactions entre les oiseaux marins et les pêcheries (Le Bot et al. 2018), mais l'intérêt de cette thèse réside dans l'utilisation de nouvelles balises permettant de détecter l'émission des radars de bateaux. Les jeux de données uniques issues des balises combinant localisation GPS et présence d'un navire sont ensuite couplés à des données de localisation de bateaux déclarés (AIS). Le traitement des données nous permet d'étudier à très fine échelle les comportements des oiseaux. En effet, grâce aux balises nous pouvons connaître les trajets des albatros avec une résolution relativement haute (une position précise à 3 mètres près toutes les 2 minutes), mais aussi les positions, la durée et la nature des interactions avec les bateaux. Couplés aux données AIS, ces éléments nous permettent de connaitre l'attraction envers ces bateaux, le type de bateau rencontré, et si ces bateaux sont déclarés ou non. Enfin, grâce aux suivis long terme des espèces effectuées depuis plus de 60 ans nous pouvons également connaitre l'ensemble des traits d'histoire de vie des individus équipés (âge, sexe, personnalité, expérience, succès reproducteur…). C'est à la fois en recueillant et en combinant ces jeux de données exceptionnelles que j'ai pu réaliser ma thèse.

Dans le chapitre 1, nous avons décrit les comportements de recherche alimentaire des albatros hurleurs et mis en évidence que ces comportements étaient plus longs, plus sinueux et situés préférentiellement sur les plateaux océaniques lorsqu'ils étaient associés à un bateau par rapport aux comportements naturels des oiseaux. De plus nous avons précisé que ces caractéristiques étaient plus marquées lors des rencontres albatros-bateaux de pêche situées sur les plateaux océaniques qui correspondent aux zones de pêcheries à la légine australe.

Dans le chapitre 2, nous avons étudié l'ensemble des populations de grands albatros de l'océan Indien (Marion, Crozet, Kerguelen Amsterdam) et développé une méthode d'estimation à fine échelle du risque de captures accidentelles en couplant des données de simples suivis GPS aux données AIS. Nous avons constaté que cette méthode, plus précise que celles utilisées couramment à plus large échelle, n'est pas équivalente en termes d'évaluation des risques en comparaison des méthodes habituelles. Par exemple, si la population d'Amsterdam est en moyenne en contact permanent avec 2 bateaux situés à moins 100 km de leur position, ils n'entrent en contact qu'avec une infime partie de ces bateaux et n'y passent que peu de temps. Alors que les oiseaux de Kerguelen qui ont beaucoup moins de bateaux navigants autour d'eux, passent au contraire bien plus de temps à leur contact. Nous avons mis ces résultats en relation avec les tendances populationnelles et constaté que les populations les moins exposées avaient le plus fort taux de croissance. Nous avons pu en déduire que l'exposition au risque de captures accidentelles dépend non seulement de l'espèce, mais aussi des populations.

Enfin dans le chapitre 3, nous nous sommes focalisés sur les populations de grands albatros de Crozet et de Kerguelen et nous avons décrit les utilisations différentes des habitats par les deux sexes de ces deux populations. Les oiseaux sont inféodés aux plateaux à Kerguelen (mâles et femelles) alors qu'ils sont beaucoup plus océaniques à Crozet, notamment les femelles qui vont plus au nord. Cette différence d'utilisation a pour conséquence une différence d'exposition au risque de captures accidentelles ; si les populations de Kerguelen sont bien plus attirées par les bateaux, elles sont moins soumises aux pêcheries non déclarées que celles de Crozet plus océaniques (notamment chez les femelles). Nous avons également constaté que les oiseaux étaient plus attirés par les bateaux de pêche que par les autres types de bateaux et tout particulièrement (quel que soit le sexe ou la population) lorsqu'il y a présence de rejets de pêche.

Dans cette discussion je reviendrai sur les méthodes utilisées, leurs avantages et leurs limites, sur les analyses des comportements de recherche alimentaire associés aux bateaux ainsi que sur les expositions au risque de captures accidentelles et sur l'ensemble des facteurs qui modifient ce risque, qu'ils soient intrinsèques aux individus ou liés aux caractéristiques des bateaux.

Enfin, j'évoquerai les conséquences de ce piège écologique que constituent ces expositions aux bateaux et les applications à la conservation qui découlent de nos résultats. Je présenterai pour terminer les perspectives de ce travail, à court terme avec les travaux en cours puis à moyen ou long terme en envisageant les possibilités qu'offrent les nouvelles technologies et les méthodes d'analyses utilisées dans ma thèse.

1. Méthodologie

1.1. Les données de localisation des albatros

La biotélémétrie permet de suivre des animaux à distance, sans changer leur comportement, en acquérant des énormes jeux de données inaccessibles autrement. Après cinq denses années de développement et de résolution des divers problèmes rencontrés sur le terrain, nos balises nous ont, non seulement, fourni des données exploitables et uniques, mais elles sont désormais opérationnelles et utilisables par tous. Même si la technologie a énormément évolué et que les composants se sont miniaturisés, des compromis doivent nécessairement être faits et des postulats avancés chaque fois que des balises sont déployées entrainant des approximations plus ou moins acceptables d’un point de vue écologique.

La durée d’échantillonnage des balises est par exemple un facteur important. Mais actuellement des données en continu ne sont pas envisageables pour des balises aussi légères sur de si longues périodes d’enregistrement. Par convention, nous considérons donc que des localisations discontinues échantillonnées régulièrement sont représentatives des déplacements de l’oiseau et que ces déplacements sont rectilignes entre ces points. Dans cette étude nous disposons de localisations toutes les minutes ou 2 minutes pour les oiseaux de Crozet, Kerguelen et Amsterdam (20 minutes pour Marion). Donc, entre chaque localisation, l’oiseau peut parcourir 5 km lorsqu’il a sa vitesse maximale seuil de 150 km/h. Des comportements peuvent nous échapper, mais ces approximations sont connues et des échantillonnages toutes les 2 minutes sur une si grande période ont une bonne représentativité écologique et sont équivalents ou supérieurs aux échantillonnages d’études traitant les mêmes sujets (Bodey et al. 2014, Collet et al. 2015, 2017b). Il faut aussi noter que la technologie étant malheureusement faillible, lors du développement de tout nouveau type de balises, les prototypes en plus d’être coûteux ont un fort risque de ne pas fonctionner dès le premier essai. C’est pourquoi il est compliqué de prévoir des projets sur une seule campagne de déploiement avec des balises n’ayant jamais été testées *in natura* au préalable.

Nous avons favorisé les périodes d’incubation, car ce sont les périodes les plus critiques pour les albatros qui sont alors très exposés au risque de captures accidentelles (Jiménez et al., 2016). Même si nous avons pu équiper quelques individus en échec de reproduction ou pour le début de leur année sabbatique, il serait intéressant d’évaluer le risque de captures accidentelles sur l’ensemble du cycle de reproduction de ces espèces, car il a été montré qu’à la fin de l’élevage du jeune (mai à décembre) les albatros hurleurs étaient de nouveau dans des zones où naviguent des bateaux de pêche (Weimerskirch et al. 1993, Jiménez et al. 2016).

1.2. Les données des bateaux

1.2.1. Par les détecteurs de radar

Les balises déployées sur les oiseaux détectent la présence des bateaux grâce à leurs ondes radar. À l’instar des données de géolocalisation, l’enregistrement n’est pas continu, mais s’avère malgré tout être le plus optimal possible dans l’état actuel de nos connaissances et des capacités des batteries des balises. Par ailleurs les ondes radar, et donc l’enregistrement du signal d’un bateau, peuvent être affectées de façons diverses. Même si l’antenne est accordée en fonction du corps de l’oiseau, en cas de mauvaise orientation vis-à-vis du navire, due aux mouvements en zigzag et à la forte houle, l’enregistrement du signal en sera affecté. De même une absence de signal peut être due aux zones d’ombre du radar provenant du bateau lui-même (Fig. 35).

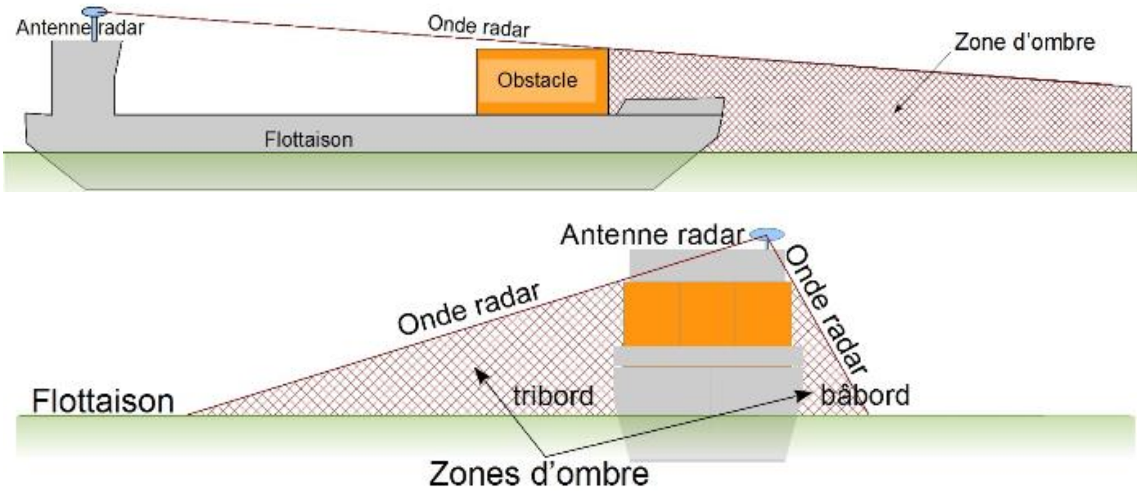

Figure 35 : illustration des zones d’ombre des radars sur les bateaux (ministère de l’Écologie)

La détection radar n’est donc pas absolue, c’est pourquoi nous avons construit des « évènements » de détection englobant les éventuelles absences de signal de moins de 2h. Malgré cela, grâce aux comparaisons avec les données AIS, nous constatons tout de même que certains bateaux ne sont pas détectés. Il y a près d’un tiers de bateaux non détectés par le radar alors qu’ils sont à proximité d’un signal AIS. Ces manques peuvent s’expliquer notamment par un contact très rapide entre l’oiseau et le bateau entrainant une absence de détection due soit à la période de sommeil du détecteur radar, soit à une altération du signal cité précédemment. Il se pose ensuite la question de la fiabilité des données AIS qui nous permettent ce constat.

1.2.2. Par les données AIS

Tout d'abord, il faut préciser que pour ces études les données AIS ont été achetées via la société CLS (Collecte Localisation Satellites) et que malheureusement, nous n'avons aucunement la main sur les extractions ni la possibilité de les vérifier. Cette solution a été choisie pour une question de facilité de transmission des données en direct par format prétraité (extrait en « .csv ») et pour la possibilité de les visualiser sur la même plateforme et directement associées aux données de nos oiseaux, transmises eux aussi par le système Argos.

Les AIS permettent maintenant d'avoir une meilleure évaluation de l'effort de pêche (de Souza et al. 2016) et une surveillance (McCauley et al. 2016) à large échelle. Cependant, il est très facile pour les équipages de couper ce signal AIS et, à ce moment-là, les bateaux sont non déclarés et peuvent être considérés comme illégaux dans les ZEE des îles du sud de l'océan Indien où les signaux AIS sont obligatoires pour tous les bateaux y naviguant. Les données AIS sont précises et le signal est transmis en moyenne toutes les 9-10 min, mais malgré cela, il peut y avoir des données manquantes. Cela peut être dû à l'arrêt volontaire ou non des transmissions par les bateaux eux-mêmes, ou bien à une transmission incomplète des informations par satellite. Nous avons d'ailleurs constaté (une seule fois) une image miroir d'un bateau signalé dans la zone d'études, alors qu'il se trouvait en réalité de l'autre côté du globe. On peut supposer que le problème de ce bateau chinois venait d'une erreur d'antenne.

Enfin, il faut noter que même si les AIS sont maintenant facilement consultables en temps quasiment réel (Marine Traffic ou Global Fishing Watch), le prix de l'accessibilité des données brutes est relativement élevé et les énormes masses de données générées (150 millions de lignes pour nos analyses en 2018-2019) ont nécessité le développement de routine d'analyses spécifiques (R ou autre).

1.3. Les analyses

Les données que j'ai utilisées dans ma thèse n'avaient jamais été directement analysées dans la littérature, c'est pourquoi j'ai employé des méthodes diverses pour exploiter ce nouveau type de données. Dans le chapitre 1 et 3, j'ai travaillé sur des méthodes de regroupement afin d'identifier les comportements des albatros. Pour le chapitre 1, j'ai déterminé des comportements de recherche alimentaire (ARS) définis par un temps plus long passé dans une zone donnée (« First Passage Time ») (Pinaud 2007). Alors que dans le chapitre 2 j'ai utilisé des modèles de Markov cachés qui permettent de définir des probabilités de changement de comportement entre chaque localisation et ainsi d'identifier un « état » pour chaque position de l'oiseau (Morales et al. 2004). Si ces méthodes sont largement utilisées dans la littérature, elles possèdent naturellement leurs avantages et leurs inconvénients.

J'ai, en premier lieu, utilisé les ARS caractérisées par un ensemble de localisation où l'albatros est en recherche active de nourriture et qui permettent de définir des comportements complets de recherche alimentaire (Weimerskirch et al. 2007). Cela m'a permis de comparer, à des échelles diverses, les comportements de recherche alimentaire naturels et ceux associés à un bateau. Toutefois, dans cette méthode, c'est l'observateur qui choisit les seuils des valeurs de FTP moyennes selon la journée et qui entraine donc inévitablement l'identification d'une ARS au moins une fois par jour. Nous avons fait ce choix subjectif de variation de seuil afin d'être le plus conformes possible à l'écologie de l'espèce et de capter la plupart des ARS réalisées par les oiseaux. En effet, ce seuil peut varier d'une journée à l'autre avec des comportements en ARS définis par des valeurs basses de FTP certains jours, dues à une moyenne de FTP journalière faible, car l'oiseau y transite fréquemment. Alors que d'autres jours, les moyennes de FTP journalières sont beaucoup plus élevées, car l'oiseau passe plus de temps posé sur l'eau.

Dans un deuxième temps, pour le chapitre 3, ce sont les HMM qui ont été utilisés. Il y a un choix de la part de l'observateur sur les valeurs seuils des paramètres, mais une fois définies, elles sont fixes pour l'ensemble des trajets. Les HMM ont l'avantage de considérer chaque localisation de l'oiseau et sont donc très intéressants pour définir différents comportements, car ils sont plus variés qu'en ARS ou non. Ici nous avons utilisé les comportements de « route », de « repos » et de « recherche » (Clay et al. 2020). Néanmoins, le désavantage de cette méthode est, contrairement à l'ARS, l'absence d'une phase unique définie comme étant « de la recherche alimentaire ». Si nous comparons les HMM et les ARS, les ARS sont composées de successions de comportements majoritairement de « repos » puis de « recherche » et de quelques comportements de « route ». Les HMM ont été utilisés ici comme un indicateur d'utilisation d'habitat et sont, dans ce cas, plus précis que les ARS.

Notons aussi que ces deux types d’analyse doivent, par principe, interpoler les localisations à intervalle parfaitement régulier, ce qui, à l’origine, constitue une légère approximation des positions de l’oiseau par l’interpolation en ligne droite. Dans le cadre de notre étude les positions étant très resserrées (toutes les 2 minutes) cette approximation est écologiquement et statistiquement tout à fait acceptable, mais c’est plus discutable pour des données excédant l’heure par exemple.

En conclusion, divers outils de plus en plus sophistiqués s’offrent à nous et permettent d’étudier des jeux de données toujours plus importants et plus complexes. C’est pourquoi il est intéressant de s’entourer d’experts en analyses, mais aussi d’experts des espèces concernées, afin de valider les conclusions issues de modèles statistiques qui ne sont pas obligatoirement réalistes biologiquement.

2. La recherche alimentaire des oiseaux marins en présence de bateaux

2.1. La présence de bateaux change le comportement des oiseaux marins

Dans le chapitre 1, après avoir décrit les comportements de recherche alimentaire (ARS) des albatros hurleurs, nous avons constaté que la présence des bateaux conduisait à un changement de comportement des oiseaux. Ce phénomène a également été observé chez les fous de Bassan dans les ZEE d’Irlande. Les fous ont tendance à basculer plus souvent vers un comportement de recherche alimentaire lorsqu’ils sont en contact avec des bateaux de pêche en activité (Bodey et al. 2014). Chez les albatros hurleurs de Crozet, s’il existe une grande variabilité au sein des individus, derrière les bateaux de pêche les oiseaux passent plus de temps, avec des trajets plus sinueux et avec plus d’ARS à petites échelles nichées dans des ARS à plus grandes échelles (chapitre 1 - Corbeau et al. 2019).

Nous avons aussi mis en évidence qu’au sein même des ARS associées aux bateaux nous pouvions différencier celles effectuées dans les eaux océaniques de celles sur les plateaux. Ces dernières sont plus longues, plus sinueuses, avec plus de temps passé dans l’eau et plus d’ARS nichées les unes dans les autres. Nous expliquions ces différences par les types de pêcheries rencontrées dans ces milieux, car les pêcheries à la légine australe se situent sur les plateaux et les pêcheries au thon en plein océan. Cependant, nous nous attendions à des résultats inverses, avec des ARS plus longues et sinueuses, en plein océan en contact avec les pêcheries aux thons qui possèdent des palangres jusqu'à deux fois plus grandes que les pêcheries à la légine. Grâce aux données AIS nous possédons maintenant de nouvelles informations sur les types de bateaux rencontrés et nous avons constaté que non seulement il existe une grande variabilité individuelle selon les oiseaux qui ne s'approchent pas ou que très brièvement des bateaux, mais aussi, que la majorité des bateaux rencontrés par les oiseaux en plein océan sont de type « transport » (Fig. 36). Ces bateaux n'offrent pas d'accès à de la nourriture et entrainent des interactions plus courtes de la part des oiseaux (chapitre 3).

2.2. Les applications méthodologiques de ce changement de comportement

Ces changements de comportements maintenant identifiables avec des variables connues nous permettent de formuler de nouvelles hypothèses et de développer des méthodes qui pourraient permettre de détecter des interactions oiseaux - bateaux à partir de simples suivis géolocalisés.

2.2.1. Un modèle basé sur les ARS

A la suite du chapitre 1, j'ai testé la prédictivité du modèle des ARS à petites échelles (Chapitre 1 - Table 1.1 – Small scales – Y = -4.232 + 0.163 durée de l'ARS + 3.6 sinuosités de l'ARS - 0.0005 distance moyenne de l'ARS à la colonie + 0.0006 bathymétrie moyenne de l'ARS -0.242 proportion de temps passé poser dans l'eau pendant l'ARS). J'ai trouvé que 95.3% (±1.5) des ARS de petites échelles dites naturelles et que 38.5% (±6.5) des ARS de petites échelles associées à un bateau ont été bien identifiées (prédiction réalisée avec la fonction R « predict » sur 70% des données et appliquée sur les 30% restantes, réitérée 1000 fois). Ce modèle n'a pas un pouvoir prédictif très important (ce qui n'était pas le but de cette étude), mais il est assez intéressant de voir qu'en général les ARS de petites échelles sont à 85.3% naturelles et à 14.7% associées à un bateau. Le modèle prédit donc plus du double des ARS associées aux bateaux par rapport à un tirage aléatoire et élimine à 95.3% le biais des ARS naturelles, le but étant de les écarter afin de repérer celles associées aux bateaux. Cependant, la faible prédictivité et la nécessité de passer par les ARS avec la méthode du First Passage Time, très chronophage, nous a conduits vers de nouvelles méthodes d'analyses qui se développent grandement.

2.2.2. Des modèles de Markov cachés inversés

Les HMM sont en plein essor et sont de plus en plus utilisés par les écologues (Joo et al. 2013). Comme je le mentionnais préalablement, les HMM consistent à définir des probabilités de changement d'état en fonction de certaines variables. Il m'est alors paru intéressant d'essayer d'inverser ce concept. Connaissant déjà les états (avec bateaux ou sans bateaux) grâce aux balises déployées et les variables pouvant influencer ces états (chapitre 1, 2 et 3) : la vitesse, la sinuosité, la bathymétrie, la distance au nid, le sexe et le paramètre jour/nuit. Je travaille actuellement avec R. Joo et collaborateurs (en préparation a) à développer un modèle permettant d'identifier un état « avec bateau » depuis un simple trajet géolocalisé.

2.2.3. Le « Machine Learning »

Lors de nos investigations sur les HMM, il nous a semblé intéressant de tenter de définir ces modèles de présence de bateau ou non, grâce à différentes méthodes de « Machine Learning » (Joo et collaborateurs en préparation b). Nous nous sommes alors confrontés à des problèmes d'ordre méthodologiques. En effet, la plupart des études (Martiskainen et al., 2009; Nathan et al., 2012…) utilisant le « Machine Learning » regroupent l'ensemble de leurs données, entrainent leur modèle avec 70 ou 80% de ces données et l'appliquent au 20 ou 30% restants. Comme nous, ils trouvent souvent de très bons résultats. Avec cette méthode, basée sur les procédures de « random forest » (Pal 2005), nous parvenons à prédire correctement 92% des interactions avec les bateaux, ce qui est assez impressionnant en écologie. Cependant, projetant une utilisation par d'autres personnes, il nous est apparu nécessaire de raisonner à l'échelle d'un trajet. En effet, une fois le modèle défini, nous avons besoin d'ajouter un trajet entier afin de déterminer où, dans ce trajet, se situent les interactions avec les bateaux. Mais c'est à ce moment-là que les prédictions diminuent drastiquement vers 55% de prédictibilité. C'est pourquoi nous réalisons actuellement une revue de différentes méthodes de « Machine Learning » et de leurs meilleures utilisations possibles à ces questions en écologie.

3. Les différentes expositions au risque de captures accidentelles

L’exposition au risque de captures accidentelles chez les oiseaux marins est directement reliée aux changements de comportement de recherche alimentaire au contact des bateaux. En effet, les divers facteurs qui influencent ces changements de comportement conduisent les oiseaux à être plus attirés et à plus s’exposer aux équipements des bateaux tels que les palangres (chapitre 1 - (Corbeau et al. 2019). L’idéal serait d’évaluer ce risque de captures accidentelles en comptabilisant la mortalité induite, directement sur les bateaux (Lewison et al. 2009) mais, il n’est hélas pas envisageable de mettre un observateur des pêches à bord de chaque bateau, en particulier sur les pêcheries océaniques pour le thon. C’est pourquoi, actuellement, l’exposition au risque de captures accidentelles est évaluée en superposant les données, à large échelle, de suivis des espèces et d’effort de pêche (résolution classique d’une grille de 5x5°) (Clay et al. 2019, Heerah et al. 2019). Toutefois une utilisation d’une échelle plus fine semble indispensable pour comprendre de quelles manières les oiseaux sont exposés à ce risque, à la fois spatialement et temporellement (Torres et al. 2013). Nos études répondent en partie au problème, car nous avons montré que nous pouvions maintenant utiliser à fine échelle les données issues de nos balises ou des signaux AIS pour détecter les rencontres avec les bateaux. L’évaluation du risque est donc plus précise et elle pourrait permettre de définir des zones de protection ciblées qui seraient par ailleurs inenvisageables sur de très larges échelles regroupant des eaux internationales et différentes eaux territoriales par exemple.

Dans cette thèse, je considère qu’une exposition au risque de captures accidentelles est associée à une rencontre avec un bateau de pêche. Ces rencontres sont identifiées soit par l’enregistreur de radar embarqué dans la balise, soit par une correspondance spatio-temporelle entre les données de géolocalisation des oiseaux et celles des AIS. Il ne s’agit pas d’une évaluation directe du risque, mais seulement du meilleur proxy actuel dans ce contexte. Je définis ici la notion d’attraction du bateau comme un changement de comportement lorsque l’oiseau est à proximité d’un bateau : c’est le rapport du temps passé posé sur l’eau à l’arrière du bateau (<5 km) divisé par le temps en contact visuel du bateau (<30 km). Avec les durées de la rencontre, ce sont les deux paramètres majeurs qui définissent l’exposition au risque de captures accidentelles dans un contexte d’exploration et d’exploitation d’une ressource par les oiseaux. Ce sont ces paramètres qui vont varier selon diverses caractéristiques intrinsèques à la fois des individus et des bateaux rencontrés.

3.1. Selon les caractéristiques des oiseaux

Les caractéristiques des individus qui jouent un rôle majeur dans l'exposition au risque de captures accidentelles vont de la notion la plus large d'espèce ou de population jusqu'au trait individuel des individus comme le sexe, l'âge ou même la personnalité.

Si peu d'espèces d'oiseaux ne sont pas en contact avec les bateaux (Grémillet et al. 2018), d'autres espèces, même semblables et habituellement attirées par les bateaux, vont interagir différemment. Dans le chapitre 2, nous avons par exemple montré qu'il existe une différence d'exposition au risque entre les albatros hurleurs et les albatros d'Amsterdam pourtant très proches physiquement et biologiquement. L'albatros d'Amsterdam, qui se nourrit dans des zones à forte densité de bateaux, rencontre et passe nettement moins des temps derrière les bateaux que les albatros hurleurs de Kerguelen ou même de Crozet et de Marion.

Les grands albatros peuvent se déplacer sur des milliers de kilomètres pour trouver de façon opportuniste les proies qui leur conviennent et ils n'ont pas de nécessité de contact avec des bateaux de pêche pour trouver leur nourriture (Weimerskirch et al. 1993). En effet, les grands albatros passent moins de 10% de leur temps de recherche alimentaire derrière un bateau, ce qui est relativement faible comparé à d'autres espèces plus petites et plus contraintes comme, par exemple, l'albatros à sourcils noirs qui y passe 25% de son temps en période d'élevage (chapitre 2; Collet et al., 2017a). Malgré cela, chez ces derniers, qui sont plus contraints dans leur temps de trajet, dans leurs proies capturées et qui sont plus fidèle à leurs sites de nourrissage, il a été montré que ces oiseaux favoriseraient une recherche de nourriture naturelle sans se spécialiser sur les bateaux de pêche (Granadeiro, Brickle, & Catry, 2014) alors même qu'ils peuvent mémoriser leurs zones de présence (Collet & Weimerskirch, 2020). En revanche, chez des espèces encore plus contraintes dans leur recherche alimentaire comme le puffin à menton blanc (*Procellaria aequinoctialis*) (Jackson 1988), nos premières analyses des populations de l'île Marion montrent que ces oiseaux vont systématiquement se focaliser sur les bateaux de pêche (78% de bateaux de pêche à moins de 5 km) alors que ce sont majoritairement des cargos et des tankers qui sont présents autour d'eux (72% de bateaux autres que des bateaux de pêche à 30 km). Pour d'autres espèces comme l'albatros brun (*Phoebetria* *fusca*), dont la biologie et le comportement sont peu connus, mais dont la chute drastique des populations est classiquement imputée aux pêcheries (Rolland et al. 2010), dans les populations de Marion les oiseaux ne privilégient et ne s'attardent visiblement pas sur les bateaux de pêche (0 rencontre de bateaux de pêche à moins de 5 km sur les 29 bateaux de tous types présents à 30 km) (Orgeret et al. *en préparation*). Ainsi, ces deux espèces, très sensibles à la mortalité dans les palangres (Barbraud et al. 2008), sont exposées différemment au risque de captures accidentelles malgré leur proximité dans leurs zones de recherche alimentaire.

L'espèce est un facteur déterminant pour évaluer le risque de captures accidentelles, mais, au sein d'une même espèce, des populations différentes montrent des expositions variables. Dans le chapitre 2, nous avons constaté une forte disparité d'exposition entre les populations de Marion, de Crozet ou de Kerguelen avec en moyenne 12% du trajet passé au contact des bateaux pour Kerguelen et seulement 1% pour Marion. Dans le chapitre 3, nous avons également observé que les albatros de Kerguelen étaient nettement plus attirés par les bateaux que ceux de Crozet. Ces différences au sein des populations pourraient s'expliquer, dans un premier temps, par une ségrégation spatiale comme nous l'avons constaté entre les populations de Marion et Crozet dans une étude réalisée avec F. Orgeret et collaborateurs (Annexe 3). De même, chez l'albatros à sourcils noirs des îles Falkland il existe des ségrégations spatiales fortes entre les populations (Catry et al. 2013), non liées aux pêcheries, mais entrainant des contacts et des expositions aux pêcheries différentes entre des populations séparées seulement de 75 km (Granadeiro, Phillips, Brickle, & Catry, 2011). Il faut toutefois noter que, malgré ces ségrégations, d'autres espèces d'oiseaux marins profitent de la présence de conspécifiques, non seulement pour repérer des patchs de nourriture, mais aussi pour augmenter leur efficacité de capture (Thiebault et al. 2014).

Les différences d'expositions aux risques peuvent également s'expliquer par une utilisation différente de l'habitat par les populations (chapitre 3). Des oiseaux exploitant pour leur recherche alimentaire un habitat plus pauvre en bateaux de pêche seront logiquement moins exposés. Toutefois, l'utilisation de l'habitat n'est pas constante dans le temps, y compris à très fine échelle temporelle, c'est-à-dire à l'échelle de la journée. Une étude menée avec A. Pajot et collaborateurs (annexe 2) a clairement montré que les rythmes d'activité des albatros dépendaient, en plus de l'espèce et de la classe d'âge, de l'heure de la journée. L'activité est bien plus importante en début et en fin de journée et elle n'est pas négligeable en pleine nuit lorsque la luminosité est importante. De plus, il a été montré en mer Baltique, que si les oiseaux marins charognards exploitent un habitat riche en sources naturelles de nourriture, ils seront moins attirés par les bateaux (Skov & Durinck 2001) et ce, de manière analogue aux albatros à sourcils noirs de Kerguelen (Collet & Weimerskirch, 2020). Notons toutefois que les stratégies de recherche alimentaire des grands albatros sont tellement opportunistes et peu fixées sur des habitats à fortes ressources naturelles que la présence des bateaux les attire immanquablement malgré d'éventuelles proies localisées en forte abondance. Il est donc fondamental de bien connaître la biologie des différentes populations étudiées et de toujours la prendre en compte lors de l'évaluation de l'exposition au risque de captures accidentelles.

L'utilisation de l'habitat et l'exposition au risque de captures accidentelles qui en résulte varient non seulement entre les espèces et les populations, mais aussi au sein même de ces populations. Les individus, et particulièrement ceux appartenant à des espèces très longévives, ont des histoires de vie et des expériences bien différentes entrainant de très grandes variations et disparités entre les sexes ou les classes d'âge (Weimerskirch et al. 1993, 2014, Weimerskirch et al. 1997).

Par exemple à Crozet (Chapitre 3) et à Marion (Nel et al. 2002), les femelles d'albatros hurleurs vont se nourrir lors de l'incubation (et à la fin de l'élevage du poussin) plus au nord, dans des eaux plus chaudes, que les mâles. Elles sont alors en contact avec des pêcheries de thon plus « meurtrières » que les mâles qui se nourrissent plus au sud ou sur les plateaux océaniques, au contact des pêcheries à la légine australe majoritairement soumises à des mesures de mitigation strictes. De même, en Géorgie du Sud, les femelles ont des taux de mortalité plus importants que ceux des mâles, car elles utilisent, elles aussi, des eaux situées plus au nord où la présence de pêcheries aux thons est plus grande (Jiménez et al. 2016). Dans l'hémisphère nord, ce sont également les fous de Bassan mâles qui utilisent majoritairement les rejets derrière les bateaux et ce sont donc les mâles qui sont plus affectés par le risque de captures accidentelles ou par les interdictions d'émission de rejet de pêche dans les eaux européennes (Votier et al. 2013).

L'âge est également un facteur important influençant les comportements chez ces espèces longévives (de Grissac et al. 2017). Si nous n'avons pas trouvé de différences d'exposition aux bateaux au sein des adultes reproducteurs (de plus de 8 ans), en revanche les jeunes, moins contraints que les adultes en reproduction, sont moins attirés et entrent moins en contact avec les bateaux que les immatures et encore moins que les adultes (Annexe 1 - Weimerskirch et al., 2020 et Weimerskirch et coll. en préparation). Notons toutefois, que les vieux mâles (>30 ans) d'albatros hurleurs font de longs trajets très au sud, jusqu'au continent antarctique, où très peu de pêcheries sévissent alors que les vieilles femelles accomplissent aussi de longs trajets, mais très au nord dans les pêcheries de thons (chapitre 3) (Weimerskirch et al. 2014a). C'est pour cela qu'il est intéressant d'associer les effets de l'âge et du sexe dans les études comportementales chez ces espèces (Weimerskirch et al. en préparation).

Pour compléter l'impact de cette variabilité individuelle, des études relativement récentes ont montré que les personnalités des albatros jouaient un rôle prépondérant dans leur stratégie de recherche alimentaire et leur reproduction (Patrick & Weimerskirch, 2015; Patrick & Weimerskirch, 2014). Il a été montré que les individus audacieux (*bold*) se nourrissent plus près de la colonie, car ils sont plus enclins à performer lors de fortes compétitions intra ou interspécifiques (Krüger et al. 2019). Or, derrière les bateaux de pêche, la compétition est très forte avec un grand nombre d'oiseaux présents. Nous nous attendons donc à ce que les oiseaux timides (*shy*) subissent cette compétition et soient moins attirés ou restent moins longtemps derrière les bateaux que les oiseaux audacieux. Mais ces interactions liées à la fois à la personnalité et au sexe (les oiseaux timides sont plus souvent des femelles) compliquent notre étude. C'est pour cela qu'avec H. Weimerskirch et collaborateurs (en préparation) nous étudions actuellement plus précisément les effets combinés du sexe, de l'âge et de la personnalité sur les comportements des albatros et les expositions au risque de captures accidentelles qui en découlent.

La grande variabilité des résultats d'exposition au risque de captures accidentelles montre l'importance d'approfondir nos connaissances chez les oiseaux marins, du niveau de l'espèce jusqu'aux traits individuels comme le sexe, l'âge ou la personnalité et l'intérêt de croiser ces paramètres qui sont tous fortement interdépendants.

3.2. Selon les caractéristiques des bateaux

Nous venons de voir qu'un grand nombre de critères spécifiques aux oiseaux influencent leurs relations avec les bateaux et leur exposition au risque de captures accidentelles, mais les particularités des bateaux jouent également un rôle très important dans ce couple oiseaux-bateaux qui peut être si meurtrier.

Les bateaux de pêche ont différentes activités qui modifient la disponibilité de la nourriture pour les oiseaux et donc leur attractivité. Il a été montré que les fous de Bassan ont surtout tendance à passer en comportement de recherche de nourriture lorsque les bateaux sont en activité de pêche (Bodey et al. 2014). Chez les palangriers, ce sont les moments de filage de la palangre qui sont les plus meurtriers pour les oiseaux et c'est d'ailleurs pour cela que les mesures de mitigation visent cette période en imposant, entre autres, les filages de nuit (Waugh et al. 2008).

Parmi les palangriers, ce sont avant tout les pêcheries à la légine australe auxquelles les albatros sont exposés autour de leurs colonies (Delord et al. 2005). Ces pêcheries qui ont lieu dans des zones de très fortes concentrations aviaires (îles subantarctiques) attirent de très nombreux oiseaux qui, à leur tour, augmentent leur attractivité. C'est au contact de ces pêcheries à la légine que les grands albatros de l'océan Indien vont passer la majorité de leur temps d'exposition aux bateaux (chapitres 2 et 3). Heureusement, ces pêcheries sont majoritairement légales, déclarées et surveillées, car opérant dans les ZEE. Les mesures de mitigation mises en place sur ces pêcheries déclarées ont conduit à une absence totale de mortalité d'albatros ces dernières années dans les ZEE françaises (Weimerskirch et al. 2018a). Ces pêcheries n'étant quasiment pas meurtrières, nous pouvons nous poser la question de l'accoutumance des populations d'oiseaux à ces pêcheries. En effet, c'est la population d'albatros hurleur de Kerguelen (chapitre 3) qui passe le plus de temps au contact des pêcheries, car elle reste sur le plateau océanique où les palangriers à la légine sont omniprésents. Il est donc possible de penser qu'aucune sélection des individus trop téméraires pour s'approcher des bateaux ne s'effectue et que cette population est habituée à aller régulièrement tenter de se nourrir derrière ces bateaux.

L'autre grande pêcherie palangrière opérant dans le sud de l'océan Indien est la pêcherie aux thons et c'est, hélas, aujourd'hui la plus meurtrière pour les albatros et les oiseaux marins de la région. Brother a montré en 1991 que 44 000 albatros mourraient tous les ans dans les palangriers Japonais au thon (Brothers 1991). Les techniques de pêche sans mesure de mitigation, les temps de filage monstrueusement plus importants dus à la taille des palangres et les filages et virages réalisés en journée, font de ces pêcheries des fléaux pour les oiseaux marins et particulièrement pour les albatros (Votier et al. 2004, Anderson et al. 2011). Fort heureusement, les albatros sont nettement moins au contact de cette pêcherie pendant la période d'incubation, car ils passent plus de temps dans les ZEE des îles où les pêcheries de thons sont absentes. Le risque de captures accidentelles étant fortement différencié entre ces deux types de pêcheries et nettement plus faible pour la légine (Waugh et al. 2008), il est très intéressant d'utiliser les données de localisation des pêcheries rencontrées pour affiner l'estimation du risque réel de captures accidentelles.

Une autre caractéristique importante de ces pêcheries est leur déclaration officielle. En effet, si le risque de captures accidentelles est faible dans les pêcheries à la légine déclarées, qu'en est-il des non déclarées, où règne un flou total, en ce qui concerne les estimations actuelles de captures accidentelles ? Les suivis des bateaux peuvent maintenant se faire par satellite grâce aux signaux AIS qu'ils émettent (McCauley et al. 2016). Cependant ces signaux AIS pouvant être facilement désactivés, il a été montré que les estimations des captures réelles de poisson sont beaucoup plus importantes que celles reportées et ce, notamment à cause des pêcheries illégales, par définition clandestines (Pauly & Zeller 2016). Les pêcheries non déclarées sont des fléaux dont il très difficile d'évaluer l'impact réel sur les oiseaux marins. Aucune mesure de mitigation n'est évidemment appliquée et il a même été montré que ces pêcheries illégales avaient une part plus importante que les changements climatiques dans les chutes des populations d'albatros (Michael et al. 2017). Il existe depuis peu des moyens détournés de quantifier ces pêcheries illégales qui, à chaque fois, montrent des chiffres hallucinants et jamais envisagés jusqu'alors. Notre étude (Annexe 1 - Weimerskirch et al., 2020) montre que 37% de bateaux rencontrés par les oiseaux ne sont pas déclarés et une autre étude récente qui combine différentes technologies satellitaires a repéré plus de 900 bateaux chinois illégaux dans les eaux de la Corée du Nord en 2017 (Park et al. 2020). Nous avons par ailleurs constaté que les diverses populations d'albatros n'étaient pas soumises aux mêmes proportions de bateaux non déclarés les unes par rapport aux autres. Ainsi la population de Crozet contacte près de deux fois plus de bateaux non déclarés que celle de Kerguelen (chapitre 3) mais nous n'avons pas encore constaté d'effet direct sur ces populations. Si nous n'avons pas trouvé de différences significatives entre les deux populations du fait des très grandes variations entre individus, malgré tout nous remarquons que les temps passés par les albatros de Crozet derrière les bateaux non déclarés sont supérieurs à ceux passés derrière les bateaux déclarés. A l'avenir, la pérennisation de cet état de fait pourrait constituer un problème en augmentant le risque de captures accidentelles pour les populations de Crozet.

Il n’y a pas que des bateaux de pêche dans le paysage des albatros. Dans la partie nord de la zone d’étude, de nombreux bateaux de « transport » (cargo, tanker…) sont présents et rencontrés par les oiseaux. Grâce aux données AIS nous pouvons connaître le type des bateaux rencontrés par les oiseaux et, dans le chapitre 3 nous avons constaté que les albatros passent moins de temps et sont moins attirés par les bateaux de transport que par les bateaux de pêche. Ce résultat est logique et s’il n’augmente pas le risque de captures accidentelles, la présence de très nombreux types de bateaux autres que ceux de pêche peut avoir un important effet de dilution. Les oiseaux, n’étant à priori pas capables de différencier les divers types de bateaux à distance, vont s’approcher de tous les types de bateaux qu’ils repèrent (Collet et al. 2017b) puis, après un certain temps, repartir lorsqu’ils constatent que ce n’est pas un bateau de pêche et qu’il n’y a pas d’accès à de la nourriture. Ce phénomène, s’il est reporté à très large échelle pour une très grande flotte de bateaux de transport, peut clairement diminuer le risque de captures accidentelles, car en visitant les autres bateaux, les oiseaux passent immanquablement moins de temps au contact des bateaux de pêche. Ce phénomène de dilution peut se retrouver au sein des bateaux de pêche eux-mêmes. Par exemple, il a été constaté qu’en Méditerranée la diminution du nombre de chalutiers entraine une plus grande attirance des puffins de Scopoli derrière les palangriers et augmente donc leur risque de captures accidentelles (Soriano-Redondo et al. 2016). Ce phénomène de dilution n’est probablement pas négligeable sur nos albatros. En effet, au-dessus de 40° sud, zones des pêcheries au thon et de présence de bateaux de transport, les grands albatros rencontrent majoritairement des bateaux de transport plutôt que des bateaux de pêche (Fig. 36) et diluent ainsi leur risque de captures accidentelles.

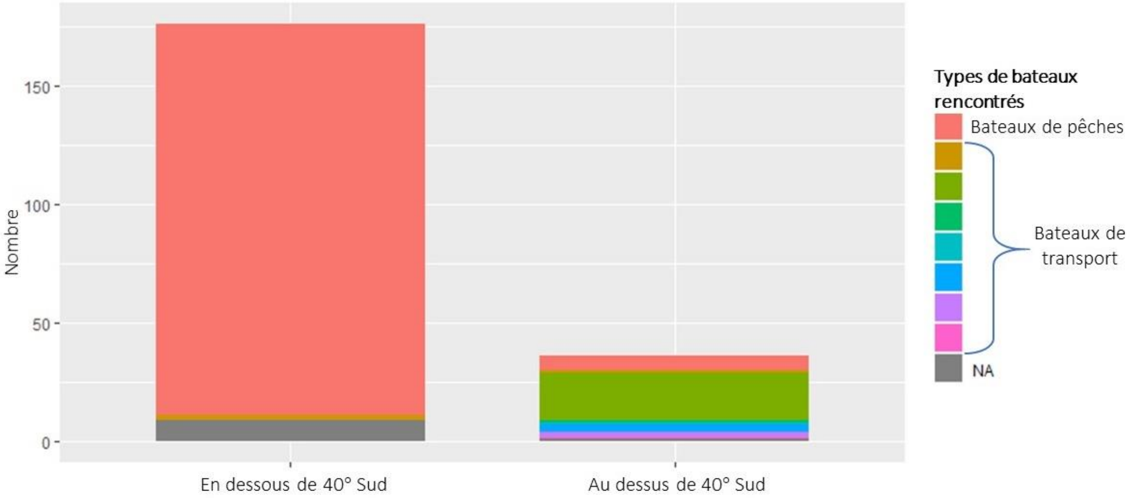

Figure 36 : Types de bateaux rencontrés à moins de 5 km par les albatros en dessous de 40° Sud (zone à pêcheries à la légine) et au-dessus de 40° Sud (zone à pêcheries aux thons et à grande présence de bateaux de transport).

La connaissance des oiseaux, de l'espèce aux traits individuels, est un enjeu majeur de l'évaluation des captures accidentelles, mais dans ces relations entre oiseaux marins et bateaux, bien connaitre les caractéristiques des flottes de bateaux soumises aux oiseaux est aussi essentiel. En plus de leur répartition, de leur nombre et de leur type, leurs pratiques et leur légalité sont de bons indicateurs du risque encouru par les oiseaux marins.

3.3. L'influence des rejets

Il est naturel de penser que les rejets ont une forte influence sur les interactions entre les pêcheries et les oiseaux marins. En effet, c'est très certainement pour ces rejets que les oiseaux marins vont chercher à rentrer en contact avec les bateaux et très tôt, il a été observé visuellement que la présence de ces rejets augmentait le nombre d'oiseaux qui suivaient les bateaux (Wahl & Heinemann 1979). Dans le chapitre 3, nous avons clairement montré que les rejets attiraient fortement les oiseaux, et ce, quel que soit la population ou le sexe. Quand il y a un rejet, quoique les albatros aient l'habitude de faire vis-à-vis des bateaux, ils vont aller voir ce rejet et tenter de s'y nourrir. Des études ont montré le problème qu'entraine cet apport de nourriture de moins bonne qualité issue des rejets (« junk food hypothesis » - Gremillet et al., 2008; Österblom, Olsson, Blenckner, & Furness, 2008), mais cette hypothèse n'est peut-être pas applicable aux grands albatros. La qualité de la nourriture est très importante pour des espèces avec de faibles capacités de stockage de nourriture et des comportements de recherche alimentaire à forte dépense énergétique (Le Bot et al. 2019), mais ce n'est pas le cas des albatros. De plus, les rejets de pêche tels que des morceaux de légine, raie, ou grenadier sont issus de poissons gras à forte valeur énergétique comparés aux calmars qui composent l'alimentation habituelle des albatros. L'influence des rejets est très dépendante de la réglementation en vigueur qui, actuellement, cherche à les faire disparaitre dans les pêcheries à la légine des TAAF. Des études ont montré que, même si les rejets pouvaient constituer une partie importante du régime alimentaire d'une population (comme c'est le cas pour les albatros (Bugoni et al. 2010)), l'interdiction des rejets, en Islande par exemple, provoque un désintérêt des fous pour les bateaux de pêche (Clark et al. 2020). De même, le traitement des rejets peut nettement modifier leur attractivité sur les oiseaux marins : les oiseaux sont moins attirés par les rejets broyés que par les morceaux entiers (Pierre et al. 2012). L'une des solutions envisagées serait de réduire les rejets par traitement ou suppression, mais quelles seraient alors les conséquences pour les oiseaux ? Actuellement, les bateaux déclarés dans les ZEE des TAAF ne sont pas autorisés à relarguer les rejets au moment de la mise à l'eau de la ligne. Idéalement les rejets devraient être stockés à bord et relargués lorsque les navires sortent des zones de pêche, cependant la taille des bateaux ne permettant pas de stocker ces rejets, ils sont alors relâchés, théoriquement, en dehors des périodes de pêche. D'un autre côté, ces rejets font maintenant partie du paysage alimentaire des espèces marines charognardes et leur suppression pourrait avoir des conséquences négatives sur la quantité de nourriture disponible engendrant des reports des prédateurs vers des espèces proies avec des conséquences importantes sur ces populations comme cela a été montré en Mer du Nord (Votier et al. 2004, Bicknell et al. 2013).

4. Un piège écologique ?

L'albatros est un « central place forager », qui est contraint de revenir à son nid tout en ayant effectué un trajet alimentaire assez productif pour lui permettre de jeûner le temps du voyage alimentaire de son partenaire (Weimerskirch et al., 1985). De ce fait, obtenir de la nourriture lors de ses voyages est nécessaire et la présence de bateaux de pêche sur les zones de nourrissage des albatros offre cette possibilité. Dans l'ensemble nous constatons que certains individus retournent plus facilement vers des bateaux que d'autres, mais sans pour autant ne dépendre que d'eux. Ce lien représente quand même un certain risque de piège écologique qui peut être défini comme une modification rapide et anthropique d'un environnent conduisant à l'utilisation d'une niche de mauvaise qualité et à ne pas pouvoir la quitter malgré un risque d'extinction (Gates & Gysel 1978). Ce risque peut tout à fait s'appliquer aux albatros. Il est même possible que ce soit déjà le cas et que les chutes drastiques des populations dues aux captures accidentelles avant les années 2000 (Delord et al. 2005) aient contre-sélectionné les individus les plus attirés par les bateaux très probablement par mortalité directe. Parallèlement, ce piège écologique comprend d'autres menaces moins directes. Si l'hypothèse de la « Junk food » mentionnée précédemment pourrait entrainer le déclin de la fitness des populations d'albatros, l'impossibilité de se nourrir derrière les bateaux pourrait également devenir une menace. Les albatros sont clairement attirés par les bateaux pour se nourrir, mais le peuvent-ils vraiment et dans quelles conditions ? Ils n'auront pas accès à la nourriture si ce n'est pas un bateau de pêche ou si les mesures de mitigation sont scrupuleusement respectées ou encore si les compétitions intra et interspécifiques sont trop importantes pour les plus timides, les plus jeunes ou les plus faibles.

Tout ce temps perdu au contact des bateaux est peut-être le réel piège écologique. Notons que, malgré tout, cette espèce est relativement peu contrainte par les bateaux dans ses trajets alimentaires (de 2 à 51 jours en incubation) allant de 12% de temps passé derrière les bateaux lors d'un trajet (pour Kerguelen) à 1% pour Marion et qu'elle peut vraisemblablement compenser cette possible perte de temps. C'est certainement pourquoi nous n'avons pas trouvé d'effet direct entre le temps passé derrière les bateaux et le gain de masse, le succès reproducteur ou même avec les tendances populationnelles générales (Marion, Crozet, Kerguelen et Amsterdam) qui ne diminuent pas (chapitre 2 et 3).

Par contre, c'est sur des espèces beaucoup plus contraintes, mais tout autant attirées par les bateaux et dont les chutes de populations sont importantes (Weimerskirch et al., 2018) telles que les albatros de Carter (*Thalassarche carteri*), les albatros bruns (*Phoebetria fusca*) ou les albatros fuligineux (*Phoebetria palpebrata*) que pourrait se refermer le réel piège écologique, et ce, sans pour autant observer de mortalité directe.

5. Application à la conservation

Les captures accidentelles sont une cause majeure de la chute des populations d'oiseaux marins (Paleczny et al. 2015) et, combinées aux effets du climat, elles affectent particulièrement les albatros (Pardo et al. 2017). C'est pourquoi lutter contre ces captures accidentelles est un enjeu majeur de conservation pour les années à venir afin de protéger, non seulement les albatros, mais aussi l'ensemble de la mégafaune marine qui subit de plein fouet ce fléau. Une meilleure estimation des proportions de pêcheries non déclarées sera un réel bénéfice en matière de conservation. Actuellement, les estimations des captures accidentelles par les palangriers déclarés dans les zones non soumises aux mesures de mitigation strictes sont fortement sous-évaluées (Zhou et al. 2019) et les données reportées par les observateurs de pêches par le biais des détachements des oiseaux morts dans les lignes le sont également (les comptages ne sont faits qu'au virage alors que les pertes se réalisent principalement au filage) (Brothers et al. 2010). De manière pessimiste, nous pourrions considérer que la chute des populations d'oiseaux dans le monde ces dernières années entrainerait une diminution de la compétition et des interactions des oiseaux avec les pêcheries, mais ce n'est pas le cas, car la compétition et l’exposition au risque sont toujours aussi présentes (Grémillet et al. 2018), ce qui suggère que les populations augmentent leurs interactions avec les bateaux. La surpêche est également de plus en plus importante avec un nombre de bateaux grandissant, des bateaux usines toujours plus énormes et des réglementations très difficiles à mettre en place du fait de l’obstruction à des accords internationaux par certaines grandes puissances diplomatiques. On peut pourtant garder l’espoir que les nombreuses études qui paraissent sur le sujet et que les outils, toujours plus performants, développés pour évaluer ce risque de surpêche conduisent à une prise de conscience internationale et à la mise en place de mesures efficaces de protection. Sachant qu’il existe actuellement une volonté de nombreux états d’augmenter leurs aires protégées, quoi de plus simple et de plus efficace que de protéger des aires marines de milliers de km² où il n’y a que peu d’enjeux humains. En outre, les collaborations internationales entre les pays possédant des ZEE subantarctiques montrent qu’il y a malgré tout des améliorations constantes des mesures de mitigation (Melvin et al. 2004) avec la construction de nouveaux types de bateau possédant une mise à l’eau des lignes située au centre et la mise en place de collaborations sur la surveillance et les méthodes de surveillance contre les pêcheries illégales. À plus large échelle, la mise en place de recommandation dans les eaux internationales et l’utilisation des accords tels que la CCAMLR pour tenter de faire respecter ces mesures, sont de grands enjeux diplomatiques qui, hélas, ne sont plus du ressort des scientifiques une fois que les preuves sont sur la table.

Dans cette thèse je me suis appliqué à développer des méthodes qui permettent cette estimation du risque de captures accidentelles ou cette surveillance des pêches. Nous avons travaillé avec plusieurs autorités de surveillance des pêches de différents pays et nous avons montré que ces outils étaient fonctionnels, disponibles et utilisables à plus large échelle. L’utilisation de ces nouvelles balises peut facilement être étendue à d’autres espèces d’oiseaux marins ou même à toute une autre mégafaune sensible aux présences des bateaux dans un but de surveillance, mais aussi de protection et de connaissances.

J’ai souligné dans cette thèse l’importance des connaissances fondamentale des espèces, mais aussi des populations et même des individus qui ne réagissent pas de la même manière au risque de captures accidentelles. Il est donc très important de continuer à développer cette recherche de savoir avant d’appliquer des mesures qui peuvent parfois être prises à « l’emporte-pièce » par manque de données et de connaissances.

6. Conclusion et perspectives

L’aspect novateur de cette thèse a été de se poser des questions d’écologie fondamentale et appliquée et de pouvoir y répondre grâce au développement de nouvelles technologies. Elle est issue d’un long processus de 5 années de tâtonnements aussi bien pour l’utilisation et le développement de nouveaux prototypes de balises que pour l’exploitation de ces données uniques. Cette thèse propose non seulement de mieux comprendre les comportements naturels des albatros et ceux associés aux bateaux, mais apporte aussi de nouvelles méthodes (matériel et analyses) pour évaluer et lutter contre le risque de captures accidentelles.

Il y a toujours la possibilité et le souhait d’améliorer les balises. À ce stade, tout dépend des compétences du fabricant, de l’argent et du temps disponible, et évidemment de l’émergence de nouvelles idées. Un point majeur à améliorer est de pouvoir augmenter la durée des enregistrements. Sur les adultes reproducteurs les résultats sont satisfaisants, car les trajets sont relativement courts (5-25 jours), mais actuellement pour les juvéniles, immatures et adultes non reproducteurs, nos balises durent au maximum 3 mois à cause de la tenue de la batterie ou du type d’attache. Le futur défi est d’obtenir des enregistrements plus longs en maintenant un poids acceptable afin notamment de pouvoir équiper les albatros sur l’ensemble de leur cycle. Il est aussi difficile de trouver des systèmes d’attaches fiables à long terme pour des espèces aux capacités de vol si complexes, et un équipement sur une plus longue période nécessite forcément de passer par un autre moyen que l’accroche aux plumes du dos. De nouveaux types de harnais (Mallory & Gilbert 2008) pourraient être envisagés comme sur les albatros à queue courte (Orben et al. 2018).

Il aurait été également idéal d’avoir eu la possibilité d’augmenter la période d’écoute de radar pour ne pas manquer des détections de bateaux et d’avoir une distance de détection des bateaux (de 30 km à 0 m) pour évaluer les réelles attractions des oiseaux équipés aux bateaux détectés, y compris ceux non déclarés. La miniaturisation permettrait aussi d’équiper un spectre beaucoup plus large d’espèces, notamment certaines plus contraintes en termes de recherche alimentaire et qui interagissent plus avec les bateaux. L’utilisation sur des espèces plongeuses, d’oiseaux marins ou d’autre mégafaune marine, nécessite aussi de développer des balises résistantes aux pressions et pouvant détecter les ondes radar sous la surface de l’eau.

Le jeu de données issues de cette thèse et du programme « Ocean sentinel » est unique et énorme avec plus de 2 millions de positions d'oiseaux et 250 millions de positions AIS et les possibilités d'études et de questions sont encore nombreuses.

Maintenant que les durées et les interactions entre les albatros et les bateaux sont mieux connues, nous ne savons toujours pas s'ils se nourrissent réellement au contact de ces bateaux. L'utilisation de sondes stomacales détectant l'ingestion de nourriture avait permis de détecter avec succès le moment précis et la quantité de nourriture ingérée dans les années 1990 et 2000 (Weimerskirch & Wilson 1992, Weimerskirch et al. 2007), mais nous ne disposions pas d'information sur la présence des navires à proximité. Lors de ma première campagne de terrain sur Crozet (2017) nous avions tenté de déployer de nouvelles générations de sondes stomacales de température afin de savoir si les oiseaux se nourrissaient réellement derrière les bateaux, mais hélas sans succès, car les sondes étaient régurgitées trop rapidement. Cette piste pourrait être envisagée afin de connaitre véritablement les prises de proies à l'arrière des bateaux.

Il serait aussi intéressant d'évaluer à plus fine échelle comment le temps passé derrière les bateaux a une influence sur le succès reproducteur et le gain de masse et pourquoi certains individus ont l'air de se spécialiser sans pour autant se nourrir uniquement derrière les bateaux. D'autre part, d'un point de vue évolutif, les albatros ont changé de comportement pour, de nos jours, interagir avec les bateaux. Mais comment ces interactions se sont-elles mises en place ? Les jeunes albatros apprennent les méthodes de recherche alimentaire sans l'aide des adultes et l'étude de l'ontogénie des relations des jeunes avec les bateaux, des immatures et des adultes est une bonne piste de compréhension de ce phénomène. Ce sont actuellement les études que nous menons avec H. Weimerskirch et collaborateurs (en préparation) qui ont tendance à montrer qu'il existe une accoutumance des jeunes albatros aux bateaux lorsqu'ils vieillissent.

À travers nos résultats, l'effet individu ressort très fortement avec des comportements propres à chaque oiseau et principalement chez des espèces longévives où l'expérience des oiseaux entraine une grande variabilité de réponse notamment aux pêcheries (Votier et al. 2010). Pour cela des études à l'échelle de l'individu ou même de la localisation seraient pertinentes. En effet, il peut ressortir des effets à très fine échelle spatiale et temporelle. Par exemple, nous avons considéré la détection visuelle à 30 km, mais n'est-il pas possible que ce soit plus loin encore, grâce à la présence d'autres oiseaux marins qui peuvent les attirer ? Cette distance est aussi régulièrement plus faible, avec les conditions météorologiques qui sont souvent mauvaises et changeantes dans ces mers australes. Tester l'effet des précipitations, ou du vent sur l'attraction serait très intéressant et pourquoi pas, ainsi, proposer aux pêcheurs des fenêtres optimales de filage des palangres en fonction de l'activité des espèces susceptibles de subir des captures accidentelles.

Enfin l'étude de nouvelles espèces pourrait aussi être un enjeu majeur pour ces questions. Je suis actuellement en train de travailler avec l'équipe sud-africaine de P. Pistorius (avec F. Orgeret et S. Banda) sur les mêmes questions que j'ai abordées dans mon chapitre 2 et 3 mais, cette fois-ci, sur des espèces plus contraintes dans leur recherche alimentaire (avec des trajets moins longs, des proies plus ciblées et une nécessité plus forte d'optimiser leur gain de masse notamment dû à leur plus petite taille) que sont les puffins à menton blanc et les albatros bruns. Peu de choses sont connues sur les interactions entre ces espèces et les bateaux et, si l'effondrement de leurs populations est classiquement inféodé aux captures accidentelles, rien n'est encore prouvé et il est nécessaire de comprendre plus en détail l'attraction et l'exposition au risque de captures accidentelles de ces populations afin de mieux les protéger. De plus, comme je le mentionnais précédent, l'extension de ce projet et de ces méthodes est tout à fait possible à travers le monde. A posteriori, d'une part, si des trajets de géolocalisation existent avec une correspondance possible avec les AIS et en direct, d'autre part, avec l'utilisation des nouvelles balises développées. Une utilisation grande échelle serait très intéressante à la fois pour la surveillance des pêches, mais aussi pour la connaissance de chaque espèce ou population sensible, que ce soient des oiseaux marins ou toutes autres mégafaunes marines sensibles. Des collaborations et utilisations de ces balises ont déjà été réalisées en Nouvelle Zélande sur les albatros des Antipodes, à Hawaï sur les albatros de Laysan, en Afrique du Sud sur les fous du Cap, actuellement en Géorgie du Sud sur les albatros hurleurs et bientôt sur les albatros à sourcils noirs à Kerguelen. Ces initiatives qui se développent à partir du projet Ocean Sentinel devraient permettre dans l'avenir une meilleure connaissance et protection du milieu marin et la réalisation d'études multi spécifiques de grande ampleur sur les répartitions et les utilisations des pêcheries par les prédateurs supérieurs.

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Annexes

Annexe 1 : Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of non-declared fishing.

Weimerskirch H., Collet J., **Corbeau A.**, Pajot A., Hoarau F., Marteau C., Filippi D., Patrick S., 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of non-declared fishing. ***Proceedings of the National Academy of Sciences***, *117(6):3006-3014*

Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing

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Edited by Hugh P. Possingham, The Nature Conservancy, Sherwood, QLD, Australia, and approved December 28, 2019 (received for review September 9, 2019)

With threats to nature becoming increasingly prominent, in order for biodiversity levels to persist, there is a critical need to improve implementation of conservation measures. In the oceans, the surveillance of fisheries is complex and inadequate, such that quantifying and locating nondeclared and illegal fisheries is persistently problematic. Given that these activities dramatically impact oceanic ecosystems, through overexploitation of fish stocks and bycatch of threatened species, innovative ways to monitor the oceans are urgently required. Here, we describe a concept of "Ocean Sentinel" using animals equipped with state-of-the-art loggers which monitor fisheries in remote areas. Albatrosses fitted with loggers detecting and locating the presence of vessels and transmitting the information immediately to authorities allowed an estimation of the proportion of nondeclared fishing vessels operating in national and international waters of the Southern Ocean. We found that in international waters, more than one-third of vessels had no Automatic Identification System operating; in national Exclusive Economic Zones (EEZs), this proportion was lower on average, but variable according to EEZ. Ocean Sentinel was also able to provide unpreceded information on the attraction of seabirds to vessels, giving access to crucial information for risk-assessment plans of threatened species. Attraction differed between species, age, and vessel activity. Fishing vessels attracted more birds than other vessels, and juveniles both encountered fewer vessels and showed a lower attraction to vessels than adults. This study shows that the development of technologies offers the potential of implementing conservation policies by using wide-ranging seabirds to patrol oceans.

bio-logging | illegal fisheries | conservation | vessel attraction | seabird

The Anthropocene era is associated with increasing threats to nature and biodiversity (1), and, as a result, conservation research is becoming increasingly sophisticated, in an attempt to protect ecosystems (2). Today, conservation studies often focus on increasing the accuracy of information used to prioritize locations for conservation actions, e.g., delimitation of areas of conservation (3). Yet, it is increasingly recognized that the implementation of conservation measures is inadequate and a major hindrance in global conservation (4). There is a crucial need to improve the implementation of conservation research into practice and policy, beyond specific species or systems studied.

Compared to terrestrial habitats, the surveillance and implementation of conservation measures is considerably more complicated in marine systems. In particular, international oceanic waters and remote areas are particularly challenging for political and logistical reasons. Fisheries are operating worldwide over National Economic Exclusive Zones (EEZs) and international waters. They have a profound effect on ecosystems through overexploitation of fish stocks, the removal of key ecosystem components, and accidental capture of marine vertebrates (5). As a result, there is an urgent need for in-depth reforms to fisheries management to improve fish abundance while increasing food security (6). Today, basic knowledge about the distribution of fishing vessels is fundamental for the regulation of fishing activities, as well for the conservation of the oceans (7). Yet, information about fishing-vessel location is very difficult to obtain. It is eventually made available to authorities or international fisheries organizations through voluntary declaration using Vessel Monitoring Systems (VMSs) or indirectly through the use of Automatic Identification Systems (AISs) (8). The former is generally used only in EEZs; the latter should be used both in EEZs and international waters to avoid collisions and may be accessed through dedicated sites (https://www.marinetraffic.com). However, AISs are not used systematically and can be switched off from the vessel. In international waters, information on fishing effort and distribution may be completely lacking or made available by Regional Fisheries Management Organizations (RFMOs), such as tuna fisheries, but at a very coarse scale and in an aggregated form, making it impossible to have real-time or regular (e.g., daily) information. Recent efforts have been made to improve this, through the use of AISs, allowing visualization, tracking, and sharing of data on global fishing activity (https://globalfishingwatch.org) (9, 10). However, this information is limited, as it is complex to access in real time, and, furthermore, at any time, AISs can be switched off, which is likely to be particular common by illegal fisheries. Yet,

Significance

New technological approaches to improving remote surveillance of the oceans are necessary if we are to implement effective conservation. Of particular concern is locating nondeclared and illegal fisheries that dramatically impact oceanic ecosystems. Here, we demonstrate that animal-borne, satellite-relayed data loggers both detected and localized fishing vessels over large oceanic sectors. Attraction of albatrosses to fishing vessels differed according to species and age. We found high proportions of nondeclared fishing vessels operating in international waters, as well as in some remote national seas. Our results demonstrate the potential of using animals as Ocean Sentinels for operational conservation.

Author contributions: H.W. designed research; H.W., J.C., and A.C. performed research; J.C., A.C., A.P., F.H., C.M., D.F., and S.C.P. contributed new reagents/analytic tools; H.W., J.C., A.C., and A.P. analyzed data; and H.W. and S.C.P. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Data deposition: Tracking database and Radar detection events have been deposited in the online open access repository Figshare (https://figshare.com/s/2481d8e6cf4aff484ffe).

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1915499117/-/DCSupplemental.

information on the location of fishing vessels is critical since in many oceanic sectors, nondeclared and illegal fisheries are negatively affecting ecosystems through overexploitation and by catch of nontarget species (11, 12). Among these species, bycatch of albatrosses and petrels is very high, and these are among the most threatened bird species, with hundreds of thousands killed by longline fisheries every year (13). Thus, there is a need to obtain better information on seabirds–fishery interactions (14).

Estimates of the overlap between seabirds and fisheries activities outside EEZ are, at best, available at a large scale from RFMOs. It is in these international waters that information on seabird–fishery interactions are badly needed to estimate global bycatch risks (15, 16). At present, risk assessments are based on the assumption that the co-occurrence of seabirds and fisheries in a large-scale sector (generally 5° squares for tuna fisheries) leads to interactions and, therefore, mortality risks. This has so far not been documented, and, until today, the real degree of overlap can only be obtained by scaling down the analysis of interactions (17) by using high-resolution VMS data and seabird tracking data. However, VMS data do not exist in international waters, and for most fisheries operating in EEZs, VMSs are rarely fully available to researchers, especially in real time. Obtaining real interaction information requires having fine-scale information simultaneously on fisheries distribution and seabird movements, which is rarely the case, generally restricted to limited EEZ areas (18). More importantly, once interactions have been located, if an intervention from authority is required, there is a need for an immediate relay of information on these interactions.

Tracking of marine animals has been used widely to determine sites to protect (19), with the ultimate goal of improving conservation (20). In addition, during recent years, seabirds, marine mammals, and turtles, fitted with a variety of loggers, have been used worldwide as oceanic samplers through equipment with biologging sensors (21, 22). These loggers have the potential to transmit information instantaneously through satellites and make them available to agencies or researchers (23, 24). Recently, a new logger detecting radar emissions of vessels has been developed, providing locations of interactions between albatrosses and vessels over vast oceanic sectors (25). Building on this new platform, we have developed a concept of operational conservation based on loggers that will allow the immediate transmission of vessel location for improving surveillance and enforcement.

By using wide-ranging large seabirds that are attracted to boats, such as albatrosses, petrels, and gannets, we have developed the concept of an Ocean Sentinel (OS). OSs aim to provide more accurate information on the distribution of fisheries in any oceanic sector and to provide instantaneous information to authorities, international fisheries agreements, or researchers on the location of fishing boats. For a large-scale test of the concept, we have used albatrosses. Large albatrosses cover huge areas of the ocean surface (22 million km^2 with 50 individuals equipped) and are highly attracted to fishing vessels, which they can detect from up to 30 km away (26), making them particularly suitable patrollers of the oceans. The concept was tested between November 2018 and May 2019 in the Southern Indian Ocean, at Crozet, Kerguelen, and Amsterdam Islands, where valuable and extensive fisheries operate, both in EEZs and in international oceanic waters. Its aim was to provide information on fisheries distribution in oceanic sectors where monitoring information is currently not available. In the Southern Ocean, surveillance of the EEZs is extremely costly, and, thus, only occasional visits by Navy ships provide monitoring for these zones. Furthermore, in international waters, such surveillance is absent.

Here, we present the first results of a 6-mo large-scale test of the OS concept carried out in the southwestern Indian Ocean. The specific aims of this paper are 1) to test whether it is possible to use animals as platforms to make research operational, especially for large-scale surveillance; 2) to compare the efficiency of the concept to the other existing surveillance systems based on VMS, AIS satellite, and naval ship-based surveillance; 3) provide an estimate of the proportion of vessels illegally deactivating their AIS, by comparing the data made available by AIS to those provided by the bird-borne radar detectors; and 4) obtain more accurate information (occurrence and location) on interactions between fisheries and two threatened species, wandering and Amsterdam albatrosses, and test the assumption that co-occurrence of seabird and fisheries results in real interaction. We also provide an estimate of the real proportion of birds attending fishing boats after co-occurrence and how it differs between species and age classes.

Material and Methods

Loggers. Since all boats at sea use radar for safety and operational reasons, the ability to detect radar emissions from geolocating loggers provides accurate information on the location of boats. We have developed, with Sextant Technology, and tested between 2015 and 2017, a logger (XGPS) that provides the global positioning system (GPS) location of the fitted animal and simultaneously detects radar emissions (25). From this platform, we developed a logger that includes this radar detector, a GPS antenna, a processor, and memory, but with the addition of an Argos antenna for real-time data transmission. It is powered by a lithium rechargeable battery, which has a solar panel capable of recharging the device when on the bird. The GPS location can be programmed to record GPS fixes at intervals of 1 s to 1 h. The Argos antenna sends this information at a programmable interval. Two models were developed: Centurion and XArgos.

The Centurion logger weighs 65 g, measures 109 × 30 × 22 mm (*SI Appendix*, Fig. S1), and records all of the information on board but sends instantaneously through Argos the location of the radar detection as soon as a vessel is detected through its radar emission. Loggers were deployed on actively breeding birds, which alternate foraging trips at sea with periods on the nest, making recovery simple. For our large-scale field-deployment test, we programmed Centurions so that the GPS recorded fixes every 2 min and the radar detector recorded the presence of radar emissions every 5 min, for a duration of 1 min. If the logger received a radar signal, the radar information (location and number of radar detections) was sent in real time through the Argos system and afterward continuously during 12 h. When no radar signals had been detected after 12 h, data were stored on the device but not transmitted through Argos. The complete information, including GPS locations every 2 min and radar detections, was then downloaded from the logger when the bird had returned to its nest. The logger must be recovered to download the entire information on the track of the bird.

XArgos loggers (55 g, 109 × 30 × 19 mm) recorded and sent the location of the bird and the summary of the radar detector scanning (scan for radar emissions recorded during 1.5 min every 15 min) every hour through Argos. They were deployed on juveniles leaving the colony, where they remained at sea for several years, without returning to land. In addition, they were deployed on immature birds, defined as birds that return to the colony for pair formation but have yet to commence breeding; postbreeding birds, which are adult birds that have successfully finished breeding; or failed breeders, which are adult birds that have attempted to breed but failed to fledge a chick. All birds were captured on the colony, but as no birds were actively breeding at deployment, the chance of logger recovery was very low, making these loggers optimal.

Deployments. A total of 169 individuals of wandering (*Diomedea exulans*) and Amsterdam (*Diomedea amsterdamensis*) albatrosses were equipped with Centurion (breeding adults) and XArgos loggers between November 2018 and March 2019 from Crozet, Kerguelen, and Amsterdam (Table 1).

The loggers were attached to the back feathers by using special tape (Tesa). For short-term deployment (Centurion loggers on breeding adults), the logger was removed after the bird returned on its nest after one foraging trip. For long-term deployment (XArgos loggers on juveniles, immature, and postbreeding adults), the attachment was reinforced by Loctite glue on the contacts between the logger and the tape. XArgos detached from birds through the loss of feathers during the molting process after 3 to 6 mo. The loggers represented 0.46 to 0.93% of the bird body weight (wandering albatrosses weigh between 7 and 12 kg and Amsterdam albatross between 6 and 10 kg), i.e., below the recommended maximum 3% of the bird's body mass for loggers attached (27).

Table 1. Numbers of individual birds equipped with Centurion loggers at Crozet, Kerguelen, and Amsterdam and percentage of time spent in international waters and in the French EEZ around Crozet, Kerguelen, and Amsterdam

	Number of birds equipped with Centurion loggers*				% time in international waters	% in French EEZ
	Crozet	Kerguelen	Amsterdam	Total		
Juveniles (XArgos)	16 (11, 8.3%)	23 (18, 27.7%)	10 (8, 37.5%)	49 (38, 23.7%)	61.7 ± 21.0	30.8 ± 23.7
Breeding adults (Centurion) – number of deployments	50 (45, 63.3%)	30 (24, 75.9%)	10 (8, 40%)	90 (77, 64.7%)	40.1 ± 35.2	55.1 ± 37.1
Postbreeding adults (XArgos)	8 (6, 70%)	2 (2, 0%)		10 (8, 53.8%)	61.7 ± 33.4	28.6 ± 33.8
Immature (XArgos)	12 (12, 81.8%)	8 (8, 50%)		20 (20, 68.4%)	33.5 ± 38.5	62.2 ± 41.0

*Number with enough location and percentage of individuals with radar detection are in parentheses.

Vessel Information and AIS Data. AIS data were made available through the Themis interface (Collecte Localisation Satellites [CLS] Toulouse) for the sector 20 to 70°S, 10 to 180°E. Through this system, all AIS emissions in the sector were recorded, and the information was downloaded every day from the CLS server and stored in a database. During the study period, more than 100 million AIS locations were obtained. For each AIS location, the following information was available: date, latitude, longitude, ship name, identity of International Marine Organization (IMO) number of the vessel, nationality, call sign, speed, heading, type of vessel (fishing, tanker, cargo, pleasure, etc.), and activity. The densities of AIS were highest along continents, and the distribution of AIS from fishing boats varied throughout the study period (Fig. 1).

Data Access and Accessibility. The information sent by the Centurion/XArgos loggers were received by the Argos satellites and made available within minutes through the Argos website. Every 10 min, the data were automatically downloaded, treated, and made available through a dedicated web page of the Terres Australes Françaises National Reserve. Access to this site was given to the researchers, the Terres Australes et Antarctiques Françaises (TAAF) administration, and to Regional Operational Monitoring and Rescue Center based on Réunion Island (CROSS), which controls the movements of boats in the Western Indian Ocean. When a boat was detected by a bird, the location appeared immediately on the interface (*SI Appendix*, Fig. S2).

During the study period, the OS website was continuously consulted and regularly verified by the TAAF administration and the CROSS Control Centre. All detections of vessels were compared by the CROSS with the AIS data available, as well as with the VMS data from the fishery operating in the Crozet, Kerguelen, and Amsterdam EEZs. Thus, the system allowed an alert to any Navy patrol vessels present in the EEZ for a control in case of a non-declared boat detected within the EEZ (Fig. 2).

Data Processing and Analyses. All information received through Argos was filtered based on a cyclic redundancy check to remove improperly transmitted locations with failures. We then applied a speed filter of 150 km·h^{-1} to remove all implausible locations of bird movements. These data were then made available on the website. Data downloaded from Centurion loggers after birds were recovered on the nest were similarly filtered, and all data filtered were then stored in a database.

All bird data were then merged with AIS data so that to each bird location was associated to AIS information of any vessel occurring within 5 km [considered as the distance of a bird nearby boat and attending it, and corresponding to the range of radar detection for the logger (25)] and within 30 km [the maximum distance of detection of a boat by an albatross, considered as an encounter (26)]. To determine bird–boat distance and time spent attending and in encounter, we used the linearly interpolated AIS location the closest in time from the bird location. Birds attracted to fishing boats come close and stay for at least a couple of hours (28), so that we are confident that a series of consecutive boat locations recorded within proximity of a bird are not due to inaccurate spatiotemporal matching. All series (at least two successive) radar detections associated to GPS locations without gaps of more than 2 h were grouped into a radar event. A radar event was considered as an association with a boat.

Then, the database was processed to associate to each bird location, each radar event, attending (AIS within 5 km), and encountering (AIS within 30 km) locations the following parameters: bathymetry, international or EEZ waters, and all information on the associated AIS boat (IMO number or, ship name, activity, and nationality).

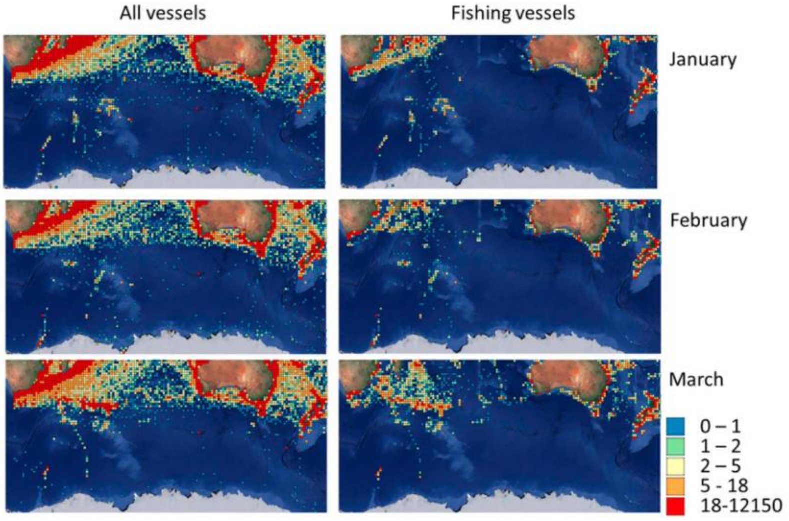

Fig. 1. Distribution of AIS locations (for all vessels [*Left*] and fishing vessels only [*Right*]) in the study sector (south Indian Ocean between Africa and New Zealand) recorded in January, February, and March 2019. Shown is the number of vessels over 4 d randomly selected every week through each month, for squares of 125 km.

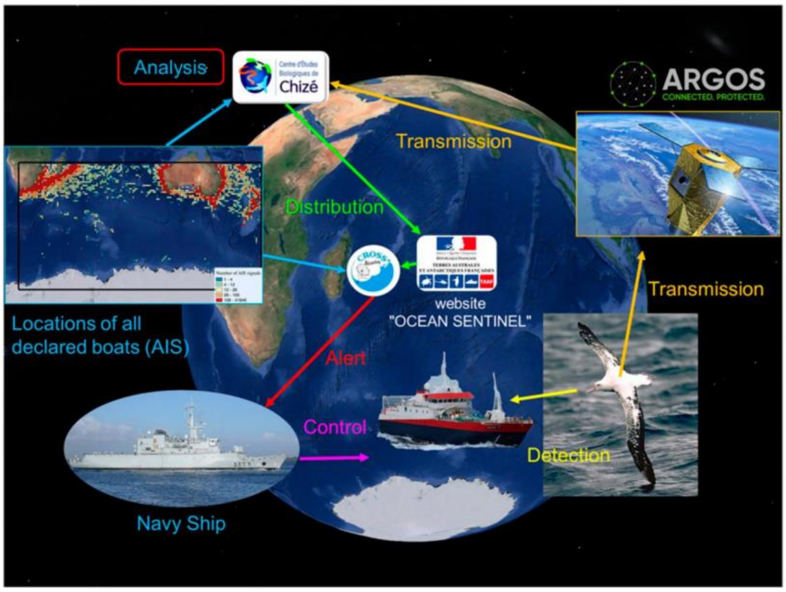

Fig. 2. Schematization of OS concept: detection by Centurion loggers fitted on foraging albatross, immediate transmission by Argos system, analysis of data, provision of data on the TAAF/OS website, comparison with VMS and AIS data, and alert in case of detection of undeclared activity, with potential control by Navy ship.

From the database, we calculated, for each individual bird, the number of vessels within 100 km of each bird location, the number encountered (within 30 km), and the number attended (within 5 km or with a radar detection). From this, we calculated first the proportion of vessels within 100 km that were encountered and attended, and then, from the number of vessels encountered, we estimated the proportion of these vessels that were attended. We also calculated for all of the encounters and attendance the proportion of all vessels that were fishing versus other types of vessels.

All data processing was performed under the R environment. Statistical analyses were performed under Statistica (Version 12). Data have been made available through the online open-access repository Figshare (https://figshare.com/s/2481d8e6cf4aff484ffe) (29).

Results

Coverage of OSs. Between the first of December 2018 and the first of June 2019, a total of 632,333 GPS locations of albatrosses, together with 5,108 radar detections, were received from Argos or downloaded from Centurion loggers. The 5,108 radar detections represented interactions with 353 different boats, considered as boat events. Adult and immature birds had a higher proportion of vessels than juveniles (Table 1). The simultaneous deployment of these loggers gave coverage of a wide area of more than 47 million km^2 (Fig. 3).

Radar detections were found throughout the albatrosses' range (Fig. 3), but with high densities within the EEZs on the edge of the Kerguelen–Heard plateau (Fig. 4) and Crozet–Del Cano plateau (Fig. 3). Proportion of time spent in international waters varied according to bird breeding status ($F_{3,133} = 5.1$, $P = 0.0049$), with juveniles and nonbreeding adults spending more time in international waters than breeding adults and immatures (Table 1). The proportion of trips spent in the French EEZ

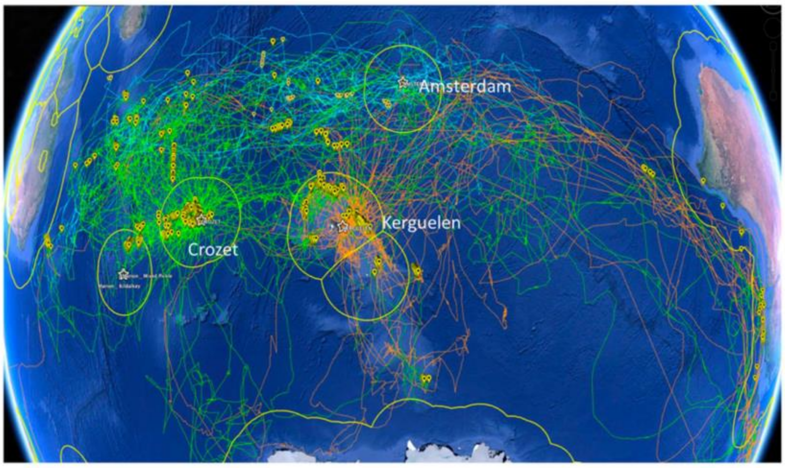

Fig. 3. Southern Indian Ocean with the tracks of Crozet wandering albatrosses (green), Kerguelen wandering albatrosses (orange), and Amsterdam albatrosses (blue). Radar detections are in yellow. EEZ limits are in the yellow line.

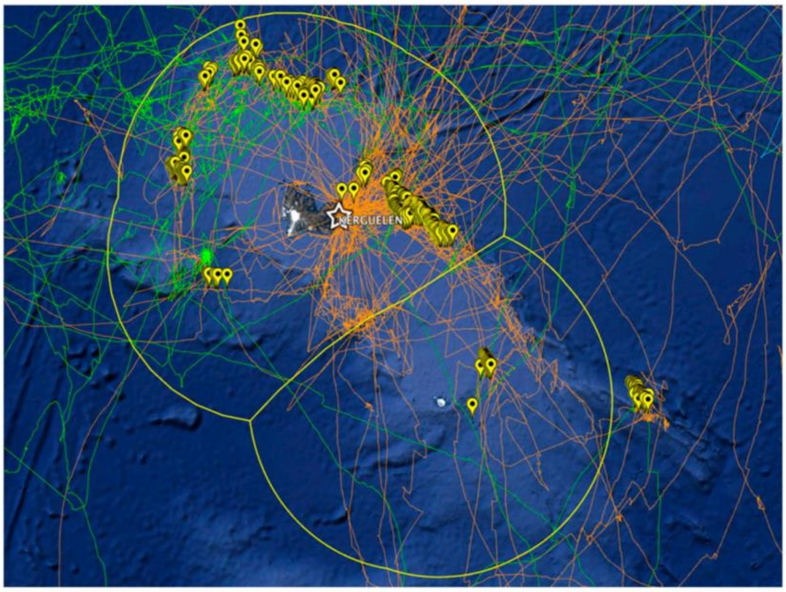

Fig. 4. Tracks of wandering albatrosses (as in Fig. 3) and location of radar detections (yellow and black points) in the sector of the Kerguelen–Heard plateau. Star indicates location of the colony. EEZ limits are in the yellow line.

differed between stages as well, with adults spending more time in the EEZ than juveniles ($F_{3,133} = 5.8$, $P = 0.0024$) (Table 1).

For Centurion loggers, fitted on breeding adults, the transmission of radar detection through Argos allowed access to the location of boats within 0.2 to 2 h of the first contact between a bird and a vessel, and this information was accessible immediately through the OS website.

Comparison with AIS. Among the 353 detections of vessels, 71.8% had a corresponding AIS signal, but 28.2% had no AIS signal within 30 km. The situation differed between EEZs and international waters. In EEZs, 74.2% of radar events had a corresponding AIS signal within 30 km; i.e., 25.8% of boats detected in EEZ had no associated AIS identification. In international waters, this percentage increased to 36.9% (the difference between EEZ and international waters was significant; Fisher exact test, $P = 0.042$). The percentage of radar-detection events without AIS differed between EEZs ($\chi^2_5 = 105.2$, $P < 0.001$) (Table 2).

For the French Crozet–Kerguelen EEZs, most of the radar detections with AIS corresponded to fishing vessels from the Réunion-based French fishing fleet. For the Crozet and Kerguelen EEZ, most of the radar detection events without AIS corresponded to the detections of surveillance ship from the French Navy (no AIS) and to the detection of declared fishing boats that had their AIS momentarily switched off but were recognized from their VMS position by CROSS. For the Amsterdam EEZ, half of the radar detections were nondeclared ships. On the border of the EEZ, several vessels were detected in operation, with AIS irregularly on (e.g., Fig. 4). This was a Spanish vessel and several Chinese long-liners fishing at the edge of the Kerguelen and Crozet EEZs.

In international waters, short encounters corresponded to encounters with vessels transiting in the range zone of albatrosses, with functioning AIS. This was particularly the case for transport ships in the high-density zone of vessels with AIS southeast of South Africa (Fig. 1). For long encounters with vessels (several hours of radar detections), half occurred with Asiatic long-liners, but half were not associated with an AIS signal, but occurred in the zone of high densities of Asiatic fishing boats operating, suggesting that within the fleets, a significant proportion of vessels had no AIS working.

We found that 77.4% of radar-detection events occurred over shelves and shelf edges, with 99 events (28.1%) being not associated with an AIS within 5 km from the bird (Fig. 5). Over oceanic waters, 39.7% of events had no AIS. We found that 28.2% of radar detection had no AIS information on the type of ship within 30 km (either no AIS at all or no AIS information on the ship type). We found that 83.3% of ships with radar detection and an AIS signal were fishing vessels, 11.1% cargo or tanker, and 5.6% other vessels. Time spent attending fishing vessels was longer than for the other vessel types (4.8 h versus 2.4 h, respectively; $F_{2,249} = 3.2$, $P = 0.045$).

In 403 events, where AIS were located within 5 km of birds, 188 (46.6%) had a radar detection, with 132 (54.8% of events) for Centurion and 56 (35% of events) for XArgos.

Table 2. Percentage of time (average ± SD) spent in international waters and in EEZs and a number of radar detection and proportion of detection with no AIS associated

EEZ	Average % time spent in EEZ	Number of radar-detection events within EEZ	% with no AIS
International	42.2 ± 35.9	78	36.9
Crozet	30.5 ± 40.4	93	14.6
Kerguelen	18.5 ± 32.4	125	14.9
Amsterdam	3.4 ± 12.9	6	50
Heard	1.8 ± 7.9	4	0
Prince Edward	1.4 ± 7.3	31	100
Australia	1.3 ± 5.2	11	18.2
New Zealand	0.3 ± 2.6	5	20.0
Antarctica	0.3 ± 2.4	0	
South Africa	0.03 ± 0.3	0	

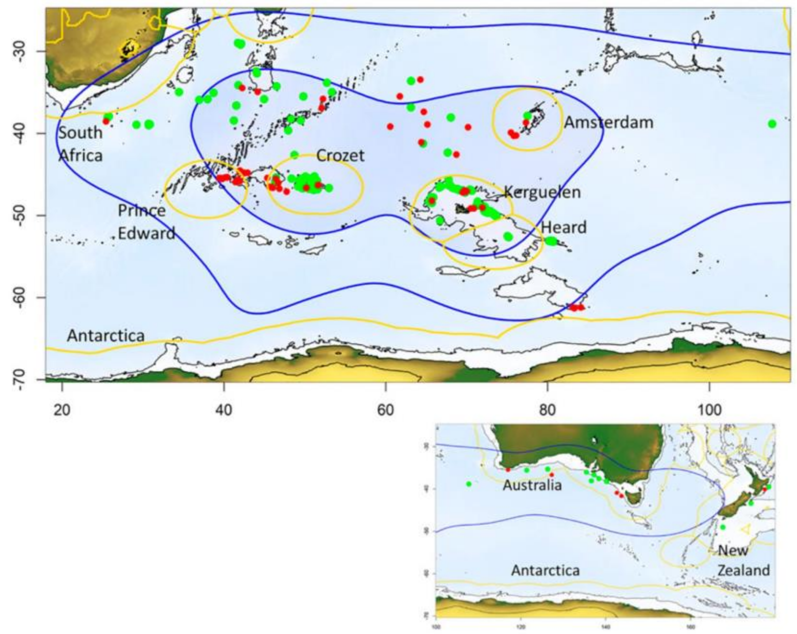

Fig. 5. (*Upper*) Study area showing the overall range (blue line; kernel 90% of all birds), core area (blue zone; kernel 50%), and the location of radar detection with AIS associated (green dots) and no AIS associated (red dots). Limit of EEZ is in yellow. (*Lower*) Eastern part of the range.

Co-Occurrence and Attraction. Only 10% of individuals did not have any vessel within a range of 100 km during their trip. For those that had at least one vessel within 100 km of their movement, 19.9 ± 20.4% came within 30 km of at least a vessel, and 6.3 ± 11.9% attended a vessel. These values varied extensively according to the age of individuals, with juveniles being less prone to encounter and approach vessels to attend it than adults ($F_{3,175} = 5.8, P < 0.0001$ and $F_{3,175} = 7.7, P < 0.001$, respectively) (Fig. 6 *A* and *B*).

When birds encountered a vessel (within 30 km), 19.8 ± 20.4% attended the vessel. Again, this value varied extensively according to the status, with juveniles having a lower propensity to attend vessels encountered ($F_{1,146} = 8.2, P < 0.001$) (Fig. 6*C*).

Attractivity of vessels varied between species, with Amsterdam albatrosses being less attracted to vessels than wandering albatrosses (8.5 ± 13.3% of Amsterdam albatrosses encountering a vessel approached at less than 5 km of the vessel compared to 21.1 ± 22.8% for wanderings; $F_{1,148} = 4.4, P = 0.038$). Wandering albatrosses were also more likely to approach a fishing vessel if encountered, compared to other vessel types: 40.3% of encounters of fishing vessels resulted in an attendance, compared to 10.9% for other vessels ($\chi^2_1 = 81.2, P < 0.001$).

Discussion

The ultimate goal of conservation research should be not only to provide ever-improving measures of priority areas to be protected, but to also provide new ways to improve on the implantation of recommendations to conserve biodiversity and sustainable resources of high importance to humans (3). In the oceans, among these processes, there is the need for new methods of surveillance of fisheries and a way to better quantify and locate nondeclared and illegal fisheries, particularly in international waters.

The first results of the OS program indicate clearly that it is possible to use animals to improve our capacity for surveillance in very isolated oceanic sectors. They also allowed us to estimate the proportion of boats operating without AIS, i.e., that were operating in EEZ and in international waters without the capacity to be located via standard monitoring systems. Finally, they provide accurate information on the interactions between two endangered species and fisheries and differences existing between adults and young individuals.

Capacity of Improving Prosecution. Our study shows that it is possible to use bird-borne loggers to survey fishing activities over large oceanic sectors. The deployment of loggers on 169 individuals during a 6-mo period gave a large coverage of the southwestern Indian Ocean, extending through to New Zealand. The quasiimmediate transmission of more than 5,000 radar detections through the Argos system to a website, accessible to authorities, confirmed that using large albatrosses as indicators of the presence of vessels is an efficient way to survey large areas where direct survey by patrolling vessels is rare and costly.

In the EEZs around Crozet and Kerguelen, where the French fishery targeting Patagonian toothfish operates, all vessels present were detected several times by breeding adults on the shelf's edges. In some cases, the declared vessels were detected by birds without associated AIS emissions: However, the identity of the vessel was confirmed by the CROSS through the VMS system. For this declared fishery, absence of AIS during radar detections was relatively rare. During the study period, no nondeclared fishing vessel was detected in the EEZs of Crozet and Kerguelen, two were detected in the EEZ around Amsterdam, and all detections in the EEZ around the Prince Edward Islands had no AIS. In addition, several vessels were detected with no AIS at the edges of the Kerguelen–Heard EEZ and of the Crozet and Prince Edward EEZ. For at least two cases, some boats had their AIS regularly switched off for long periods. In the EEZ around Crozet and Kerguelen, the fishery is strictly controlled today by authorities using mitigation measure to reduce seabird mortality to very low numbers (30, 31).

In the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) zone and in international waters, at least half of the radar detections over several hours, corresponding

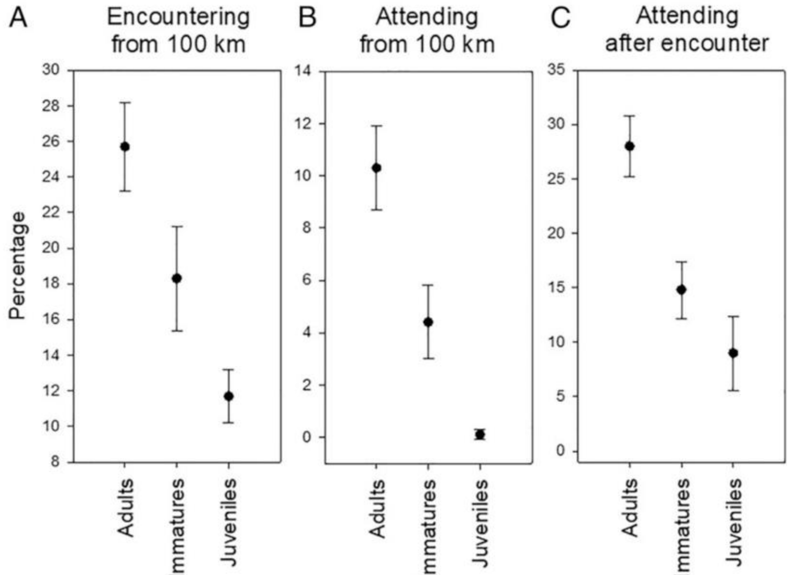

Fig. 6. Average (±SE) percentages of albatrosses of different age classes that encountered (within 30 km from a vessel) (*A*) and attended (within 5 km from a vessel) after being in a 100-km range from a vessel (*B*) and average percentage of albatrosses attending a vessel after encountering it (*C*).

to typical vessels in fishing operation, had no AIS associated. Most detections occurred in subtropical waters, where large Asiatic fisheries operate targeting tuna (32). Typically, the fleets are located through clusters of vessels with AIS, but with irregular AIS transmissions and incomplete information on the identity of vessels. It is in these areas of tuna fisheries where AISs are often not transmitted that a significant number of radar detection occurred with no AIS (Fig. 5). Although the Indian Ocean Tuna Commission (IOTC) requires that fishing boats targeting tuna use at least two seabird-mitigation methods selected from a range of methods (33), and that best practice to reduce mortality in these fisheries is well established (34), most tuna fisheries do not use mitigation measures, apart from some countries which have adopted to use them voluntarily (15, 32, 35). Thus, it is in these waters that mortality risks in long-line fisheries are the highest, and, hence, seabirds are at the highest risk.

The OS concept appears offer a way forward to help develop tools for surveillance and improved enforcement. First, OS provides researchers or international agreements for fisheries management (such as Tuna Commissions, IOTC, the Commission for the Conservation of Southern Bluefin Tuna, etc.) or for conservation (such as CCAMLR) unprecedented information on the distribution of fisheries in remote areas, where conventional methods are not available. We have shown that OS was able to provide to national and regional authorities direct information about the presence of fishing boats in the region they manage. This is critical information for regions where surveillance by maritime or aerial patrols is not possible because of their remoteness and/or because of the extensive cost of surveillance. The Radar-Sat system (https://www.asc-csa.gc.ca/fra/satellites/radarsat2/) can provide information on the potential presence of boats in a particular region through the detection of metallic masses. However, the cost for obtaining images is extremely high (for example, 1.4M€/y for the TAAF area), and the information depends on the coverage by the satellite bands. More importantly, the detections provide only "potential" signals of boat presence. Our preliminary examination shows that satellite images are available irregularly, and, when available, not all boats are detected by the system.

The only open-access system providing information on fisheries is the Global Fishing Watch (https://globalfishingwatch.org/) that potentially enables anyone with an internet connection to see fishing activity anywhere in the ocean, with a 2-d delay. The system is based on the detection of AIS signals sent by boats. We have shown that a significant proportion of vessels detected by our birds had no AIS. Since AIS can be switched off, and this probably occurs in illegal fisheries, full coverage of fishing activity using AIS is not possible. OSs appear to be a complementary tool for surveying fisheries in remote areas.

Apart from these two systems based on satellites, surveillance can be made by patrol boats or airplane, but the more remote the area, the more difficult and costly the surveillance. For example, in the Kerguelen and Crozet EEZs, airplanes cannot be used, and naval or surveillance vessels are infrequently present in these remote areas. When present in the zone, they had access to OS information. The CROSS used the OS data to survey the zone, indicating that the program has the potential to improve surveillance, and in case of the detection of illegal activities within EEZ, to improve enforcement efficiency.

Co-Occurrence, Attraction, and Risk Assessment. Tracking of marine animals has been used extensively to delineate hot spots of biodiversity (19, 36–38), with the ultimate goal of improving conservation through the setting of marine protected areas or the enforcement of conservation measures (20). In this context, overlapping seabird or turtle distribution with fisheries activities (when available, at various spatial scales) allows the estimation of interaction and estimate risks of bycatch (7, 39). However, this risk assessment is generally based on the strong assumption that the co-occurrence of seabirds and fisheries leads to interaction and mortality risks. This assumption may be correct when overlapping fine-scale fishery activities, but these are rarely available (28), especially in international waters, where the information on fisheries distribution is at best available at large scales from RFMOs (15, 16). Based on the results of OS, our study tests the hypothesis that co-occurrence at various scales leads to interaction. This hypothesis has been tested by using vessels equipped with VMS in EEZs (14, 17, 26), whereas our study used a system detecting not only vessels in EEZs, but also in international waters. Several seabird species, such as albatrosses, are well known to be attracted to fishing vessels. However, the attractivity of vessels to seabirds is difficult to study (14) and is generally examined indirectly through the comparison of numbers of seabirds in co-occurrence with vessels at different spatial scales (40). Attraction of seabirds to fishing vessels is believed to be mainly the result of local, small-scaled co-occurrence (41). Our loggers have allowed us to estimate co-occurrence at various scales and attraction to vessels for two different species and different age classes. Juvenile individuals, during their first months at sea, encountered fewer boats than adults or immature birds, and when co-occurring within 100 km of a vessel had almost a zero probability of attending the vessel, whereas for adults, 10% of birds attended such vessels. The low attendance rate of juvenile was the result of the low density of vessels in the range of juveniles, but also because juveniles were less attracted to vessels than adults. Amsterdam albatrosses forage in a sector with high boat densities, especially large tuna fisheries, compared to wandering albatrosses, yet the population is increasing with very low mortality rates at all ages (42, 43). Examination of encounter rates followed by attendance at the boat suggests that Amsterdam albatrosses attend fewer fishing boats compared to wandering albatrosses, despite encountering more boats. These results have strong implications for future risk-assessment plans since they provide a figure for the attraction of albatrosses to fishing boats and show that attraction differs extensively between age classes and species.

Our data also indicate that adult albatrosses are more attracted to fishing vessels than to other types of boats. Short encounters at vessels in international waters generally correspond to birds crossing the route of large transport ships within the range of albatrosses. Birds never follow these boats for long periods (maximum 2 h). Conversely, for fishing boats in operation, encounters are followed by long attendance periods. In the EEZ, attendance can last several hours on the shelf edge, corresponding to long-liners, targeting Patagonian toothfish (28).

Conclusions

The concept of OS is flexible and can be applied to many other systems. According to the area and requests of local authorities, the accessibility of the data can be fully open access through the web (for example, in the case of international waters) or with limited access restricted to authorities through a password system (for example, in EEZs where regulated fisheries operate). The system can be exploited in any situation where large seabirds attracted by boat (for example, albatrosses are attracted by boat at a distance of up to 30 km and cover millions of square kilometers during foraging trips) can be fitted with the OS concept. Preliminary tests have been made with our loggers on other albatross populations in Hawaii and the New Zealand region. The loggers can be deployed on smaller-size seabird species such as gannets to detect fishing boats (44). However, our results show that the species and age class have to be selected carefully: In our case, adult wandering albatrosses appear to be excellent sentinel species, since they are very attracted by fishing vessels and can detect them at 30-km distance. In addition, the system has the potential to provide unpreceded information on the attraction and attendance of seabirds to vessels, opening perspectives for the study of behavior of seabirds in relation to vessels, but also giving access to crucial information for risk-assessment plans. The concept of OS is complementary to other efforts aiming at providing independent information on fisheries distribution (9). It is a good example of how the development of technologies applied to conservation make operational conservation possible and could be used in other animal taxa such as sea turtles or sharks, where conservation actions and independent bycatch locations are critically required (45, 46).

ACKNOWLEDGMENTS. The study is a contribution to the Program EARLYLIFE funded by a European Research Council (ERC) Advanced Grant under the European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 [to H.W.) and to the Program OS funded by the ERC under European Community's H2020 Program (Grant Agreement ERC-2017-PoC_780058 [to H.W.]). The fieldwork was also funded by Institut Polaire Français Paul-Émile Victor Program 109 and was only possible thanks to the help of fieldworkers, especially Jeremy Dechartre, Aude Schreiber, Tobie Getti, Yuseke Goto, Yoshi Yonehara, and Florent Lacoste. The field procedures and manipulations on Crozet, Kerguelen, and Amsterdam were given permission by the Préfet of Terres Australes et Antarctiques Françaises. We thank the Reserve Nationale des TAAF for help with the development of the website and for funding loggers deployed on Amsterdam Island and Florient Orgeret for comments on the manuscript.

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SUPPLEMENTARY INFORMATION

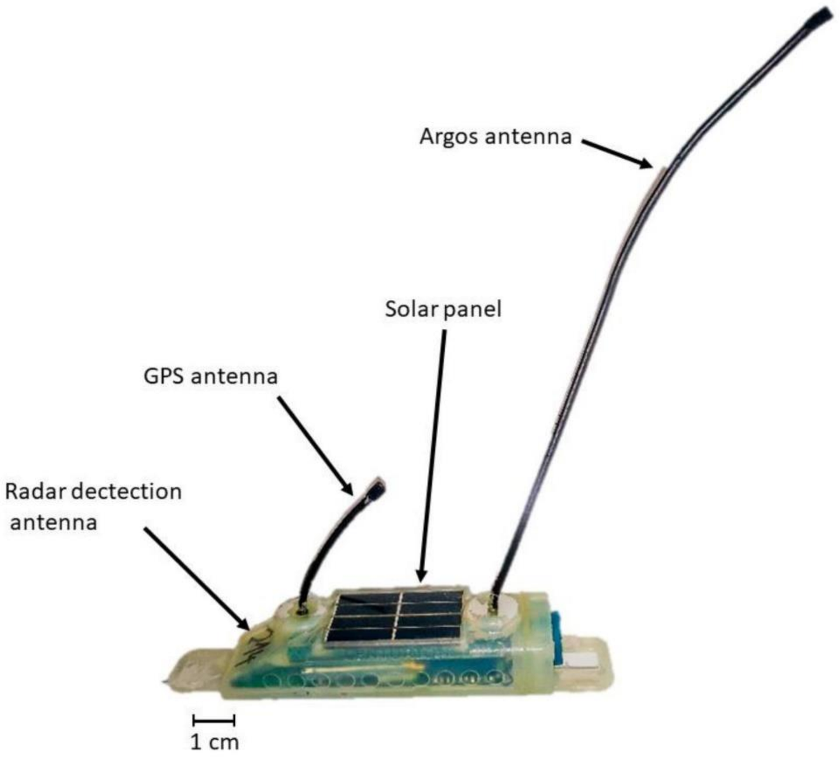
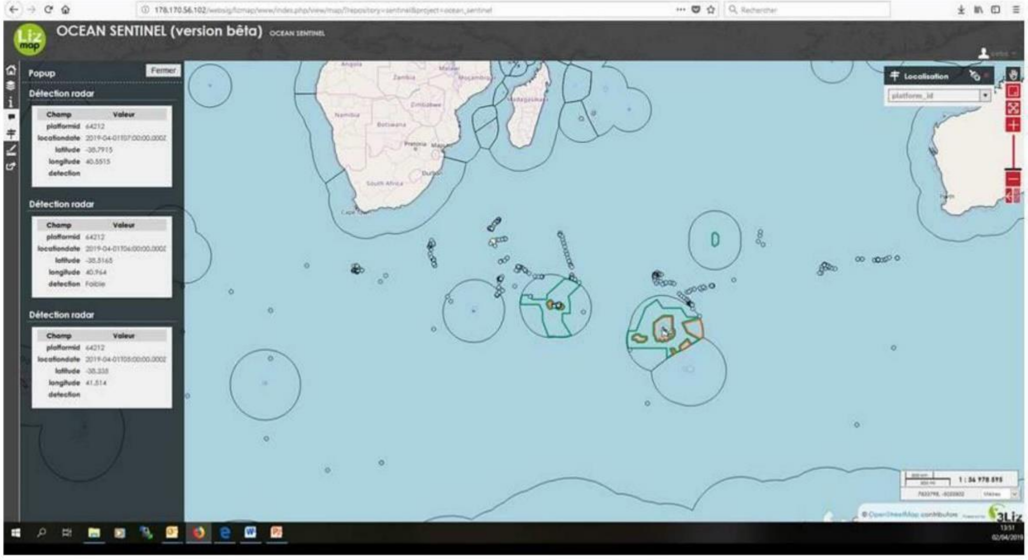


Figure S1 - A centurion logger with the short GPS antenna, the radar detector at the front, solar panel and the long Argos antenna for the transmission of the data.

www.pnas.org/cgi/doi/10.1073/pnas.1915499117



Détection radar

Champ	Valeur
platformid	64212
locationdate	2019-04-01T07:00:00.000
latitude	-38.7915
longitude	40.5515
detection	

Détection radar

Champ	Valeur
platformid	64212
locationdate	2019-04-01T06:00:00.000
latitude	-38.5165
longitude	40.964
detection	Faible

Détection radar

Champ	Valeur
platformid	64212
locationdate	2019-04-01T05:00:00.000
latitude	-38.335
longitude	41.514
detection	

Figure S2 – Webpage of the Ocean Sentinel program giving the location during the past 12 hours of albatrosses equipped with XArgos tags, and the detection of Radars (white dot).

Annexe 2 : Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging behavior

Pajot A., **Corbeau A.**, Weimerskirch H., 2020. Diel at sea activity of two species of great albatrosses: the ontogeny of foraging behaviour. ***Journal of Avian Biology*** *(sous presse).*

Abstract

The first year of life is a period of high mortality in animals. Reduced foraging capacities of naive individuals might be the primary cause of their mortality. These capacities are supposed to be progressively acquired during the first months of life. In this study, we investigate the ontogeny of flight capacities, by day and night, of first-year individuals, and compare it with adults from two closely related species of great albatrosses: Amsterdam (*Diomedea amsterdamensis*) and wandering (*Diomedea exulans*) albatrosses which forage in different environmental conditions. We used 71 tracks of 71 juvenile birds and 141 of 116 incubating adults to compare both age categories. In order to explore the effect of moon light on night activity, we elaborated a new formula which improves the precision of the proxy of moon illumination. By day, we found that juveniles of both species reach some adult foraging capacities in less than two months. By night, albatrosses have reduced activity increasing during the first weeks at sea for juveniles and changing in accordance with moon illumination for both juveniles and adults. A peak of flight activity at dawn and dusk was apparent for both species. Interspecific comparison underlined that Amsterdam albatrosses were more active than wandering albatrosses, suggesting a difference in food and foraging strategy. Overall, we highlighted how life history traits, environmental conditions and time of the day affect the foraging activity of two related species seabirds.

Keywords: Seabirds, *Diomedea*, Albatross, Flight behavior, Night activity, Foraging activity, Moon illumination, Diel activity pattern

Introduction

In seabirds, as in many other animal species, survival of juveniles during their first year at sea is low. Drivers of this mortality are not fully understood. One of the most recognized and studied hypothesis considers that first-year animals are physically immature and lack experience, resulting in inferior foraging and movement abilities (Lack 1954, Ashmole 1963, Lindström 1999). Therefore, it is assumed that juveniles acquire abilities during their early-life, reaching an optimum behavior by themselves or with experienced individuals (Clutton-Brock et al. 2001, Mazur & Seher 2008, Rotics et al. 2016).

Learning of foraging techniques during early life has been previously studied in different species (e.g primates (Lefebvre 1995), bears (Mazur & Seher 2008), dolphins (Fragaszy & Perry 2008), seals (Breed et al, 2011) or insects (Boivin et al. 2010)). For seabirds in particular, where juveniles leave the colony alone, there is an increasing number of studies focusing on the first year of life (MacLean 1986, Yoda et al. 2004, Daunt et al. 2007, Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Campioni et al. 2019, Ramos et al. 2019, Corbeau et al. 2020, Collet et al. 2020) and the immature period (Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Clay et al. 2018, Campioni et al. 2019). However, studying this period of learning at sea is challenging for oceanic species such as albatrosses since they do not return on land before the fourth or fifth year, and cover huge distances in extreme oceanic conditions (De Grissac et al. 2016). With the recent development of new sensors and bio-logging technologies, it is now possible to follow birds for a longer time, to have more precise locations and store many data, considering the habitat of the bird (Harcourt et al. 2019, Yoda 2019).

Using these technologies, Yoda and his colleagues (Yoda et al. 2004) were the first to study daily changes of flight behavior on captive-bred seabirds, investigating parameters such as duration of foraging trips, time spent gliding and proportion of time spent in flight. Subsequent studies (Daunt et al. 2007, Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Clay et al. 2018, Ramos et al. 2019, Corbeau et al. 2020, Collet et al. 2020) explored juveniles' behaviors and their changes over time and compared it to adults. All highlighted that some parameters of juveniles' flight behavior improved to attain adults' ones but in variable time durations and assumed that the long immaturity of seabirds was partly due to this long period of learning. Other parameters were considered as innate (Riotte-Lambert & Weimerskirch 2013). These studies indicate that the duration of the acquisition of foraging abilities varied between species (De Grissac et al. 2016). These differences could be related to the fact that they belong to different taxonomic groups and/or forage in very contrasted environments (tropical versus temperate or polar) with different ranges of sea surface temperature, wind, resource availabilities, night duration and light conditions.

Although many seabirds are not active in complete darkness, many species take advantage of illuminated nights to increase foraging effort. This aspect, to our knowledges, has never been studied in juvenile seabirds. In adult seabirds, at-sea night activity varies among species (Harper 1987, Weimerskirch & Guionnet 2002, Phalan et al. 2007, Mackley et al. 2010) from low for wandering albatrosses – Diomedea exulans (Weimerskirch & Wilson 1992, Weimerskirch et al. 1997b) to high for white-chinned petrels – Procellaria aequinoctialis (Mackley et al. 2011) or even exclusively at night in swallow-tailed gull – Creagus furcatus (Cruz et al. 2013). Night-behavior of albatrosses, particularly from great albatrosses of the Diomedea genus, is assumed to be reduced probably because they are less able to fly and find prey in darkness (Weimerskirch et al. 1997b, Phalan et al. 2007). Nonetheless, seabirds' at-sea night activity changes with moon illumination (Yamamoto et al. 2008, Regular et al. 2011, Pinet et al. 2011, Cruz et al. 2013), which increases visibility and improves detection of prey. Furthermore, many preys such as zooplankton, squid and fishes do a dial migration and approach sea surface at night (Gliwicz 1986a, Luecke & Wurtsbaugh 1993, Hays 2003). This phenomenon is moon dependent as it decreases in intensity during bright nights (Gliwicz 1986b, Lowry et al. 2007) which possibly impacts foraging strategies of albatrosses mainly feeding on cephalopods and small fishes (Cherel & Klages 1998, Imber 1999, Cherel et al. 2017).

In this paper we studied daily changes in the flight behavior of juveniles of two closely related albatross species, Amsterdam albatross – Diomedea amsterdamensis (Roux et al. 1983) and wandering albatross – Diomedea exulans (Linnaeus, 1758). While wandering albatross has been the subject of many studies on its foraging ecology since the first tracking studies (Jouventin & Weimerskirch 1990), Amsterdam albatross, an endemic species of the Amsterdam island, has only been recently described (Roux et al. 1983) and little is known on its ecology at sea, especially during non-breeding stages (Thiebot et al. 2014). Although closely related, both species live in two different habitats with different constraints: Amsterdam albatross is a subtropical species throughout its life cycle

(Thiebot et al. 2014) whereas wandering albatrosses forage over a more varied number of habitats, especially in subantarctic and Antarctic waters.

In this study, we compared the first months at sea of juvenile birds from both species in order to examine differences in the foraging and movement ecology during a critical period for their life. We examined whether juveniles improve their foraging efficiency to attain those of adults for two flight parameters: proportion of time spent flying and speed, during daytime, but also at night, according to light intensity.

We wanted to test several hypotheses:

1) Acquirement of foraging skills by juveniles should be gradual and might differ between both species. Acquired skills might be different from adults.

2) Light availability at night may affect juveniles differently from adults; because of their lower foraging abilities during the first months, juveniles may spend more time foraging at night to increase foraging time.

3) A higher moon illumination should affect night behavior of albatrosses by increasing their flight time. Juveniles might be less affected because of their lower foraging abilities.

4) Because each species forages in different environmental conditions, foraging strategies might differ between Amsterdam and wandering albatrosses in both age categories.

5) As bycatch rates by long-liners were high during twilight (Murray et al. 1993), flight activity is expected to be more important around dawn and dusk, when diel vertical migration is still undergoing, and visibility higher than at night.

Material et Methods

Loggers technology and deployments

Two types of loggers developed by Sextant Technologies (New Zealand), measuring precise GPS locations, were used for this study:

- XArgos satellite transmission loggers (55 g, 109 x 30 x 19 mm) programmed to record and send a location every hour. Deployed on juvenile birds, loggers were attached on the back feathers using Tesa tape (Tesa, Germany) and thus should remain on the bird for several months, and at the latest until the first moult (maximum after 9 months).

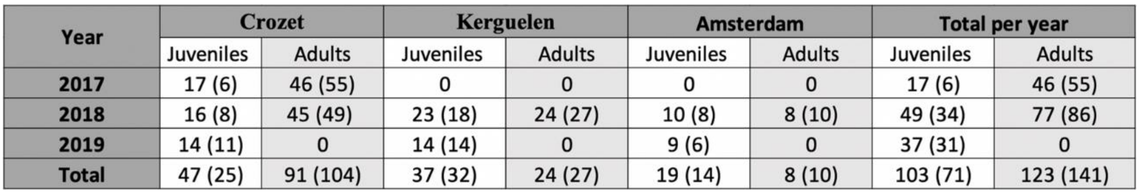
- Centurion data archival loggers (65 g, 109 x 30 x 22 mm), programmed to record a location every two minutes. Deployed on incubating breeders, loggers were attached to the back feathers only using Tesa tape in order to remove them after one, two or three trips at sea. Each track represents a foraging trip. Data were downloaded after the logger was removed from the bird returning from a trip.

The loggers weigh respectively 55 g and 65 g which represents between 0.4% and 0.7% (median = 0.6%) of the body mass of juveniles for the first, and between 0.5% and 0.9% (median = 0.8%) of the body mass of adults, much less than the 3% recommended (Phillips et al. 2003).

During three consecutive fieldwork campaigns between 2017 and 2019, 103 juvenile albatrosses ready to take off were equipped at Crozet, Kerguelen and Amsterdam Islands, providing 71 tracks (Table1). As a comparison, we used 141 complete tracks from 123 incubating breeders equipped in 2017 and 2018 on the three islands (Table 1). We used complete foraging trips for adults and trips lasting at least 5 days (maximum time to reach 100 km from the nest) before the logger stopped transmitting for juveniles or juveniles died. We found no case of transmitters drifting during 2 days or more before stopping transmitting, which may have resulted from a dead bird floating at the surface.

Details of the loggers and deployments are given in Weimerskirch et al. (2020).

Table 1 - Number of loggers deployed on albatrosses each year on the three islands. In brackets the number of usable tracks (n=141 in total)



Year	Crozet		Kerguelen		Amsterdam		Total per year	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
2017	17 (6)	46 (55)	0	0	0	0	17 (6)	46 (55)
2018	16 (8)	45 (49)	23 (18)	24 (27)	10 (8)	8 (10)	49 (34)	77 (86)
2019	14 (11)	0	14 (14)	0	9 (6)	0	37 (31)	0
Total	47 (25)	91 (104)	37 (32)	24 (27)	19 (14)	8 (10)	103 (71)	123 (141)

Data processing

In order to perform similar standardized analyses, we resampled the Centurion data to obtain hourly locations for adults. With 187 loggers we collected 244 tracks on which we applied various filters. After having removed spurious Argos score locations (Cyclic Redundancy Check was generated for each location, we kept CRC=”OK” and removed

CRC=”Error”), duplicates and all (but the last) location on land before departure, we applied a speed filter (120 km.h-1 (Weimerskirch et al. 2002)) on each track to remove implausible bird locations. We considered a bird to be flying when speed was above 10 km.h-1 (Weimerskirch et al. 2002).

Once each track was filtered, we added environmental variables to each GPS location. Sea surface temperature (SST, °C), 10 meters wind u and v components (m.s-1) and total cloud cover (TCC, %) data were downloaded from Copernicus platform as NetCDF files, extracted from “ERA5 hourly data on single levels from 1979 to present” (Copernicus, 2017), a reanalysis of the global climate data (spatial resolution: 0.25 degrees per 0.25 degrees grid, temporal resolution: one hour).

Wind direction and speed were derived using following formulas (Ostrenga 2019):

$$wind_{speed} = \sqrt{\vec{u}^2 + \vec{v}^2}$$

$$wind_{direction} = \tan^{-1}(\vec{u}, \vec{v}) * \frac{180}{pi} + 180$$

We also added celestial parameters:

- Sun presence was calculated with ‘TripEstimation’ R © package (Sumner et al. 2009) using respectively ‘*elevation()*’ and ‘*astro()*’.
- Sunrise and sunset time were obtained with ‘suncalc’ R © package (Thieurmel and Elmarharoui, 2019) in order to calculate night duration (difference between sunset time and sunrise time for each location) and to identify locations during day, night, civil dawn or dusk (Furness et al. 2018). Dawn was considered to begin when the sun is six degrees below the horizon and ends at sunrise time. Dusk begins at sunset time and ends when the sun is six degrees below the horizon.
- Night duration was calculated for each location with the difference between sunset and sunrise time.
- Moon parameters (presence -when above the horizon-, altitude, illuminated fraction) were extracted with ‘oce’ R © package (Kelley et al., 2020) using some outputs of the ‘moonAngle()’ function.

These latter parameters were used to establish a new formula to have a better proxy of moon illumination. Indeed, previous studies about the impact of moon illumination on seabirds only used the illuminated fraction of the Moon (Fig. 1a) or the moon phase as a proxy of moon illumination (Phalan et al. 2007, Yamamoto et al. 2008, Regular et al. 2011, Cruz et al. 2013), without taking into account either moon altitude or total cloud cover. It has been recently criticized by Kyba et al (2020) who indicated that such measures do not provide the real light conditions encountered. In order to precisely measure real illumination at the albatross location, we elaborated a simple formula to have a better proxy of this parameter.

We calculated moon illumination taking into account illuminated fraction of the Moon (between 0 and 1), moon altitude (angle between -90° and +90°) and moon presence (0 or 1) as advised by Kyba et al (2020).

Therefore, we used the following formula that considers the moon illumination to be maximal when the Moon reaches her zenith (moonaltitude = +90°) (Fig. 1b):

$$moon_{illumination} = moon_{presence} * \sin\left(moon_{altitude} * \frac{pi}{180}\right) * moon_{illuminated\ fraction}$$

However, even if the previous formula should increase the precision of the real moon illumination received on earth at a given place and time, it doesn't take into account the impact of cloud cover. With the highly precise open source data set online on Copernicus platform, we elaborated a formula to consider the effects of the total cloud cover (TCC), using diffusion and transmission coefficient (Fig. 1c):

$$moon\ illumination_{calculated} = moon_{illumination} * \mathrm{k}_{diffusion} * \mathrm{k}_{transmission} + moon_{illumination} * \left(1 - k_{diffusion}\right) * k_{transmission}$$

$\mathrm{k}_{diffusion}$ = 0.9 * TCC + 0.1. The more clouds there are the more diffusion there is, but with a TCC of 0 there is still a bit of diffusion.

$\mathrm{k}_{transmission}$ = (1-TCC) * 0.95 + 0.05. It considers that a total cloud cover of one almost annihilates transmission, leaving only a bit of light passing through.

This new formula generates a proxy of moon illumination which is generally lower compared to standard estimates of moon illumination (Fig. 1) : Moon illumination modulated by total cloud cover and moon altitude is lower than moon illumination modulated by only moon altitude (student test, t = -106.18, df = 62341, p-value < 2.2e-16) and also lower than moon illumination using only the illuminated fraction of the satellite (student test, t = 150.02, df = 54330, p-value < 2.2e-16).

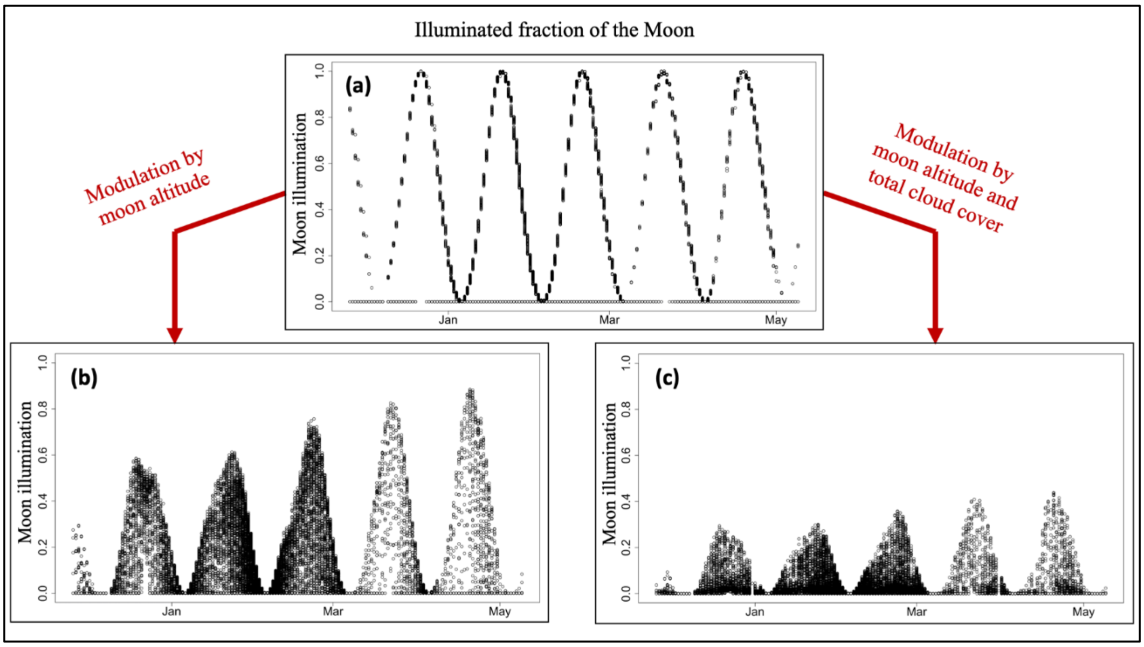


Figure 1 - Differences in formula impacts on moon illumination proxy. One dot represents the illumination received by an albatross during one night location within the 2018-2019 season

Analyses

R For relative comparison purposes, we created a spatial point class object for both age categories of bird from both species with ‘SpatialPointsDataFrame()’ R© function (from ‘sp’ R© package). From these, we produced kernel utilization distributions (UDs 50% and 90%), using the ‘kernelUD()’ R© function from ‘adehabitatHR’ R© package (smoothing parameters, h=1 degree). We then calculated overlaps on UDs 90% between both species and age categories with ‘kerneloverlaphr()’ R© function (Sanchez et al. 2018). This function calculates a ratio of superposition between one kernel distribution and another.

In order to study the foraging and movement ecology of both species of albatrosses we estimated two parameters of bird flight behavior. For these, the shortest distance between two locations (i.e. the great-circle distance) was calculated using ‘distCosine()’ function from ‘geosphere’ R© package.

1) For each day, we calculated the proportion of time spent in flight during daylight, at night, at dusk and at dawn which is the number of locations with the bird flying over the total number of locations during the defined period.

2) For each location, we calculated the speed of the bird when flying. Also known as ground speed, it is the distance between the previous and the current location divided by the interval of time between both locations. At a one-hour scale, this parameter is not the absolute value representative of the real speed between two locations. Indeed, birds are not going in straight line each time they are flying. However, relatively, we can evaluate differences in the foraging and movement behaviour between groups of albatrosses using this parameter (see De Grissac et al. 2016).

From these parameters, we performed analyses using generalized linear models (GLM), linear (LMM) and generalized linear mixed models (GLMM ('lme4' R© package (Bates et al. 2015))). Distribution of the two flight parameters were: binomial for time spent in flight and negative binomial for speed.

To test our first hypothesis, change over time of juvenile flight behavior, we fitted GLMMs. One model was performed for each flight parameter, for both groups of juveniles, from each species and by day and night (i.e. 8 models (Table 3)). The random structure was established by AIC selection between two random factors: ring number (for individual identification) and date of departure. In particular, we tested the effect of individual identification on the slope to evaluate the effect of logger duration on the total model. The covariate was the number of days or nights since departure.

We tested whether the response was linear or logarithmic (by log-transforming the covariate). When a logarithmic growth was significant, we modelled the equation by computing three commonly used growth curves (Ricklefs 1983, Benharzallah et al. 2015): Von Bertalanffy, Gompertz and logistic equations (Ricklefs 1983). We chose the one that fitted best to the data by AIC selection and extracted two parameters from it: the threshold and the time to reach it.

From these models, we explored our third hypothesis on the effect of light availability at night by adding the proxy of moon illumination as a covariate to the GLMMs representing night flight behaviour of juveniles. Again, we tested whether the response to this proxy was linear or logarithmic. For adults, we performed GLMMs for each flight parameter with moon illumination as covariate and ring number as random factor.

After having studied the evolution of both flight parameters over time and change of these latter with moon illumination, we compared the value of each flight parameter between each category of albatrosses with LMMs and GLMMs. We studied:

1/ The difference between juveniles and adults (covariate = ‘age’, Table 3) – Hypothesis 1

2/ The difference between day and night for each group of albatrosses (covariate = ‘day_night’, Table 4) – Hypothesis 2

3/ The difference between both species’ individuals of similar ages (covariate = ‘species’, Table 5). – Hypothesis 4

Individual identification was always used as random factor.

Finally, to examine our last hypothesis concerning the diel activity pattern of each group of birds, we used the ratio of time spent in flight throughout the day. First, each location was characterized as a proportion of day or night duration centered on sunrise. Therefore, a whole day is represented by values between -1 and +1 with 0 being the sunrise location.

For example:

1/ A location three hours after sunrise for a day lasting six hours has a value of 0.5.

2/ A location four hours before sunrise for a night lasting twelve hours has a value of -0.33.

This method is called the “equinoctial anchoring” presented by Vazquez et al. (2019). It enables us to overcome the issue of different day lengths between all birds foraging in different habitats under different latitudes. Then, we plotted the data with a ‘geom_smooth()’ regression (‘ggplot2’ R© package) to observe the pattern.

All data processing and analyses were made under R© environment (R Core Team, 2017).

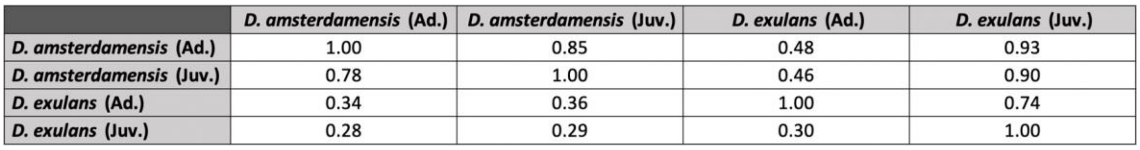
Results

During the study period, we received a total of 116 520 GPS locations from 187 birds. Centurion transmitters were left on adult breeders during one trip at sea, lasting on average for 11 days (Amsterdam albatrosses: 10 days, wandering albatrosses: 11 days). XArgos loggers, because of a technical problem, did not function as long as expected, lasting continuously on average for 41 days (Amsterdam albatrosses: 58 days, wandering albatrosses: 37 days).

Spatial segregation

Juvenile and breeding adult Amsterdam albatrosses were not segregated in space (Fig. 2, Fig. S1, Fig.S2, Table 2), whereas for wandering albatrosses only 30% of the 90% kernel of juveniles overlapped with those of adults. Breeding adult wandering albatrosses were highly segregated from adult and juvenile Amsterdam albatrosses (Fig. 2, Fig. S1, Fig.S2, Table 2). The differences in ranges between juveniles wandering albatrosses and Amsterdam albatrosses resulted from the eastern movements of juvenile wandering albatrosses toward Australian coasts.

Table 2 - Overlap ratio of 90% kernel for each category of albatrosses. As an example, 0.78 signifies that the range of the juveniles from Amsterdam is overlapped at 78% by the one of Amsterdam adults.



	***D. amsterdamensis* (Ad.)**	***D. amsterdamensis* (Juv.)**	***D. exulans* (Ad.)**	***D. exulans* (Juv.)**
***D. amsterdamensis* (Ad.)**	1.00	0.85	0.48	0.93
***D. amsterdamensis* (Juv.)**	0.78	1.00	0.46	0.90
***D. exulans* (Ad.)**	0.34	0.36	1.00	0.74
***D. exulans* (Juv.)**	0.28	0.29	0.30	1.00

Sea surface temperatures encountered were significantly different between adults of both species (t.test, t = 1 17.18, df = 2090.4, p-value < 2.2e-16). Wandering albatrosses forage in sub-Antarctic waters, 10 °C colder than tropical and subtropical waters where Amsterdam albatrosses forage. The difference between juveniles of both species was less important but still significant (t.test - t = 155.29, df = 52885, p-value < 2.2e-16). However, even if the difference was significant between both age classes (t.test - adults: t = -2.5749, df = 1820.7, p-value = 0.01011 / juveniles: t = -31.66, df = 28856, p-value < 2.2e-16), wind speeds encountered by both species were similar with less than 1 km.h-1 of difference in mean for adults and 3 km.h-1 for juveniles. Finally, as both species foraged on average at different latitudes, night duration was different, particularly during summer. Night duration was longer for Amsterdam albatrosses than for wandering albatrosses in both age categories (t.test - adults: t = 250.62, df = 2602.2, p-value < 2.2e-16 / juveniles: t = 216.36, df = 21503, p-value < 2.2e-16).

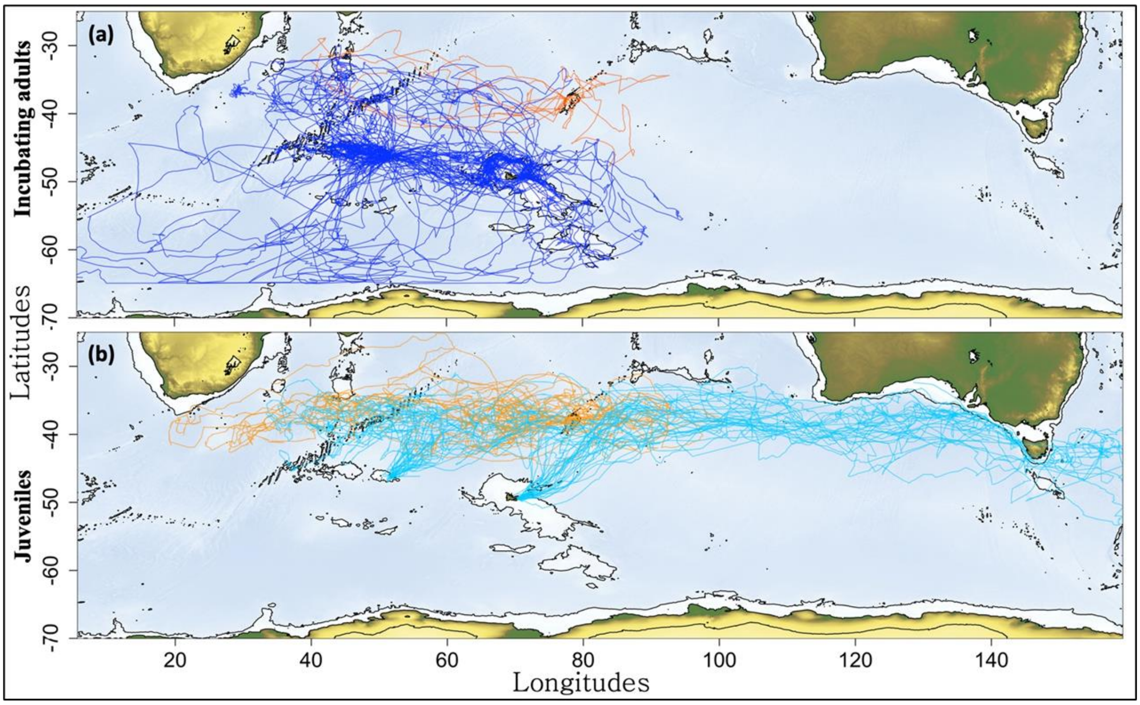


Figure 2 - Study area with all the tracks (n=212) of both species, Amsterdam albatrosses in orange and wandering albatrosses in blue: (a) adults are on upper map and (b) juveniles are on lower map

Daily changes in flight behavior of juveniles and comparison with adults

Between both parameters estimated for juveniles, only the ratio of time spent in flight increased significantly with time for both species by day and at night (Table 3, Table S3). By day, Amsterdam albatrosses reached a threshold, acquired in 41 days, which was not different from the average value of adults. For wandering albatrosses, juveniles reached the same value as adults in 26 days (Fig. S4). In both species, the time spent in flight by night was lower for juveniles than for adults. That parameter changed logarithmically for Amsterdam albatrosses and linearly for wandering albatrosses. However, at the end of loggers functioning, juveniles of both species were still increasing their ratio of time spent in flight by night. Therefore, to obtain a reference value for comparison, we used the time necessary to reach a threshold value during daytime.

Flight speed did not change over time in juveniles and was similar to adults' one for both species, except for juvenile wandering albatrosses that had a slower night speed than adults (Table 3, Table S3).

Table 3 – Change of flight parameters over time and comparison between adults and juveniles of a same species. (a Night threshold values calculated after to the time necessary to reach a threshold by day). p-values ** and *** represent p<0.01, and p<0.001.

Flight parameter	***Day/Night***	Change over time			Adults - Juveniles comparison			
		Daily evolution	***Trend***	***Pr(>|z|)***	***Juveniles' reference value***	***Time (days) to reach threshold (when change over time)***	***Adults' reference value***	***Pr(>|z|)***
Amsterdam albatrosses - *Diomedea amsterdamensis*								
Ratio time spent in flight	Day	YES	Log	<2e-16 ***	0.607 ± 0.488	41	0.733 ± 0.443	0.111
Speed		NO	NA	NA	39.483 ± 29.371	No	38.834 ± 15.594	0.663
Ratio time spent in flight	Night	YES	Log	0.000971 ***	$0.183^a \pm 0.387^a$	41^a	0.602 ± 0.490	2.81e-05 ***
Speed		NO	NA	NA	31.610 ± 22.829	No	31.619 ± 12.577	0.194
Wandering albatrosses - *Diomedea exulans*								
Ratio time spent in flight	Day	YES	Log	<2e-16 ***	0.512 ± 0.500	26	0.546 ± 0.498	0.8657
Speed		NO	NA	NA	36.650 ± 24.833	No	37.036 ± 16.904	0.929
Ratio time spent in flight	Night	YES	Linear	1.09e-12 ***	$0.158^a \pm 0.364^a$	26^a	0.263 ± 0.440	0.00594 **
Speed		NO	NA	NA	32.494 ± 24.184	No	30.781 ± 14.724	1.99e-08 ***

Day-night comparison and effects of moon illumination

For each group of albatrosses, flight parameters values were significantly lower by night (Table 4). However, when moon illumination was brighter, both parameters were increasing (either linearly or logarithmically) for each group of albatrosses. Only the speed of juvenile wandering albatrosses did not increase with moon illumination (Table 4).

Table 4 - Comparison of flight parameters between day and night and the effect of moon illumination by night for each category of birds. p-values *, **, and *** represent respectively p<0.05, p<0.01, and p<0.001.

Group	***Flight parameter***	Day - Night difference		Effect of moon illumination		
		Estimate	***Pr(>|z|)***	***Trend***	***Estimate***	***Pr(>|z|)***
Amsterdam albatrosses - *Diomedea amsterdamensis*						
Juveniles	Ratio time spent in flight	-2.213	1.6e-07 ***	Log	0.25476	1.66e-07 ***
	Speed	-0.34756	7.34e-12 ***	Log	0.06497	0.00903 **
Adults	Ratio time spent in flight	-0.593	2.57e-06 ***	Log	0.7465	2.06e-11 ***
	Speed	-0.2968	0.0201 *	Linear	41873.989	2.67e-09 ***
Wandering albatrosses - *Diomedea exulans*						
Juveniles	Ratio time spent in flight	-1.9716	<2e-16 ***	Linear	0.11152	0.000419 ***
	Speed	-0.30513	<2e-16 ***	Linear	0.006995	0.701
Adults	Ratio time spent in flight	-1.34919	<2e-16 ***	Log	0.5339	< 2e-16 ***
	Speed	-0.23151	1.99e-08 ***	Log	0.05881	8.88e-08 ***

Interspecific comparison

By day or night, for both age classes (juvenile and adults), Amsterdam albatrosses spent more time in flight than wandering albatrosses. Nonetheless, speed was not different by day or night between albatrosses of the same category of age (Table 5).

Table 5 - Interspecific comparison of birds of the same age category for each flight parameter. p-values *, **, and *** represent respectively p<0.05, p<0.01, and p<0.001.

Group	***Day/Night***	***Flight parameter***	Interspecific comparison		
			Amsterdam albatross value	**Wandering albatross value**	**Pr(>|z|)**
Juveniles	Day	Ratio time spent in flight	0.607 ± 0.488	0.512 ± 0.500	0.029295 *
		Speed	39.483 ± 29.371	36.650 ± 24.833	0.186
	Night	Ratio time spent in flight	0.183 ± 0.387	0.158 ± 0.364	0.631
		Speed	31.610 ± 22.829	32.494 ± 24.184	0.859
Adults	Day	Ratio time spent in flight	0.733 ± 0.443	0.546 ± 0.498	0.00262 **
		Speed	38.834 ± 15.594	37.036 ± 16.904	0.51
	Night	Ratio time spent in flight	0.602 ± 0.490	0.263 ± 0.440	1.97e-06 ***
		Speed	31.619 ± 12.577	30.781 ± 14.724	0.267

Diel activity pattern

For all categories of albatrosses, the diel flying activity of each group of albatrosses throughout a day (Fig. 3) was at the highest value just after sunrise (Fig. 3, Table S5). Later during daylight, after being slightly lower, activity of adults from both species increased again at dusk to attain its lowest value at night (Fig. 3). We observed a similar pattern in juveniles with their ratio of time spent in flight decreasing after the peak around sunrise to be close to zero by night and without peaking at dusk (Fig. 3, Table S5).

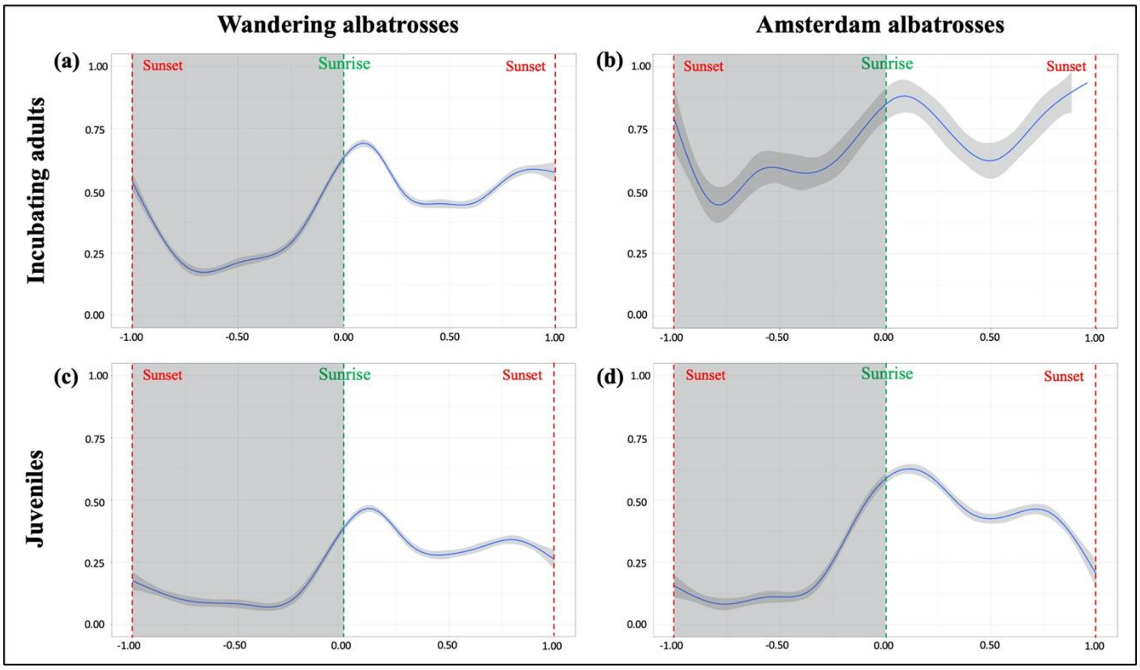


Figure 3 - Diel activity pattern of Wandering and Amsterdam albatrosses. (a) Incubating adults of wandering albatrosses (b) Incubating adults of Amsterdam (c) Juveniles of wandering albatrosses (d) Juveniles of Amsterdam. Activity is the ratio of time spent in flight between all locations from each group at a given moment of the day. Confidence interval is the 95% level interval computed by ggplot() R function.

Discussion

Studying juveniles' foraging and movement ecologies in comparison to adults' performances may enable us to understand the drivers of a higher juvenile mortality (Weimerskirch et al. 1997a, Fay et al. 2015). In this paper, we provided the first comparison of changes in movement and foraging parameters, by day and night, through the first weeks of independence at sea of two closely related species of Diomedea albatrosses. This learning period is a topic of growing interest among seabirds (Yoda et al. 2004, Riotte-Lambert & Weimerskirch 2013, Votier et al. 2017, Sherratt & Morand-Ferron 2018, Campioni et al. 2019, Corbeau et al. 2020, Collet et al. 2020).

In our paper we used a different approach to explore this issue by studying either the linear or the logarithmic change over time, by day and night.

We found that the ratio of time spent in flight by juveniles increased over time, by day and night. By day, for both species, it reached a threshold similar to the reference value of adults. Thus, within a few weeks, juveniles become able to fly during an important proportion of the daytime. The fact that juveniles reached a plateau, suggests that they either developed physical maturity or learned how to minimize their energy expenditure through the development of flight efficiency. Both hypotheses have been recently studied on geese (Gatt et al. 2020) and authors showed that the 'physical development hypothesis' has a more important role in decreasing energy expenditure than the development of flight efficiency. Albatrosses practicing dynamic soaring, this remains to be proven, for example by measuring energy expenditure with heartrate sensors.

Juvenile Amsterdam albatrosses take more time to reach adults' values compared to wandering albatrosses. However, the higher asymptotic value for juvenile Amsterdam albatrosses compared to wandering albatrosses could be an explanation for that difference.

By night, juvenile individuals of both species increased the ratio of time spent in flight without reaching a plateau. Nonetheless, loggers did not function as long as expected and stopped before birds potentially reached this threshold. In each case, flying activity of juveniles is lower than the one of incubating adults leading us to reject our second hypothesis assuming that juveniles have a higher night activity to compensate a lower foraging efficiency during daylight.

The other studied parameter, speed, did not change over time by day or night and was identical between both age classes of a same species. In albatrosses, flight speed is highly dependent on wind utilization (Alerstam et al. 1993, Reinke et al. 1998, Richardson et al. 2018). Therefore, juveniles could be using winds optimally as soon as they leave their nest, which has been previously suggested for wandering albatrosses (Riotte-Lambert & Weimerskirch 2013) but not for Amsterdam albatrosses.

Exploring night activity allowed us to investigate a poorly explored topic for animals and especially for juvenile seabirds (Kronfeld-Schor et al. 2013). Juvenile seabirds' night behavior has, to our knowledge, never been explored before and, for our two targeted species, only been studied in adult wandering albatrosses (Weimerskirch & Wilson 1992, Weimerskirch et al. 1997b, Phalan et al. 2007, Nevitt et al. 2008). These studies show that, like other albatrosses, wandering albatrosses have a reduced activity by night. Our results support this observation. For each of the four groups (juveniles and adults of both species) we compared day and night activity values for both parameters. Ratio of time spent in flight and speed were lower by night than by day.

There are several assumptions to explain why albatrosses spend less time in flight by night than by day which are reviewed by Phalan and his colleagues (2007). First, foraging efficiency could be reduced because it is harder to fly, detect and catch prey at low light levels. Second, albatrosses may use another feeding strategy, the 'sit-and-wait' technique at night (Weimerskirch et al. 1997b). Based on the diel vertical migration (DVM), this hypothesis is explained by a higher concentration of prey at the surface by night (Gliwicz 1986a, Luecke & Wurtsbaugh 1993). Then the balance between energy consumption and energy gain seems better for birds when sitting-and-waiting for smaller and less energetic prey than flying in the dark for bigger prey – similar to the ones they catch during the day – (Weimerskirch et al. 1997b).

Our analyses support both hypotheses because with reduced light, both species of albatrosses reduce their flight activity to sit on water. However, seabirds' night activity increases with moon illumination for many species (Yamamoto et al. 2008, Regular et al. 2011, Pinet et al. 2011, Cruz et al. 2013) and also for wandering albatrosses (Weimerskirch et al. 1997b, Phalan et al. 2007, Nevitt et al. 2008, Mackley et al. 2010). In our study we have examined the effect of a more precise proxy of moon illumination on the activity of both studied species. This proxy considers the altitude of the Moon and the cloud cover at the location date and hour. Commonly, the illuminated fraction of the Moon serves as proxy of moon illumination. It is a 29-day cycle through which the amplitude of the illumination ranges from 0 during new moon to 1 in full moon. Our formula keeps the same cycle, following the classical curve but with a lower amplitude because birds' locations are not often during the Moon zenith and cloud cover was very high during the study period (mean of total cloud cover by night from our data = 73%). Therefore, we have a better measure of the real illumination encountered by the birds and can measure more precisely its impact on flight behavior. We assume this proxy, inspired by the technique used in a recent study (Portugal et al. 2019), to be closer to reality than proxies used in other ecological studies. Correlated with a brighter moon illumination, the speed and the ratio of time spent in flight by night increased for both species and both age categories. Only the speed of juveniles of wandering albatross did not, probably due to the high standard deviation of the parameter. Those results are supporting the hypothesis about the impact of darkness on albatrosses' activity which could be explained by a better visual acuity of individuals.

Therefore, with parameters studied continuously during 24 hours we were able to explore the diel activity pattern and particularly the flying activity during dawn and dusk which has little been studied in albatrosses and in seabirds more generally.

For adults and juveniles of both species we found a peak of activity at dawn. With DVM happening at night, prey availability must be higher during duskiness hours than during daylight ones, as indicated by the increased activity of many seabirds observed behind longliners at dusk and dawn (Murray et al. 1993). We observed a peak of activity at dusk only for adult birds. In contrast, juveniles flying activity seemed to decrease progressively during the day to stop after sunset. We can therefore assume that the second activity peak observed in adults might be acquired later during the immature phase. A second hypothesis is that energy requirements are higher for adults than for juveniles, therefore incubating birds should spend more time foraging than juvenile ones.

From both studied parameters only the ratio of time spent in flight differed between adults of both species: Amsterdam albatrosses spent more time in flight than wandering albatrosses by day and night. Amsterdam albatrosses have very high values of time spent in flight at night and during the day (both above 60%) whereas wandering albatrosses spent less than 60% of the time flying by day and around 30% by night, suggesting different feeding strategies between the two species.

By day, wandering albatrosses are known to forage over extensive distance, detecting prey visually or by olfaction (Nevitt et al. 2008). It is called the 'foraging-in-flight' strategy which is the lowest energy consuming feeding strategy for wandering albatrosses (Weimerskirch et al. 1997b). However, this strategy tends to change when birds are incubating, with birds spending more time on water (Phalan et al. 2007, Louzao et al. 2014) leading to a more important utilization of the 'sit-and-wait' technique. This technique is used at night by wandering albatrosses when they spend around 70% of their time on water. (Weimerskirch et al. 1997b). It appears to be efficient in productive area where DVM is important (Weimerskirch et al. 2005).

Incubating Amsterdam albatrosses spent 75% of their time flying by day and around 62% by night, twice the value of wandering albatrosses. Foraging activity and especially nocturnal activity has been proven to change in accordance to SST for a same species with populations foraging in different habitats (Dias et al. 2012). Amsterdam albatrosses live in a less productive area with a lower DVM compared to wandering albatrosses. Therefore, the 'sit-and-wait' technique might be not efficient enough to compensate the energy allocated for the incubation and to search for food. Amsterdam albatrosses could spend more time searching for scarce prey in poorer subtropical waters, like their counterparts from Hawaii island do (Fernández & Anderson 2000). However, another aspect may explain such an important night activity: predator avoidance. It has already been proved that marine predators such as sharks feed on seabirds and albatrosses (Fisher 1975). Since they are also visual predators, bright light conditions enable them to see more easily what happens on the water surface, which has consequences on prey' activity. Most of shark species live in warm sea temperature, which might increase the time spent in flight for Amsterdam albatrosses, especially under bright moon. A last hypothesis could be that visual acuity of Amsterdam albatrosses is better at night than wandering albatrosses, which would allow them to fly more easily in dark conditions.

Food and foraging strategy of Amsterdam albatross was unknown: we show here that it differs from wandering albatross in the time spent in flight per day. However, during this flying time, speed is not different between species, neither for juveniles nor for adults suggesting that flying behaviour is the same. This might be explained by the relatively close anatomy of both species and a similar use of the wind conditions, which are quasi-identical between foraging areas of both species.

Conclusion

In conclusion, juvenile albatrosses acquired several movement capacities through their early life, a critical period with high mortality. The time of acquirement and foraging strategy, by day or night, differed between species possibly in relation to prey

availability. The latter has to be further examined, particularly in subtropical areas where the Amsterdam albatrosses (until recently a critically endangered species) forage, but the results already underline the importance of environmental and trophic conditions to understand how seabirds and especially juveniles behave. With the development of new technologies deployed on marine predators and the emergence of more comprehensive and complete datasets exploring the influence of biotic and abiotic conditions, more precise studies on the ontogeny of movement and foraging behaviour are now possible and needed.

Funding and acknowledgements

The study is a contribution to the Program EARLYLIFE funded by a European Research Council (ERC) Advanced Grant under the European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 and to the Program OS funded by the ERC under European Community's H2020 Program (Grant Agreement ERC-2017-PoC_780058). The fieldwork was also funded by Institut Polaire Français Paul-Émile Victor Program 109 and was only possible thanks to the help of fieldworkers, especially Célia Lesage, Jeremy Dechartre, Aude Schreiber, Tobie Getti, Yuseke Goto, Yoshi Yonehara, Florent Lacoste, Mélissa Goepfert, Théo Chateaugiron, Cécile Vansteenberghe and Anthony Le Nozahic. An important thanks to Julien Collet for its fieldwork but also for the many advices and point of views he gave me.

Thanks also to Pierre-Loup Jan and Dominique Filippi for help with the analyses.

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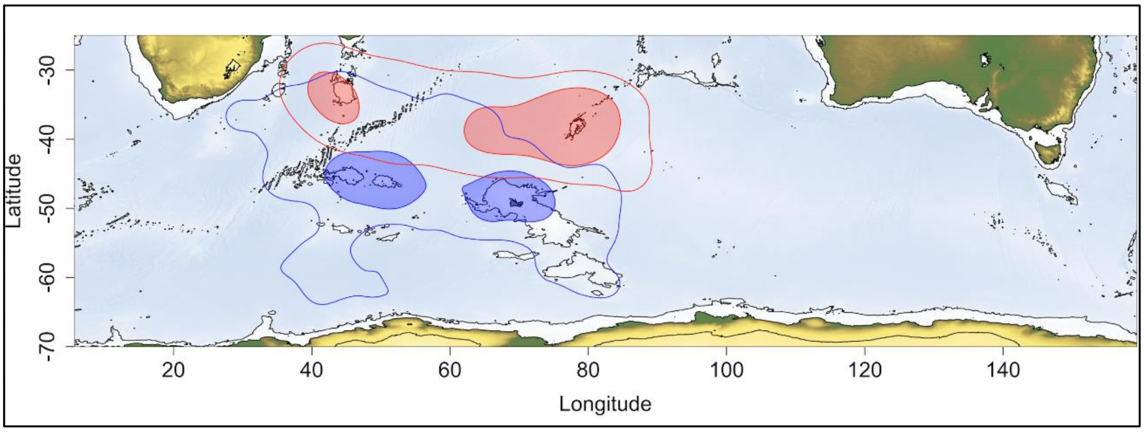
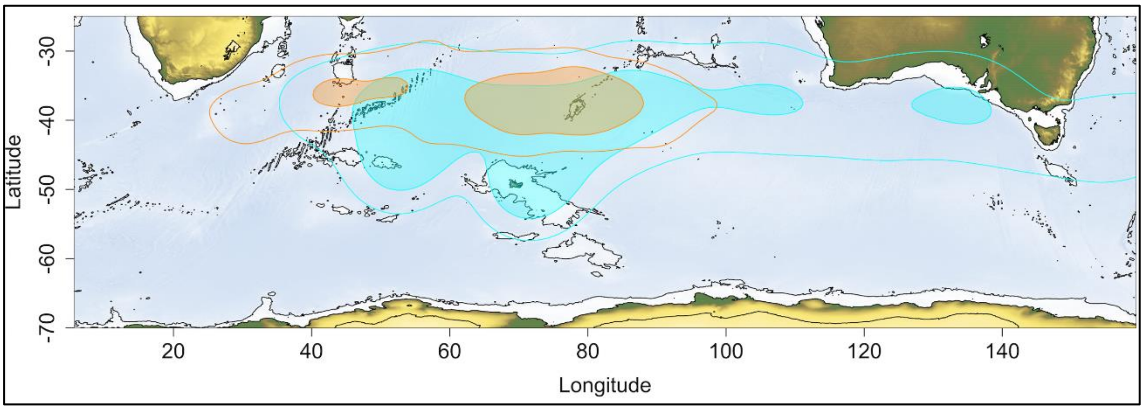
Supporting information



S1 - Figure: 50% and 90% Kernel of adults from both species. In orange Amsterdam albatrosses, in blue wandering albatrosses.

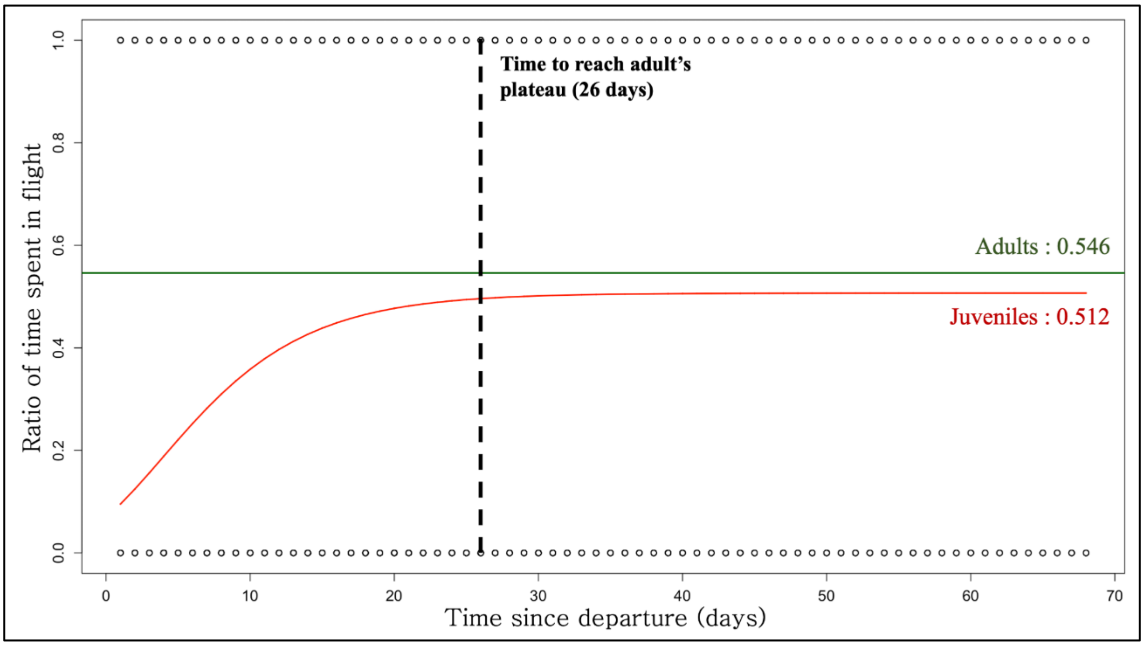


S2 – Figure: 50%, and 90% Kernel of juveniles from both species. In orange Amsterdam albatrosses, in blue wandering albatrosses.

S3 – Table: Change over time of flight parameters of juveniles from both species by day or night.

	Change over time									
	Flight parameter	*Day/Night*	*Daily evolution*	*Trend*	*Estimate*	*Standard Error*	*z value*	*Pr(>|z|)*	*Rsquared marginal*	*Rsquared conditional*
Amsterdam albatros (*Diomedea amsterdamensis*)										
	Ratio time spent in flight	Day	YES	Log	1.3681	0.1118	12.23	<2e-16 ***	0.256	0.473
	Sinuosity		NO	Linear	-0.0001888	0.0040195	-0.047	0.96255	0.000	0.121
	Speed		NO[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]
	Ratio time spent in flight	Night	YES	Log	0.48906	0.14826	3.299	0.000971 ***	0.060	0.359
	Sinuosity		NO	Log	-0.47424	0.12125	-3.911	9.19e-05 ***	0.062	0.092
	Speed		NO[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]
Wandering albatros (*Diomedea exulans*)										
	Ratio time spent in flight	Day	YES	Log	1.02357	0.05045	20.29	<2e-16 ***	0.132	0.562
	Sinuosity		NO	Linear	0.013	0.001879	6.917	4.63e-12 ***	0.011	0.060
	Speed		NO[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]
	Ratio time spent in flight	Night	YES	Linear	0.85126	0.11958	7.119	1.09e-12 ***	0.141	0.354
	Sinuosity		NO	Linear	0.17489	0.0998	1.752	0.07971 .	0.012	0.170
	Speed		NO[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]	NA[a]

a Significates that models could not have been done because they did not fit, trend being inexistent



S4 – Figure: Change of the ratio of time spent in flight over time for juveniles of wandering albatross compare to adults.

S5 – Table: T.test t_values and p_values (under brackets) for each comparison to evaluate diel activity pattern of each category of albatrosses

			Day	Dusk	Night
Amsterdam albatrosses	Juveniles	**Dawn**	8.0622 (2.062e-15 ***)	18.752 (< 2.2e-16 ***)	26.952 (< 2.2e-16 ***)
		Day		17.565 (< 2.2e-16 ***)	43.847 (< 2.2e-16 ***)
		Dusk			3.7879 (0.0001608 **)
	Adults	**Dawn**	3.797 (0.000247 **)	0.84781 (0.3978)	8.1556 (3.518e-13 ***)
		Day		3.9048 (9.58e-05 **)	7.4339 (1.891e-13 ***)
		Dusk			6.8715 (1.683e-10 ***)
Wandering albatrosses	Juveniles	**Dawn**	2.3582 (0.0185 *)	4.246 (2.263e-05 **)	22.534 (< 2.2e-16 ***)
		Day		17.565 (< 2.2e-16 ***)	66.76 (< 2.2e-16 ***)
		Dusk			27.854 (< 2.2e-16 ***)
	Adults	**Dawn**	12.896 (< 2.2e-16 ***)	7.6699 (2.224e-14 ***)	36.772 (< 2.2e-16 ***)
		Day		-2.3501 (0.01886 *)	51.046 (< 2.2e-16 ***)
		Dusk			25.785 (< 2.2e-16 ***)

Annexe 3 : Differentiating the effect of intra- and interpopulation competition on spatial segregation in a central place forager

Orgeret F., Reisinger R. R, Carpenter-Kling T., Keys D. Z., **Corbeau A.**, Bost C-A., Weirmerskirch H., Pistorius P. A., 2021 Differentiating the effect of intra- and interpopulation competition on spatial segregation in a central place forager. ***Journal of Animal Ecology*** (*en revision*).

Abstract

1.Intraspecific competition is increasingly recognized as an important selective pressure driving species distributions. However, few studies have investigated the relative importance of inter- *vs.* intrapopulation competition in relation to habitat availability and selection. Ecological niche theory, together with density dependence models, predicts that for non-territorial and central place foragers, such as seabirds, the effects of intrapopulation competition should be stronger than the effects of interpopulation competition.

2.We tested this hypothesis in two populations of an extreme wide-ranging and sexually dimorphic seabird, investigating the relative role of intrapopulation (sex-specific) and interpopulation competition in influencing the distribution and habitat preferences.

3.Using GPS loggers, we tracked 192 wandering albatrosses *Diomedea exulans* during four consecutive years (2016-2019), from two neighbouring populations in the Southern Ocean (Prince Edward and Crozet archipelago). We simulated pseudo-tracks to create a null spatial distribution and used Kernel Density Estimates (KDE) and Resource Selection Functions (RSF) to distinguish the relative importance of habitat preference, accessibility and competition.

4.In accordance with our expectations, KDE showed that only intrapopulation sexual segregation was significant, and that tracks between the two colonies resulted in greater overlap than expected from the null distribution. RSF confirmed these results but highlighted asymmetrical relationships within and between populations. Within populations, females were less likely to select areas preferred by males, whereas the inverse was not evident for males. Birds from the different populations tended to select the same areas, but this was not the case for males from Crozet, which avoided areas selected by birds from the neighbouring population. These differences in intraspecific segregation and aggregation between sites and sexes were associated with striking differences in habitat preferences, as expected according to niche theory and density dependence models.

5.Our results suggest that even with low at-sea population densities, intrapopulation competition in wide-ranging dimorphic seabirds could drive individual niche specialization while shared habitat preferences between populations could lead to at-sea aggregation. Accordingly, we provide a framework to study competition within as well as between populations of marine predators. This is relevant for understanding their distribution patterns and population regulation, which could potentially improve management of threatened populatiuon.

Introduction

The distribution of a species is influenced by both (i) the biotic environment, including intra- and interspecific interactions such as competition or predation and (ii) the abiotic environment in which species can survive and reproduce as well as the (iii) area accessible to the species via their movement and dispersion capacities (Matthiopoulos, 2003; Soberon & Peterson, 2005). Together, these abiotic factors ('fundamental niche') and biotic factors define the ecological niche ('realized niche') of a species (sensu Hutchinson, 1957). Ecological niche theory predicts that species with similar ecological niches should segregate spatially, temporally and/or trophically, to limit competition for resources (Connell, 1980; Schoener, 1974). Interspecific interactions clearly influence the distribution of species, within and across trophic levels, and by several mechanisms such as competition, resource-consumer interaction, mutualism or facilitation (reviewed in Wisz et al., 2013). However, intraspecific interactions also play an important role in the coexistence and distribution of individuals, and potentially give rise to diverging behaviours, diet preferences or habitat specializations within a species (Bolnick et al., 2003; Polis, 1984).

Disentangling the respective influence of different components (within and between populations) of intraspecific competition for resources on the distribution of individuals is fundamental in ecology but is particularly challenging in highly dynamic environments such as marine ecosystems (Melo-Merino, Reyes-Bonilla, & Lira-Noriega, 2020). Intraspecific competition has frequently been reported between age classes and sexes in animals (Polis, 1984; Ruckstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008). There is a large body of literature on seabirds and ungulates that has demonstrated that sexes segregate by foraging in distinct habitats (Giery & Layman, 2019; Phillips, Lewis, González-Solís, & Daunt, 2017; Ruckstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008). There are several non-exclusive hypotheses potentially explaining why sexes segregate (Wearmouth & Sims, 2008) but for species exhibiting sexual size dimorphism, the most likely explanations relate to different energy requirements, activity budgets or foraging efficiencies between males and females. Sexual segregation could arise through competitive exclusion (direct competition), niche divergence (indirect competition) and both, potentially manifested as differences in habitat preferences (Barbraud, Delord, Kato, Bustamante, & Cherel, 2019; Cleasby et al., 2015; Paiva, Pereira, Ceia, & Ramos, 2017).

Thanks to advances in bio-logging technologies, at-sea distributional segregation between different populations of the same species have increasingly been reported for marine predator species (e.g. Baylis, Tierney, Orben, Staniland, & Brickle, 2018, for marine mammals), especially in the case of seabirds (reviewed in Bolton, Conolly, Carroll, Wakefield, & Caldow, 2019). Many marine top predators, such as seabirds, are central place foragers (Orians & Pearson, 1979), which means that they must commute between at-sea foraging areas and a central place on land where they breed in colonies, fulfilling their breeding duties (swapping with brooding or incubating partner, feeding and care of young). In addition, accessibility to potential foraging grounds is restricted in space and time, accessibility being inversely related to the distance travelled from the central place (Matthiopoulos, 2003; Orians & Pearson, 1979). In a dynamic marine environment characterized by patchy resource availability (Riotte-Lambert & Matthiopoulos, 2020), segregation between populations is expected depending on prey field distribution, species dispersion capacities, distances between colonies and their relative population sizes, as characterized by the Density Dependent Hinterland model (DDH, Wakefield et al., 2013). In the DDH model, which combines both Ashmole's (1963) and Cairns's (1989) models, competition is a function of both population size and distance of foraging grounds from the colony. Therefore, the DDH model predicts (i) elevated competition at the interface of dense, neighbouring colonies but also (ii) aggregation of individuals from small colonies at more distant foraging grounds (Bolton et al., 2019). In order to minimize competition near the colony, some individuals are therefore expected to commute longer distances in search of productive areas further away from the colony (Dean et al., 2015; Evans, Dall, Bolton, Owen, & Votier, 2016). In accordance with the DDH model, partial or complete segregation between close and dense neighbouring seabird populations have often been reported (e.g. Lewis, Sherratt, Hamer, & Wanless, 2001; Wakefield et al., 2013, reviewed in Bolton et al., 2019). However, few studies have described the second DDH model prediction, i.e. that overlap in foraging areas should occur between individuals from small-sized neighbouring colonies with low at-sea densities.

Spatial segregation between individuals arising due to both within and between population processes is thought to limit intraspecific competition, but very few seabird studies have separately examined these two mechanisms during the breeding period, when individuals are the most constrained in space and time (but see Pinaud & Weimerskirch, 2007; Yamamoto et al., 2011). Using tracking data, both Pinaud and

Weimerskich (2007) (wandering albatrosses Diomedea exulans) and Yamamoto et al. (2011) (streaked shearwaters Calonectris leucomelas) concluded that populations segregated spatially at-sea not only by sex but also by populations; however, the authors did not investigate the relative importance and the potential interactions between these two sources of competition. Within-population competition, such as sex-specific competition, is theorized to have a stronger effect on seabird distribution compared to competition between populations (Fretwell, 1992; Lewis et al., 2001). This is because the rate at which competition varies with distance away from a breeding colony is expected to be equal for all individuals at the colony since seabirds are non-territorial at sea (ideal free foragers, Fretwell, 1992; Lewis et al., 2001; Wakefield et al., 2013). To demonstrate competition, however, confounding factors such as habitat availability and accessibility should ideally be taken into account and results must be compared with an appropriate null model that assumes no segregation (Bolton et al., 2019). To date there has been limited progress in this regard.

In this study, we investigated the relative importance of intraspecific competition within and between two populations of one of the most sexually dimorphic and wide-ranging seabird species, the wandering albatross (Shaffer, Weimerskirch, & Costa, 2001; Weimerskirch, Lequette, & Jouventin, 1989). The two populations, one on the Prince Edward Archipelago (Marion Island) and the other on the Crozet Archipelago (Possession Island) are situated in the Southern Indian Ocean, ~1000 km apart. The two populations together contain more than half of the world population: ~ 3,000 breeding pairs at Prince Edward Islands and ~ 2,000 breeding pairs at Crozet archipelago (Ryan, Jones, Dyer, Upfold, & Crawford, 2009; Weimerskirch et al., 2018). Wandering albatrosses are remarkable in that they are able to cover up to 15 000 km in a foraging trip during the incubation phase, through dynamic soaring flight (Jouventin & Weimerskirch, 1990). This low-cost flight strategy to cover extensive areas in search of prey is likely an adaptation to their diet, which consists of scavenged squid and fish, which have a patchy and extensive distribution (Grémillet, Prudor, le Maho, & Weimerskirch, 2012). Wandering albatrosses have been shown to exhibit partial sexual segregation in their at-sea distribution during the breeding season, especially during incubation (Clay et al., 2020; Froy et al., 2015; Nel et al., 2001; Pinaud & Weimerskirch, 2007; Weimerskirch, Salamolard, Sarrazin, & Jouventin, 1993) but this apparent segregation has never been tested for wandering albatrosses against a null model constructed by randomization or simulation (e.g. Barbraud et al., 2019; Cleasby et al., 2015; Ito, Watanabe, Kokubun, & Takahashi, 2020) nor explicitly linked to differences in habitat preferences (sensu Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008; Wakefield et al., 2011).

Our aim was to investigate the relative importance of inter- vs. intrapopulation competition in the wandering albatross. Synchronously between populations and over four consecutive years, we tracked 192 wandering albatrosses (110 males, 82 females) during the incubation period. Tracking data were analyzed using two approaches. Firstly, we compared Kernel Density Estimates (KDE) of the tracking data against a null model to investigate whether spatial segregation or aggregation occurs more than expected by chance (Ito et al., 2020). Secondly, we used Resource Selection Functions (RSF, Boyce & McDonald, 1999) to investigate the relative influence of (i) intraspecific competition, (ii) habitat availability and (iii) habitat accessibility, and to estimate at-sea densities for the two populations, weighted by their relative population size (following Wakefield et al., 2011). Based on the DDH model (Wakefield et al., 2013), we predict that intrapopulation competition should influence distribution more than competition between populations. This is expected to result in more pronounced sexual segregation than interpopulation segregation, and birds of the same sex from different colonies should have more similar habitat preferences than males and females from the same population, potentially resulting in areas of aggregation. However, because the Prince Edward Archipelago has ~30% more breeding pairs, we also expect that birds from this population should have a larger distribution range (due to greater intrapopulation competition), compared to birds breeding on the Crozet Archipelago and exert a greater influence on the distribution of Crozet birds due to interpopulation competition.

Materials and methods

Data collection and processing

Wandering albatrosses from Possession Island, Crozet Archipelago (46°24’S, 51°46’E) and Marion Island, Prince Edward Archipelago (46°54’S, 37°48’E), were individually sexed from field observations or from genetic analyses. GPS loggers (CatLog-S and Igot U GPS at Marion, and X-GPS and Igot U at Crozet) were deployed on incubating birds and attached to the back feathers using Tesa© tape and left on birds for one (180 individuals) or two (12 individuals) at-sea trips. Tracking was conducted synchronously at Marion and Crozet. A total of 192 birds (Crozet: 66 males and 55 females totaling 121 birds; Marion: 44 males and 27 females totaling 71 birds) were tracked during four subsequent years (2016-2019) with a relatively similar sample size (N) and sex ratio (SR; percentage of males) per year: 2016: N=42, SR=36%; 2017: N=35, SR=40%; 2018: N=48, SR=48%; 2019: N=67, SR=45%. GPS sampling rates were programmed to record locations at intervals from 1 to 90 min, depending on site and year.

Data processing and analyses were conducted in R v.3.6.3 (R Core Team 2020). Locations within 2 km of the islands were removed and locations were regularly interpolated every 90 min using the crawl package (Johnson, London, Lea, & Durban, 2008). Analyses described hereafter were performed with data projected in Lambert Equal-Area Azimuthal projection, centered on the study area. We did not aim to investigate the interannual variability specifically, and therefore pooled data from different years, unless stated otherwise.

Null model and pseudo-tracks simulations

To examine the effect of intraspecific competition on the movements of birds, we used pseudo-tracks simulated with the availability package (Raymond et al., 2015) for two different purposes. Firstly, we simulated 1,000 pseudo-tracks per individual to build a null model that assumes no intraspecific competition between sexes and populations. This set of pseudo-tracks was used to quantify the degree of overlap expected by chance (Ito et al., 2020). Secondly, we randomly selected 20 pseudo-tracks per individual (resulting in a total dataset with ~1 million locations) and used these to characterize the oceanic environment potentially available to birds (that is, where they could have been if they did not have any habitat preferences). Combined with the real tracks, the pseudo-tracks allow for a case-control design to be used in the habitat selection models (i.e. RSF, details below).

Pseudo-tracks were simulated by fitting a first order vector autoregressive model based on the parameters estimated from the real tracks; the pseudo-tracks maintain the step length and turning angle distributions of the real tracks to realistically estimate null movements for each population and sex (details in Raymond et al., 2015). A land mask was used to avoid pseudo-track locations on land.

Kernel density estimations and overlaps

To quantify the spatial overlap between populations and sexes we calculated Utilization Distributions (UD, see protocol framework in Fig. 1a) using Kernel Density Estimation (KDE) in the adehabitatHR package (Calenge, 2006). Following Lascelles et al. (2016), we estimated the smoothing parameter (h) based on the spatial scale of area-restricted search estimated with the first passage time method (adehabitatLT package, see details in Pinaud & Weimerskirch, 2007) and then averaged over all individuals (h=85 km). We calculated 95% UD, which represents most of the distribution range of the population, and 50% UD, which represents core distribution. To assess the effect of tracking sample size on the estimation of UD, we calculated 'Representative Values' from saturation curves, following Lascelles et al. (2016). Specifically, we randomly selected an increasing number of individual trips and at each step calculated the resulting UD size as a percentage of the UD size for all trips. We obtained Representative Values >85% for each population; this is considered sufficiently representative of the tracked populations (Lascelles et al., 2016).

We then used Bhattacharyya's Affinity (BA) index to calculate overlap between populations and sexes (Fieberg & Kochanny, 2005) for both the observed tracks and the 1,000 pseudo-tracks per individual. To estimate whether segregation and/or aggregation was greater than expected, P-values were determined as the proportion of 1,000 simulated overlaps that were smaller (segregation) or higher (aggregation) than the observed overlap (following Ito et al., 2020).

Resource Selection Functions (or Habitat selection analysis)

Following Aarts et al. (2008), we used a habitat selection approach to investigate the relative effects and importance of habitat availability, accessibility and competing groups on the distribution and habitat preferences of populations and sexes.

(i) Environmental covariates

We first selected three environmental variables that are known to have the most influence on albatross habitat preferences, namely sea surface temperature, wind speed and bathymetry (e.g. Louzao et al., 2011; Wakefield et al., 2011). Sea surface temperature (SST, °C) and wind speed (WS, m.s-1) variables were downloaded from U.E Copernicus Marine Service Information (http://marine.copernicus.eu/) at a monthly, 1/12° grid resolution and were extracted for each location along the real and pseudo-tracks using the SDMtools package. Bathymetry (m) was extracted at each location using the marmap package from the NOAA ETOPO1 1 arc-minute global relief model.

(ii) Accessibility covariates

As central place foragers, albatrosses are constrained in space and time during the breeding season and therefore habitat preferences must be controlled by habitat accessibility (Matthiopoulos, 2003). Following Aarts et al. (2008), we thus calculated distance from departure colony for each location along the real and pseudo-tracks using the sf package. We then used these distances as accessibility covariates within each habitat model (see below).

(iii) Intraspecific competition covariates

In order to test for intraspecific competition within each study group, we first estimated habitat preferences models for each site and sex, which were then used to predict competition covariates for the other site and sex combinations (see protocol framework in Fig. 1b). For example, under each location for Crozet males, the habitat preferences of Crozet females, Marion males and Marion females were predicted separately, using estimates of each of the other corresponding three models (Fig. 1b).

We assessed habitat preferences (probability to select a grid cell relative to its availability) by modelling the ratio of used vs. available locations as a function of the three environmental covariates (SST, Wind and Bathymetry) and the accessibility covariate. Because it allows non-linear relationships, we used Generalized Additive Mixed Models (GAMM) with a binomial distribution and a logit link, fitted in the mgcv package (Wood, 2017). The 1/0 response value represented each cell in the study area that contained either real (1) or only pseudo-locations (0) (Aarts et al., 2008). Fitting random effects in large case-control tracking data-sets can be computationally demanding (e.g. Raymond et al. 2014). However, greater efficiency has been achieved with recent GAMM algorithm techniques (Li & Wood, 2020) which we adopted to fit individuals (IDs) as random effects, thus taking the hierarchical structure of the data into account (Aarts et al., 2008). We therefore modeled habitat preference w following Wakefield et al. (2011):

$$Wi,j = b0 + years + s1(x1,j) + ... + sj(xi,j) + (1|IDs) \qquad (1)$$

The inverse logit of w gives the habitat preference for each site i and sex j, given the environmental and accessibility covariates xi,j, while 1|IDs corresponds to the random effects structure. Smooth functions of all covariates were fitted as cubic regression splines s1->j with shrinkage to prevent over¬fitting (Wood, 2017). Study 'years' were added as a fixed effect to account for potential interannual variability in habitat preferences and b0 corresponds to the model intercepts.

(iv) Disentangling effects of environment, accessibility and intraspecific competition

For each site and sex, we finally used habitat selection GAMMs as above, but this time using all three types of covariates: three environmental covariates, one accessibility covariate and three competition covariates (Fig. 1b). Here, we therefore made the assumption that if all groups have the same preferences for a given cell, accounting for habitat preference and relative accessibility, the second set of models will result in probabilities of spatial aggregation (or conversely, segregation) among sites and sexes (Fig. 2).

We then used Akaike's Information Criterion corrected for small sample size (AICc, Burnham & Anderson, 2002) to select the most parsimonious model against all possible models including a null model, excluding covariates other than year and the spatial structure and random effects (see online supporting information for details).

At-sea density estimates

To estimate the effect of relative at-sea population densities (birds.km-1) on the observed at-sea distribution, we firstly estimated accessibility probabilities (a) for each site i and sex j with the same GAMM structure:

$$ai,j = b0 + years + s(di,j) + (1|IDs) \qquad (2)$$

with di,j being the distances from the colony for the corresponding site and sex. Following Aarts et al. (2008) and Wakefield et al. (2011), we then estimated spatial densities by calculating the probability of spatial usage (f) for each site and sex as:

$$fi,j= wi,j / (1-wi,j) * r * ai,j \qquad (3)$$

with r = k0/k1 where k0 is the number of pseudo-locations (0) and k1 the number of real locations (1) for a given cell. We normalized f to the range 0-1 and then weighted estimates by the relative population size (Prince Edward islands = 3000/2 breeding pairs and Crozet archipelago=2000/2 breeding pairs) for each site and sex, assuming equal sex ratio (Weimerskirch, Lallemand, & Martin, 2005).

Results

Maximum distance and duration of trips

On average (±SD), trips lasted 12.6±5.3 days and maximum range from the colony was 1523±971 km (Table 1). Both maximum distances travelled (Linear Mixed Effect, LME, models with IDs in random effects, +457.1±173.5 km, p<0.001) and trip durations were longer for Marion birds (LME, +2.9±1.0 days, p<0.001). No significant differences were detected between sexes for maximum distance (male vs. females: LME, +144.6±164.2 km, p=0.379) or trip duration (male vs. females: LME, +0.34±0.93 days, p=0.717), nor for the two-way interaction between site and sex (Table 1).

Sex and site-specific overlap in at-sea distribution

Birds ranged over an extensive area, from the Subtropics (up to 30°S) to Antarctica (up to 70°S) and from 42°W to 102°E, giving average 95% UD of ~9.0 million km2 and 50% UD of ~1.4 million km2 (Fig. 3). At both Marion and Crozet, females tended to travel further north than males (Fig. 3). Even though overlap between sites and sexes varied substantially, sometimes reaching high values (ranging from 0.03 to 0.61, Table 2), differences in UD indicated pronounced spatial segregation (Fig. 4). However, only intrapopulation segregation (i.e. between sexes) was significant even though these were also the highest overlap values (Table 2). Surprisingly, there was greater interpopulation overlap than expected by chance, resulting in more aggregation (Fig. 5) than expected, especially for the same sexes from different sites (Table 2).

Resources Selection Functions

For each RSF built per site and sex, every full model (i.e. with environmental, accessibility and competition covariates) was retained (ΔAICc>2). This means that each covariate explained a significant part of the deviance, even if the relative importance of each covariate differed between sites and sexes (Fig. 6).

Females from both sites avoided grid cells selected by males from the same site, but rather selected areas preferred by birds from the neighboring islands regardless of their sex (Fig.

7). Crozet males also avoided the grid cells selected by females from the same sites, but less markedly, and this was not evident for Marion males (Fig. 7). Crozet males avoided grid cells selected by individuals (both sexes) from Marion Island. Marion males were more likely to select grid cells selected by Crozet males (i.e. asymmetric relationship between males from the two islands) but they were less likely to select grid cells selected by Crozet females (Fig. 7).

Environmental variable preferences were broadly similar for sites and sexes, but there were some striking differences (Fig. 8). All groups preferred shallower waters, but Crozet birds more so. While all groups preferred relatively warm water (>20°C, especially Marion males and Crozet females), there were clear differences in preference for lower sea surface temperature (<15 °C). Crozet males preferred the lowest temperatures whereas Marion males and Marion females preferred intermediate temperature (~8 °C). Finally, Marion females avoided the highest wind speeds whereas males from both sites preferred high wind speed (more so for Crozet males). Crozet females also had a moderate preference for intermediate wind speed (between 12 and 13 m.s-1). Lower wind is also preferred for all the bird groups. The relationships with accessibility (i.e. distance from colony) followed a bell-shape for Crozet birds (preferences for intermediate distances) whereas preference increased with distance for Marion birds (Fig. 8).

When mapped, habitat preferences indicated clear important areas in common between sites and sexes (Fig. 9) whereas predicted densities (habitat preference weighted by population size) overlaid on the observed tracks revealed very low at-sea densities, but also key important areas missed by the KDE (Fig. 9).

Discussion

This study demonstrates that for two populations of an extremely wide-ranging seabird, only intrapopulation (i.e. sexual) segregation in at-sea distribution occurs, whereas more overlap than expected by chance was found between the two study populations. These conclusions were supported through the use of appropriate null models, constructed by pseudo-track simulations. Furthermore, habitat selection approaches (or RSF) show that the effects of competition were asymmetric: the direction of the effects was opposite between males and females per population, and between males from the two different populations. These relationships were also illustrated by key differences in distributional ranges and habitat preferences, in accordance with the predictions of both ecological niche theory and the DDH model (Wearmouth & Sims, 2008, Wakefield et al., 2013). By using RSF to disentangle the relative importance of preferences within the different groups, environmental availability and accessibility (sensu Aarts et al., 2008 and Wakefield et al., 2011) we were able to highlight important selected areas that would not have been apparent through the use of KDE analyses alone (Fig. 9).

Intrapopulation sexual segregation

Numerous studies have demonstrated that sexual segregation is widespread in animals (Ruckstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008), confirming the importance of sexually selected traits in ecology (Giery & Layman, 2019). This segregation seems to be exacerbated for some central place foragers, such as seabirds, especially during the breeding season (reviewed in Phillips et al., 2017) due to restricted foraging ground access in time and space (Orians & Pearson, 1979). The three main hypotheses commonly used to explain sexual segregation in central place foragers are (H1) competitive exclusion (through direct competition, e.g. Phillips, Silk, Phalan, Catry, & Croxall, 2004), (H2) niche divergence (through indirect competition, e.g. Phillips et al., 2004) and (H3) differences in reproductive roles and/or energy requirements (Wearmouth & Sims, 2008).

In support of the first hypothesis (H1) it has been suggested that because wandering albatross males are ~20% larger than females (Shaffer et al., 2001), size-mediated competition could exclude females from some feeding grounds (Weimerskirch et al., 1993). This hypothesis has also often been used to explain sexual segregation in a scavenger specialist, the giant petrels Macronectes spp. (e.g. Gonzalez-Solis, Croxall, & Wood, 2000; but see Granroth-Wilding & Phillips, 2019). However, our study suggests that because of very low at-sea population densities (<1.2 bird.km-2, Fig. 9), the likelihood of detection between birds must be very limited, and such at-sea exclusion through direct competition is unlikely to occur. This is particularly the case during incubation, when the distributional range is extremely vast compared to the brooding period (Weimerskirch et al., 1993). In comparison, the at-sea density of black-browed albatrosses Thalassarche melanophrys can vary between 15 and 75 birds per km2 in some areas during incubation and brooding (Wakefield et al., 2011) and in that case direct competition may be more prominent.

Using habitat preferences from the different site and/or sex groups as a proxy of intraspecific competition (Fig. 7), we demonstrated that within each population the effect of male grid cell preferences on female grid cell preferences was clearly negative (Fig. 7). This suggests shared constraints on females to prefer areas not selected by males from their own population (Giery & Layman, 2019). This was not evident in the case of males that were not affected by habitat preferences of females from the same population. Males therefore seem to be less constrained in their habitat choices, probably because of the competitive advantage due to their larger size (in favor to H1). However, between populations, females were more likely to select areas also selected by birds from the neighboring population regardless of their sex (Fig. 7), counter to the expectation that sexual segregation should occur both within and between populations. Surprisingly, males were more likely to avoid areas selected by females from the neighboring population (Fig. 7).

Together, these results suggest that sexual size dimorphism might have had an influence on niche divergence, but from an eco-evolutionary perspective (in favor to H2, Connell, 1980; Giery & Layman, 2019). Interestingly, wandering albatrosses have a unique courtship mating behaviour, where females can evaluate the wing size and quality of the males (Pickering & Berrow, 2001), probably resulting in sexual selection for larger males during these display rituals (Xavier & Croxall, 2005). Different wing loading between males and females influences their flight capacities (Schaffer et al., 2001) and this could in turn have resulted in different windscape habitat specializations. This might explain the different wind preferences observed for males and females (Fig. 8), which are also linked to differences in SST (Fig. 8) with both SST and wind having latitudinal gradients (Orsi, Whitworth, & Nowlin, 1995). Therefore, probably as a result of sexual selection (Giery & Layman, 2019), wandering albatross males with their higher wing-loading are more constrained as they would require windier conditions for their gliding flight and taking-off (Clay et al., 2020; Cornioley, Börger, Ozgul, & Weimerskirch, 2016; Shaffer et al., 2001). Moreover, it seems that age also plays a role in segregation for males; it has been shown that only older wandering albatross males forage in Antarctic waters whereas young breeder males do not forage south of the Antarctic polar front (Lecomte et al., 2010).

Another hypothesis (H3) is that sexual segregation in seabirds is due to or promoted by differences in reproductive roles. We did not find sex differences in trip ranges and duration, potentially indicating similar foraging effort during incubation. Metrics of foraging behaviour together with the effect of environmental conditions may, however, be required to elucidate differences in foraging effort that may only be evident in periods of relatively low food availability when competition is exacerbated (Paiva et al., 2017; Weimerskirch et al., 1993). Because of the high energetic cost of egg production and differences in moult physiology (Weimerskirch, 1991), energy requirements may be higher for females during incubation, potentially explaining the higher foraging effort in females, compared to males, during incubation described in another study (Weimerskirch, 1995). However, when rearing chicks, it has been shown that the provisioning rate of males is lower than that of females (Weimerskirch, Barbraud, & Lys, 2000). Even though this is dependent on offspring sex and the male's body condition (Cornioley, Jenouvrier, Börger, Weimerskirch, & Ozgul, 2017), it does result in unequal parental contributions at least during chick rearing.

Sexual segregation has, however, also been described in monomorphic seabird species (Phillips, McGill, Dawson, & Bearhop, 2011) suggesting that factors other than sexual size dimorphism can lead to sexual segregation, such as changes in environmental conditions (Paiva et al., 2017), differences in reproductive roles (Yamamoto et al., 2011), breeding stages (Granroth-Wilding & Phillips, 2019), habitat preferences (Cleasby et al., 2015, Barbraud et al., 2019) and diet differences (Phillips et al., 2011). Furthermore, reversed sexual size dimorphism in red-footed boobies Sula sula (where females are larger) is not associated with spatial segregation, but with differences in diving behaviour between sexes. It is therefore likely that several non-exclusive factors (size dimorphism, habitat preferences, parental roles, breeding stages, foraging behaviour, age and diet) interact and should therefore be investigated together to better understand how sexual selection might influence observed ecological processes shaping individual's distribution (Giery & Layman, 2019).

Interpopulation aggregation

Most previous studies on the distribution of neighbouring marine predator populations found partial or complete segregation (e.g. Baylis et al., 2018, and reviewed for seabirds in Bolton et al., 2019). Indeed, very few studies demonstrated aggregation of central place foragers in shared foraging areas (Dean et al., 2015, Evans et al., 2016). In our study, even though absolute overlap between populations' at-sea distributions were relatively low (Table 2), the overlap was higher than expected from the null model. Our study is, to our knowledge, one of the first to robustly describe this configuration (Bolton et al., 2019).

The absence of interpopulation segregation could be viewed in relation to the relatively large distance between the two islands (~1000 km) and the very low population density at sea potentially indicating low levels of competition (Fig. 9). However, wandering albatrosses rely on rare, patchily distributed resources and therefore are able to cover far greater distances on a single incubation trip than the distance between the islands (our study, Jouventin & Weimerskirch, 1990). Furthermore, shared areas were mainly on the Del-Cano Rise and Kerguelen Plateau (Fig. 5), which are known to be productive areas also targeted by other marine predators (Koubbi et al., 2012; Thiers, Delord, Bost, Guinet, & Weimerskirch, 2017) including wandering albatrosses from these two populations (Nel et al., 2001, Louzao et al., 2011) and from the Kerguelen Archipelago (Pinaud & Weimerskirch, 2007).

RSF outputs also confirmed that birds other than Crozet males preferred areas selected by birds from the other population. Crozet males, in contrast, avoided these areas (Fig. 7). In fact, the spatial interaction between Marion females and Crozet males seems to be negligible (lowest values of 50% UD ~0.03%, Table 2, and large Confidence Interval in selection probabilities, Fig. 7). These results suggest that most of the wandering albatrosses did not experience great interpopulation direct competition but rather were more likely to select common areas. However, males from the smaller Crozet population tended to avoid interpopulation competition, especially with Marion males, by selecting different areas. Crozet males preferred areas with lower SST and shallower waters compared to Marion males (Fig. 8). Interestingly, this was reversed for Marion males, which were more likely to select the same areas as Crozet males, suggesting an asymmetrical relationship in interpopulation competition between males (Fig. 7). This can be viewed in light of the DDH model predictions, where individuals from the smaller colony should avoid areas used by individuals from the larger colony (Wakefield et al., 2013, Bolton et al., 2019). In accordance with DDH, Marion birds had greater distribution range, travelling further and longer (Table 1) while targeting distant locations, whereas Crozet birds preferred locations at intermediate distances (Fig. 8b). Here our results demonstrate that the effect of interpopulation competition is sex-biased; the higher-than-expected observed overlap between males from the two populations resulted in Marion birds going toward Crozet birds' preferred areas, especially over the Del-Cano Rise and the Kerguelen Plateau (Figs 4 & 5).

Why then did we not observe this asymmetrical relationship for females between the two populations? Females from both populations also mainly aggregated over the Del-Cano Rise and showed common areas of preference situated over the east of the South African shelf (Fig. 9). However, RSF also showed only slight differences in habitat preferences between Marion and Crozet females especially in relation to SST and bathymetry (Fig. 8). Females from Marion also preferred areas further away from their colony compared to Crozet females (Fig. 8) suggesting that segregation for females could possibly be more subtle and scale dependent (Barbraud et al., 2019; Pereira, Paiva, Phillips, & Xavier, 2018).

One important factor that was not considered in terms of influencing observed aggregation patterns is association of albatrosses with fisheries, especially over the Del-Cano Rise and Kerguelen Plateau where most of the overlap between populations was observed (Fig. 5). Indeed, albatrosses are known to target fisheries in this region (Weimerskirch et al., 2020). Our results therefore raise fundamental questions about the relationship between habitat selection, intraspecific competition and fisheries in marine predators (see Catry et al., 2013). These questions need further investigation using recent biologging technologies (Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018) and data on the location of legal and illegal fisheries (Park et al., 2020; Weimerskirch et al., 2020) since the issue has important conservation implications.

Conclusions

We here introduced a novel framework (Fig. 1) for the study of intraspecific competition in central place foragers and demonstrated that intrapopulation competition of a wide ranging, dimorphic seabird had a stronger influence than interpopulation competition. Even if multiple causes could result in sexual segregation as a mechanism to reduce intraspecific competition, it appears that niche divergence resulting in differential habitat selection is an important driving force that could largely explain the distribution of wandering albatrosses from these two populations. In line with the DDH model (Wakefield et al., 2013), we also demonstrated that interpopulation trajectories, even with low at-sea density, resulted in complex patterns of aggregation that differed according to sex. The framework developed in this study can be used to investigate the relative importance of different sources of intraspecific competition over and above which additional factors can be tested. Notably, the relative importance of seabird-fisheries interactions which may be critical in the context of rapid changes in resource availability due to climate change and overfishing (Grémillet et al., 2018) should be considered in future studies.

Acknowledgments

We are grateful to all those involved in data collection at Possession Island and Albert Snyman, David Green and Stephan Keys who helped with the Marion field work. All experimental procedures were approved by the French ethics committee, the French Polar Environmental Committee and South African National Antarctic Program and conducted in accordance with their guidelines. The Institut Polaire Français and the Terres Australes Antarctique Françaises provided logistical and financial support at the Crozet Islands. The study is a contribution to the Program EARLYLIFE funded by a European Research Council Advanced Grant under the European Community’s Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 to Henri Weimerskirch) and to the Program Ocean Sentinel funded by the ERC under European Community’s H2020 Program (Grant Agreement ERC-2017-PoC_780058 to Henri Weimerskirch). Research on Marion Island is made possible through the logistical support from South Africa's Department of Environment, Forestry, and Fisheries. Financial support was received from the South Africa's National Research Foundation (NRF), through its South African National Antarctic Programme, as a grant to Pierre Pistorius (grant number SNA093071).

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Tables and figures

Table 1: Trip parameters (mean±SD) per site and sex with corresponding sample size (number of individuals: N)

Site	Sex	N	Max distance (km)	Trips duration (days)
Crozet	Females	55	1265±674	11.4±4.3
Crozet	Males	66	1350±1117	11.7±6.3
Marion	Females	27	1647±855	14±4.0
Marion	Males	44	2265±1077	15.2±6.1

Table 2: Kernel Utilization Distribution (50% and 95% UD) overlap (Bhattacharyya Affinity index) between the two sites - Crozet (CRO) and Marion (MAR) - by sex (Males = M, Females = F). When the observed overlaps were significantly higher or lower than the overlaps calculated from the 1000 simulated tracks, we interpreted this as aggregation or segregation, respectively, between sites and sexes. Note that intrapopulation competition systematically resulted in segregation between sexes, with a higher rate than interpopulation competition that, in contrast, resulted in more aggregation than expected for 50% UD and 95% UD (but see MAR.F vs. CRO.M with marginally significant segregation). Intrapopulation competition overlaps are highlighted in grey.

Site.sex1	Site.sex2	UD	Observed overlaps	Simulated (average)	Simulated (sd)	pvalue	Code	Interpretation
CRO.F	MAR.F	50%	0.10	0.00	0.00	<0.001	***	aggregation
CRO.F	CRO.M	50%	0.32	0.46	0.01	<0.001	***	segregation
CRO.F	MAR.M	50%	0.18	0.01	0.02	<0.001	***	aggregation
MAR.F	CRO.M	50%	0.03	0.00	0.00	<0.001	***	aggregation
MAR.F	MAR.M	50%	0.19	0.40	0.02	<0.001	***	segregation
CRO.M	MAR.M	50%	0.16	0.01	0.02	<0.001	***	aggregation
CRO.F	MAR.F	95%	0.55	0.34	0.06	<0.001	***	aggregation
CRO.F	CRO.M	95%	0.61	0.86	0.01	<0.001	***	segregation
CRO.F	MAR.M	95%	0.35	0.39	0.07	0.305	ns	null
MAR.F	CRO.M	95%	0.27	0.38	0.06	0.036	*	segregation
MAR.F	MAR.M	95%	0.41	0.81	0.02	<0.001	***	segregation
CRO.M	MAR.M	95%	0.53	0.44	0.07	0.068	ns	null

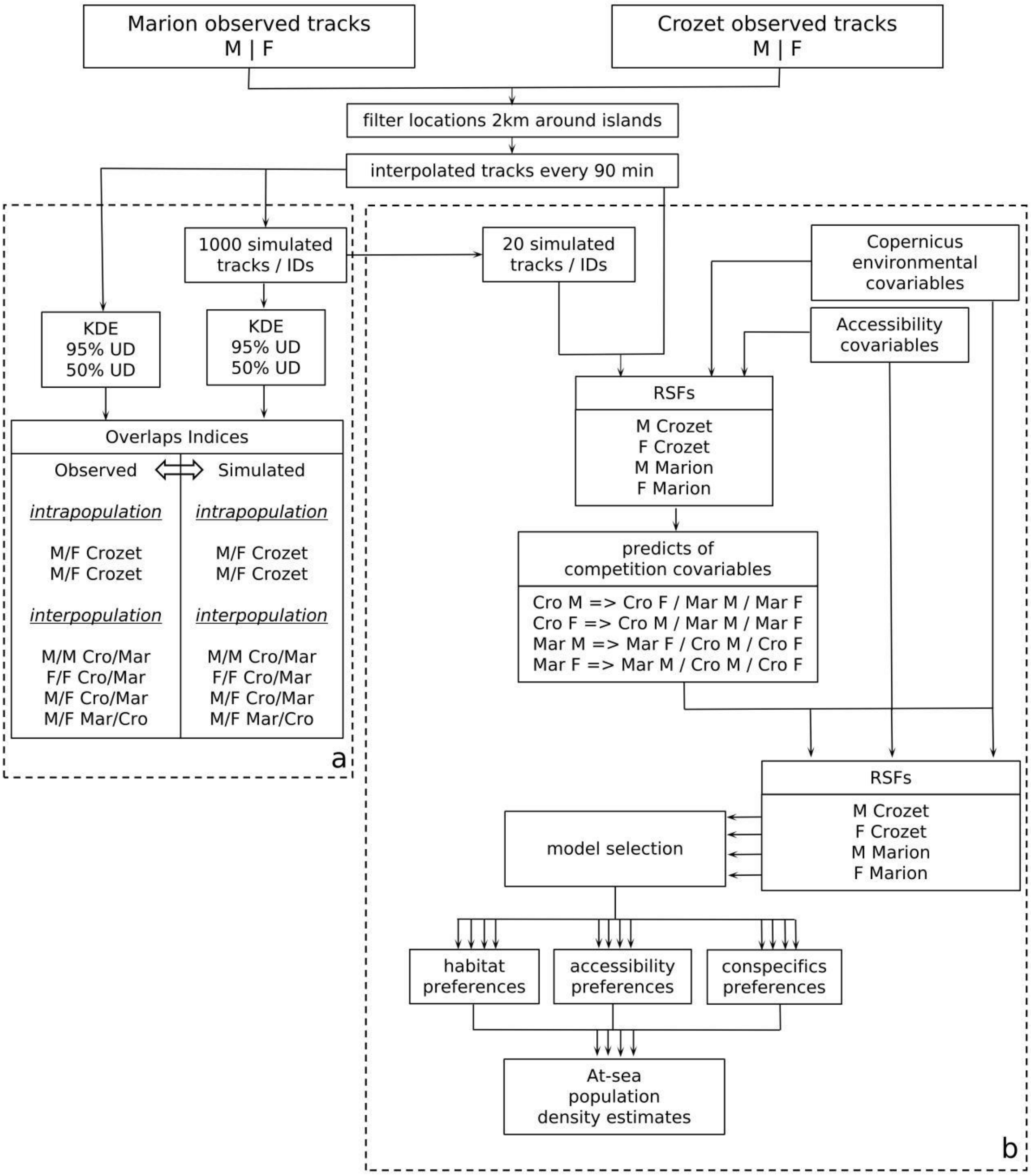


Figure 1: Schematic representation of the analytical protocol. The two main aims were: a. To compare overlap values between observed tracks and pseudo-tracks that assume no intraspecific competition for each site (Marion [Mar] *vs.* Crozet [Cro]) and sex (Males [M] *vs.* Females [F]) b. To disentangle effects of environmental, accessibility and competitions covariates to estimate wandering albatross *Diomedea exulans* densities at-sea for each site and sex.

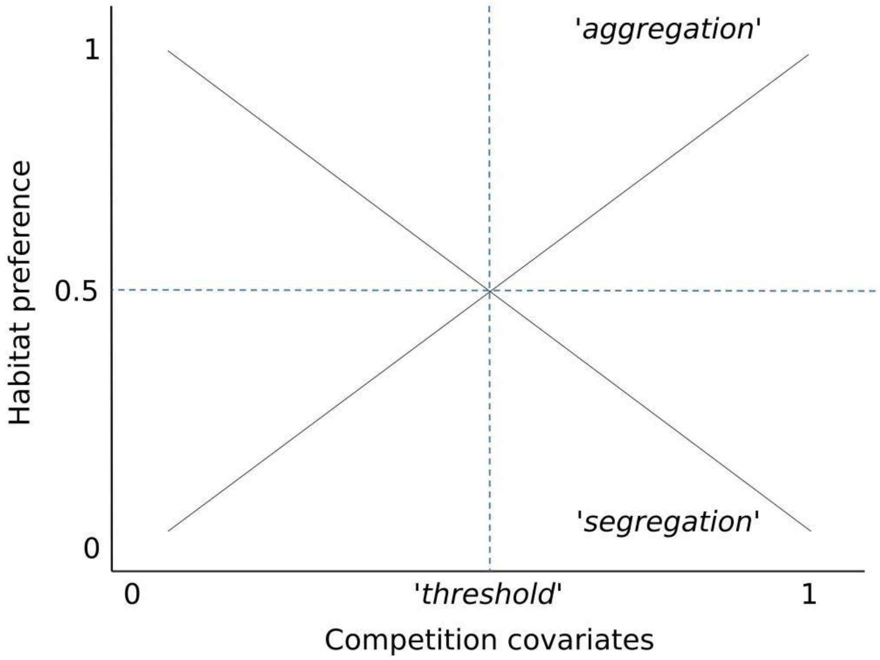


Figure 2: Assumptions underlying the competition covariates estimated from the first set of RSF (see Fig. 1b): ‘aggregation’ will be more likely to occur where individuals from different sites and sexes tend to prefer the same cells and ‘segregation’ occurs when they prefer different cells. The ‘threshold’ line indicates the values at which aggregation is differentiated from segregation.

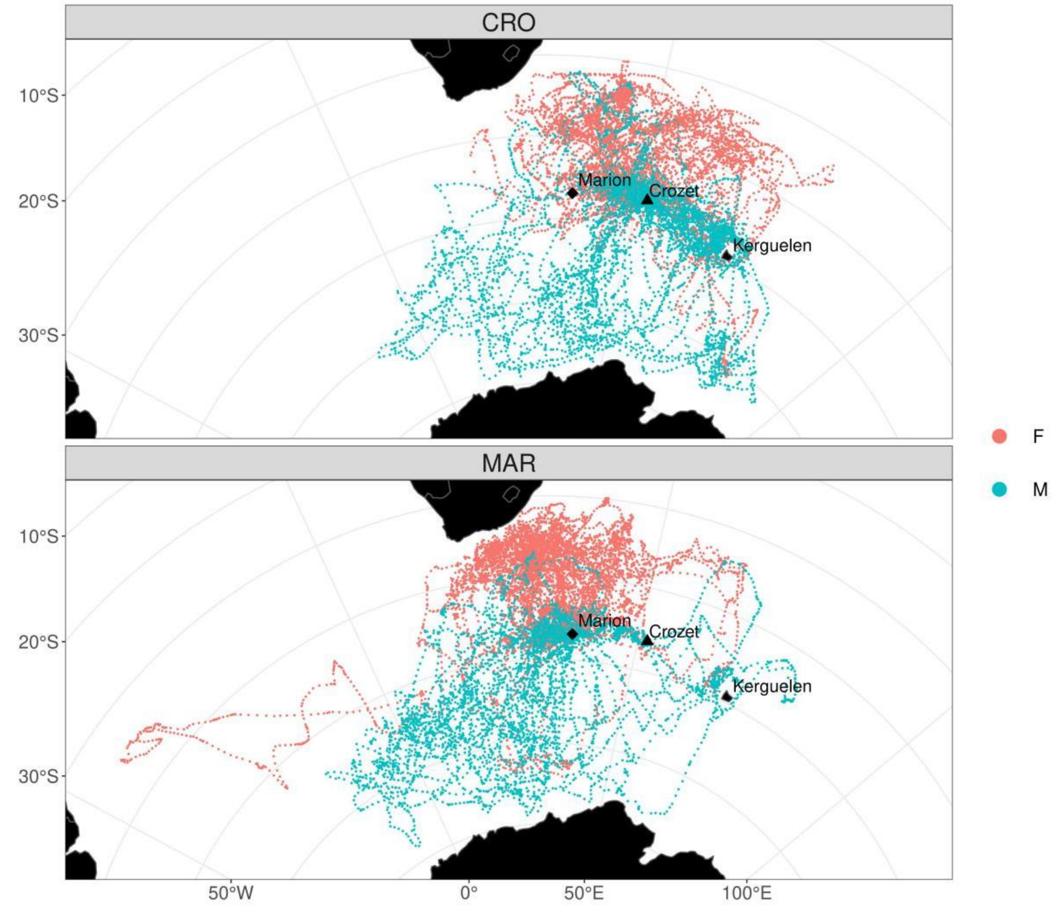


Figure 3: Apparent sexual segregation in the foraging distribution of incubating wandering albatross from two neighbouring populations: Marion (MAR) and Crozet (CRO) islands.

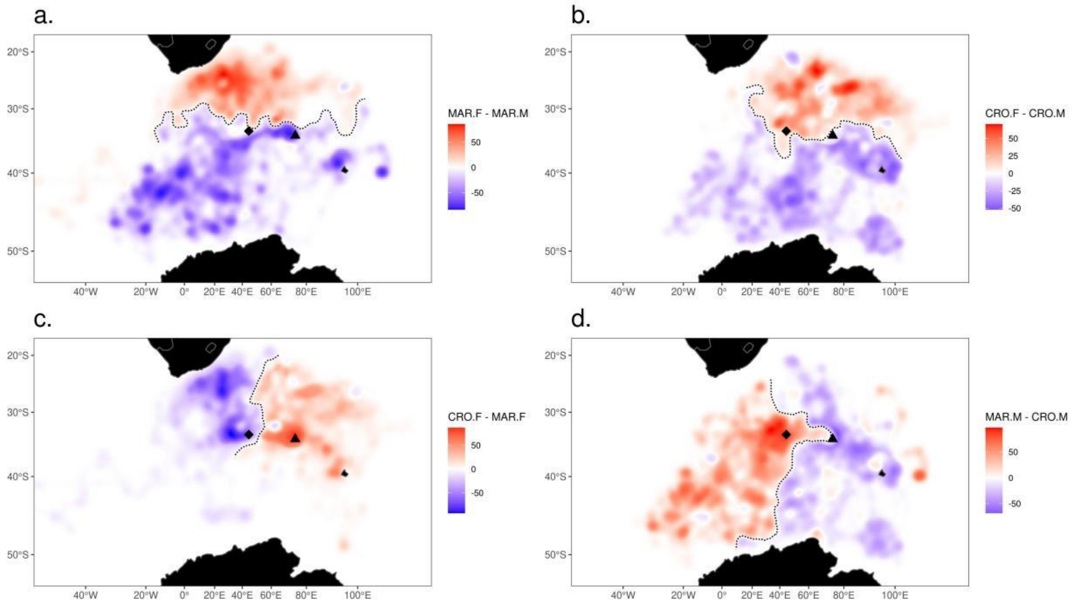


Figure 4: Difference in Kernel Utilization Distributions between populations and sexes. Interface (black dashed lines) indicates equal utilization between the two considered groups, and could be considered as the border of the partial segregation (see Ito et al. 2020). Sites indicated as in Fig. 3.

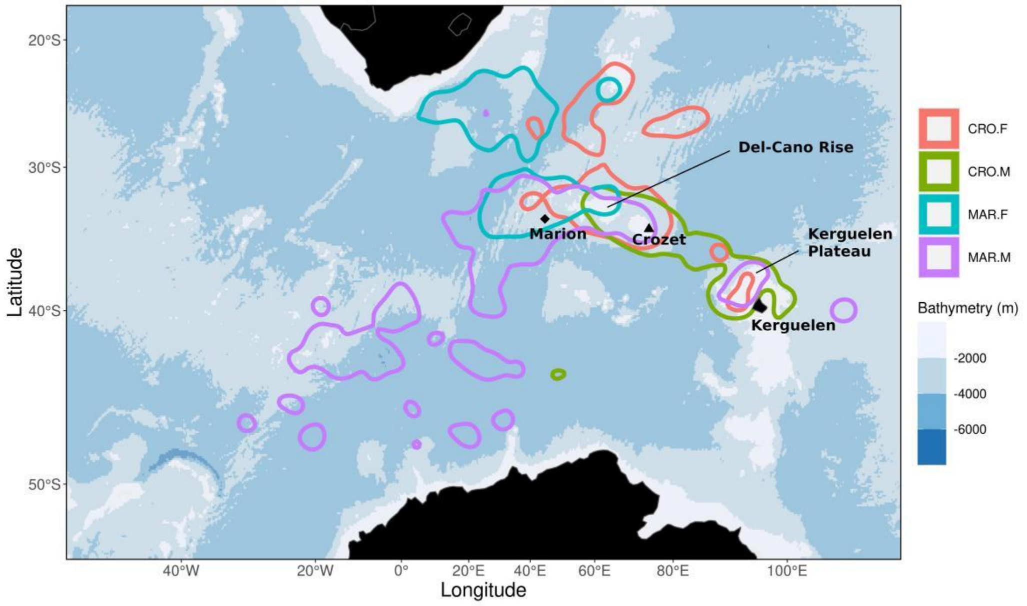


Figure 5: Kernel Utilization Distribution overlaps between populations and sexes at 50% UD. Most overlaps occurred over the Del Cano Rise and Kerguelen Plateau.

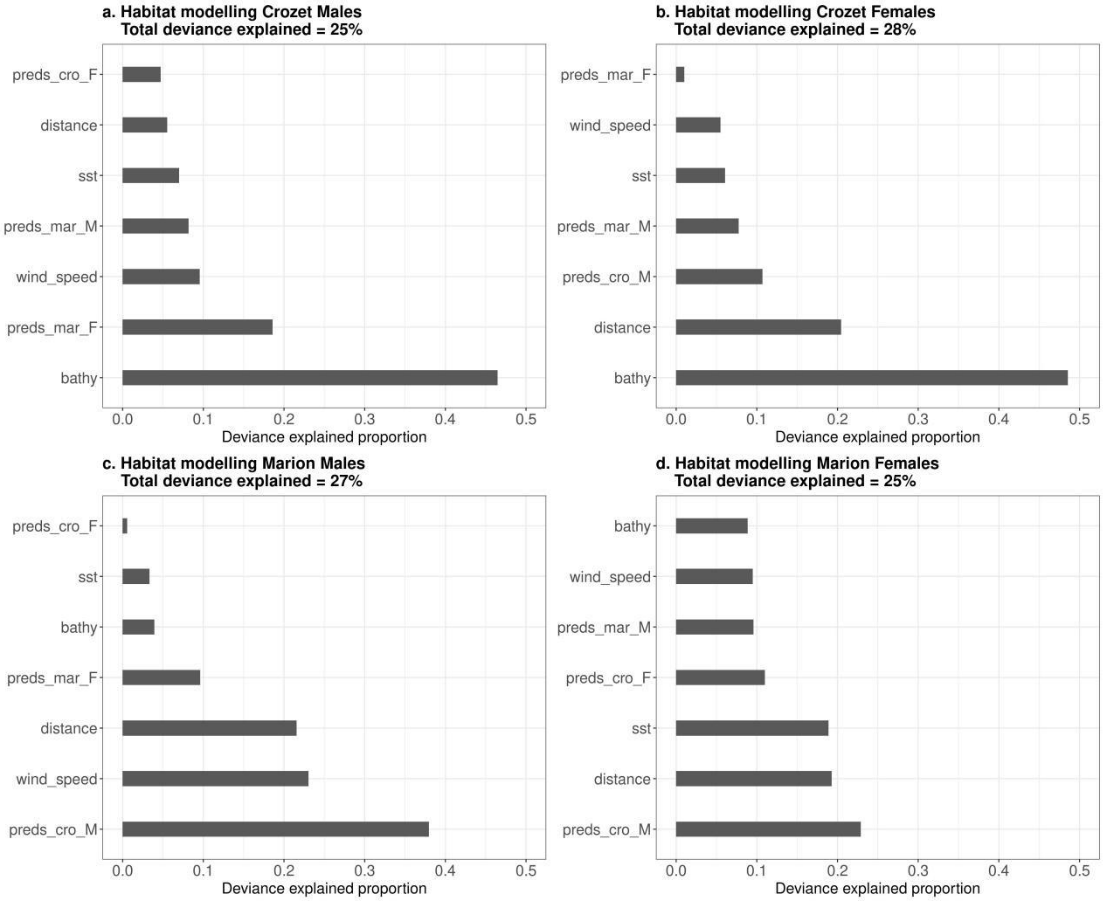


Figure 6: Proportion of the deviance explained per environmental variable for each best model by site and sex (see details in online supporting information). Covariates 'preds' correspond to the competition covariates estimated by the first series of RSF (see Fig. 1b).

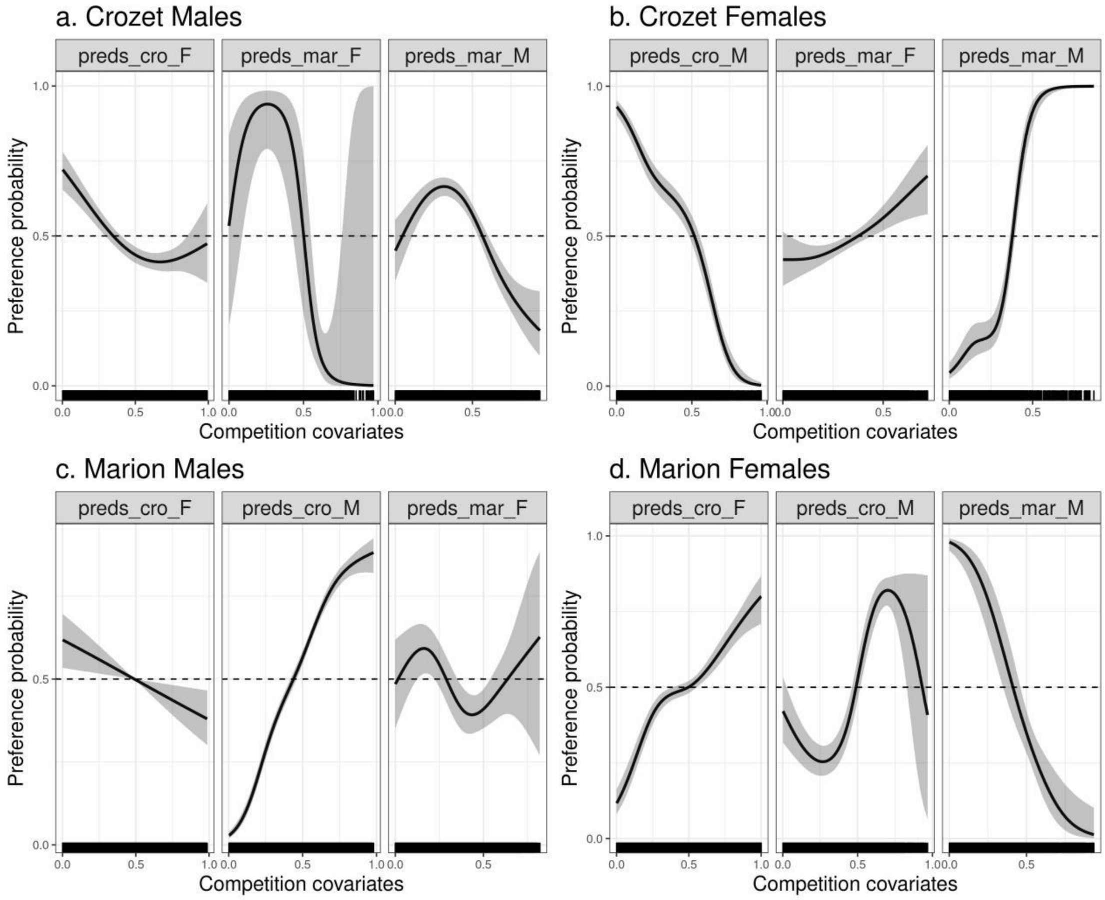


Figure 7: Preference probabilities for the best GAMM per site and sex (a, b, c and d), showing different responses curves of probability of habitat preference (with 95%CI indicated by grey shaded area) as a function of the competition covariates (‘preds’, i.e. habitat selection probability predicted by the first series of RSF, see Fig. 1b). The 0.5 horizontal dashed lines represent a null effect where preferences of the response and explanatory variable (site-sex group) is equally likely. Positive relationships can be interpreted as increase in selection of the response in relation to increase in preference for the same area for the other sex or site-sex considered (see Fig. 2).

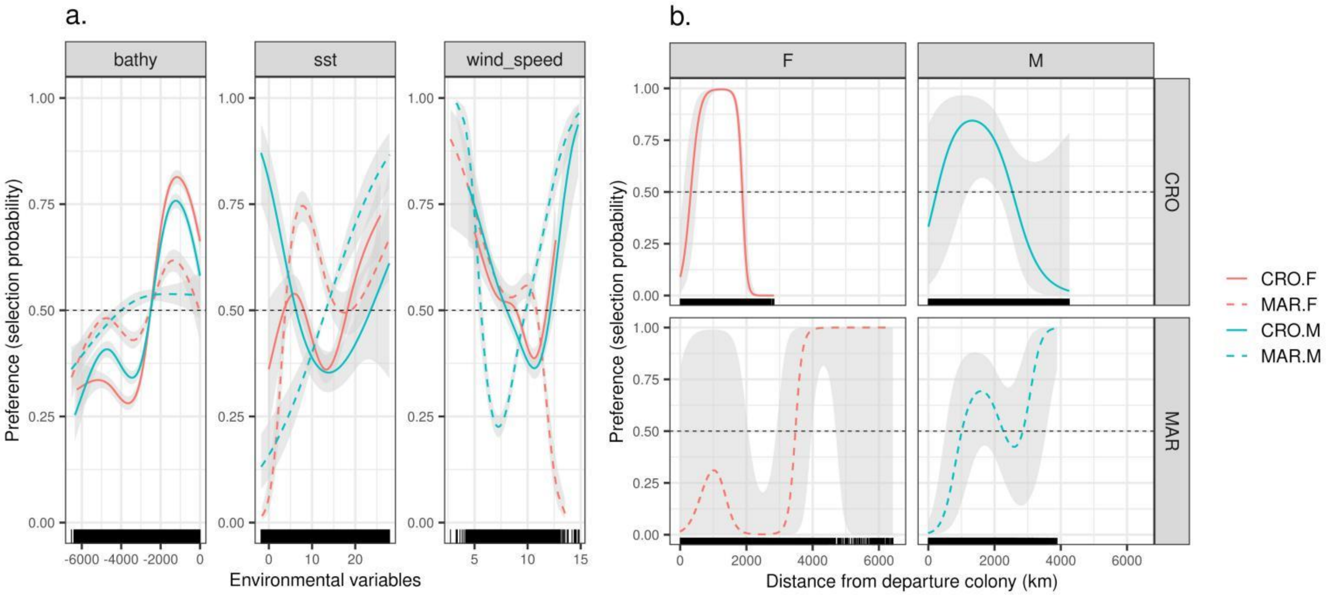
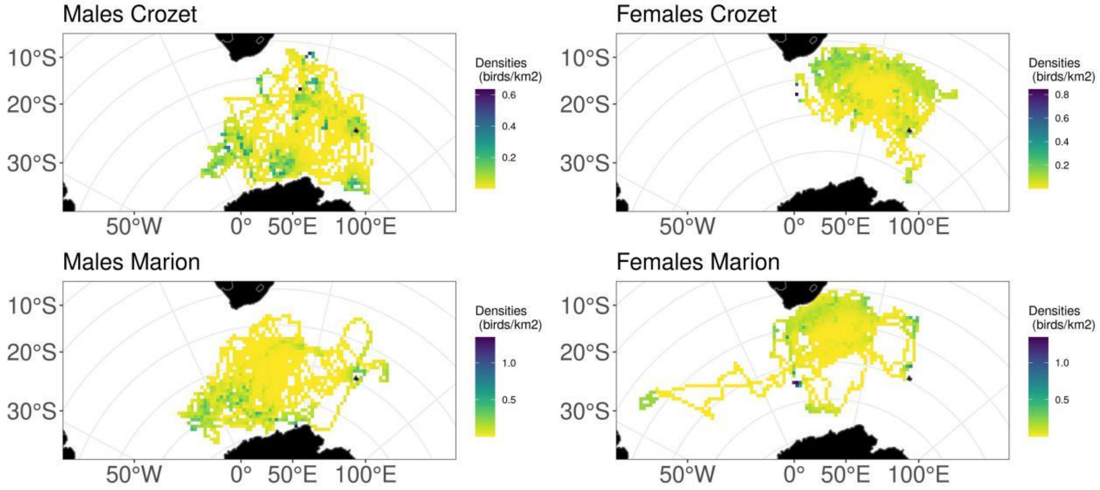
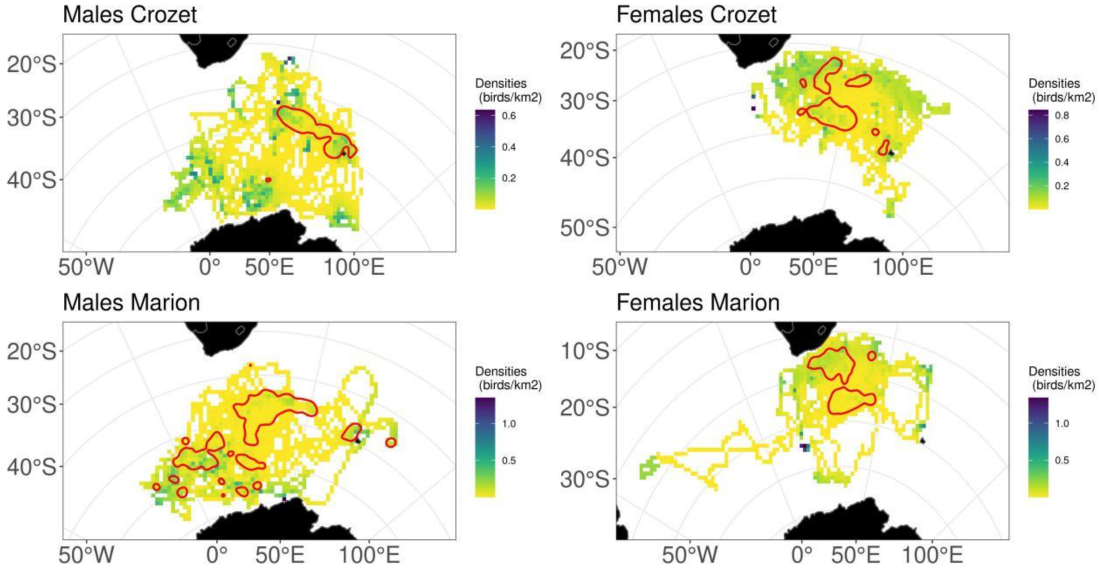


Figure 8: Habitat preference (ratio of used habitat [1] defined by real tracks to available habitat [0] defined by simulated tracks) represented by change in selection probability against each environmental variable (a): bathymetry (m), sea surface temperature (°C), and wind speed (m.s^{-1}) for each site and sex. Lower panel (b) indicates accessibility (distance from corresponding departure colony, km) preferences.



a. Predicts from best models



b. Densities vs. Kernels

Figure 9: Discrepancies between habitat preference probabilities (top panel a.) and predicted populations densities at sea with corresponding 50% Kernel Utilization Distribution (lower panel b., red contours), over the observed tracks. Values have been averaged per 100 km^2 grid cell.

Supporting information

To estimate the proportion of Deviance Explained (DE) for each covariate j we used:

$$\Delta j = (\text{deviance} (wj) - \text{deviance} (wbest)) / \text{deviance} (w0) \quad (4)$$

with wj corresponding to the deviance for a model with only the covariate j, wb corresponding to the deviance explained of the best model (estimated by AICc) and w0 to deviance explained of the null model (S. Wood 2011, public comm. at https://stat.ethz.ch/ and also see Clay et al. 2016).

Covariates of the different competition covariates were highly correlated per sex between each population, which could cause estimation biases (Dorman et al. 2007). We therefore also conduced the analyses without these highly correlated competition covariates (|r|>0.7), investigating the effects on the estimation of each other covariate. We found no strong effect of correlated covariates on the estimation of the other covariates (see Figs S3 to S6 below), and since our aim was to investigate the relative influence of the 3 other groups, we retained all of them.

Finally, we also added an additional smoother - a two-dimensional spline on geographical projected coordinates - to take into account the spatial structure of the data (Beal et al. 2010). We did not use this spatial smoother in the first set of models since it would result in models that are not spatially transferable (that is, they could not be used to extrapolate the habitat preference of competition covariates, see Péron et al. 2018).

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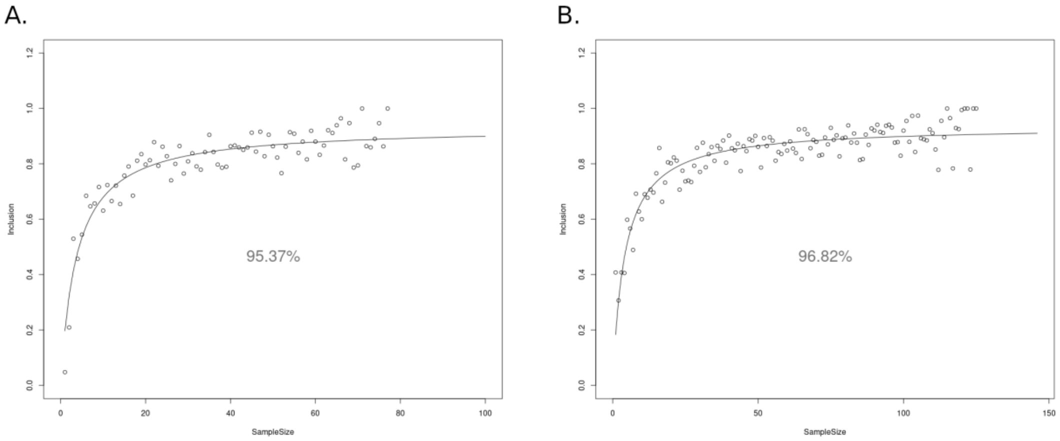

Fig. S1: Assessment of the Representative Values (or Inclusion rate) for the tracking sample size for Marion (A.) and Crozet (B.) islands. The graphs represent the proportion of out-of-sample locations that were located within the 50% UD estimated from sampled locations relative to an increasing number of foraging trips (sample size, horizontal axis). The representativeness of the tracking data set is based on the estimated asymptote of the nonlinear regression (see Lascelles et al. 2016). For each population, Representative Values were >85%; the tracking data are thus considered to be sufficiently representative of the respective populations.

Table S1: Linear mixed effect model (with bird ID as random effects) outputs comparing maximum distance traveled (km) per population and between males and females.

term	estimate	std.error	df	statistic	p.value
(Intercept)	1615	155.9	185	10.36	0
siteMAR	457.1	173.5	185	2.634	0.0091
sexM	144.6	164.2	185	0.881	0.3795
yr2017	-521.6	205.3	185	-2.541	0.0119
yr2018	-316.2	190.7	185	-1.658	0.0989
yr2019	-579.7	175.6	185	-3.301	0.0012
siteMAR:sexM	474	272	185	1.743	0.0831

Table S2: Linear mixed effect model (with bird ID as random effects) outputs comparing trip duration (days) per population and between males and females.

term	estimate	std.error	df	statistic	p.value
(Intercept)	12.7	0.8833	185	14.38	0
siteMAR	2.873	0.9828	185	2.923	0.0039
sexM	0.3365	0.9269	185	0.363	0.717
yr2017	-3.221	1.16	185	-2.776	0.0061
yr2018	-0.5702	1.076	185	-0.5297	0.5969
yr2019	-1.523	0.995	185	-1.531	0.1275
siteMAR:sexM	0.881	1.54	185	0.5722	0.5679

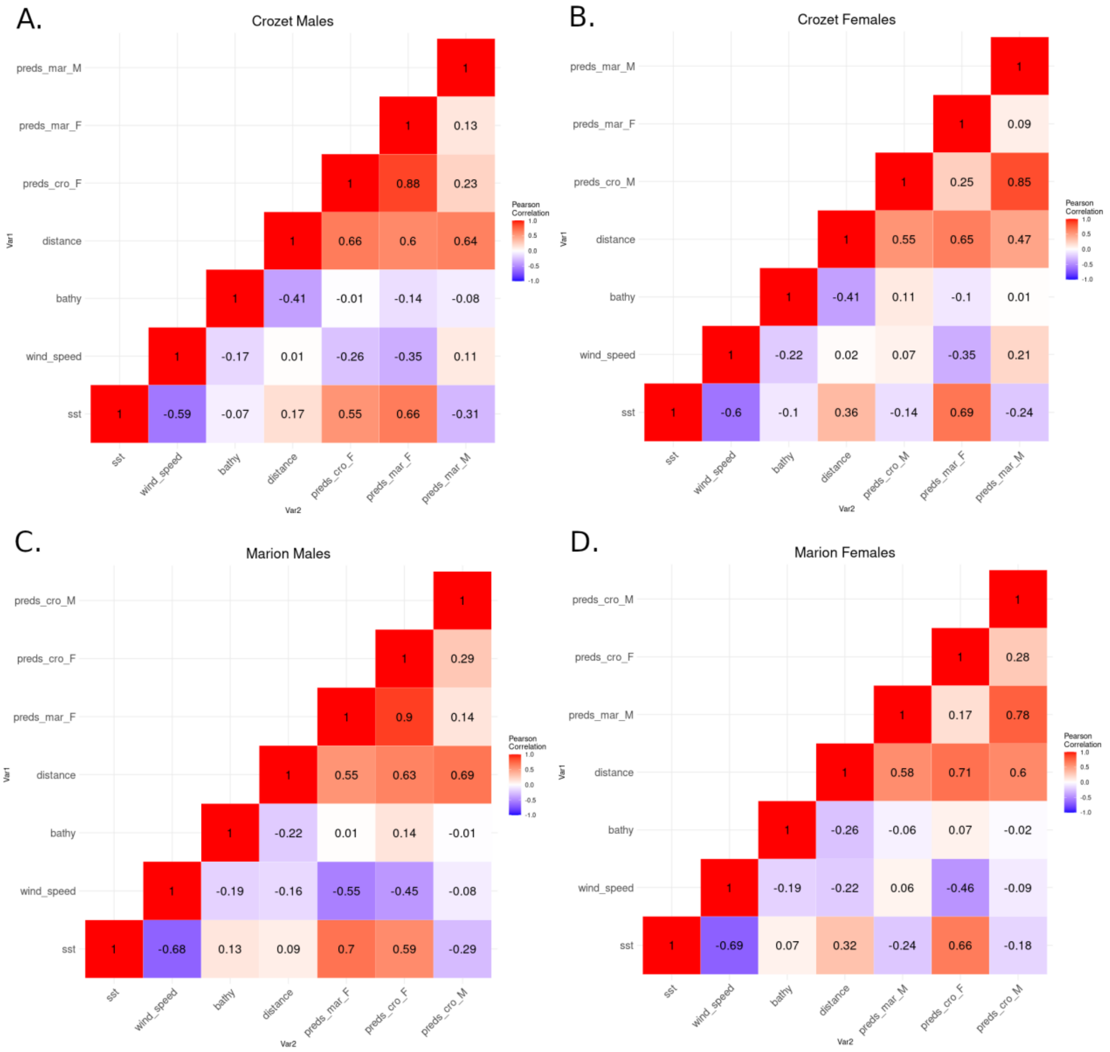

Fig. S2: Pearson correlation coefficient matrices between covariates for the 4 separate models that are testing intraspecific competition (A. Crozet males, B. Crozet females, C. Marion males and D. Marion females).

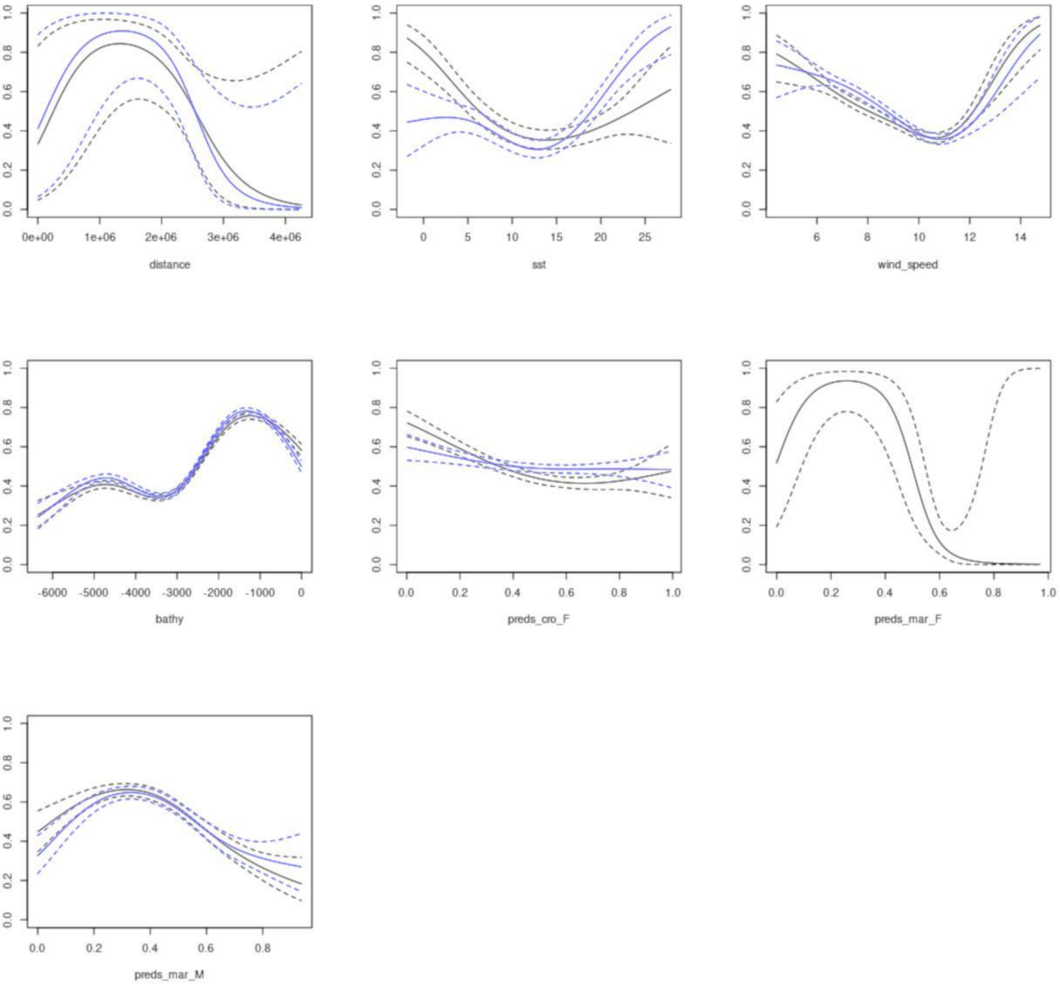

Fig. S3: For the Crozet males model, investigating the effect of removing the most correlated competition covariates, on the other covariates probability estimates. Full model outputs (all covariates) are in black and model estimates without the Marion females competition covariate are in blue.

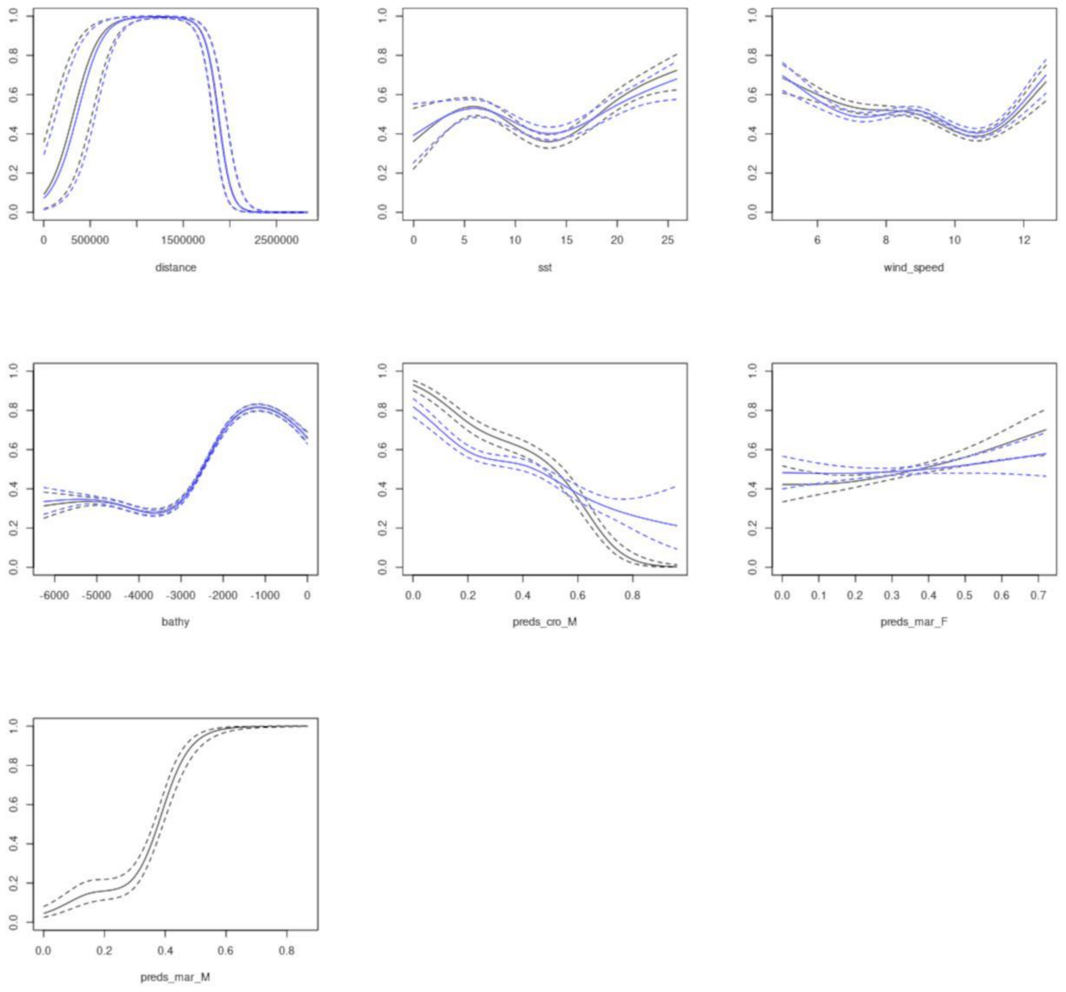

Fig. S4: For the Crozet females model, investigating the effect of removing the most correlated competition covariates, on the other covariates probability estimates. Full model outputs (all covariates) are in black and model estimates without the Marion males competition covariate are in blue.

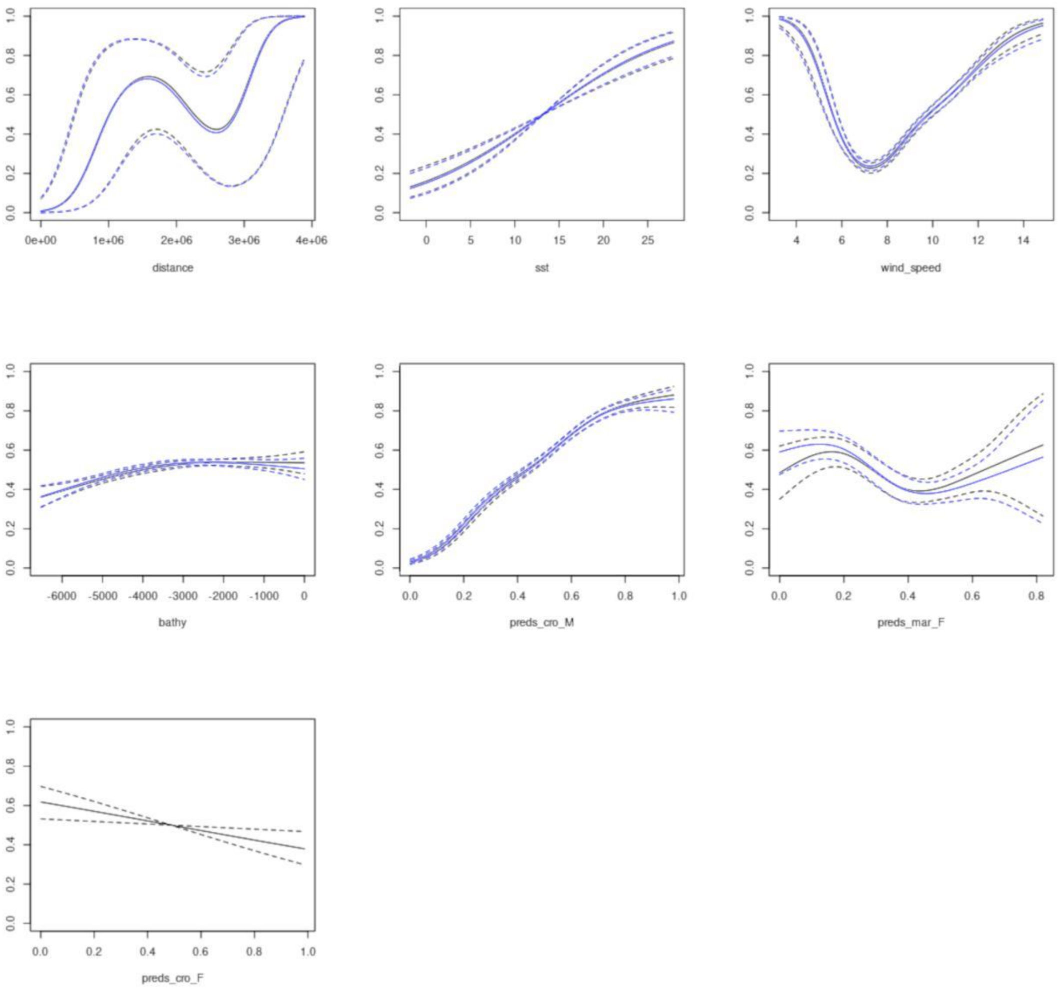

Fig. S5: For the Marion males model, investigating the effect of removing the most correlated competition covariates, on the other covariates probability estimates. Full model outputs (all covariates) are in black and model estimates without the Crozet females competition covariate are in blue.

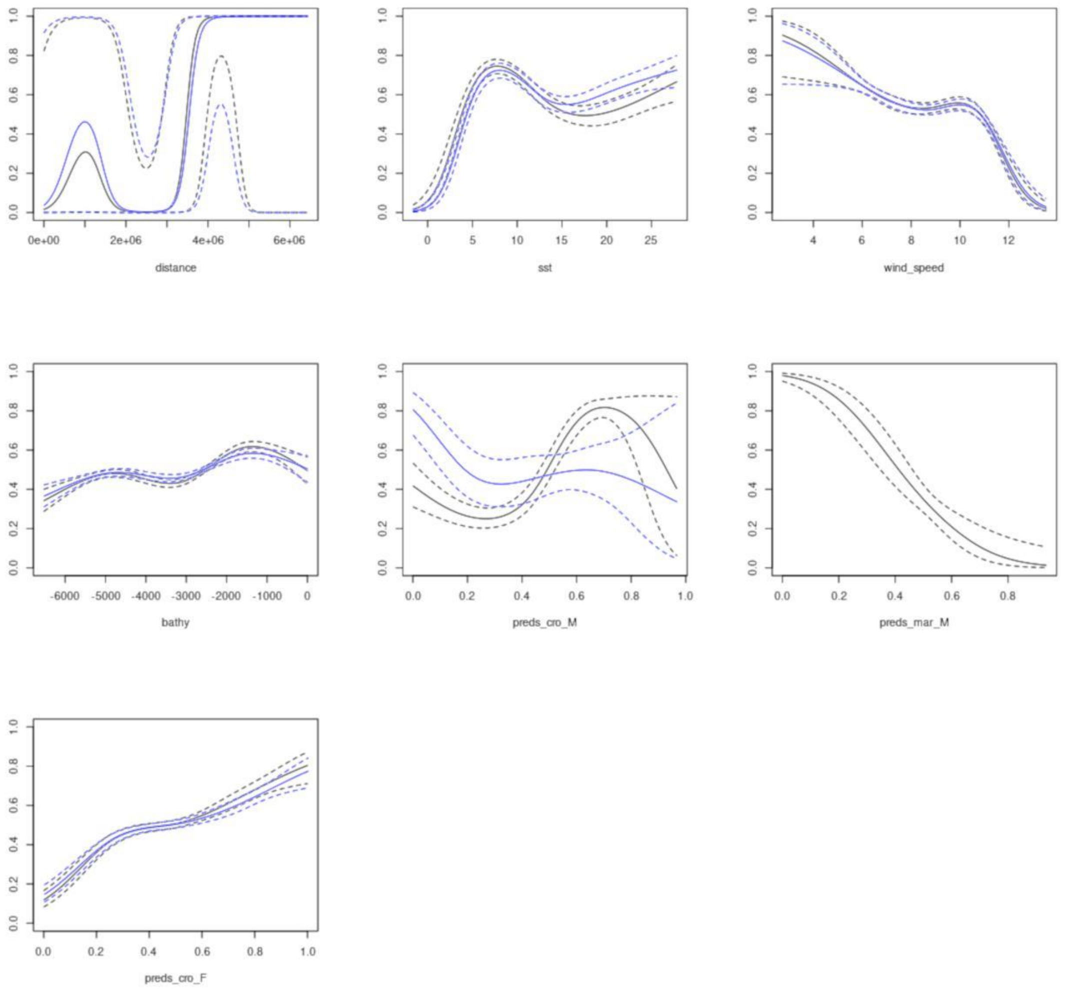

Fig. S6: For the Marion females model, investigating the effect of removing the most correlated competition covariates, on the other covariates probability estimates. Full model outputs (all covariates) are in black and model estimates without the Marion males competition covariate are in blue.

Table S3: For Crozet males, outputs from models of occurrence probabilities against environmental, accessibility and competition covariates (best GAMM with deviance explained of 25%).

Crozet Males

parametric coefficients

term	estimate	std.error	statistic	p.value
(Intercept)	-8.02	0.888	-9.03	1.70E-19
yr2017	0.829	0.358	2.32	2.05E-02
yr2018	0.00323	0.31	0.0104	9.92E-01
yr2019	0.656	0.287	2.29	2.22E-02

smooth terms

term	edf	ref.df	statistic	p.value
s(distance)	3.31	3.78	107	2.36E-13
s(sst)	3.37	3.8	62.1	3.61E-10
s(wind_speed)	3.81	3.98	144	7.07E-30
s(bathy)	3.98	4	699	3.45E-149
s(mu.x,mu.y)	28.2	28.8	2749	0
s(id)	50.2	51	4983	1.01E-22
s(preds_cro_F)	3.02	3.47	68.3	1.80E-12
s(preds_mar_F)	3.02	3.17	188	3.54E-32
s(preds_mar_M)	3.66	3.94	118	3.73E-24

Table S4: For Crozet females, outputs from models of occurrence probabilities against environmental, accessibility and competition covariates (best GAMM with deviance explained of 28%).

Crozet Females

parametric coefficients

term	estimate	std.error	statistic	p.value
(Intercept)	-3.06	0.347	-8.81	1.22E-18
yr2017	0.276	0.299	0.924	3.56E-01
yr2018	0.154	0.285	0.542	5.88E-01
yr2019	-0.0257	0.259	-0.0992	9.21E-01

smooth terms

term	edf	ref.df	statistic	p.value
s(distance)	3.96	3.99	334	2.11E-69
s(sst)	3.89	3.99	103	1.12E-21
s(wind_speed)	3.91	4	92	3.47E-19
s(bathy)	3.99	4	793	2.92E-170
s(mu.x,mu.y)	28.4	28.9	1750	0
s(id)	61.2	62	14568	1.05E-60
s(preds_cro_M)	3.8	3.97	179	2.00E-37
s(preds_mar_F)	2.52	3.11	15.9	1.43E-03
s(preds_mar_M)	3.83	3.98	123	9.91E-26

Table S5: For Marion males, outputs from models of occurrence probabilities against environmental, accessibility and competition covariates (best GAMM with deviance explained of 27%).

Marion Males

parametric coefficients

term	estimate	std.error	statistic	p.value
(Intercept)	-1.49	0.459	-3.26	0.00113
yr2017	-0.0449	0.432	-0.104	0.917
yr2018	0.244	0.401	0.609	0.543
yr2019	0.355	0.41	0.866	0.387

smooth terms

term	edf	ref.df	statistic	p.value
s(distance)	3.87	3.97	256	2.70E-48
s(sst)	1	1	43.9	3.50E-11
s(wind_speed)	3.95	4	323	1.56E-68
s(bathy)	2.67	3.21	46.5	9.66E-10
s(mu.x,mu.y)	28.2	28.9	2163	0
s(id)	22.7	24	3045	3.81E-43
s(preds_mar_F)	3.54	3.86	48.9	5.76E-08
s(preds_cro_F)	1	1	7.43	6.42E-03
s(preds_cro_M)	3.86	3.99	510	6.75E-108

Tables S6: For Marion females, outputs from models of occurrence probabilities against environmental, accessibility and competition covariates (best GAMM with deviance explained of 25%).

Marion Females

parametric coefficients

term	estimate	std.error	statistic	p.value
(Intercept)	-2.83	2.23	-1.27	0.205
yr2017	0.506	0.32	1.58	0.113
yr2018	0.796	0.304	2.62	0.0088
yr2019	1.04	0.286	3.64	0.000274

smooth terms

term	edf	ref.df	statistic	p.value
s(distance)	3.58	3.76	150	6.68E-30
s(sst)	3.97	4	199	1.74E-41
s(wind_speed)	3.89	3.99	85.2	1.87E-17
s(bathy)	3.94	4	88.2	9.90E-18
s(mu.x,mu.y)	28.5	28.8	2842	0
s(id)	39.4	41	16994	9.51E-57
s(preds_mar_M)	2.35	2.9	86.1	1.80E-18
s(preds_cro_F)	3.83	3.98	116	5.21E-24
s(preds_cro_M)	3.83	3.98	207	9.02E-44

Relations entre oiseaux marins et pêcheries : Albatros sentinelles de l'océan Austral

La 6ème crise majeure d'extinction des espèces qui sévit actuellement n'épargne pas les oiseaux marins, notamment les albatros. Leurs populations ont chuté de 70% au cours des 60 dernières années essentiellement par mortalité dans les palangriers. Les grands albatros couvrent d'énormes distances pendant leurs trajets de recherche alimentaire et leur curiosité et leur opportunisme favorisent les rencontres régulières avec des bateaux. Ils constituent ainsi des modèles privilégiés pour étudier les relations entre les oiseaux marins et les pêcheries. Au cours de cette thèse, grâce au développement de nouveaux prototypes de balises déployés sur les albatros hurleurs et d'Amsterdam de l'océan Indien et à de nouvelles méthodes d'estimation du risque de captures accidentelles, nous avons pu démontrer que les comportements de recherche alimentaire naturels diffèrent de ceux associés à un bateau. De même, les caractéristiques intrinsèques des oiseaux (espèce, population, sexe, âge et personnalité) entrainent des différences d'exposition au risque de captures accidentelles notamment par l'utilisation d'habitats différents. Enfin nous avons mis en évidence que les caractéristiques des bateaux avaient également une forte influence sur ce risque de captures accidentelles, notamment par le type de bateaux rencontrés, leur légalité, les pratiques utilisées et la présence de rejets de pêche. Nous concluons par la présentation de nouvelles méthodes pour mieux estimer le risque de captures accidentelles et la nécessité de connaissances fondamentales des espèces et populations pour mieux protéger les milieux marins toujours plus en danger.

Mot clés : AIS ; capture accidentelle ; écologie alimentaire ; interaction bateau ; prise accessoire ; télémétrie

Relations between seabirds and fisheries: Albatrosses as sentinels of the Austral Ocean

The current 6th major species extinction crisis is also affecting seabirds, especially albatrosses. Their populations have decreased by 70% over the last 60 years, mainly due to mortality in longline fisheries. Large albatrosses cover enormous distances during their foraging trips and their curiosity and opportunism favour regular encounters with boats. Thus, they constitute privileged models for studying the relationships between seabirds and fisheries. During the course of this thesis, thanks to the development of new prototype loggers deployed on Wandering and Amsterdam albatrosses in the Indian Ocean and new methods for estimating by-catch risks, we were able to observe that natural foraging behaviours differ from those associated with a boat. Similarly, the intrinsic characteristics of birds (species, population, sex, age and personality) lead to differences in exposure to by-catch risk, particularly through the use of different habitats. Finally, we have shown that the characteristics of boats also have a strong influence on the risk of by-catch, in particular through the type of boats encountered, their legality, the fishing practices used and the presence of discards. We conclude by presenting new methods to better estimate the risks of by-catch and the need for fundamental knowledge of species and populations in order to better protect marine environments that are increasingly endangered.

Keywords: AIS; biologging; boat interaction; by-catch; foraging ecology

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