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Solène Derville

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Sorbonne Université

Ecole doctorale ED129 Sciences de l'Environnement
Institut de Recherche pour le Développement, UMR Entropie
Ecologie Marine Tropicale des Océans Pacifique et Indien

Écologie spatiale des baleines à bosse en zone de reproduction : habitats, distribution et mouvements dans le Pacifique Sud

*Spatial ecology of humpback whales in breeding areas: habitats,
distribution and movements in the South Pacific*

Par Solène Derville

Thèse de doctorat en sciences de l'environnement,
Spécialité : Ecologie Marine

Présentée et soutenue le 3 décembre 2018

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Abstract

Understanding the social and environmental drivers of the distribution and movements of marine megafauna is essential to their conservation. Cetaceans are elusive and mobile species, whose management requires an improved understanding of habitat use patterns. This thesis is aimed at investigating the spatial ecology of an endangered population of humpback whales (*Megaptera novaeangliae*) in the South Pacific Ocean. Using a multidisciplinary dataset collected between 1995 and 2018 in New Caledonia and Oceania, this thesis addressed three objectives, 1) investigate best practices to cetacean species distribution modeling, 2) acquire fundamental knowledge on the distribution, habitats and movements of humpback whales in Oceania breeding grounds, and 3) predict priority conservation areas and potential threats to humpback whales. Modeling the distribution of a migratory large whale from non-systematic visual survey and citizen science data provided valuable space-use predictions when uneven survey effort and statistical overfitting were specifically addressed. Generalized Additive Models were favored for their complexity trade-off, ecological interpretability and transferability. Models of habitat use revealed a preference for a diversity of shallow habitats (low island and atoll lagoons, barrier reef and high island slopes, banks and seamounts) spread over a relatively large thermal range over Oceania. Shallow seamounts and banks were identified as major breeding and nursing habitats and play a key role in the connectivity within and between populations. This unique and unexpected use of pelagic waters has important consequences for the spatial management of humpback whales. The predictions of present and future suitable humpback whale breeding habitats at multiples scales provide science-based evidence for priority conservation areas, and enable mitigation of threats from anthropogenic activities and climate change in the South Pacific.

Key words: Humpback whale, Species Distribution Models, Movements, Habitat mapping, Spatial management

Résumé

Comprendre les facteurs sociaux et environnementaux de la distribution et des mouvements de la mégafaune marine est essentiel à sa conservation. Les cétacés sont des espèces rares et mobiles, dont la gestion nécessite une meilleure compréhension des habitats qu'ils occupent. Cette thèse a eu pour but d'étudier l'écologie spatiale d'une population en danger de baleines à bosse (*Megaptera novaeangliae*) dans l'océan Pacifique Sud. En utilisant un ensemble de données multidisciplinaires collecté entre 1995 et 2018 en Nouvelle-Calédonie et en Océanie, cette thèse a poursuivi trois objectifs : 1) étudier les meilleures pratiques de modélisation de la distribution des cétacés, 2) acquérir une meilleure compréhension de la distribution, des habitats et des mouvements des baleines à bosse dans leur zone de reproduction d'Océanie, 3) prédire les zones de conservation prioritaires et les menaces potentielles pour les baleines à bosse dans cette région. La modélisation de la distribution d'une grande baleine migratrice à partir de données de recherche non systématique et issues de la science participative a fourni des prédictions de bonne qualité, tant que l'hétérogénéité spatiale de l'échantillonnage et la tendance statistique au surapprentissage étaient correctement prises en compte. Les modèles additifs généralisés ont été privilégiés pour leur équilibre en termes de complexité des relations modélisées, leur rendu écologiquement explicite et leur capacité de transférabilité. Les modèles d'utilisation de l'habitat à différentes échelles spatiales ont révélé une préférence pour une diversité d'habitats peu profonds répartis dans une large gamme de température des eaux en Océanie. Les monts sous-marins et bancs peu profonds ont été identifiés comme d'importants habitats de reproduction et de développement pour les baleineaux. Ces reliefs sous-marins jouent également un rôle clé dans la connectivité au sein et entre les populations. Cette utilisation unique et inattendue de l'habitat pélagique a des conséquences importantes sur la gestion spatiale des baleines à bosse. La prédiction des habitats de reproduction présents et futurs à des échelles multiples fournit une base scientifique pour la désignation de zones de conservation prioritaires et la protection contre les menaces générées par les activités humaines et le changement climatique dans le Pacifique Sud.

Mots clés : Baleine à bosse, Modèles de distribution d'espèces, Déplacements, Cartographie d'habitats, Gestion spatiale

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Scientific contributions

First author publications

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Derville, S., Torres, L. G., Iovan, C., and Garrigue, C. (2018) Finding the right fit: Comparative cetacean distribution models using multiple data sources and statistical approaches. *Diversity and Distribution*. doi: 10.1111/fog.12163

Derville, S., Torres, L. G., Albertson, R., Andrews, O., Baker, C. S., Carzon, P., Constantine, R., Donoghue, M., Duthiel, C., Gannier, A., Oremus, M., Poole, M. M., Robbins, J., Garrigue, C., (In review) Whales in warming water: assessing breeding habitat diversity and adaptability in Oceania's changing climate. *Global Change Biology*.

Derville, S., Torres L. G., and Garrigue, C. (In review) From land and sea, long-term data reveal persistent humpback whale breeding habitat in New Caledonia. *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Other publications

Chero, G., Pradel, R., Gimenez, O., Bonneville, C., **Derville, S.**, Garrigue, C. (In review) High breeding capacity highlights recovery potential of humpback whale populations in the Southern hemisphere. *Biological conservation*.

International conferences

Derville, S., Aucan, J., Le Gendre, R., Menkes, C., Oremus, M., Torres, L. G., Garrigue, C. (2017) Why do humpback whales aggregate around seamounts in South Pacific tropical waters? New insights from diving behaviour and ocean circulation analyses. 22nd Biennial Conference on the Biology of Marine Mammals, Halifax, Canada.

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Workshops

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Garrigue, C., Constantine, R., **Derville, S.**, Dodémont, R., Perard, V. (2016) Kermadec Islands constitute a migratory corridor for the humpback whales breeding in New Caledonia. In B Golder and A Connell (Eds.) Proceedings of Kermadec - Discoveries and Connections. Paper presented at Kermadec - Discoveries and Connections, Wellington, New Zealand. p51-53. The Pew Charitable Trusts.

Derville, S., & Garrigue, C. 2017. Synthèse des études sur les dynamiques de distribution des baleines à bosse dans le Grand Lagon Sud de la Nouvelle-Calédonie. Rapport non publié pour le CCCE, Vale. 67p

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Garrigue, C., Bonneville, C., **Derville, S.**, Dodemont, R., Oremus, M., Pérard, V., Schmidt N., Williamson, M., (2018) Field work report for the 2017 humpback whale expedition in the Chesterfield-Bellona MARACAS 3. 28p.

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Glossary of abbreviations

ARGOS	Advanced Research and Global Observation Satellite
BRT	Boosted Regression Tree
DTSI	Direction des Technologies et des Services de l'Information
EEZ	Economic Exclusive Zone
ENSO	El Niño Southern Oscillation
GAM	Generalized Additive Model
GEBCO	General Bathymetric Chart of the Ocean
GIS	Geographic Information Systems
GLM	Generalized Linear Model
GPS	Global Positioning System
IMMA	Important Marine Mammal Areas
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
KDE	Kernel Density Estimate
MPA	Marine Protected Area
MARACAS	Marine Mammals of the Coral Sea surveys
NASA	US National Aeronautics and Space Administration
NOAA	US National Oceanic and Atmospheric Administration
RF	Random Forests
SAM	Southern Annular Mode
SDM	Species Distribution Model
SOI	Southern Oscillation Index
SPWRC	South Pacific Whale Research Consortium
SVM	Support Vector Machines

Foreword

This work was primarily based on data collected by the NGO Opération Cétacés. A long-term monitoring has been ongoing for more than 20 years in the South Lagoon, where I participated in this fieldwork in 2015 and 2016. The Comité Consultatif Coutumier Environnemental participated in funding the analysis of this data. In addition, this PhD was conducted as part of the WHERE project (Humpback Whale Habitat Exploration to improve spatial management in the natural park of the CoRal Sea) launched in 2015. Between 2015 and 2018, I participated in five out of six research cruises 'MARACAS' (MARine mAMMALS of the CorAl Sea, doi: [10.17600/17003700](https://doi.org/10.17600/17003700)). This project and the MARACAS surveys were funded by the Ministère de la Transition Ecologique et Solidaire, the New Caledonian Government, the World Wildlife Fund for Nature and the NGO Opération Cétacés. I was personally awarded the Louis M. Herman Research Scholarship by the Society for Marine Mammalogy to conduct part of this research. In addition, I received financial support by the French Ministry for Europe and Foreign Affairs (Fond Pacifique grant), under collaboration with the Secretariat of the Pacific Regional Environment Programme (SPREP). These funds, along with a collaboration with members of the South Pacific Whale Research Consortium, provided the opportunity to extend the study of humpback whale distribution to the South Pacific Ocean and participate in the 'Whales in a Changing Ocean' conference in Tonga. Finally, most of my time was spent at the Institut de Recherche pour le Développement in Nouméa, New Caledonia (UMR Entropie). I also spent a total of five months in the Marine Mammal Institute of the Oregon State University (US). My regular trips to Oregon allowed a close collaboration with Dr Leigh Torres, who welcomed me in the Geospatial Ecology of Marine Megafauna Lab and greatly contributed to the supervision of this PhD.



Synthèse des travaux en français

1. Contexte et objectifs

L'étude de la distribution des espèces et des liens entretenus avec leur environnement est un pilier de l'écologie. Fondée sur le concept de niche écologique (Hutchinson, 1957), la modélisation des distributions permet de décrire les habitats occupés par une espèce et de prédire leur distribution géographique à plus ou moins grande échelle. La production de cartes de distribution est ainsi essentielle à la mise en place de mesures de conservation d'espèces rares ou en danger d'extinction.

Les cétacés représentent une part importante des espèces dites de la « mégafaune marine ». A ce jour, 89 espèces de cétacés vivent de par le monde, assurant leur rôle de prédateurs supérieurs au sein d'une grande variété d'écosystèmes marins. Des eaux côtières aux plus pélagiques, les cétacés sont exposés à diverses menaces d'origine humaine : chasse, prise accessoire, collisions avec des navires, pollution, dégradation des habitats et changement climatique (Parsons *et al.*, 2013a; Avila *et al.*, 2018). La protection de ces espèces repose en grande partie sur la mise en place d'Aires Marines Protégées (AMP) de grande envergure (Wilhelm *et al.*, 2014; O'Leary *et al.*, 2018). Cependant, ces AMPs doivent inclure les habitats essentiels des espèces concernées pour pouvoir les protéger avec succès. Etant généralement rares, difficiles à observer en mer et très mobiles, les cétacés sont des espèces en danger dont les déplacements et habitats sont souvent méconnus. La collecte de données multidisciplinaires et l'utilisation d'outils de modélisation adaptés sont donc cruciales pour permettre la conservation de ces espèces.

La baleine à bosse (*Megaptera novaeangliae*) est une espèce appartenant à la famille des Balaenopteridae, ou rorquals. Elle est cosmopolite (observée dans tous les océans du globe) et réalise chaque année l'une des plus grandes migrations du règne animal (Robbins *et al.*, 2011). En effet, la majorité des baleines à bosse se déplace entre des zones d'alimentation estivales situées à proximité des pôles et des zones de reproduction et de mise bas hivernales situées sous les tropiques (Johnson and Wolman, 1984). Les avantages évolutifs à réaliser ces migrations de grande ampleur sont encore mal connus mais semblent partagés avec d'autres espèces de mysticètes (ou baleines à fanons). Thermorégulation des baleineaux, saisonnalité des proies, et pression de prédation sont autant d'hypothèses émises pour expliquer le comportement migratoire des grandes baleines (Brodie, 1975; Corkeron and Connor, 1999; Clapham, 2000b), dont les déplacements de la baleine à bosse forment l'archétype. De par ce comportement saisonnier migratoire, les baleines à bosse de l'hémisphère sud et de l'hémisphère nord sont isolées et génétiquement distinctes. Au sein de chaque hémisphère,

plusieurs populations et sous-populations sont distinguées et gérées comme des entités séparées à des fins de conservation (Jackson *et al.*, 2014, 2015).

En effet, la baleine à bosse a été tout particulièrement touchée par les chasses industrielles de la fin du XIX^{ème} siècle et du début du XX^{ème} (Parsons *et al.*, 2013b). A l'échelle du globe, les populations de baleines à bosse ont été en grande partie décimées, et ce, particulièrement dans l'hémisphère sud (IWC, 1998). En 1986, les pays membres de la Commission Baleinière Internationale (CBI) ont signé un moratoire permettant un arrêt (provisoire) des chasses. Depuis, la plupart des populations de baleines à bosse ont montré des signes de rétablissement encourageants, qui ont amené l'Union Internationale pour la Conservation de la Nature (UICN) à reclasser l'espèce comme « préoccupation mineure » à l'échelle mondiale. Cependant, certaines petites populations à faible taux d'accroissement demeurent « en danger » d'extinction (Childerhouse *et al.*, 2009) : la population du golfe d'Arabie et celle d'Océanie.

La baleine à bosse est aujourd'hui une espèce charismatique, particulièrement appréciée par le public. Chaque année, des milliers de personnes effectuent des sorties en mer de « whale-watching » pour observer ces animaux (O'Connor *et al.*, 2009; Cisneros-Montemayor *et al.*, 2010). Cette activité touristique en croissance représente un important débouché économique, notamment pour les pays insulaires (Orams, 2002; Hoyt, 2005; Schaffar and Garrigue, 2007). Les enjeux entourant l'étude de la distribution et du comportement de ces grandes migratrices sont donc tout à la fois scientifiques, conservationnistes, culturels et économiques.

L'océan Pacifique Sud est l'une des régions les plus riches du globe en terme de biodiversité (Tittensor *et al.*, 2010; Ceccarelli *et al.*, 2013). Ce vaste océan est recouvert d'une multitude d'îles, atolls et monts sous-marins qui attestent de l'intense activité tectonique et volcanique de cette région. Ces reliefs forment autant d'habitats tropicaux et sub-tropicaux susceptibles d'accueillir des baleines à bosse pendant leur saison de reproduction et de mise bas hivernale (Dawbin, 1966). Les sites de reproduction de la population de baleines à bosse d'Océanie s'étendent ainsi de l'ouest de la Nouvelle-Calédonie à l'est de la Polynésie Française, et de l'équateur à approximativement 30°S de latitude. Cette population classée comme « en danger » par l'UICN compte environ 6,404 individus (intervalle de confiance : 5,491-7,595; Jackson *et al.*, 2015) et enregistrait un taux de reconstitution de 47 % en 2015 comparé à ses effectifs pré-chasses industrielles.

La population de baleines à bosse d'Océanie est géographiquement structurée en sous-populations qui forment des entités génétiques et démographiques distinctes (Olavarría *et al.*, 2007; Childerhouse *et al.*, 2009) affichant des degrés variables de connectivité (Garrigue *et al.*, 2011a; Steel *et al.*, 2017). En particulier, les baleines à bosse de Nouvelle-Calédonie, considérées comme appartenant au sous-stock E2 selon la classification de la CBI, sont à la frontière entre la population Est Australienne et le reste de la population Océanienne. La Nouvelle-Calédonie, collectivité française située au sein de la Mer de Corail, est le lieu de regroupement annuel d'une population d'environ 500 baleines (estimations de 2008; Garrigue *et al.*, 2012). Cette petite population est relativement isolée des populations voisines, ce qui accroît sa vulnérabilité (Garrigue *et al.*, 2004a; Olavarría *et al.*,

2007; Garrigue *et al.*, 2011a).

La connaissance des habitats occupés par les baleines à bosse en Océanie est principalement limitée à quelques sites (e.g., Vava'u à Tonga et Tutuila aux Samoa Américaines; Lindsay *et al.*, 2016). Les eaux relativement chaudes et les abris procurés par les eaux côtières et peu profondes des îles d'Océanie semblent constituer un environnement favorable aux regroupements hivernaux. Cependant, l'utilisation de l'espace pélagique, durant la migration ou à des fins de reproduction, est encore trop peu explorée. En Nouvelle-Calédonie, le suivi satellitaire de baleines à bosse a permis de mettre en évidence l'utilisation de monts sous-marins et de récifs éloignés des côtes (Garrigue *et al.*, 2015). Or, le Parc Naturel de la mer de Corail a justement été créé en 2014 afin de protéger l'intégralité des eaux de la zone économique exclusive de Nouvelle-Calédonie, jusque dans ces zones les plus reculées. Dans ce contexte, il apparaît essentiel d'appréhender l'ensemble de la diversité des habitats occupés par les baleines à bosse afin de pouvoir protéger ces grandes migratrices.

Cette thèse comprend une introduction générale, cinq chapitres basés sur des articles publiés ou en cours de publication, et une discussion générale. Les chapitres 2 à 6 s'échelonnent selon une échelle spatiale croissante, du Lagon Sud de Nouvelle-Calédonie à l'ensemble de l'Océanie, et répondent à trois objectifs majeurs :

- 1. Effectuer une recherche méthodologique des approches de modélisation des distributions de cétacés appliquée au cas de la baleine à bosse.**
- 2. Acquérir des connaissances fondamentales sur l'écologie des baleines à bosse durant leur saison de reproduction.**
- 3. Appliquer les connaissances d'écologie spatiale à la conservation des baleines à bosse dans le Pacifique Sud.**

2. Suivi de long-terme d'un site de reproduction de baleines à bosse dans le Lagon Sud de Nouvelle-Calédonie

Le suivi de long-terme des populations est essentiel à la compréhension et à la protection d'espèces longévives. En Nouvelle-Calédonie, un suivi régulier de la population de baleines à bosse a été effectué depuis 1995 sur le site de reproduction côtier du Lagon Sud. Une méthode originale de collecte de données combinant l'observation par bateau et l'observation terrestre depuis le site du Cap N'Doua a permis de maximiser le taux d'observation. Entre 1995 et 2017, 2651 groupes de baleines ont ainsi pu être observés dans le Lagon Sud, dont 1167 par les observateurs à terre et 1484 par les observateurs en mer (parmi lesquels 30 % avait initialement été détectés depuis la terre). Ces observations dénotent une présence persistante sur ce site côtier. La composition sociale des groupes est relativement constante d'une année à l'autre, en moyenne 32 % de paires d'individus adultes, 25 % de baleines solitaires, 14 % de groupes compétiteurs, 17 % de mères-baleineau avec ou sans

escortées et 6 % de mâles chanteurs. Le taux de rencontre général (nombre de baleines observées par heure d'effort) est à l'augmentation (16.9 % entre 1995-2003 et 2012-2017). Les baleines occupent principalement les eaux situées entre le Cap N'Doua, l'île Ouen et le récif Gué, entre 10 et 200 m de profondeur et ouvertes sur l'océan. Cette zone d'utilisation préférentielle est caractérisée par des eaux à la température relativement froide (22°C) et stable en hiver austral. Les eaux très peu profondes situées au sein de certains complexes récifaux denses sont peu utilisées par les baleines à bosse. Ainsi, très peu d'observations ont été réalisées dans la réserve intégrale Merlet, principalement récifale. De façon générale, les aires marines protégées de la zone ne constituent pas une protection efficace pour ces cétacés. La croissance des activités industrielles et touristiques dans le lagon calédonien pourrait représenter une menace pour les baleines à bosse qui viennent s'y reproduire et mettre bas. Cette étude apporte donc des éléments importants qui permettront d'améliorer les mesures de gestion dans le Lagon Sud de la Nouvelle-Calédonie.

3. Ségrégation sociale des femelles suitées en zone côtière et pélagique dans le sud de la Nouvelle-Calédonie

Comme le montre le chapitre 2, les baleines à bosse sont bien connues pour leur utilisation des eaux côtières durant la période de reproduction, en particulier les femelles accompagnées d'un baleineau. En revanche, leur usage du milieu océanique demeure méconnue. En Nouvelle-Calédonie les baleines à bosse occupent les écosystèmes côtiers et pélagiques : entre autres le complexe récifal du Lagon Sud et les monts sous-marins offshore tels que le mont sous-marin d'Antigonia et le banc de la Torche situés au sud-est de la Nouvelle-Calédonie. La répartition spatiale et l'utilisation des habitats par les femelles suitées ont été analysées sur la base de 20 ans d'observations réalisées au cours de missions de recherche en mer dans le Lagon Sud et sur les monts sous-marins. De 1995 à 2015, 206 groupes comprenant un baleineau ont été observés dans le Lagon Sud et 74 sur les monts sous-marins. Dans le Lagon Sud, les groupes avec baleineau ont été plus fréquemment observés dans les eaux peu profondes et proches des côtes que les autres groupes sociaux. En revanche, cette ségrégation sociale n'a pas été observée sur les monts sous-marins, où les groupes avec baleineau ne sont pas spatialement isolés des autres types de groupes sociaux. La proportion de groupes avec baleineau y était également plus élevée. L'analyse comparative de photographies de baleineaux collectées dans ces deux écosystèmes suggère une utilisation des monts sous-marins à une phase plus tardive de leur développement : les mères pourraient préférentiellement s'éloigner des côtes lorsque leur baleineau est suffisamment grand pour affronter les conditions du large. De plus, alors que les mères évitent tout contact avec d'autres baleines dans le Lagon Sud, cette ségrégation n'est pas observée à Antigonia où elles sont plus fréquemment accompagnées d'une ou plusieurs escortes mâles. Dans l'ensemble, cette différence de comportement soulève donc de nouvelles questions quant aux facteurs environnementaux et sociaux qui poussent les baleines à bosse à se regrouper sur les monts sous-marins au large des côtes Néo-Calédoniennes.

4. Modélisation des habitats de reproduction à partir de données multi-sources

Prédire la distribution des cétacés à grande échelle est une étape essentielle pour assurer leur conservation. Cependant la modélisation de cette distribution est limitée par la qualité et la quantité de données disponibles pour ces espèces souvent rares et difficiles à observer. Cette étude s'est donc attachée à 1) comparer les performances de plusieurs algorithmes utilisés pour modéliser la distribution de cétacés à partir de données collectées en mer de manière non-systématique, et 2) évaluer le potentiel de données de science participative pour améliorer ces prédictions. La distribution de la baleine à bosse dans la Zone Economique Exclusive de Nouvelle-Calédonie a été utilisée comme cas d'étude. Cinq approches statistiques ¹ ont été comparées afin de modéliser l'habitat préférentiel des baleines à bosse à partir de 1360 observations réalisées au cours de 14 saisons de recherches en mer. Les cinq algorithmes ont différé en termes de complexité des relations environnementales modélisées, de leur interprétation écologique, et de leur capacité d'extrapolation. Bien que la calibration des paramètres ait eu un effet important sur le résultat de chaque approche statistique, cette étude révèle une faible capacité prédictive des GLM, une difficulté d'interprétation des SVM, et une production de tendances bruitées des BRT. MAXENT et les GAM semblent proposer un équilibre en termes de complexité des relations modélisées et des distributions prédites, ainsi qu'un rendu écologiquement explicite. Dans l'ensemble, les cinq modèles suggèrent une préférence des baleines à bosse pour des eaux peu profondes (0-100 m), côtières ou pélagiques, et relativement fraîches, entre 22 et 23°C. Par ailleurs, 625 observations opportunistes ont été modélisées à l'aide d'un GAM selon trois approches dites de « presence-background ». Le but de ces approches était de corriger les modèles de distribution de baleines à bosse en prenant en compte l'hétérogénéité spatiale de l'effort d'observation du public. Les résultats mettent en avant l'intérêt des données de sciences participatives dont les tendances modélisées ont convergé avec celles des modèles issus des données de recherche scientifique. Dans l'ensemble, il apparaît que la modélisation des distributions de cétacés peut être réalisée à partir de recherche en mer non-systématique, mais aussi dans une certaine mesure à partir de science participative. L'évaluation intégrative de la qualité des modèles, la calibration d'algorithmes spécifiquement sélectionnés et la validation indépendante des résultats sont des points clés assurant la qualité des prédictions de distribution à grande échelle.

5. Impact du changement climatique sur les habitats de reproduction à l'échelle de l'Océanie

Dans le présent contexte de changement climatique, le succès des efforts de conservation de la mégafaune marine repose sur la compréhension des facteurs environnementaux affectant

¹GAM = Generalized Additive Models, GLM = Generalized Linear Models, SVM = Support Vector Machine, MAXENT = maximum entropy, BRT = Boosted Regression Trees.

leur distribution. Parmi les mammifères, les baleines à bosse effectuent les migrations saisonnières les plus longues, mais l'étendue de leur migration et de leurs habitats de reproduction demeure imprécise. Nous avons utilisé plus de 20 ans de données issues de campagne de recherche en mer provenant de 7 pays et territoires d'Océanie (1376 jours de suivi) pour étudier la diversité des habitats de reproduction des baleines à bosse dans cette vaste région et leur capacité d'adaptation aux changements climatiques. A fine échelle, l'influence majeure de la topographie du fond marin sur la distribution des baleines à bosse a été mise en évidence. Ainsi, tous les groupes sociaux ont montré une affinité pour les eaux peu profondes (< 400 m), proches des côtes ou dans les lagons coralliens, mais aussi sur des monts sous-marins et bancs offshore. Par ailleurs, les baleines à bosse utilisent des sites de reproduction présentant une large gamme de températures de surface de l'eau : de 22,3 à 27,8°C en août, avec des variations entre les années allant jusqu'à 2,0°C sur un site donné. Dans le Lagon Sud de Nouvelle-Calédonie, où le suivi des baleines à bosse a été effectué sur la plus longue durée (774 jours de suivi, 1996-2017), le taux de rencontre moyen augmente lorsque la température diminue (avec un optimum autour de 20.5°C). Cependant, cette influence de la température de surface sur la présence de baleines à bosse semble découplée de l'oscillation climatique d'El Niño et de l'oscillation Antarctique. Les projections de l'évolution des températures de l'eau pour la fin du siècle suggèrent qu'une grande partie des sites de reproduction actuels des baleines à bosse d'Océanie deviendront potentiellement inadéquats car trop chauds pour cette espèce (supérieurs au maximum de 28°C décrit par [Rasmussen et al., 2007](#)). Cependant, l'extrapolation des modèles de distribution prédit l'existence d'habitats adaptés aux baleines à bosse en dépit du réchauffement climatique. Les archipels et monts sous-marins du sud de l'Océanie pourraient constituer des zones de refuge futures. Bien que le comportement philopatryque des baleines à bosse puisse limiter leur dispersion vers de nouveaux sites de reproduction, leur apparente plasticité comportementale et la diversité des habitats disponibles favorisent leur capacité adaptative en réponse au réchauffement climatique en Océanie durant la saison de reproduction.

6. Etude des déplacements et du comportement de plongée en milieu pélagique

Les chapitres précédents ont montré la diversité d'habitats occupés par les baleines à bosse dans leur zone de reproduction d'Océanie. En particulier, l'utilisation d'eaux peu profondes (monts sous-marins et bancs) pélagiques a été mise en lumière en Nouvelle-Calédonie. Le nombre important de baleines observées dans ces eaux suggère un intérêt adaptatif encore inconnu à se rassembler dans ces habitats. Entre 2016 et 2018, 18 balises de télémétrie satellitaire ont été déployées sur des baleines à bosse adultes de sexe et de classes sociales variés, afin de mieux comprendre leur utilisation de l'espace pélagique. En particulier, ces balises ont permis d'enregistrer les déplacements le comportement de plongée de ces animaux, en plus de leurs déplacements. Les baleines ont ainsi été suivies jusqu'à 125 jours, incluant 4.8 à 33.8 jours au sein de la région de reproduction incluant les eaux de Nouvelle-Calédonie, la mer de Corail et la côte Est Australienne. Des déplacements ont été observés entre les reliefs sous-marins peu profonds situés au sud de la Nouvelle-Calédonie, ainsi

qu'entre ceux se trouvant le long de la chaîne des guyots de Lord Howe. De plus, deux mâles ont réalisé de longs déplacements longitudinaux entre la Nouvelle-Calédonie et la côte Est Australienne. La plupart des 7 986 plongées enregistrées ont eu lieu au-dessus de 80 m (88,5 %) mais des plongées profondes (> 80 m, max 616 m) ont également été régulièrement enregistrées (11,5 %), y compris par des femelles suitées. Les plongées profondes ont souvent eu lieu en série et ont été caractérisées par des formes en U et des durées relativement longues. Les profondeurs maximales observées dépassent les limites connues de plongée des baleines à bosse et supposent une dépense d'énergie importante mais dont la fonction demeure inconnue. A la lumière de la littérature existante, trois hypothèses peuvent être émises quant à l'intérêt adaptatif d'un tel comportement : une aide à l'orientation et à la navigation, le résultat d'interactions sociales entre individus, et/ou une stratégie d'alimentation opportuniste en eaux sub-tropicales. L'analyse des déplacements en milieu pélagique a souligné l'influence des monts sous-marins peu profonds (< 500 m de profondeur) sur le comportement des baleines à bosse pendant la saison de reproduction. En effet, le temps de résidence augmente à proximité des monts sous-marins (13 % de déviance expliquée) ainsi que la profondeur des plongées, dans une moindre mesure. Cette étude apporte donc un nouveau regard sur un habitat des baleines à bosse en saison de reproduction précédemment négligé. Compte tenu de l'augmentation des menaces anthropiques pesant sur les monts sous-marins en Nouvelle-Calédonie et dans le monde, ces résultats ont des implications en matière de conservation.

7. Conclusions et perspectives

La modélisation précise de la distribution et des habitats des cétacés est essentielle à la mise en place d'une gestion spatiale adaptée. Au cours de cette thèse, la baleine à bosse a été utilisée comme cas d'étude afin de comparer diverses approches pour modéliser les distributions de cétacés. Il est apparu que la calibration et le type d'algorithme choisi pour réaliser ces modèles ont un effet important sur les prédictions qu'ils fournissent. En particulier, les approches statistiques testées ont différé en termes de complexité des relations environnementales modélisées, de leur interprétation écologique, et de leur capacité d'extrapolation. Une fois ces choix méthodologiques appliqués, les données issues de recherche en mer non-systématique et de science participative peuvent être valorisées pour modéliser des distributions à grande échelle, malgré leur biais respectifs. La prise en compte des biais d'échantillonnage spatiaux est notamment une étape essentielle pour améliorer la qualité des prédictions. Les limites de nos principales méthodes de terrain, la question de la calibration et de la transférabilité des modèles de distribution de cétacés sont abordées dans la discussion (Chapitre 7).

En perspective de ce volet méthodologique, l'intérêt des approches de modélisation mécanistes (ou « process-based ») et des nouvelles technologies numériques et électroniques est abordé. En particulier, des méthodes de collecte de données prometteuses afin d'étudier la distribution des cétacés sont présentées : imagerie satellitaire, drones aériens et applications mobiles de science

participative.

L'étude de la distribution, des habitats et des déplacements des baleines à bosse dans leur région de reproduction du Pacifique Sud forme le cœur de cette thèse. Tout d'abord, l'analyse des conditions environnementales favorables à ce stade de vie de la baleine à bosse a montré une préférence marquée pour les eaux peu profondes (environ 0 - 200 m) comme habitat de regroupement. Les baleines à bosse occupent ainsi une grande diversité d'habitats peu profonds : pentes externes d'îles et de récifs barrière, lagons des îles et des atolls, bancs et monts sous-marins offshore. Un lien étroit entre baleines à bosse et monts sous-marins a été mis en évidence dans la région Néo-Calédonienne, apportant ainsi un regard nouveau sur la niche écologique occupée par ces animaux durant leur phase de reproduction.

L'analyse de la distribution des baleines à bosse en fonction de la température de surface de l'eau a montré diverses préférences dépendant de l'échelle spatio-temporelle de l'échantillonnage. Alors qu'à l'échelle de l'Océanie, elles utilisent des sites de reproduction couvrant une grande gamme de température (22.3°C – 27.8 °C en moyenne en août), une préférence pour les eaux relativement froides (21°C - 22°C) a été révélée localement dans le Lagon Sud de Nouvelle-Calédonie. La longue série temporelle disponible sur ce site a montré que cet effet de la température sur le taux de rencontre des baleines à bosse est cependant découplé des fluctuations climatiques de basse fréquence telles que le phénomène El Niño.

Par ailleurs, l'influence des facteurs sociaux sur les déplacements et la distribution des baleines à bosse a été analysée, indépendamment des facteurs abiotiques. Les résultats obtenus ont révélé que les baleines à bosse se distribuent suivant une structuration spatialement hiérarchisée à plusieurs échelles. Les individus se répartissent de façon hétérogène au sein des sites de reproduction (par ségrégation sociale des mères-baleineau). Plusieurs de ces sites sont eux-même répartis en un réseau au sein duquel les baleines réalisent des déplacements locaux fréquents. Enfin, de grands déplacements longitudinaux intra-saisonniers peuvent permettre aux baleines de rejoindre des régions de reproduction éloignées.

En perspective, les monts sous-marins de Nouvelle-Calédonie et du Pacifique Sud en général méritent de plus amples recherches afin de comprendre le rôle de ces habitats pélagiques peu connus pour les baleines à bosse. L'apport de données océanographiques et de mesures de densités des cétacés par transects linéaires apparaît comme un point clé des futures recherches à mener sur ce sujet. Par ailleurs, les recherches portant sur la connectivité de la sous-population Néo-Calédonienne avec les sites d'alimentation des eaux Antarctiques, sont identifiées comme une étape essentielle pour évaluer l'impact des changements climatiques sur l'ensemble du cycle de vie de la baleine à bosse.

Pour finir, les connaissances obtenues au cours de ces travaux sont directement applicables à la conservation et permettront d'améliorer les mesures de gestion des baleines à bosse en Nouvelle-Calédonie. Rappelons que ces dernières appartiennent à la population d'Océanie, classée comme en danger par l'UICN. Tout d'abord, le Lagon Sud de la Nouvelle-Calédonie a été confirmé comme un site côtier d'importance pour la sous-population de Nouvelle-Calédonie. Le dérangement et

les collisions qui peuvent résulter du trafic maritime et touristique dans ces eaux sont identifiés comme les principaux risques pour les baleines visitant le Lagon Sud. En particulier, les femelles accompagnées d'un baleineau préférant les habitats côtiers et peu profonds sont les plus exposées aux risques anthropiques, notamment en fin de saison hivernale (fin août - début septembre). En l'état actuel, le réseau d'AMPs du Lagon Sud ne protège que très peu ces zones occupées par les baleines à bosse. A l'échelle de la ZEE, plusieurs sites de reproduction ont été identifiés dans les eaux reculées du Parc Naturel de la Mer de Corail. En particulier, des zones à fort intérêt de conservation ont été identifiées au niveau des monts sous-marins, récifs et îles de la ride de Norfolk (Antigonia, banc de la Torche), de la ride des Loyautés (Banc de l'Orne, Walpole), des plateaux de Chesterfield-Bellona, des bancs de Faiway-Landsdowne, et de la chaîne des guyots de Lord Howe (Kelso, Capel). Ces régions ont fait l'objet de propositions au statut UICN d'Important Marine Mammal Areas. La zone des « monts sous-marins et bancs du sud de la Nouvelle-Calédonie » a définitivement acquis ce statut en 2017, et celle des « Monts sous-marins et récifs de Chesterfield-Bellona » est actuellement en attente d'une re-évaluation.

En perspective de ces découvertes, il apparaît essentiel de valider in situ les prédictions des modèles d'habitats dans le Parc Naturel de la Mer de Corail, et potentiellement même en Océanie. La chaîne des guyots de Lord Howe est ainsi la région la plus prometteuse pour une expédition exploratoire, au vu des résultats de modélisation et de télémétrie satellitaire. La collection de données individuelles in situ (photo-identification et échantillons génétiques) sur les baleines visitant les monts sous-marins de Kelso et Capel apporterait beaucoup à notre compréhension de la connectivité et des dynamiques de population de la mer de Corail. Pour finir, bien que l'exploration de nouvelles régions soit une perspective majeure de ce travail, elle ne doit pas être faite au détriment du suivi à long terme réalisé dans des sites de référence tel que le Lagon Sud de la Nouvelle-Calédonie ou l'île de Tutuila aux Samoa Américaines. En effet, seules les séries temporelles enregistrées sur de nombreuses années peuvent permettre d'appréhender l'effet des changements climatiques présents et à venir.

I. General introduction

1.1 Spatial ecology: understanding where and when species occur

The description of species diversity and distribution is deeply rooted in the history of civilizations and science. The need to understand where and when animals and plants might be observed (and harvested) goes back to the dawn of man. More than a science, the spatial ecology of organisms has always been a key knowledge for human survival. Any fisherman knows the close link between fish aggregations and tide cycles, any hunter recognizes the type of forest in which he is most likely to encounter his favorite game bird. Although in the past century the need to understand species distributions has shifted from a mostly consumerist to a conservationist goal, the fascination has remained intact. Theories and tools have emerged over the last century to understand how the geographic distribution of species is shaped by interactions among organisms and with their environment.

1.1.1 The ecological niche concept

The **niche theory** is a key concept to describe the distribution of species and understand the underlying mechanisms driving where and when a species occurs.

The niche theory has now grown to be a symbol of ecology as a field (Real and Levin, 1991). This concept was first defined by Grinnell (1928) as the 'ultimate distributional unit within which each species is held by its structural and functional limitations'. In Grinnell's definition, the geographic space in which the species lives was therefore a central characteristic of its niche, hence being later interpreted as a 'place concept of niche'. In parallel, Elton (1927) proposed a definition centered on the role played by an organism in a group: 'the status of an animal in its community', that can be interpreted as a 'functional niche concept'. Gause (1934) extended Elton's concept by adding the notion of interspecific competitive interactions. It was only by the late 1950s that Hutchinson (1957) 'concluding remarks' combined the Eltonian and Grinnellian niche concepts. Hutchinson mathematically materialized the '**fundamental niche**' as the hypervolume N describing a species' requirements in n -dimensions. The revolutionary insight of Hutchinson was therefore to transfer the niche concept from a geographic to a geometric concept. The interactions between species, or external limitations to their dispersal were introduced as restrictive drivers forcing the species to remain in a portion of its fundamental niche, a subset known as the '**realized niche**' (Fig. 1.1).

Although a major concept of theoretical ecology for a century, the niche concept is still challenged and built upon. In the last decades, it has become possible to test and question the foundations and assumptions of niche theory (e.g., Soberón and Arroyo-Peña, 2017). While Hutchinson focused on inter and intraspecific **competitive exclusion** as the main constraint to realized niches, other driving forces have been highlighted since then to explain the absence of species in otherwise suitable habitats. Among them, **dispersal limitations** may restrict species within a certain geographic or environmental space (Fig. 1.1). For instance, land masses constitute obvious barriers for marine species. Thereby, Holt (2009) introduced the problem of species dispersion, and the distinction

between the **establishment niche** and the **persistence niche** of a population. Building on the original concept of the fundamental niche, Holt introduced a metapopulation component, as species disperse and fragment into populations of varying sizes. The concept is **density-dependent**: habitats where populations can have positive intrinsic growth rate as long as their density is low, belong to the establishment niche. On the contrary, the persistence niche describes the habitats of positive density dependence, where growth rate is viable only above some threshold density. The Allee effect provides a good example of a density-dependence link to the realized niche. Operating in populations at low numbers (for instance, in establishment), the **Allee effect** describes a positive correlation between population density and growth rate, through an increased individual fitness resulting from various behavioral mechanisms such as cooperative feeding or specific anti-predator strategies (Courchamp *et al.*, 1999).

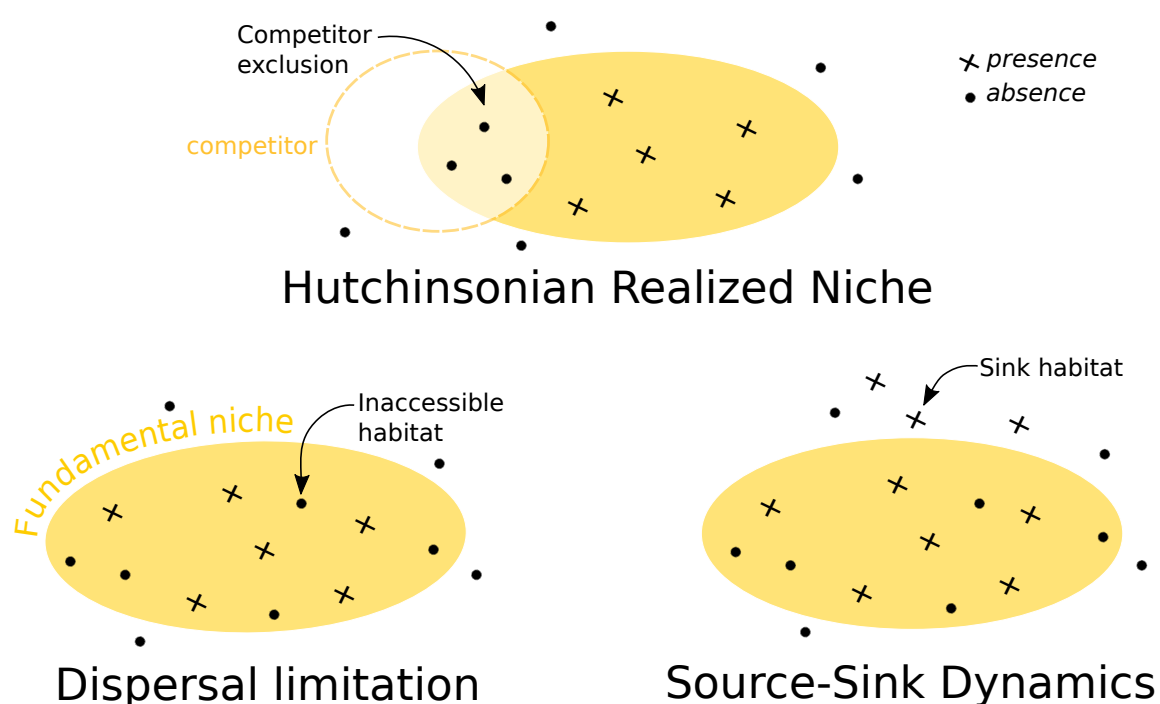


Figure 1.1 The ecological niche concept (based on Pulliam, 2000).

Another interesting expansion of the niche concept is that of the **source-sink model** (Pulliam, 1988, 2000), in which a species may also exist outside its fundamental niche (Fig. 1.1). In this view, a species' realized niche may effectively constitute a superset of its fundamental niche, rather than a subset. Pulliam suggests that in the context of a **metapopulation** composed of several connected populations, a large fraction of individuals may be living in 'sink habitats' where the intrinsic population growth rate is negative (mortality > reproduction), whereas other individuals persist in 'source habitats' where suitable conditions allow for positive growth rate (reproduction > mortality). Immigration of individuals from the productive source habitats to the unsuitable sink habitats allows for the latter to be maintained. An equilibrium may settle in the metapopulation as long as these fluxes are sustained between source and sink. Sink habitats exerting attraction on individuals to

the detriment of neighboring higher-quality habitats have been called '**ecological traps**' (Battin, 2018; Delibes *et al.*, 2001). For instance, the eastern Caribbean region has been suggested to be an attractive sink habitat for sperm whales (*Physeter macrocephalus*) to explain the discrepancy between the positive observed population growth rate and the estimated negative growth rate. Locally high mortality from anthropogenic causes coupled with immigration from neighboring populations was hypothesized (Whitehead and Gero, 2015).

These reflections further reveal the importance of considering niches through time. Indeed, the concept of **niche conservatism** describes the tendency of species to maintain some aspects of their fundamental niche over time (Wiens and Graham, 2005). Niche conservatism is an important framework to understand historical biogeography or the impact of climate change. Although this theory has been hard to test empirically (Araújo and Peterson, 2012), there is evidence that some species do seem to move in response to environmental changes within their range, to track suitable conditions into new territories. For instance, many species have shown geographic or phenological shifting in response to global warming during the last decades (e.g. global meta-analysis from 1,700 species, Parmesan and Yohe, 2003). However, the capacity of species adaptation is challenged by the rapidity with which human-induced environmental changes can occur (Sih *et al.*, 2011).

1.1.2 SDMs: the study of species distributions

Based on the study of species niches, **Species Distribution Models (SDMs)** have evolved since the 1980s to characterize the natural distribution of species and describe their relationships to the environment. These numerical tools are also referred to as bioclimatic models, climate envelopes, ecological niche models, habitat models or resource selection functions. The diverse topology used in this field results from conflicting definitions of the conceptual grounding of SDMs into the niche theory (or theories; Austin, 2002; Peterson, 2006; Soberón, 2007; Kearney and Porter, 2009).

SDMs are divided into **mechanistic and correlative models** (for reviews see Dormann *et al.*, 2012; Peterson *et al.*, 2015) with the latter being by far the most popular approach. Correlative approaches rely on statistical algorithms to fit empirical observations of species occurrence to environmental conditions. On the contrary, mechanistic approaches (also referred to as process-based, Kearney and Porter, 2009) relate functional traits (e.g., behavioral, morphological, physiological traits) to the spatial habitat occupied by a species. Hence, these approaches differ fundamentally, as defined by Dormann *et al.* (2012): 'In correlative models, parameters have no a priori defined ecological meaning and processes are implicit. In contrast, process-based models [mechanistic] are built around explicitly stated mechanisms and parameters have a clear ecological interpretation that is defined a priori'. Hence, correlative SDMs tend to be considered as a representation of the realized niche rather than the fundamental niche. They are criticized for not representing causal relationships between a species' presence and environmental variables, and even less in terms of physiological responses or direct constraints on organisms (Kearney and Porter, 2009). On the other hand, mechanistic

SDMs, because they integrate physiologically-based relationships, are more likely to capture the fundamental niche of a species. However, mechanistic approaches are based on assumptions about niche dimensions and dispersal abilities that may be hard to validate. Claims have been made that hybrid models, where both strategies are combined, are conceptually and practically superior, but they pose technical challenges and have so far rarely been applied (Boulangeat *et al.*, 2012; Dormann *et al.*, 2012; Peterson *et al.*, 2015; Sadoti *et al.*, 2017).

Although it appears essential to design and interpret SDMs with a strong conceptual ecological framework in mind, the practical tool (SDMs) and the theoretical object (the niche) should not be confused. In line with Elith and Leathwick (2009) and Mcinerny and Etienne (2012), I will simply consider the observed species distribution that is modeled in SDMs, as an outcome of its realized niche. In this sense, SDMs are modeling an approximation of part of the species' niche. It is our responsibility as ecologist to apply a 'healthy skepticism' (Elith and Leathwick, 2009) to the ecological grounding of model predictions. To this extent, I will use the neutral terminology, '**correlative SDM**', to describe any model that 'relates species distribution data (occurrence, presence-absence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations' (Elith and Leathwick, 2009). In practice, a set of geographic points in \mathbb{R}^2 ¹ is projected in an environmental space in \mathbb{R}^n , with n being the number of environmental variables of interest (e.g., depth, distance to the coast, temperature, salinity etc.; Fig. 1.2). Based on the observed species occurrence patterns at these points (whether it is present, absent or present with a measured abundance), a hypervolume can be modeled to encompass the environmental conditions suitable to the species (Blonder, 2017). This hypervolume may then be reprojected to the geographic space as a **map of suitability or presence probability** (depending on the type of data used to calibrate the model).

Rapid methodological advances have enhanced SDM capacities and applicability. The development of **Geographic Information Systems (GIS)** has greatly improved the capacity of ecologists to manipulate and analyze environmental and biological data for the purpose of modeling species-habitat relationships (Miller, 1994; Foody, 2008). However, the collection of ever larger datasets implies the need to model complex relationships over multiple scales (Benhamou, 2014). Indeed, the study of spatial and temporal processes is defined by two related concepts of scale: the **range** (or extent) and the **resolution** (or grain). Although for obvious technical reasons, these two parameters are usually inversely correlated, recent technological advances have made it possible to collect and process data over increasing extents and at ever higher resolutions (for a review of scales considered in marine environments see Witman *et al.*, 2015). But with better tools, also comes conceptual problematics, namely the chosen scale at which processes should be considered. It is not a surprise that spatio-temporal scales have become a key concept of ecology (Wiens, 1989), and a core question in species distribution modeling (Guisan and Zimmermann, 2000).

¹For any natural number n , the set \mathbb{R}^n consists of all n -tuples of real numbers (\mathbb{R}). \mathbb{R}^2 is a two dimensional space (e.g., a plane in latitude and longitude).

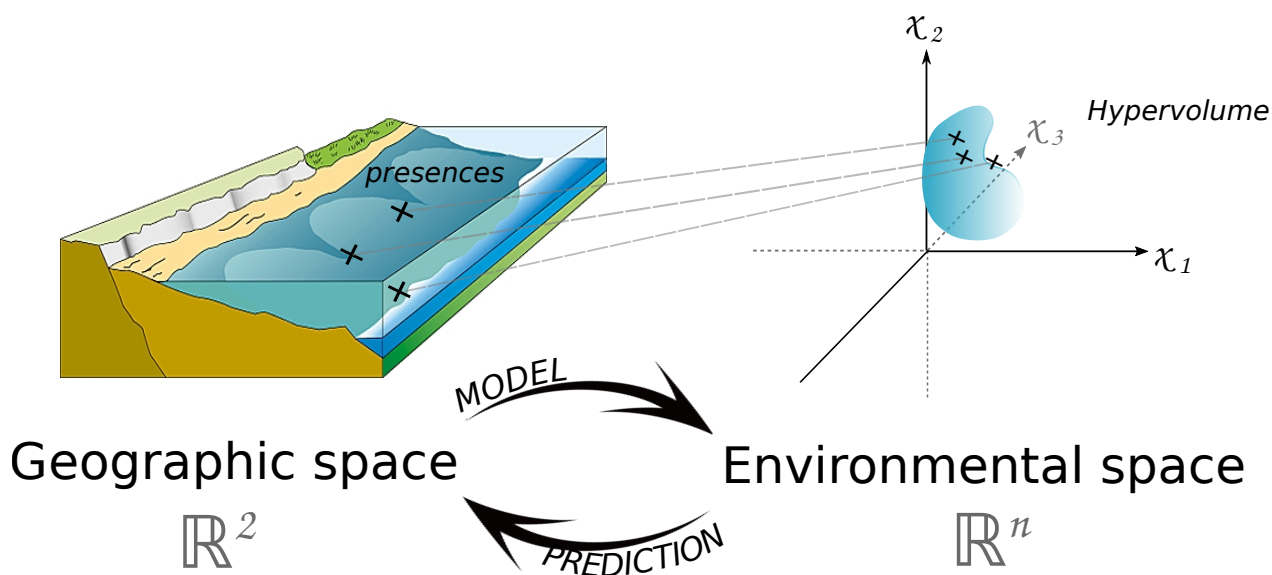


Figure 1.2 Schematic representation of Species Distribution Models. Species are observed at 'presence locations' with coordinates $\in \mathbb{R}^2$ (longitude-latitude). Each of these locations is characterized by a series of n environmental variables $\{x_1, x_2, \dots, x_n\}$ representing the environmental space $\in \mathbb{R}^n$. A species distribution can be modeled as an hypervolume in environmental space. In return, the hypervolume can be reprojected into the geographic space to predict the species distribution over the study area.

In a review of SDM, [Guisan and Thuiller \(2005\)](#) highlighted three main factors influencing species at multiple scales: the **resources** (e.g., food, mates), the **regulators** (eco-physiological parameters, e.g., temperature), and the **disturbances** (natural or human-induced perturbations of the environment, e.g., extreme climatic events). The intensity with which each of these factors influences a species distribution varies through time and space, often in a hierarchical manner. For instance, disturbances can be recurrent and/or rare events and their impact on species would only be detectable over long time frames. Moreover, food resources tend to be distributed in patches of variable sizes and quality ([Wiens, 1989](#)). Patches are dynamic through time and space, specifically in the marine environment, as food resources might go depleted or appear in response to environmental changes. The size of the study area dictates our capacity to detect the hierarchical organization of patches through space ([Barve et al., 2011](#)). Consequently, our ability to characterize a species distribution pattern is a function of the combined spatio-temporal range and resolution of sampling.

1.1.3 Integrating the species' movements

Environmental conditions and resources have complex multi-scale patterns of heterogeneity through space and time. In addition, organisms themselves do not have constant requirements throughout their life. From birth to death, and over their reproductive cycles, organisms have specific needs. **Movement** is an ubiquitous ecological process that allows organisms to cope with environmental heterogeneity and varying life-history traits ([Nathan et al., 2008](#)). Movement modes

have diversified across all major forms of life, from active displacement to passive transportation. In turn, movement is a key component of species distribution that has long been neglected in SDMs (Holloway and Miller, 2017). Indeed, modeling the distribution of mobile species constitute a challenge compared to sessile species (Elith and Leathwick, 2009), as the spatial extent at which they interact with environment may be far larger than the sampled areas.

As a result, movement is considered a key element in the **BAM diagram** (Biotic-Abiotic-Movement) conceived by (Soberón and Peterson, 2005) to characterize species distributions (Fig. 1.3). The BAM diagram represents how Biotic (B: interaction with other species), Abiotic (A: physiological tolerance to external environment / fundamental niche) and Movement (M) factors interact. M therefore represents the area accessible to the species based on its current dispersal capacities. Therefore, the intersection between suitable biotic and abiotic factors, the '**invadable distribution**' G_i , represents the species potential distribution, which may be viewed as the realized niche. Finally, the **occupied distribution** G_o is the area where the species is actually present, as a result of A, B and M. SDMs have much to gain from properly accounting for factors limiting the area accessible to a species (Holloway and Miller, 2017). The study of movement ecology may provide a better understanding of the M component through the estimation of the **navigation capacity** (traits enabling the individual to orient in space/time, e.g., sensory systems), **motion capacity** (traits enabling the execution of the movement, e.g., biomechanisms), **external factors** (e.g., geographical barriers) and **internal drivers** (internal state motivating the movement, e.g., breeding) of mobility (Nathan *et al.*, 2008; Benhamou, 2014).

Movement mechanisms are diverse and their classification is somewhat confusing. The word '**migration**' that constitutes one of the archetypal movement behavior, yet has been applied in many contexts. An early definition by Baker (1978) considered any 'act of moving from one spatial unit to another' as a migration, hence covering all types of movement. Dingle and Drake (2007) over-viewed the characteristics of migration at an individual level, rather than attempting to draw a single definition. They describe migration as an adaptation to the spatio-temporal fluctuations of resources, which supports habitat use when it is most favorable (Ramenofsky and Wingfield, 2007). Migration is often preemptive, as the organisms will be leaving a given habitat before it becomes too unsuitable. Migration may be distinguished from daily movements (e.g., foraging excursions) as it leads the individual outside its temporary home range over prolonged periods of time (permanently or seasonally) and leads to another life history phase. Migration differs from dispersion or ranging as it is characterized by an oriented movement, with a spatial determinism. Indeed, until they reach their final destination, migrating individuals may transit through suitable habitats without settling. Finally, migration often involves specific physiological adaptations (e.g., energy storage, muscle performance; Weber, 2009).

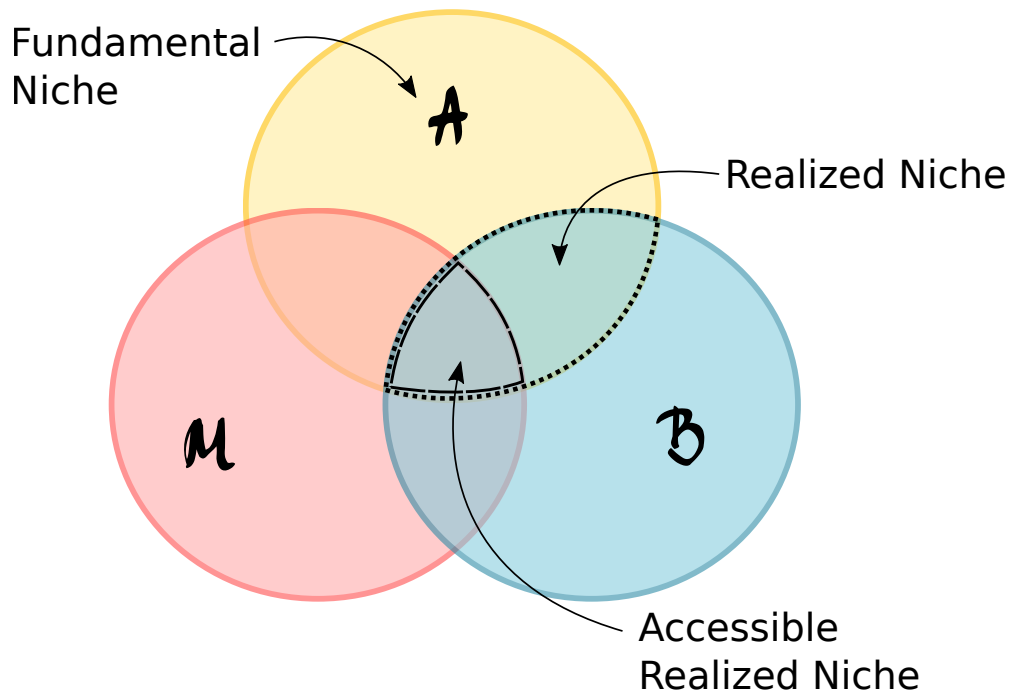


Figure 1.3 The BAM diagram based on (Soberón and Peterson, 2005). The area A represents the fundamental niche, the appropriate abiotic factors for the species. The area B represents the region with appropriate biotic interactions from the presence of other species. The intersection between A and B therefore represents the Hutchinsonian realized niche. Finally, the area M represents the region accessible to the species given its movement capacities. The intersection between A, B and M represents the portion of the realized niche that is currently accessible to the species.

1.2 Cetaceans: a case for marine megafauna species in need for conservation

Like most marine megafauna species, cetaceans are mainly wide-ranging species that occupy a diversity of marine ecosystems worldwide. Many cetaceans face anthropogenic threats and are in need for conservation. Describing and understanding their distribution, habitats and movements at multiple spatio-temporal scales is a prerequisite to efficient management.

1.2.1 General aspects

Phylogeny

To date, there are nearly 89 species of cetaceans in the world (www.marinemammal-science.org, last updated July 2017). The Cetacea infraorder (part of the Artiodactyla order) is represented by two suborders: the Mysticetes (or **baleen whales**) and the Odontocetes (or **toothed whales**). The term 'large whale' is usually used to refer to the baleen whales and sperm whales (Fig. 1.4), which share some common ecological and conservation issues.

Baleen whales are split into four families: the Balaenidae, the Neobalaenidae, the Eschrichtiidae, and the Balaenopteridae (Parsons *et al.*, 2013d). Unlike odontocetes and most terrestrial mammals, baleen whales do not have enamel-covered teeth but instead are characterized by a filter-feeder system made of keratin baleen plates. Baleen whales are also characterized by their large size: from 6 m for the pygmy right whale (*Caperea marginata*) to more than 30 m long for the blue whale (*Balaenoptera musculus*).

Adaptations to marine life

Cetaceans have conquered a great diversity of marine ecosystems (Parsons *et al.*, 2013c). They have adapted to life in a fluid environment within a variety of habitats: from the freezing waters of the Antarctic to the hot seas of the Arabian Gulf, from freshwater rivers of the Amazon to the open oceans, and from the shallow reefs and mangroves of the tropics to the deep waters of the abyssal plains.

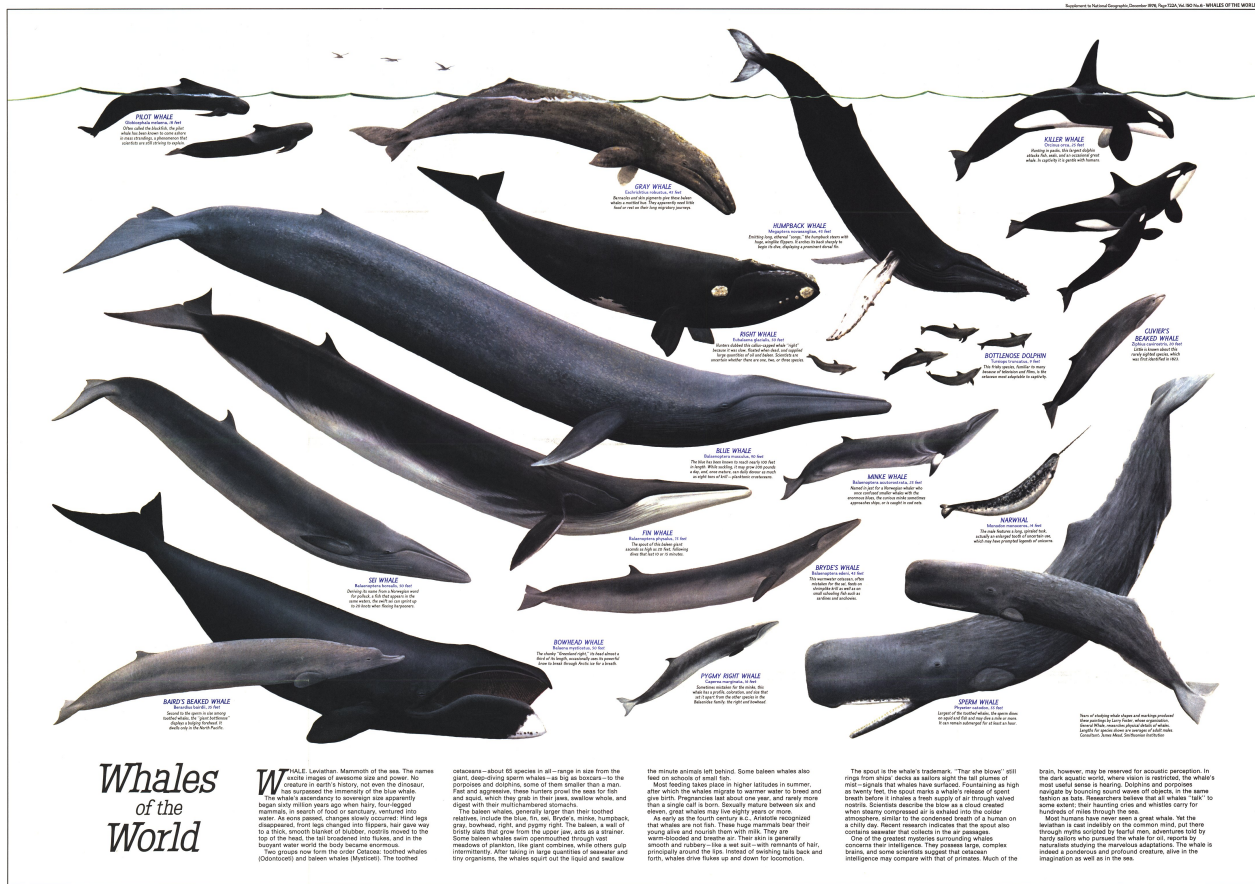


Figure 1.4 'Whales of the world' non-exhaustive representation of odontocete and mysticete specimens revealing the diversity of sizes and shapes in the Cetacea infraorder. (source: National Geographic 1976).

All cetaceans are hydrodynamic fast-moving species. **Swimming** capacities of cetaceans have adapted through the loss of hind limbs, specialized forelimbs in a paddle-like shape, and

reduced or lacking zygapophyses increasing the flexibility of the backbone, hence favoring mobility by undulation. Sprinting speeds above $45 \text{ km}\cdot\text{h}^{-1}$ have been recorded for Sei whales (*Balaenoptera borealis*; Williams, 2002). **Buoyancy**, the upper force that keeps something afloat, is maintained in cetaceans through body shape and fat that is mainly stored in the **blubber layer**. Fat is also the key to the **thermoregulation** of cetaceans. Considering that the thermal conductivity of water is 25 times greater than air, marine **endotherm species** such as cetaceans need specific adaptations to prevent heat loss to the surrounding environment, including 1) a large body size with small appendages, and 2) increased insulation provided by a thick blubber layer (e.g., up to 50 cm for bowhead whales, *Balaena mysticetus*). Furthermore, feeding on prey that live underwater involves important **diving capacities**. Cetaceans have evolved a variety of traits improving diving depth and duration, such as high oxygen access and storage. Compared to terrestrial mammals, cetaceans have higher levels of myoglobin, a lower blood viscosity, a larger spleen and an intricate blood capillary network to store and redistribute oxygen more rapidly. Finally, deep diving cetacean species (e.g., Cuvier beaked whale, *Ziphius cavirostris*, recorded at 2,992 m deep (Schorr *et al.*, 2014) have physiological adaptations to prevent decompression sickness (Lonati *et al.*, 2015).

1.2.2 Collecting spatial data for cetaceans

The study of the spatial ecology of cetaceans relies on a great variety of data collection approaches (Fig. 1.5), which show varying degrees of technical complexity, financial cost and spatio-temporal scales. Also, these methods allow the collection of data from the individual to the population level, which can then be explicitly integrated in SDMs (presence/absence, abundance), or used to study spatio-temporal behavioral patterns through other types of models (e.g., spatial connectivity, regional fidelity, interactions etc.).

Visual observation

Visual surveys are typically conducted to study cetacean presence using **systematic line transect sampling**, from a ship or an aircraft (Forney, 2002). Aerial surveys advantageously allow the coverage of a great area in a set amount of time (e.g., Mannocci *et al.*, 2015; Lambert *et al.*, 2016). On the other hand, boat-based surveys allow the collection of additional data at sea (e.g., biopsy, photo-identification) and can be conducted far offshore. Aerial or boat-based surveys can be conducted in **passing mode** (cetaceans are not approached upon detection) or in **closing mode** (cetaceans are approached upon detection). Closing mode surveys often allow a more accurate identification of species observed. In both cases, in order to derive abundance estimates, line transect surveys must follow a certain number of assumptions, including an equal coverage probability design, a certain detection on the transect line, independent observations, and the limited mobility of animals with respect to the transect lines. Factors affecting detection (speed, sea state, glare, ship height or aircraft altitude) are controlled to allow the estimation of cetacean densities (Hammonds, 2010).

Accurate measurement of the perpendicular distance of animals to the transect line is paramount to estimate the detection function and deduce abundance.

Alternatively, many boat-based surveys are conducted with **non-systematic search** following a haphazard sampling design (Corkeron *et al.*, 2011) of varying speed and effort extent. The term 'haphazard' designates a sampling protocol that is not explicitly randomized, nor a systematic regime. This protocol is typically adapted to small vessels in study sites where effort has to target accessible areas and/or areas of expected cetacean presence. In practice, non-systematic survey designs are often implemented to maximize encounter rates, at the cost of a heterogeneous coverage of the study area. They emphasize the **focal follows** of cetacean groups during which behavior, biological samples and photographs can be collected. Parameters affecting detection are not necessarily controlled nor measured. Although this approach to surveying is commonly applied, its application to spatial distribution studies has been relatively disregarded due to survey bias in comparison to line transect surveys.

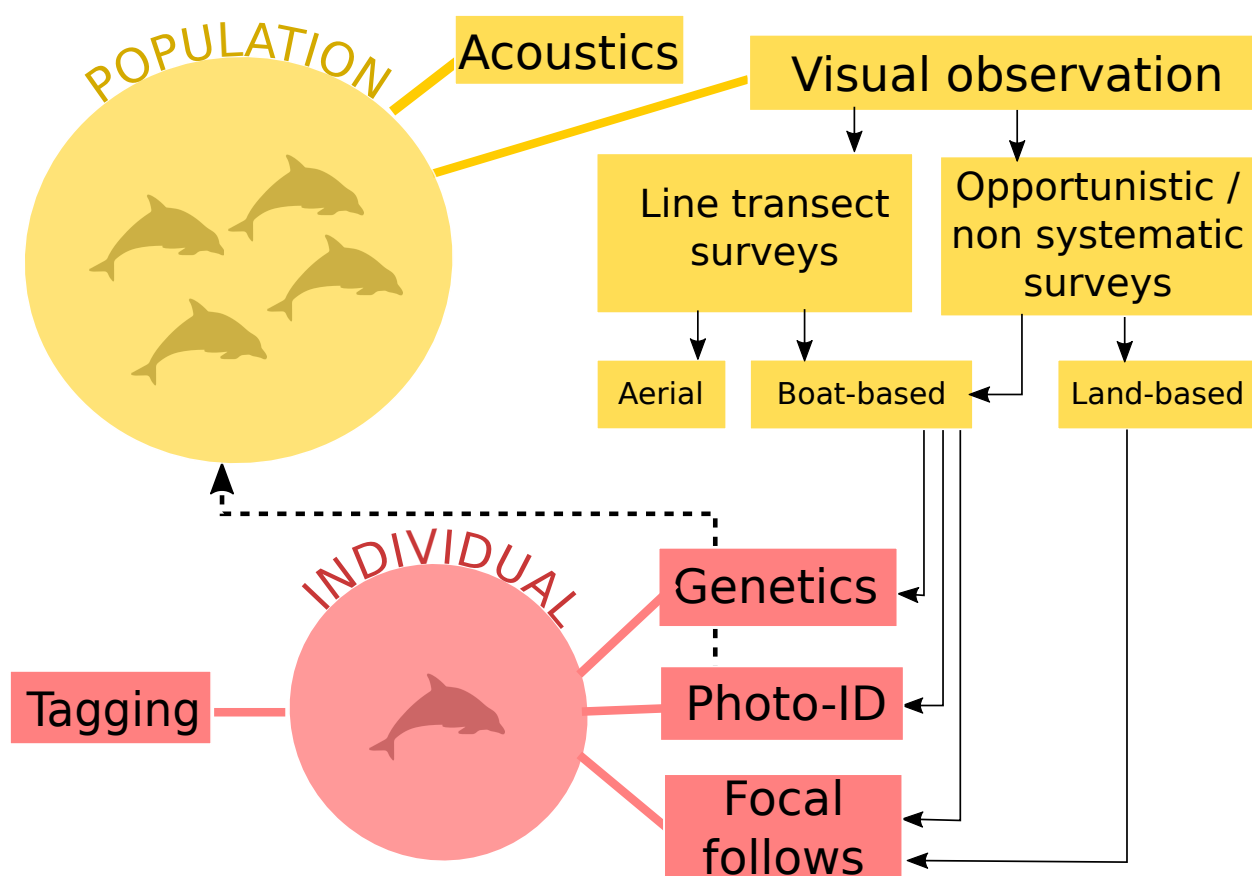


Figure 1.5 Methods for spatial data collection on cetaceans. Pink boxes represent methods that are primarily applied at the individual scale whereas yellow boxes represent population-level methods. Links can be drawn between these two scales: genetics and photo-identification (when georeferenced) can allow population-level studies of abundance or biogeography. On the other hand, boat-based visual surveys can be applied both to study distribution at population scale, or to collect photographs, biopsy samples, and record individual behavior during focal follows.

Visual observation can also be conducted during **land-based surveys**, which have the great

advantages of being cheap, less technically challenging and the least impactful for animals (Aragones *et al.*, 1997; Giacoma *et al.*, 2013). Although coverage is relatively limited, observing from a fixed point holds advantages to measure temporally varying patterns (e.g., cetaceans migrating along a coast, such as gray whales along the US West Coast, Sullivan and Torres, 2018). Furthermore, land-based surveys can be conducted with the help of a theodolite, a movable telescope that accurately locates marine mammals at the sea surface with a simple trigonometric calculation. The recorded geographic positions can then in turn be used to model spatio-temporal patterns of distribution.

Finally, **opportunistic surveys** regroup all surveys conducted from a non-dedicated platform of observation such as whale-watching boats, ferries, oil and gas platforms, cargo ships or fishing boats between others. Commercial whaling records also represent one of the largest opportunistically collected dataset of cetacean occurrence (Kaschner *et al.*, 2006; Torres *et al.*, 2013; Hann *et al.*, 2016; Johnson *et al.*, 2016). These opportunistic surveys may be conducted by scientists (onboard platforms of opportunities) or by members of the general public. The latter case falls under the **citizen science** category, defined as 'the engagement of non-professionals in scientific research' (Miller-Rushing *et al.*, 2012). The reliability and accuracy of opportunistic observations is variable and affected by confounding factors, such as the expertise of observers. On the other hand, citizen science is cost effective and serves a role in raising public awareness on environmental conservation issues. From individual photo-identification (see 'Happy Whale' identification project: <https://happywhale.com>) to overall species and population spatio-temporal occurrence, opportunistic surveys can provide a great diversity of information.

All visual surveys are limited by **perception bias** (not all cetaceans at the surface are recorded by the observer) and **availability bias** (cetaceans under the surface, hence unavailable, are not recorded by the observer; Redfern *et al.*, 2006), which together contribute to **imperfect detection** of animals in an area (Monk, 2014). Moreover, both visual and acoustic surveys are subject to a **spatial sampling bias**, which results from an inhomogeneous or incomplete coverage of the spatial and environmental range of a species or a population (Kramer-Schadt *et al.*, 2013; Fithian *et al.*, 2014). This bias is particularly problematic in opportunistic or non-systematic cetacean surveys that do not display an explicitly randomized nor systematic sampling.

Acoustics

Acoustic methods for cetacean studies can be categorized into **passive acoustics** that involve listening/recording sounds and **active acoustics** that involve sound production (Parsons *et al.*, 2013e). Passive systems can be anchored to the seabed, and record ocean and marine mammal sounds (Mellinger *et al.*, 2007). Vessel-based passive systems include simple hand-held hydrophones lowered over the side of the boat or more sophisticated devices such as towed hydrophones or hydrophone arrays. After analysis of the sound spectrograms, acoustic data can provide an indication of the occurrence of species through time at fixed positions (e.g., Carlén *et al.*, 2018; Ceyrac *et al.*, 2018)

or over transect lines (e.g., sperm whales, [Lewis et al., 2007](#); vaquita, *Phocoena sinus*, [Gerrodette et al., 2011](#)). For some species and with properly calibrated equipment, it is now possible to model cetacean densities using passive acoustics [Marques et al., 2013](#); [Jacobson et al., 2017](#). Finally, passive devices can be included in animal-borne tags (e.g., D-Tags). Active acoustics include play-back experiments and echo-sonars that may be used to detect cetaceans that do not vocalize or produce sounds. Contrary to visual surveys, acoustic approaches are not limited by sea state and weather, and can assess occurrence at low cost over long periods of time in the case of moored hydrophones.

Biologging

Biologging is defined as the 'use of miniaturized animal-attached tags for logging or transmission of data about the movements, behavior, physiology, or environment of an animal' ([Hays et al., 2016](#)). The word biologging may be used synonymously with **biotelemetry** although the latter rather designates tags involving a remote transmission of data, and does not encompass data loggers that must be recovered for download. Animal movements can be tracked with **passive tags** such as natural markings (genetics, coloration etc.), conventional tags (non-electronic: spaghetti tags, flipper tags, Discovery tags, etc.) or passive integrative transponders (PIT tags). **Active tags** include some form of active data collection about the animal and its environment. They were used on large whales as early as the 1970s, when implantable radio tags were deployed on northern right whales, *Eubalaena glacialis* ([Watkins and Schevill, 1977](#)).

Archival tags are active animal-borne devices that record data about the individual's internal and/or external state. With the exception of pop-up archival transmitting tags (PAT), archival tags are not developed to transmit the data they recorded, and need to be recovered for download. They are mounted with multiple sensors recording fine-scale movements such as 3-axis acceleration, depth, temperature, sounds, and video ([Calambokidis et al., 2007](#)). They have particularly been applied to study the fine-scale foraging behavior and feeding strategies of baleen whales ([Goldbogen et al., 2013](#)). In the case of large whales, archival tags are typically attached with suction cups and have short attachment durations (hours).

Transmitting tags are equipped with a technology allowing the transmission of the data recorded during tracking. The first tags of this kind used Very High Frequency (VHF) **radio-tracking** where an observer had to be present in the field to home in on the radio signal produced by the tag, using a directional receiving antennae. Obviously this method is not very time effective and challenging for marine species that spend much of their time below the surface, where VHF signals do not propagate. **Acoustic tags** rely on an array of acoustic receivers that detect the presence of a tagged individual in the vicinity ([Heupel et al., 2006](#)). This method is limited by the spatial coverage achieved with the receiver array (e.g., dugong, *Dugong dugon* ([Zeh et al., 2015](#))). In the case of wide-ranging marine mammals, satellite tags have become an indispensable tracking device. Both the geolocation of animals and data transmission can be performed using the Advanced Research and

Global Observation Satellite (**ARGOS**) system. Global Positioning System (**GPS**) receivers have been inserted in ARGOS tags to improve the quality of tracking over fine scales (e.g., FastLoc GPS, [Witt et al., 2010](#)).

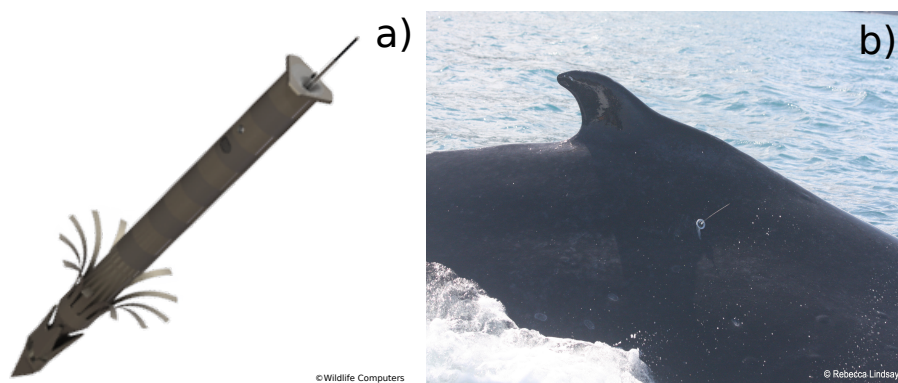


Figure 1.6 SPLASH10 transdermal cetacean tag (Wildlife Computers, Seattle, WA), before (a) and after deployment (b) on a humpback whale, *Megaptera novaeangliae*.

However, this technology is not available yet in the transdermal long-term tags used to track the extensive movements of large whales (e.g., SPOT and SPLASH Wildlife Computers tags; [Garrigue et al., 2015](#); [Zerbini et al., 2015](#); [Riekkola et al., 2018](#); Fig. 1.6). While intermediate-duration systems have been developed such as the Advanced Dive Behavior (ADB) tag ([Mate et al., 2017](#)) or the Wildlife Computer Limpet tags ([Henderson et al., 2018](#)), the wide-ranging movements of large whales remain a constraint for data recollection using archival methods. Satellite tracking sample sizes have long been limited by financial cost and tagging technical challenges. Collaborative datasets are progressively allowing the study of movement at community level and contribute to an ecosystem-wide conservation approach ([Block et al., 2011](#); [Lowther et al., 2015](#); [Citta et al., 2018](#); [Sequeira et al., 2018b](#)), notably in the face of climate change ([Hazen et al., 2013](#)).

Photo-identification

Individual identification is a key component of any cetacean monitoring program, as it provides information about social interactions (e.g., transience of affiliations, [Mobley Jr. and Herman, 1985](#)), life history traits (e.g., age at first calving of humpback whales, [Gabriele et al., 2007](#)) and spatio-temporal connectivity (e.g., movements across Oceania humpback whale breeding grounds, [Garrigue et al., 2011a](#)). Resightings can help quantify ranging patterns, site fidelity or habitat use at individual level. Mark-recapture models derived from individual identification are also used to study population dynamics and produce abundance estimates ([Hammond, 2006](#)). Contrary to species that can be handled (e.g., pinnipeds during haul-out on land), cetaceans must be identifiable based on their **natural markings** in the marine environment. Color variations or scars, on the back, the fluke or the dorsal fin of animals contribute to individually distinctive patterns. For instance, humpback whales can be identified from the unique black and white pattern, and trailing edge of their

caudal fluke (Katona *et al.*, 1979). Photographs are then compared to known individuals, visually or using a computer-assisted matching program such as FlukeMatcher (Kniest *et al.*, 2010) to assemble encounter histories (Fig. 1.7).



Figure 1.7 Photographs of a humpback whale's caudal fluke collected at several years interval in New Caledonia (whale HNC127).

Genetics

Genetic analysis can be conducted on **tissue samples** that are routinely collected on cetaceans. Samples of skin and blubber can be taken in the field using a crossbow with specially adapted bolts (Lambertsen *et al.*, 1994) or a modified capture veterinary rifle (Krutzen, 2002). Skin samples may also be skimmed from the surface when animals lose sloughed skin (during intense surface activities for instance). Nuclear and mitochondrial DNA can be extracted and analyzed for a multitude of research purposes. The most evident application is the sexing of individuals by the amplification of a male-specific SRY marker (Gilson and Syvanen, 1998) for species that do not display evident sexual dimorphism. **Sexing** individuals observed in the field is important for the study of sex-specific habitat use patterns or connectivity. Genomic DNA is also regularly used to **identify individuals** based on microsatellite polymorphism (e.g., Garrigue *et al.*, 2004a). Genetic identification of individual can be used in combination with photo-identification to infer identities and encounter histories. Finally, genetic analysis can provide important information regarding biogeography, structure and differentiation at population-level (Jackson *et al.*, 2014; Kershaw *et al.*, 2017).

1.2.3 The study of cetacean distribution and habitats

Cetacean data

When properly georeferenced, all of the data types described above can be more or less explicitly modeled within SDMs. Three major types of data are included in SDMs: presence-only data, presence-absence and abundance (Elith and Leathwick, 2009). **Presence-only** data record the positions where the species occurred without recording the areas where it did not. This type of data is typically recorded by citizen scientists who opportunistically reported on their observations, without providing information as to the places they visited but where no animals were observed. Similarly, satellite tracking only provides locations where the cetacean surfaced and the tag transmitted. Finally,

acoustic data also provides presence-only data as the absence of sound does not necessarily reflect the absence of the cetacean, but rather the absence of a vocal behavior. **Presence-absence** and **abundance** are provided by systematic research surveys such as line transect sampling. Indeed, perception and availability biases can be accounted for when a certain number of assumptions are upheld to assess detection probability. During non-systematic research surveys, these assumptions are not necessarily valid and absence cannot be recorded with certainty. However, data regarding the spatio-temporal intensity of survey effort is often available to inform models. For instance, GPS tracklines followed by a research vessel can be used to estimate sightings per unit of effort, also referred to as **encounter rates** (e.g., [Garaffo et al., 2011](#); [Arcangeli et al., 2015](#)). Alternatively, this data can be treated as presence-only, while accounting for survey effort in the form of **pseudo-absence or background approaches** ([Chefaoui and Lobo, 2008](#); [Phillips et al., 2009](#); [Aarts et al., 2012](#)). The environmental conditions at presence locations are then compared to a sample of the environmental space available to the species and surveyed by observers.

Environmental data

The performance of an SDM not only depends on the amount of cetacean data it is based on, but also on the quality and careful choice of the environmental variables used to describe the surrounding habitat. It is worthwhile noting that some SDM are purely 'spatial', hence rely on geographic rather than environmental variables. In this introduction, I will focus on environment-based SDMs. Variables describing the marine environment can be classified into two categories: the static (or topographic, or physical) variables that are fixed through time, and the dynamic variables that vary at a given position through time.

Static variables typically describe the topography of the environment in which cetaceans live, including the seabed depth, slope, aspect (orientation of the slope), or roughness. Distance to coastlines, reefs or specific isobaths are also used to describe the type of habitat species live in (e.g. coastal vs deep diving species, species associated with the continental shelf). Topographic variables can be derived from worldwide bathymetric charts that are freely available, such as the GEBCO international organization (General Bathymetric Chart of the Ocean) or the NOAA ETOPO (National Oceanic and Atmospheric Administration) datasets. They estimate **topographic complexity**, that is 'the shape, geometry and configuration of natural terrain surfaces in three-dimensional space' ([Bouchet et al., 2015](#)). Many studies have highlighted topography as a good predictor of cetacean distribution. For instance, different social group types of humpback whales (singers, mother-calf) in Tonga and Samoa showed spatial segregation with respect to depth, distance to reefs and slopes ([Lindsay et al., 2016](#)). In the mid-Atlantic Bight, short-finned pilot whales, *Globicephala macrorhynchus*, had an affinity for steep bathymetric features such as the shelf break and submarine canyons ([Thorne et al., 2017](#)).

Dynamic variables usually describe the physical, chemical or biological oceanographic

characteristics of cetacean habitats. They can be estimated with three main approaches: in situ sampling, satellite remote sensing, and numerical ocean circulation models (Redfern *et al.*, 2006).

In situ sampling is conducted simultaneously or asynchronously with the cetacean surveys. Measurements of oceanographic factors include water temperature, fluorescence, salinity, dissolved oxygen or chlorophyll-a. Conditions at depth can be estimated with CTD casts (Conductivity, Temperature and Depth) or XBT expendable bathythermograph (e.g., Becker *et al.*, 2016). The biological environment such as potential preys can also be sampled. Active acoustic devices (e.g., echosounders) can be applied during oceanographic cruises to record the vertical and horizontal distribution of prey (Benson *et al.*, 2002; Laidre *et al.*, 2010; Friedlaender *et al.*, 2011). Direct prey sampling can also be performed at discrete sites with various fishing/sampling techniques (e.g., trawl nets, Torres *et al.*, 2008; Witteveen *et al.*, 2008). All of these in situ approaches provide valuable direct measurements of the biotic environment, both at the surface and at depth. However, in situ sampling is often technically challenging and costly. For these reasons, biological conditions and prey distribution are often approximated by oceanographic variables that can be estimated remotely and act as proxies.

Satellite remote sensing offers a cheap and practical solution to estimate a great number of environmental variables over large spatial scales: sea surface temperature, salinity, chlorophyll-a concentration, turbidity, net primary productivity, dynamic height or weather. Scales of the measurements vary from 1 km to several degrees of latitude/longitude, and from daily measurements to monthly averages. In some regions, cloud cover can significantly affect data acquisition (Scales *et al.*, 2017). Another major limitation of satellite derived data is that it only estimates conditions in the superficial water layer, from 10 μm to 1 mm (<https://podaac.jpl.nasa.gov/SeaSurfaceTemperature>). Hence, these variables can provide a biased view of environmental conditions in areas with strong vertical heterogeneity.

Finally, **ocean circulation models**, also referred to as Regional Ocean Model Systems (ROMS), can provide habitat data for cetacean SDMs. These models can advantageously provide very fine scale predictions (e.g., hourly and meters resolutions) in 3 dimensions. They estimate oceanographic conditions at depth, such as the mixed layer depth (Mannocci *et al.*, 2015; Becker *et al.*, 2016; Breen *et al.*, 2016), a major predictor of ocean primary productivity. Models may be constrained, improved and validated through the assimilation of historical in situ and remotely sensed data. The interpolation of these various sources of data has allowed the mapping of average ocean circulation and conditions worldwide, referred to as global climatologies. The performance of cetacean SDMs built on modeled ocean products has been demonstrated for various species in the California Current Ecosystem (Becker *et al.*, 2016). The most sophisticated models can include biological processes at lower trophic levels (Redfern *et al.*, 2006), hence allowing the prediction of apex predator distributions through an ecosystem-wide approach (Fiechter *et al.*, 2016).

Scales in marine environments

The modeling of cetacean distributions is limited by several challenges. These **mobile species** can cover great distances in a small amount of time and are often wide-ranging (specifically in the case of large whales, e.g., [Robbins et al., 2011](#)). Movements of species in the marine environment induce potential mismatches between the scale over which the species can occur and the scale at which environmental variables are recorded ([Bruneel et al., 2018](#)). Also, the marine environment they live in is characterized by a **high spatio-temporal variability** compared to terrestrial ecosystems. As a result, cetacean-habitat relationships operate over multiple hierarchical scales, which are not necessarily within the reach of researchers. As there is no single natural scale at which process should be studied ([Elith and Leathwick, 2009](#)), careful examination should be dedicated to the spatial (meter, kilometer, degree of latitude/longitude, ocean basin) and temporal scale (daily, monthly, annually) at which to model ecological relationships ([Wiens, 1989](#); [Chave, 2013](#)). This issue has been addressed empirically ([Fernandez et al., 2018](#)), theoretically ([Mannocci et al., 2017a](#); [Torres, 2017](#)) and by simulation ([Fernandez et al., 2017](#); [Scales et al., 2017](#)) for the case of marine mammals.

[Mannocci et al. \(2017a\)](#) established a framework to classify temporal resolutions as either instantaneous, contemporaneous, or climatological, and argues that the choice for one scale over another should depend on the type of cetacean-habitat association we wish to model. For instance, the relationship between cetaceans and ephemeral prey patches are best modeled with **instantaneous data** (conditions in the immediate perceptual range of the animal, in seconds to hours). **Contemporaneous data** (average conditions in a daily-monthly time window) are valuable when studying mesoscale oceanographic features. Finally, **climatologies** (average conditions over several years) are best applied to ecosystems with strong seasonality and weak inter-annual variability (Fig. 1.8). As cetacean space use patterns occur over a range of scales ([Torres, 2017](#)), it might be necessary to combine multiple scales from this framework depending on the question at hand.

The social organization of cetacean species also complicates the modeling of their distribution at fine scale as it can result in spatial autocorrelation of observations ([Redfern et al., 2006](#)). Indeed, the aggregation of individuals may influence their spatial arrangement irrespective of environmental conditions ([Montoya et al., 2009](#)) and the detection of such processes is directly related to the scale of sampling ([Hui et al., 2010](#)). Positive **spatial autocorrelation** is an important issue for all SDMs ([Dormann et al., 2007](#); [Crane et al., 2012](#)), and perhaps even more so for social cetacean species ([Redfern et al., 2006](#)). When not accounting for autocorrelation, models risk displaying spatially autocorrelated residuals violating the assumption of independent errors and increasing the frequency of Type I errors (i.e. when a non-significant relationship is erroneously considered to be significant). Overall, although their impact is expected to be significant, **intraspecific interactions** are rarely accounted for in SDMs ([Sadoti et al., 2017](#)).

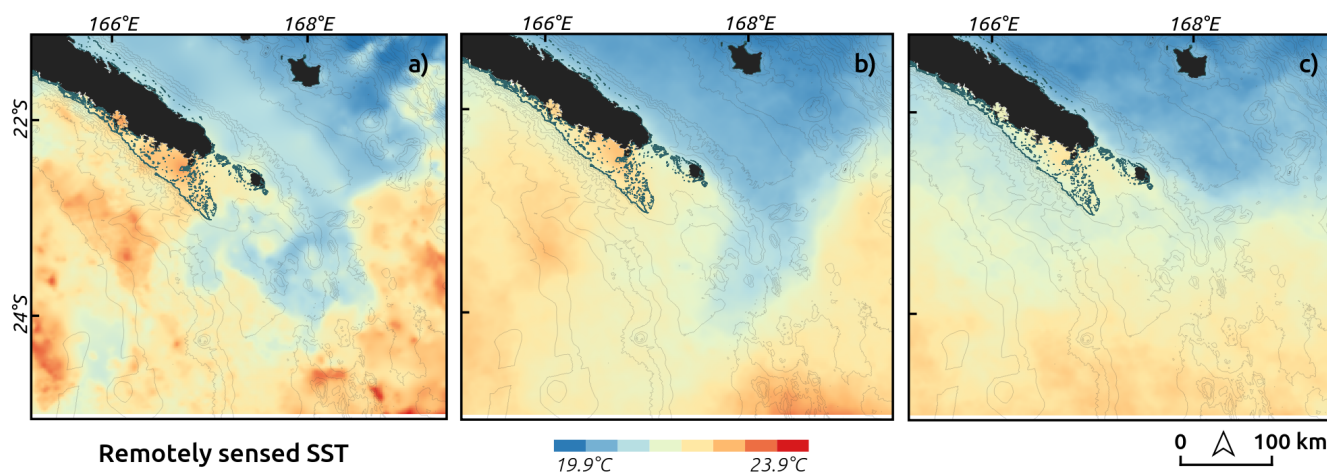


Figure 1.8 Satellite remote sensing of sea surface temperature (SST) at three different temporal scales: instantaneous (a; daily), contemporaneous (b; monthly) and climatological (c). SST was acquired for a) August 15th, 2003, b) the month of August 2003 and c) the average SST measured on August 15th from 2002 to 2018. Multi-scale Ultra High Resolution SST was acquired from the JPL MUR SST project (https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST). This blended product includes data from several satellite infrared and microwave sensors, as well as in situ data to produce a gap-free interpolated map at 1 km spatial resolution.

A diversity of modeling approaches

A great number of algorithms have been used to fit correlative SDMs. Their definitions are relatively loose, given that many 'hybrid' approaches have also emerged. These approaches are sometimes classified depending on the type of response data they are based on, whether it is 'presence-only' or 'presence-absence'. However, because some of these models may be used with all types of data, including pseudo-absence/background cases, I favored the classification of SDM algorithms into three main groups: profile methods, regression methods and machine learning methods.

Profile approaches - Profile methods, also referred to as environmental envelopes, are specifically used to model presence-only data. Examples include envelope-based methods such as BIOCLIM (Nix, 1986), and distance-based methods such as DOMAIN (Carpenter *et al.*, 1993) or the Mahalanobis distance (Mahalanobis, 1936). These approaches are truly 'presence-only' as they do not require the sampling of pseudo-absences or background data. In contrast, Ecological Niche Factor Analysis ENFA (Hirzel *et al.*, 2002) is a profile method that also uses information about the environmental conditions outside the presence locations. Applications of ENFA to cetacean include studies of sperm whale, pilot whale, *Globicephala melas*, and Risso's dolphin, *Grampus griseus*, in the Mediterranean Sea (Praca and Gannier, 2007) and harbour porpoise, *Phocoena phocoena*, in the Scottish Sea of Hebrides (Macleod *et al.*, 2008).

Regression approaches - Regression methods are perhaps one of the most common statistical approaches to cetacean SDMs (Redfern *et al.*, 2006). They organize in various loose categories, depending on 1) characteristics of the response variables, 2) linearity of the relationships modeled, and 3) presence of random effects. Linear regression are based on an assumption of normality and homoscedasticity of the response variable/residuals. When this assumption is not met, which is frequent in ecological studies, a **Generalized Linear Model** (GLM, McCullagh and Nelder, 1989) can be applied. Generalized models therefore have the capacity to model response variables such as the presence/absence of species (Binomial distribution), the number of individuals at a given location (Poisson distribution), or the percent individuals in a certain state (Beta distribution), and other applications. When the relationship between the response and each predictor is not expected to be linear, it can be modeled with a parametric transformation such as a polynomial regression. However, if the relationship cannot be modeled with a simple function, non-parametric smoothing can be applied using a **Generalized Additive Model** (GAM; Hastie and Tibshirani, 1990). GAMs have been extensively applied to model cetacean-habitat relationships, for instance: blue whales (Redfern *et al.*, 2017), California Current cetacean assemblages (Becker *et al.*, 2017), and harbor porpoises (Gilles *et al.*, 2016). If random effects are present they can be accounted for using the mixed-effect versions GAMM (Generalized Additive Mixed Models) or GLMM (Generalized Linear Mixed Models).

Machine learning approaches - Machine learning approaches designate a great variety of increasingly popular approaches. Some algorithms are defined as **classification methods**, because they assign observations to classes based on combinations of environmental predictors (Guisan and Zimmermann, 2000). Such is the case for the **Classification and Regression Trees** (CART), which is based on the binary recursive partition of the response data into subsets of homogeneous covariate values. **Boosted Regression Trees** (BRT, (Friedman, 2001) and **Random Forests** (RF; Breiman, 2001) are more sophisticated forms of classifiers that combine decision trees with a boosting or bagging algorithm (review in Carvalho *et al.*, 2017). Applications to cetacean study cases include belugas, *Delphinapterus leucas*, in Alaska (Goetz *et al.*, 2007), bottlenose dolphins, *Tursiops truncatus*, in Australia (Zanardo *et al.*, 2017) and in northwestern Atlantic (Torres *et al.*, 2003), and southern right whales, *Eubalaena australis*, in the Australasian region (Torres *et al.*, 2013).

Maxent (Phillips *et al.*, 2006) is certainly one of the most popular approach to producing SDMs (Radosavljevic and Anderson, 2014). Maxent estimates the geographic range of species by modeling the distribution's maximizing entropy, in other words, closest to a geographically uniform distribution (Phillips *et al.*, 2017). This distribution is subject to environmental constraints estimated at recorded presence locations for the species. Maxent relies on a maximum likelihood exponential model, but has also recently been formulated as an inhomogeneous Poisson process (Aarts *et al.*, 2012; Renner *et al.*, 2015; Phillips *et al.*, 2017). Maxent is typically applied in 'presence-only' data cases, such as citizen science sightings (e.g., spinner dolphins, *Stenella longirostris*, in Hawaii, Thorne *et al.*,

2012) or historical whaling records (e.g., sperm whales, south western in Australia, [Johnson et al., 2016](#)). Indeed, environmental conditions at presence locations are automatically contrasted with environmental conditions at background positions that are randomly generated over the study area. However, when possible, spatial sampling effort can be reflected in the background samples in order to account for an inhomogeneous distribution of survey effort across a study region ([Phillips et al., 2009](#)). In the case of cetacean visual surveys at sea, boat GPS tracklines have been used to delineate the surface appropriate for background sampling (e.g., [Lindsay et al., 2016](#)).

Finally, with increasing computational power and memory, several machine learning approaches to SDMs have recently gained in popularity. **Support Vector Machines** (SVMs, [Boser et al., 1992](#)) are supervised learning methods capable of fitting nonlinear effects and interactions by projecting the predictors into a high dimensional space, where habitat relationships can be solved with a linear solution. The interpretation of such a model is therefore argued to be closely related to the original Hutchinsonian niche definition as a multidimensional environmental hypervolume ([Drake et al., 2006](#)). SVM can be applied either as a two-class approach to classify presences vs absences or pseudo-absences, or as a one-class approach to model distribution from presence-only ([Guo et al., 2005](#)). The latter is similar in essence to profile approaches described above. SVMs have been relatively rarely applied to SDMs, and mostly to terrestrial cases (e.g., [Guo et al., 2005](#); [Drake et al., 2006](#); [Pouteau et al., 2012](#)). **Artificial Neural Networks** (ANNs) also constitute a promising machine learning tool to produce SDMs ([Guisan and Zimmermann, 2000](#)). ANNs are well-known for their performance as classifiers for speech and image recognition ([Lek and Guégan, 1999](#)), and have specifically been applied to detect whale and dolphins sound in passive acoustic recordings ([Potter et al., 1994](#)). They have been applied in marine species SDMs ([Palialexis et al., 2011](#)), including for cetaceans ([Aïssi et al., 2014](#)). Finally, **Gaussian Processes** (GPs) have shown high predictive accuracy in comparison to BRTs and GAMs ([Golding and Purse, 2016](#)) but their application to SDMs is computationally intensive and has remained limited so far.

Occupancy models - These models do not belong to the types of approach listed above, but may be seen as a peculiar type of correlative SDM ([MacKenzie, 2006](#)). Dynamic occupancy models have the potential to explicitly model non-equilibrium species distributions ([MacKenzie et al., 2003](#)). Occurrence at a site is modeled as a chain of Markov states through time and the probability of each site being in a given state and transitioning between states (colonization, extinction) is estimated. This approach allows for the explicit modeling of imperfect detection using a Hidden Markov model ([Kéry et al., 2013](#)), as well as the inclusion of environmental predictive covariates. [Sadoti et al. \(2017\)](#) used this approach to model the distribution of lek-mating birds over multiple seasons. This approach has only rarely been applied to cetacean cases ([Pennino et al., 2016](#); [Currie and Stack, 2018](#)).

1.2.4 Cetacean conservation & applicability of spatial knowledge

Currents threats to cetaceans

Direct takes of cetaceans for human consumption has occurred for millennia. Rock carvings attest of the hunting of large whales in Korea as early as 6000 BC (Lee and Robineau, 2004). Modern whaling was marked by the development of explosive harpoons in the 1840s, steam-driven ships in the 1860s and factory ships in 1925 (Parsons *et al.*, 2013b). These technologies greatly increased the efficiency of the whaling activities, making it possible to hunt whales faster and further into remote waters of the globe. Whale products had many uses, but overexploitation was primarily boosted at the end of the 19th century by the ever increasing demand for whale oil used in lamps, soaps and food before the development of the petroleum industry and vegetable oils (Coleman, 1995). Millions of whales were killed throughout the history of commercial whaling: about 250,000 humpback whales, 350,000 blue whales, 500,000 fin whales, 1,000,000 sperm whales and hundreds of thousands of animals from other species (Parsons *et al.*, 2013b). In 1946, the main whaling nations created the the **International Whaling Commission** (IWC) and signed the International Convention for the regulation of whaling, but the measure was relatively ineffective to limit the catastrophic decline of large whales. For instance, illegal whaling operations conducted by the USSR between 1948 and 1979 led to 179,000 unreported whale catches, mostly taken in the Southern Hemisphere and revealed only recently (Ivashchenko and Clapham, 2014). A moratorium signed by the IWC members took effect in 1986 to prohibit direct takes on large whales. Since then, over 25,000 large whales have been killed by Norway, Japan and Iceland under legal (although criticized) rights of reservation or scientific research (Parsons *et al.*, 2013b). Indigenous whaling represents a small fraction of direct takes, with a few hundred whales hunted as part of annual quotas in Nordic communities of US (Alaska), Greenland, St Vincent and the Grenadines, and Russia (Tchoukota) (IWC, 2012).

Accidental entanglement is one of the main anthropogenic source of cetacean mortality today, killing at least 300,000 whales and dolphin every year (Parsons *et al.*, 2013a). Entanglement may occur as bycatch in fishing gear in active use, or in interaction with discarded or broken gear such as 'ghost nets'. Commonly used in the 1960s, drift nets are infamous for their damage to cetacean populations, and marine megafauna species at large. Purse seine nets targeting schools of tuna in the eastern Pacific had a great impact on spinner dolphin (*Stenella longirostris*) and spotted dolphins (*S. attenuata*), which despite some regulation have not shown signs of recovery (Gerrodette and Forcada, 2005). Gillnets have led to a substantial number of entanglements of dolphins and porpoises (Reeves *et al.*, 2013). Gillnets are also known to cause entanglement of large whales (Reeves *et al.*, 2013; Thomas *et al.*, 2015), as do trap and pod fisheries that have been identified as a leading cause of mortality of the endangered North Atlantic right whale (Knowlton *et al.*, 2012). Finally, large whales are also subject to entanglement in large mesh shark control nets used in South Africa and Australia (Meÿer *et al.*, 2011), and bycatch by artisanal fisheries.

Vessel strikes have become a major cause of cetacean mortality since the 1950s and the

largest threat to baleen whales (Avila *et al.*, 2018), as both the number of ships and their speed has increased worldwide (Laist *et al.*, 2001). Although many of these incidents go unreported (Peel *et al.*, 2018), recent research has highlighted the main factors of risk. Severe or lethal injuries are usually caused by ships over 80 m and/or traveling 14 knots or faster (Laist *et al.*, 2001). Vessel strikes are therefore specifically threatening to populations with ranges that overlap shipping routes, major ports, offshore industrial sites or ferry routes (e.g., Redfern *et al.*, 2013). The North Atlantic right whale in southern New England is affected at a population-level from intense shipping traffic, as 57 % of fatalities reported in 2017 in the Gulf of St. Lawrence were due to ship collisions (while the remaining 43% were due to entanglement or were undetermined, Meyer-Gutbrod *et al.*, 2018). Collision risk is not limited to large and fast cargo ships. Despite their smaller size and lower speed, whale and dolphin watching boats may be also responsible for collisions, probably because they target waters where cetaceans are most likely to occur (Van Waerebeek *et al.*, 2007).

Chronic threats such as disturbance, pollution or resources depletion have a more pernicious, yet important cumulative impact on cetaceans (Thomas *et al.*, 2015; Clapham, 2016; Avila *et al.*, 2018). Many anthropogenic activities are documented as causing potential disturbance to cetaceans, but noise-generating activities are probably of highest concern. Indeed, sound is the primary means by which cetaceans communicate and navigate. Industrial and shipping noises have the potential to mask the animal's vocalizations, impair hearing, and induce physiological stress. For instance, Blair *et al.* (2016) showed that humpback whale foraging behavior was affected by high levels of shipping noises in the Gulf of Maine, Massachusetts, USA. Habitat degradation also results from direct impacts (e.g., dredging) or pollution (oil spills, industrial waste, sewage, litter etc.) and can affect cetaceans directly (diseases) or indirectly (prey depletion; Reijnders and Aguilar, 2002).

Finally, the 'big unknown' (Clapham, 2016) and major concern for cetaceans in the immediate future is the effect of **climate change**, and the numerous environmental changes that will ensue from it. Ocean acidification affects calcifying organisms such as plankton (Doney *et al.*, 2012), which sustain entire ecosystems and are a major food resource for baleen whales. Moreover, polar waters are warming up faster than the rest of the globe and the decline in winter sea ice in these regions is already affecting Arctic and Antarctic ecosystems. Summer krill densities have decreased since the 1970s in the southwest Atlantic (Atkinson *et al.*, 2004). Profound changes are expected in food webs as a result of warming, acidification and krill decline, and will impact polar high order consumers (Flores *et al.*, 2012). Top predator distribution shifts are already being observed in response to climate-related changes (e.g., Chambault *et al.*, 2018) but the full extent of its impact is a subject of speculations (Macleod, 2009; Hazen *et al.*, 2013; Sydeman *et al.*, 2015).

Importance of spatial management for cetaceans

Site-based environmental protection is rooted in the history of conservation through the early creation of terrestrial wildlife reserves and natural parks (Carr *et al.*, 2003). This spatial approach to

risk management has been applied to marine ecosystems through the creation of **Marine Protected Areas** (MPAs, <http://www.mpatlas.org/>), defined by the IUCN (Kelleher, 2002) as 'any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment'. One of the rising new areas of marine conservation is the development of large-scale MPAs (Lewis *et al.*, 2017), also referred to as 'giant MPAs' (Pala, 2013), which extend protection to vast areas that encompass the high seas. The first world's high-sea giant MPA was created in 1999 in the Mediterranean sea: the Pelagos Sanctuary for Mediterranean Marine Mammals (87,500 km², Hoyt, 2005) and many have followed since then, especially in the Pacific Ocean (O'Leary *et al.*, 2018).

Cetaceans are often the lucky beneficiaries of MPAs, but rarely are the reasons for which they were established in the first place. Conservationists emphasize the need to spatially identify **critical habitats** as the 'parts of a cetacean's range, either a whole species or a particular population of that species, that are essential for day-to-day survival as well as for maintaining a healthy population growth rate' (Hoyt, 2005). Critical habitats may include areas used for feeding, mating, calving or even migrating. Great efforts have been employed by ecologists to model and predict critical habitats of cetaceans to explicitly help spatial management (e.g., Cañadas *et al.*, 2005; Leathwick *et al.*, 2008; de Castro *et al.*, 2014).

1.3 The study species: humpback whales

The humpback whale (*Megaptera novaeangliae*, Borowski 1781, Fig. 1.9) is a **Balaenopteriidae** of Mysticete suborder, or baleen whales. Among all the cetacean species cited above, it is likely one of the most studied. Although many aspects of the behavior of humpback whales remains mysterious, the amount of data available for this species makes it a great study case to deepen our understanding of cetacean spatial ecology at large.

1.3.1 Morphology and life-traits

Early studies of humpback whales were conducted in association with commercial whaling activities. Hence, much of the basic knowledge regarding morphology, physiology, reproduction and diet of humpback whales was acquired during whaling of the mid 20th century (e.g., Chittleborough, 1958; Dawbin, 1959; Chittleborough, 1965). Adult humpback whales average 12 to 15 meters in length (Chittleborough, 1965). They are easily recognized from other large whales because of their long pectoral flippers (4 - 5 m long, about one third of the body length), which led to the name 'Mega' (latin: large), 'ptera' (latin: wings). These oversized appendages provide a great maneuverability that could be advantageous during feeding, intrasexual competition (Clapham, 2000a), or to repel predators (Pitman *et al.*, 2016).

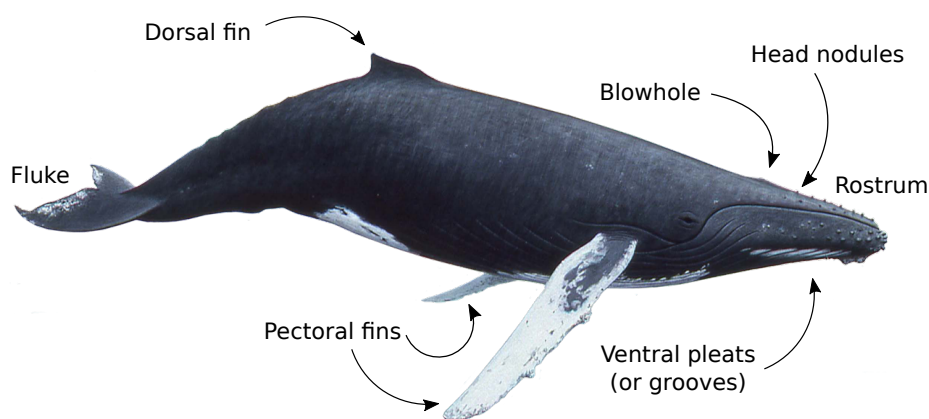


Figure 1.9 Humpback whale, *Megaptera novaeangliae*. The white coloration of the upper side of pectoral fins is more common in the Northern Hemisphere.

Like other cetaceans, humpback whales are **long-lived species**. They have a maximum verified lifespan of 95 years (Chittleborough, 1965), if single ear plugs are considered to accrue annually (Gabriele *et al.*, 2010). They also have a long generation time (i.e., average time between two consecutive generations), estimated at 21.5 years (Taylor *et al.*, 2007). As a comparison, the average human generation time is about 25 years (Eyre-Walker and Keightley, 1999). It is now possible to age live whales through molecular analysis (Polanowski *et al.*, 2014), and to date this new technique has actually revealed few individuals more than 30 years old (Riekkola *et al.*, 2018) in contrast to the estimates made in the 1960s (Chittleborough, 1965). Sexual maturity is reached around 5 (Chittleborough, 1965; Clapham and Baker, 2002) to 12 years old (Gabriele *et al.*, 2007). The **birth interval** is estimated between 2 and 3 years (Chittleborough, 1958; Baker *et al.*, 1987; Craig and Herman, 2000; Rankin *et al.*, 2014). However, recent evidence in the Southern Hemisphere suggests that annual calving may be more common than expected (Chero, 2017; Pallin *et al.*, 2018; Riekkola *et al.*, 2018).

1.3.2 Migration

Patterns of migration

Humpback whales are migratory like most baleen whales. They seasonally migrate between polar feeding areas, and tropical / subtropical breeding areas, both in the Northern and the Southern Hemispheres (Johnson and Wolman, 1984). The only exception to this North-South migration pattern is the Arabian Sea humpback whale population that is sedentary and restricted to the Northern Indian Ocean all year long (Pomilla *et al.*, 2014; Willson *et al.*, 2014). Humpback whale's annual movements are the archetype, and perhaps one of the most famous examples of migration in the animal kingdom. To date, they are thought to undertake among the longest seasonal migrations of any mammalian species (Robbins *et al.*, 2011). Migratory routes are an example of vertically transmitted culture (Rendell and Whitehead, 2001), as the fidelity to breeding and feeding grounds

is maternally driven (Baker *et al.*, 2013; Herman, 2017). While many aspects of these extensive movements remain mysterious, I attempt to define humpback whale migrations within the framework established by (Dingle and Drake, 2007). First, at individual level, although it has long been thought to be obligate, it appears that not all individuals undergo the migration. Indeed, some individuals appear to overwinter in their feeding grounds (Alaska, Straley, 1990; Gulf of Maine, Clapham *et al.*, 1993). The humpback whale migration may therefore be considered 'partial' (to a degree that remains to be identified), or even 'differential' if we consider the hypothesis of Brown *et al.* (1995) that overwintering individuals are mostly females. Second, it can spatially be defined as a 'round-trip', since individuals generally go back and forth between the same areas (Baker *et al.*, 2013; Herman, 2017). In some ocean basins, humpback whales are suspected to follow different paths on the outward and return journeys (Valsecchi *et al.*, 2010), hence their round-trip migration could be defined as a 'loop'. Third, humpback whales migrate repeatedly over their long life-span and are therefore considered as 'seasonal' migrants. Finally, humpback whales use an 'active' locomotion medium to migrate, as they appear to compensate for current drift (Horton *et al.*, 2011).

Benefits of migration

Humpback whales are a good example of **capital breeders**. In contrast with income breeders that directly allocate ingested resources to reproduction, capital breeders build up reserves when and where resources available, then reinvest them into reproduction at some future date (Sainmont *et al.*, 2014). Humpback whales have a marked seasonal cycle as they feed and accumulate energetic reserves, then fast during winter migration and breeding, depending on the energy stored during summer. Fasting has been confirmed by whaling catches reporting empty stomachs and low adiposity of whales returning from the wintering grounds (Chittleborough, 1965; Dawbin, 1966). Though still subject to an ongoing debate, the primary driver explaining the evolutionary persistence of migration appears to be calf development and survival. The reduced risk of killer whale (*Orcinus Orca*) predation in tropical and sub-tropical breeding grounds (Corkeron and Connor, 1999) and warm waters in these regions (Clapham, 2000b) are assumed to contribute to greater calf survival.

Corkeron and Connor (1999) suggested **predation** as the primary driver of baleen whale migrations, on the grounds that killer whales were more abundant in polar waters than elsewhere in the world. Hence, giving birth in tropical and seemingly predation-free waters was an adaptive strategy of whales to decrease predation risk during the ontogeny of the calf. Killer whales are known to attack calves of humpbacks (Pitman *et al.*, 2015), proof is the high proportion of humpback whales showing teeth rakes and apparent bite marks on their flukes (33 % in the North Atlantic, Katona *et al.*, 1979). However, the location and the preponderance of these attacks is debated (Clapham, 2000b). It has been argued that aggressions are rarely observed in feeding and breeding grounds (Clapham, 2000a; Mehta *et al.*, 2007), but mostly occur during the first migration of newborn calves from their tropical place of birth. As a result, predation was contested as being the main selective force of humpback whale migrations.

The same interrogation may emerge when considering other possible predators of humpback whales. Although limited, predation from large pelagic sharks is more likely to occur during migration and under tropical latitude than in polar waters. Attacks on humpback calves have been observed from dusky sharks, *Carcharhinus obscurus* (Dicken *et al.*, 2015), and tiger sharks, *Galeocerdo cuvier* (Mazzuca *et al.*, 1998). Interesting correspondances have also been drawn between the timing of white shark migrations, *Carcharodon carcharias*, and humpback breeding season in Hawaii (Domeier and Nasby-Lucas, 2008) and New Caledonia (Bonfil *et al.*, 2009). While scavenging sharks are commonly observed around floating whale carcasses, direct attacks are actually rarely sighted.

The alternative (although not exclusive) hypothesis that had been brought forward by Corkeron and Connor (1999) and subsequently supported by Clapham (2000b) concerns the **thermoregulation** of calves. Although the exact thermal tolerance range of adult or newborn humpback whales is not known, Rasmussen *et al.* (2007) estimated that breeding grounds were all included in a 21.1 - 28.3 °C range, irrespective of latitude. Calf survival or fitness and reproductive success of the future adult could be increased by early development in warm waters. However, this hypothesis fails to explain why males and non-pregnant females would undertake these long and costly migrations. Some other hypothesis would have to explain why migration to low latitudes would be energetically profitable to the whole population. **Seasonally varying prey availability** was proposed as an alternative or at least as a contributing driver of whale migrations. Comparing the energetics (lipid stores, morphology, migratory patterns) of cetaceans, Brodie (1975) suggested that baleen whales migrate so that they could feed in cold waters in the summer when they are most productive, and switch to warmer waters when resources in feeding grounds are too scarce to compensate for the energy deployed in thermoregulation. Finally, Durban and Pitman (2012) noted that migration to warmer waters can allow whales to shed diatoms and barnacles that grow on their skin in feeding grounds. **Physiological maintenance** migration allowing for skin regeneration was suggested as a driver of killer whale movements to subtropical waters but could apply to other whale migrations.

Multi-scale aspects of distribution

Humpback whales present a **cosmopolitan distribution** and have been observed in all oceans of the globe (Fig. 1.10). However, separate populations are identified in each ocean basin. As early as 1929, Kellogg (1929) identified the migratory routes and destinations of the main humpback whale populations of the Northern and Southern Hemisphere. Admixture between the two hemispheres is almost nonexistent, as 1) breeding grounds rarely go beyond the equator, and 2) breeding season covers the austral winter for Southern Hemisphere whales (July - October on average) and the boreal winter for Northern Hemisphere whales (December – March on average). Breeding grounds off the Central America Pacific coast constitute the only example of a trans-equatorial migration, as whales visiting these regions originate both from feeding areas off California and Antarctic feeding grounds, and share genetic traits that suggest exchanges (Medrano-González *et al.*, 2001). Aside from this exception, recent worldwide genetic studies support discontinuous migratory patterns resulting in

discrete regional populations. Specifically, the humpback whale populations of the North Pacific, North Atlantic and Southern Hemisphere are suggested to form three sub-species that follow separate evolutionary trajectories (Jackson *et al.*, 2014).

Within each of these populations, humpback whales display an extensive range as a result of their seasonal north-south migrations from feeding to breeding grounds. The first description of population migratory routes dates back to the launch of the Discovery program in 1924 in the Southern Ocean (Rayner, 1940). Discovery marks were small metal cylinders implanted in whales during whaling activities and later retrieved when whales were killed and carcasses were processed. Between 1932 and 1984, more than 23,000 marks were deployed on 11 species of cetaceans. These marks provided the first overview on connectivity at basin scale and resulted in the identification of stocks (Mackintosh, 1965) necessary to the implementation of whaling quotas. The IWC currently recognizes 7 breeding stocks in the Southern Hemisphere (A to G; IWC, 1998) associated with 6 Antarctic feeding areas (I to VI; Fig. 1.10). Since then, photo-identification, genetics and satellite telemetry have contributed to a better understanding of the linkages between breeding and feeding grounds worldwide.

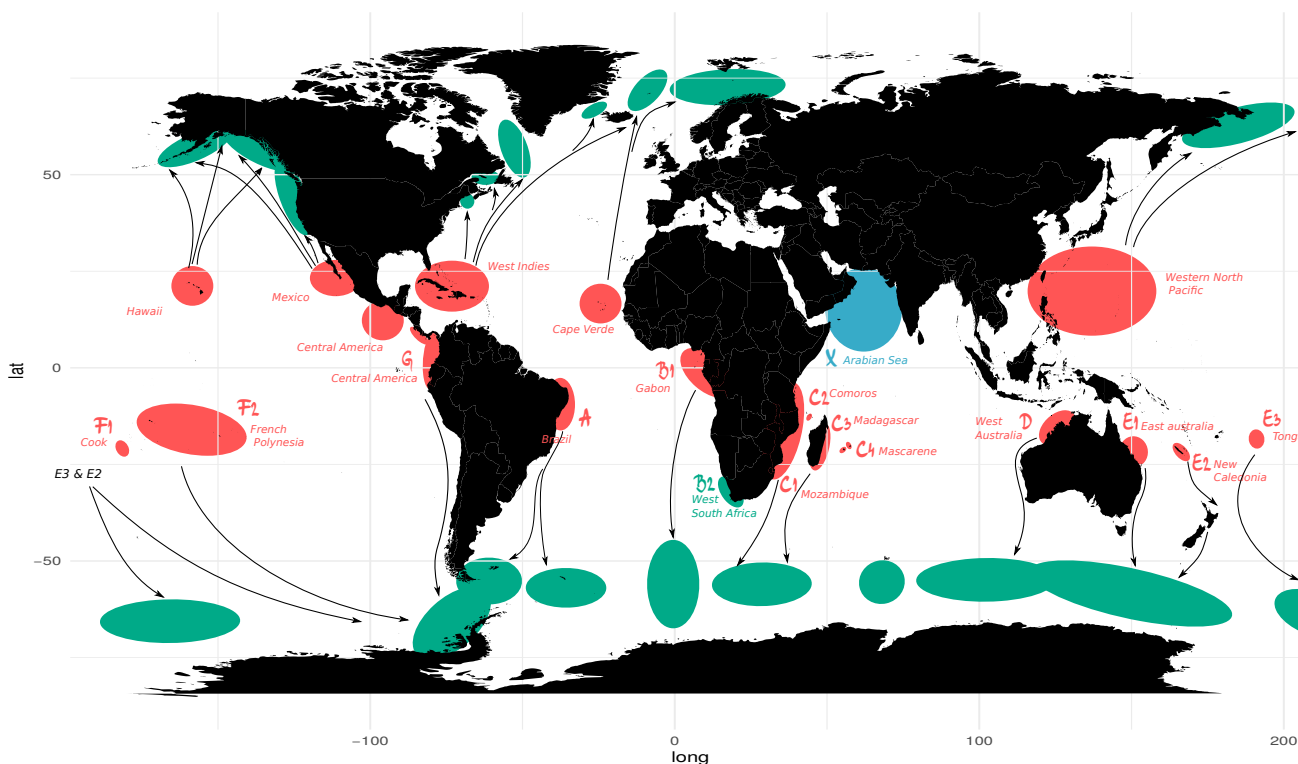


Figure 1.10 Global map of humpback whale distribution, with migratory routes, main feeding (in green) and breeding grounds (in red), with IWC stock and sub-stock names indicated. Breeding ground of stock B2 is unknown. The Arabian Sea stock X represented in blue is the only non-migratory humpback whale population.

Studies of individual movement have progressively underlined the complexity of humpback whale migrations. For instance, wide movements have been reported between seasons (e.g., whale photographed in Hawaii & Japan during the subsequent winter, Darling and Cerchio, 1993). Simi-

larly, using genetic analysis, migratory interchanges between seasons have been detected between Columbia and French Polynesia, or between Tonga and Australia (Steel *et al.*, 2017). As for within season movements, satellite tracked humpback whales have shown longitudinal movements from New Caledonia coastal waters, in the direction of Australia, late in the breeding season (Garrigue *et al.*, 2015), hence suggesting the potential for extensive localized movements at the scale of a breeding region.

1.3.3 Behavior

The feeding season

Like all rorquals, humpback whales use a **gulping feeding strategy**. They engulf schools of fish or invertebrates and close their mouth, causing their ventral pleats to extend from all the prey and water they gulped. Then they use their tongue to expel the water out of their mouth, through their baleen plates, leaving the prey trapped inside the mouth cavity. This feeding strategy is very energetically demanding (Goldbogen *et al.*, 2007, 2008; Potvin *et al.*, 2009; Goldbogen *et al.*, 2011) because of the high drag required for engulfment. As a result, to maintain a positive energetic balance, whales have to be selective as to the quality of the prey patches they feed on. The density and nutritive quality of prey patches has to be large enough to compensate for the energy deployed during feeding (e.g., Hazen *et al.*, 2009).

Humpback whales feed on schools of fish (e.g. sardine, anchovy, sand lance and herring) or **krill** (crustaceans of the order Euphausiacea). Feeding is largely restricted to the summer season, when humpback whales are within their polar feeding grounds. In the Southern Hemisphere, the primary food source of humpback whales is the Antarctic krill (*Euphausia superba*). However, humpback whales can have a relatively strong diet plasticity, particularly in response to changes in their environment. Using stable isotope tracers, Bengtson Nash *et al.* (2018) show inter-annual dietary fluctuations for humpback whales migrating along the East Australian coast. Fleming *et al.* (2016) showed a similar flexibility in the California Current System. Humpback whales are also known to adapt their generalist diet to reduce interspecific competition for preys with varying relative abundance (Fossette *et al.*, 2017). Finally, some whales on the East Australian coast are thought to supplement their energy supplies by feeding on fish in temperate waters during their migration (Eisenmann *et al.*, 2016).

As well as being rather generalist, humpback whales also display a diversity of feeding strategies (Fig. 1.11), such as **lunge feeding** (Goldbogen *et al.*, 2008), **bubble-feeding** (Jurasz and Jurasz, 1979) and lobtail feeding (Allen *et al.*, 2013) among others. Humpback whales have also been observed bottom-feeding on sand lance (Hain *et al.*, 1995). The same individuals may alternate between these strategies depending on prey availability, prey types or the time of day (Friedlaender *et al.*, 2009). Specifically, humpback whales have been shown to adapt to the nighttime **vertical migration** of the deep scattering layer and to feed at varying depth over the diel cycle (Hazen *et al.*,

2009; Friedlaender *et al.*, 2013). Due to the aggregated distribution of their preys, dense groups of humpback whales may be observed feeding in close proximity. The '**super-groups**' recently observed in South Africa offer a demonstrative example of such concentrations: large tightly-spaced groups of 20 to 200 individuals were discovered to feed late in the austral winter in the southern Benguela system (Findlay *et al.*, 2017).



Figure 1.11 Humpback whale feeding tactics: (a) bubble feeding, (b) lobtail feeding in the Gulf of Maine, where the whales slaps the surface with its caudal fluke before diving, (c) super-groups feeding observed in South Africa.

The breeding and calving season

The organization of humpback whales during the breeding season has been attributed to a lekking system (Herman and Tavolga, 1980), defined as a gathering of males engaged in competitive or vocal and visual display to attract females. This concept has been elaborated on by Clapham (1996) who suggested the term of a 'floating lek' to reflect the absence of territoriality in leks of humpback whales. The congregation areas where humpbacks regroup are called 'arenas' and their spatial distribution is theoretically independent from resource availability, other than the presence of conspecifics (Herman, 2017). Within arenas, individuals form small and unstable groups (Clapham, 1996). Social interactions have been extensively studied in the West Indies and 70% of humpback whales were found to stay in pairs or singletons (Mattila *et al.*, 1994). Larger groups are mostly of competitive nature and are composed of a mature female (the nuclear animal) followed by a principal escort (male with the dominant position) and challengers trying to remove the principal escort and access the female (Tyack and Whitehead, 1983; Clapham *et al.*, 1992). These groups are characterized by intrasexual competition through intense surface activities and violent aggressions between males (Fig. 1.12). Competitors often show superficial wounds as a result of these agonist interactions (Chu and Nieukirk, 1988). Serious injuries have only been reported on one occasion, in Hawaii where a male died while in interaction with a competitive group (Pack *et al.*, 1998).

One of the most remarkable aspect of humpback whale male display is their singing behavior (Payne and McVay, 1971). Songs are exclusively produced by mature males, while intra-specific communication in general is performed with short and quiet sounds called 'social sounds' (Dunlop, 2017). The function of songs is not exactly known, whether its is meant to attract females to individual

singers (or generally to a male aggregation), or to facilitate male-male interactions (Herman, 2017). Given the relatively high frequency at which songs are produced (100 Hz – 4,000 Hz; Tyack and Clark, 2000), and the harmonics up to 24,000 kHz in (Au *et al.*, 2006), the range of propagation is limited to a few kilometers (~20 km, Garland *et al.*, 2015). However, there is potential for larger scale attraction to be exerted 'in cascade' and for songs to play a role in spatial aggregation of individuals (Clapham and Zerbini, 2015; Herman, 2017).

Breeding grounds are also where nursing takes place. Pregnant females migrate to tropical waters and give birth at some point during migration or once arrived at their breeding grounds. Indeed, it is not precisely known where birth occurs with respect to breeding grounds, as the event has never been observed (with the possible exception of Faria *et al.*, 2013), and when a calf is encountered it is not possible to age it accurately. Humpback whales neonates can only be recognized from their small size, pale flank pigmentation (Chittleborough, 1953) and a furled dorsal fin (Cartwright and Sullivan, 2009b). Along the West Australian coast, neonates have recently been observed in July and August 1,000 km further south than the accepted southward limit to calving grounds for this population (22.7°S instead of 18°S limit, Irvine *et al.*, 2017). Mothers and their calf are always observed in close proximity to each other, and show varying degrees of social segregation with the rest of the breeding groups, which often results in a habitat use segregation (Smultea, 1994; Martins *et al.*, 2001; Ersts and Rosenbaum, 2003; Oviedo and Solís, 2008; Félix and Botero-Acosta, 2011; Craig *et al.*, 2014; Guidino *et al.*, 2014; Trudelle *et al.*, 2018).



Figure 1.12 Social group types and behaviors observed in breeding grounds. a) Mother with a calf escorted by a male (bottom right), b) competitive group, c) antagonist interactions between a male and a calf within a competitive group following a mother.

Mother-calf pairs are sometimes observed in the company of another whale, the 'escort' (Fig. 1.12). Escorts are almost exclusively mature males, who are thought to follow females to seek a mating opportunity or 'guard' them after mating has occurred. The 'bodyguard hypothesis' further suggests that maternal females seek the protection of an escort to avoid male harassment and injuries to their calf (Mesnick, 1997; Fig. 1.12). Indeed, direct deadly injuring of calves is rarely observed in humpback whales, but there is proof for increased energy expenditure by calves in the presence of adult males (Darling *et al.*, 2006; Cartwright and Sullivan, 2009a) and increased strandings of calves in areas where the density of males is high (southern right whales, Elwen and Best, 2004). However, the bodyguard hypothesis has been contested as the presence of a single escort sometimes appears to

disrupt calf behavior (Craig *et al.*, 2014).

1.3.4 From whaling to whale-watching

Humpback whales have been hunted intensively during the last two centuries. In early modern whaling, they were the main target of whalers because of their coastal distribution that made them easier to capture (Parsons *et al.*, 2013b). Populations of humpback whales worldwide were reduced to a few percent of their pre-exploitation numbers, particularly in the Southern Hemisphere (Jackson *et al.*, 2015).

It was only in the 1960s and up until the 1980s that public awareness and declining whale stocks pushed industrial whaling to a term. The 'Save the whales' campaign was key in concentrating public attention around the terrible fate of large whales. Far from the mysterious sea monsters they used to be, they became the symbol of human immoderate use of natural resources. The charismatic humpback whale became an umbrella species of conservation (Albert *et al.*, 2018), whose protection benefits to marine ecosystems from the poles to the tropics. In the past decades, humpback whales have shown encouraging signs of recovery leading to the reclassification of most populations by the IUCN from 'vulnerable' to a species of 'least concern' at a global scale.

The iconic value of humpback whales is supported by the recent increase in tourism, and with it, the actual capacity of people to observe whales in the wild. Since the moratorium on commercial whaling effective in 1989, humpback whales have grown as a valuable addition to coastal and island economies, thanks to the development of whale watching tourism. Cisneros-Montemayor *et al.* (2010) estimated the potential yearly revenue of this growing industry to 2.5 billion USD, creating 19,000 jobs around the world. Humpback whales are the main focus of many tours (O'Connor *et al.*, 2009), as they are appreciated for their proximity to the coast and demonstrative surface activities.

1.4 The study region: the South Pacific Ocean

The South Pacific is the geographic region located between the equator and the Southern Ocean (or Austral Ocean) surrounding Antarctica, and the study region for the present thesis. It is characterized by a complex topography, resulting in a network of scattered trenches, ridges, islands, reefs and seamounts. The South Pacific encompasses many groups of islands spread over Melanesia, Micronesia, Polynesia (Fig. 1.13), plus Australia and New Zealand. South Pacific islands are characterized by relatively low population densities and large Economic Exclusive Zones (EEZ; 30 million km²).

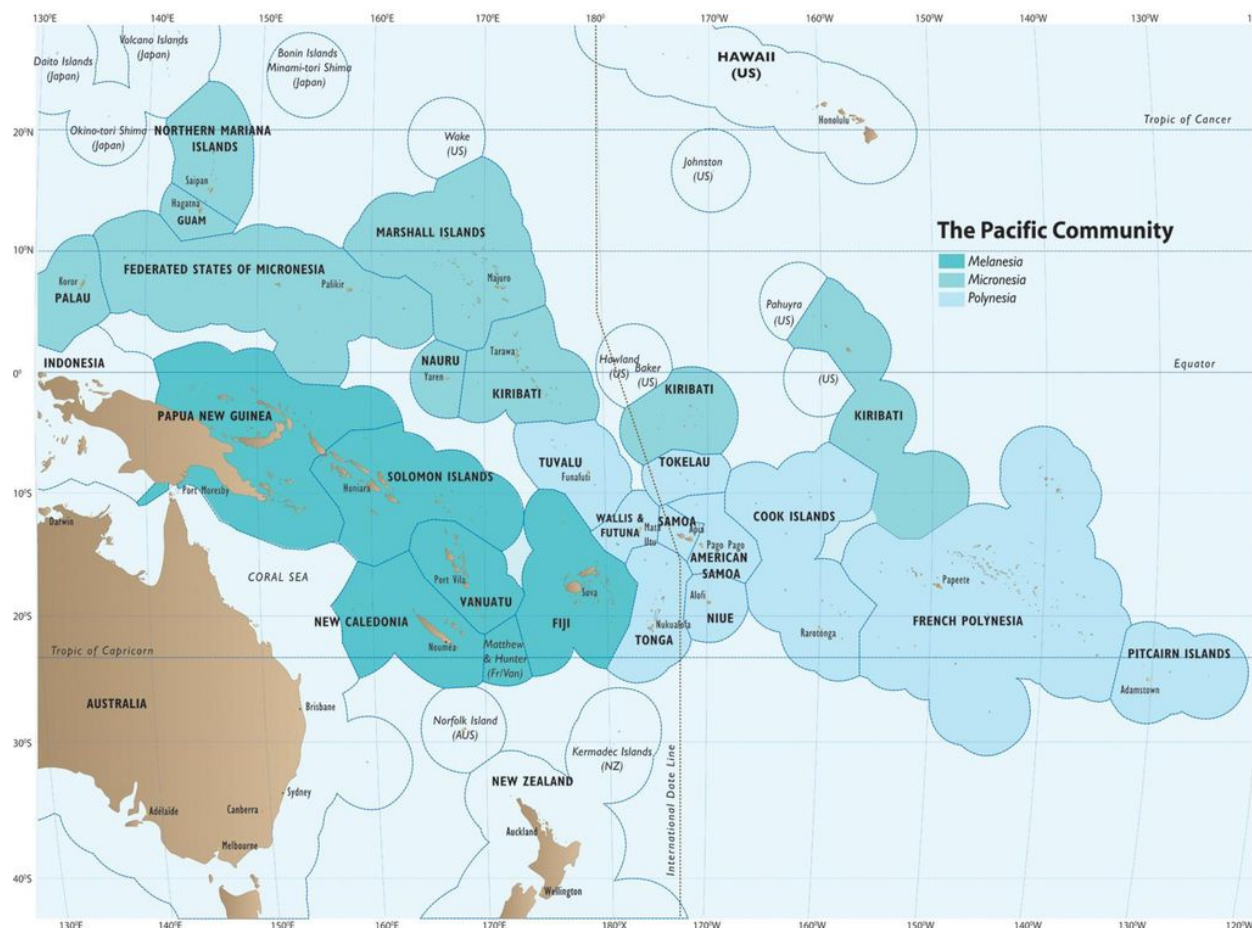


Figure 1.13 Geopolitical map of the South Pacific region showing the EEZ of countries and territories.

1.4.1 Ocean circulation in the South Pacific

The South Pacific region is dominated by the westward warm South Equatorial Current (SEC), and the Equatorial Counter Current (ECC) that flows below it (Fig. 1.14). To the West of the basin, the SEC flows into the intensified East Australian current, from where it then branches with the Antarctic Circumpolar current (the West Wind Drift) and finally completes the gyre as the Peru Current (the Humboldt current). The whole circuit around the South Pacific is known as the South Pacific Gyre. In this gyre, nutrients rich waters flow westward from the upwellings of the Peruvian coast. However, the SEC rapidly impoverishes as it warms up and photosynthesis consumes its nutrients in the tropical Pacific area. The south western pacific is known for having one of the lowest nutrient levels in the world, although localized nutrient inputs occur in coastal areas as a result of erosion, leaching and marine microorganism diazotrophic activity.

The vast Pacific Ocean is characterized by differential climatic conditions. To the West, air pressure is low and precipitations are abundant (around northern Australia, Indonesia and New Guinea). To the East, higher air pressure induces dry weather on the South American coast. Strong

southeast trade winds blow across the equatorial South Pacific as a result of this pressure difference, forming the Walker Circulation Cell (Fig. 1.15).

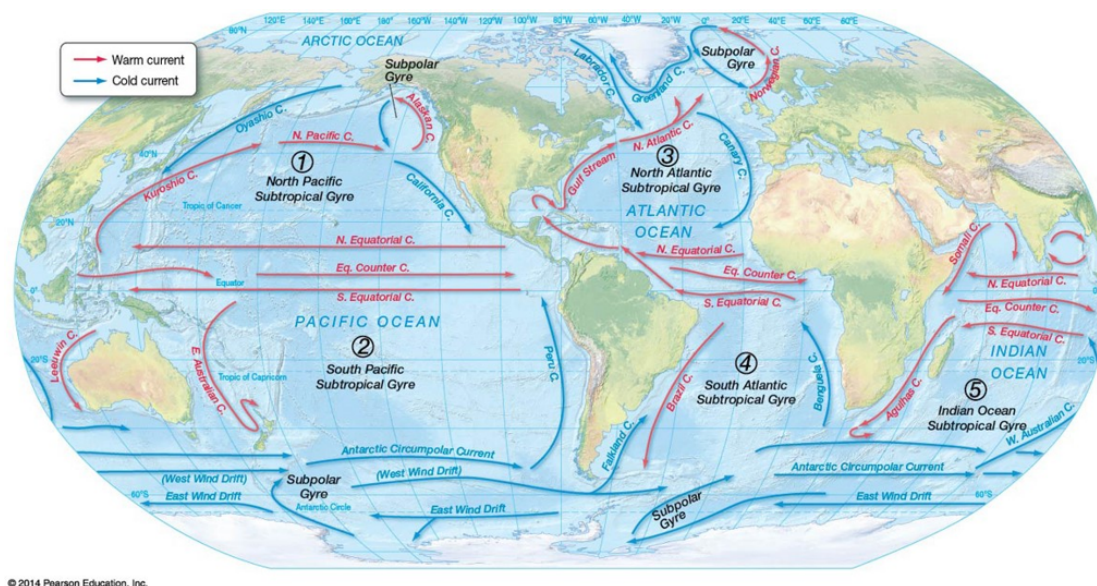


Figure 1.14 Schematic map of worldwide ocean circulation (Thurman and Trujillo, 2004).

The Pacific Ocean is characterized by the strong cyclical influence of the El Niño Southern Oscillation (ENSO). During the El Niño phase, the Walker Circulation Cell is weakened by a decreased pressure difference across the Pacific (Fig. 1.15). As trade winds decrease in strength (or may even be reversed) the warm pool of waters initially located to the western side of the Pacific begins flowing across the Pacific towards the east. On the contrary, La Niña phases correspond to a strengthening of the pressure difference across the Pacific, along with the trade winds. Upwellings along the South American coast are intensified and cold waters are transported at the surface from east to west. The alternating pattern between El Niño, La Niña and neutral years is shown by a variety of atmospheric and oceanic indexes, including the Southern Oscillation Index (SOI) based on the observed sea level pressure differences between Tahiti, in French Polynesia, and the city of Darwin on the north coast of Australia. Although these events are part of a natural climate cycle, ENSO is thought to intensify as a result of global warming (Cai *et al.*, 2015).

ENSO has a major influence on ecosystem functioning, from the tropical waters of the Pacific, down to the Southern Ocean, and from primary productivity, up to the top of the food chain. Cetacean distribution shifts have already been recorded in response to ENSO phases (Benson *et al.*, 2002; Sprogis *et al.*, 2017). These climatic fluctuations have impacts on sea-ice concentration in the Antarctic, which in turn impacts biological productivity (Zhang *et al.*, 2014). Breeding and birth rates have been shown to echo environmental fluctuations associated with ENSO in some marine mammals (sperm whales, Whitehead, 1997; southern right whales, Leaper *et al.*, 2006; dugongs, Fuentes *et al.*, 2016) and migratory seabird species (Laysan and black-footed albatrosses, *Phoebastria immutabilis* & *P. nigripes*, Thorne *et al.*, 2016).

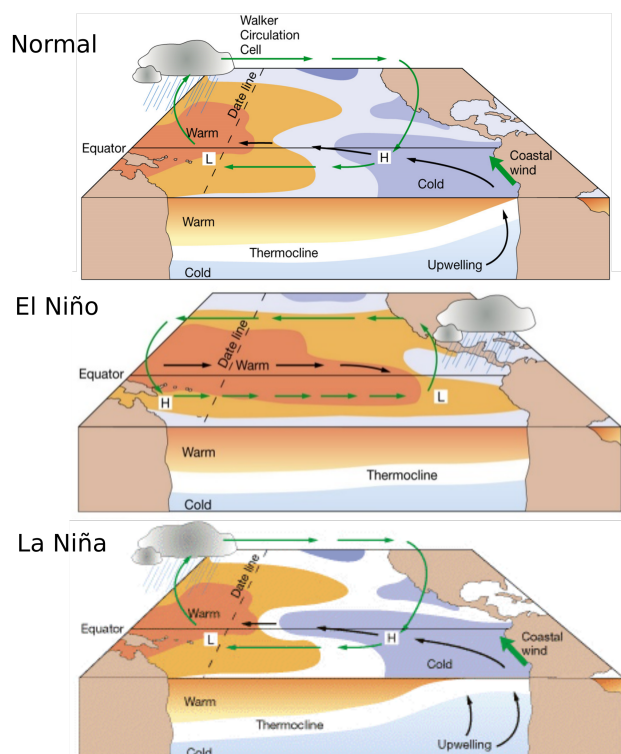


Figure 1.15 Schematic presentation of oceanic and atmospheric conditions during El Niño and La Niña phases (source: [Thurman and Trujillo, 2004](#)).

1.4.2 Tropical habitats: from reefs to high seas

The South Pacific is scattered with islands and atolls formed by the intense volcanic and tectonic activity around ridges, subduction zones and hotspots. Oceania only encompasses about 500,000 km² of surfacing land, spread over 200 high islands and 2,500 low islands and atolls ([Miller, 2007](#)). Four main types of islands exist: volcanic islands, continental islands, atolls and raised coral islands. Recently appeared volcanic islands are also referred to as 'high islands' because of their tortuous and elevated topography, sometimes towering above the height of 1,500 m (e.g., Tahiti, the Marquesas). These islands are typically surrounded by fringing reefs that develop along the margin of landmasses, where the temperature, depth and salinity is most suitable to reef-building corals. On the external slope of these reefs, depth increases rapidly. As landmasses subside and lagoons form, fringing reefs become barrier reefs. After some time, the volcano may completely disappear under water, while the coral reef continues to build up towards the surface and forms an atoll. Lagoons inside atolls or surrounding islands typically enclose shallow (30-50 m) and sheltered waters. Large reef systems (e.g., Great Barrier Reef, New Caledonia lagoons) often include several intermediate reef complexes scattered in the lagoon between the coast and the barrier reef. In some instances, raised coral islands can emerge from coral reefs that have been lifted out of the water through tectonic activity or sea level fall (e.g. Niue, Loyalty Islands). Finally, New Caledonia mainland and New Zealand form large islands of continental origin.

The Pacific seabed is also covered with bathymetric features that are not necessarily visible from the surface: seamounts. In general, seamounts are formed by two separate processes: small

seamounts with no clustering pattern are produced as active volcanoes along the crest of the mid-ocean ridges formed by divergent plate boundaries, while seamounts of various sizes are produced in linear groups as a result of surfacing mantle plumes in hotspots (e.g., the Hawaii chain). This relationship between tectonic activity and seamounts explains their heterogeneous distribution among the world's ocean basins (Pitcher *et al.*, 2008). No wonder that the western Pacific Ocean has some of the highest seamount density in the world considering its intense tectonic and volcanic activity (Wessel, 2001; Allain *et al.*, 2008).

Bathymetry of the ocean floor influences the water circulation. Small scale bathymetric features such as seamounts play a formerly overlooked role in the turbulent mixing of deep water with shallower and warmer waters (Kunze and Llewellyn Smith, 2004). Between other phenomenons, water circulation is affected around seamounts by localized circulation cells (e.g., Taylor columns), the amplification and modification of tidal motions and an increased vertical mixing (Fig. 1.16). These large vertical water excursions due to internal waves, together with vigorous turbulences and mixing, lead to nutrient export towards the surface and to the stimulation of biological production (Pitcher *et al.*, 2008; Fig. 1.16). Enriched and dynamic waters trigger local trophic cascades around seamounts (Morato *et al.*, 2010), which are now recognized for their exceptional levels of benthic fauna biodiversity and endemism (Richer de Forges *et al.*, 2000).

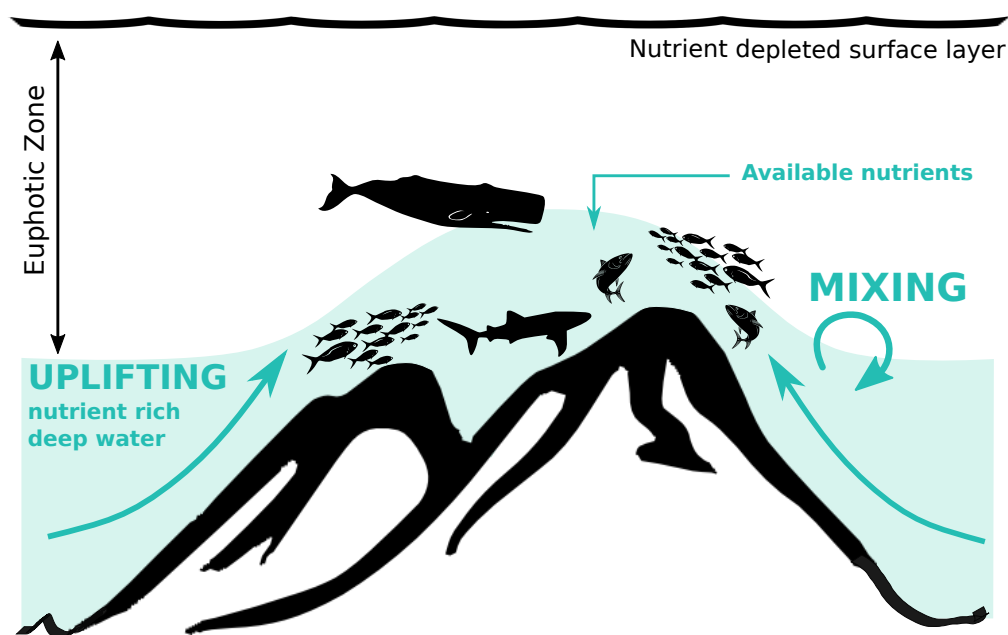


Figure 1.16 Vertical nutrient fluxes resulting from dynamic ocean circulation around seamounts (inspired by Pitcher *et al.*, 2008).

In turn, these features are also attractive to top-predators (Bouchet *et al.*, 2015). For instance, the attraction for seamounts has been highlighted in various species of odontocetes (e.g., Johnston

et al., 2008; Morato *et al.*, 2008; Hann *et al.*, 2016). Associations with baleen whales are less commonly reported (e.g., Sei whales, Waring *et al.*, 2008; humpback whales, Lammers *et al.*, 2011). Interestingly, shallower seamounts appeared to have stronger aggregation effects for top predators in the Azores region (< 400 m, Morato *et al.*, 2008) where common dolphins, *Delphinus delphis*, were specifically found in association to seamounts. Similarly, Hann *et al.* (2016) reported an association between sperm whales and seamounts of varying summit depth depending on the season (200-400 m or > 400 m).

1.4.3 The Oceania humpback whales

The South Pacific encompasses a remarkably large extent of suitable breeding habitat for humpback whales (Valsecchi *et al.*, 2010). Among the South Pacific islands, humpback whales have been recorded in American Samoa, Cook Islands, Fiji, French Polynesia, New Caledonia, Niue, Pitcairn, Samoa, Tonga, Vanuatu and Wallis and Futuna (Fig. 1.13). There are anecdotal reports of humpback whales visiting Papua New Guinea and the Solomon Islands. Finally, the species is unreported to date in all of the northernmost countries of the South Pacific: Kiribati, Nauru, Tokelau and Tuvalu (Miller, 2007).

The **humpback whale population of Oceania** is delineated by its breeding range, as defined by the IUCN (Childerhouse *et al.*, 2009): from 145°E to the west (between New Caledonia and eastern Australia), to 120°W to the east of the Pacific (between French Polynesia and South America), and from the equator at 0°S, up to approximately 30°S to the south of the Pacific.

Industrial whaling of the 20th century has particularly impacted Southern Hemisphere humpback whales, and among them the humpback whale population of Oceania. But with whaling also came the first information regarding the migratory routes and distribution of humpback whales in this vast region. In recent years, genetics, photo-identification and satellite tracking have begun to clarify the connections between feeding and breeding grounds of the South Pacific, as well as among breeding grounds.

Connectivity to feeding grounds

Whaling catch records and Discovery tags tracking first led scientists and whalers to think that humpback whales visiting the breeding grounds of Oceania were associated to the Antarctic feeding Area V (130°E and 170°W), and later to Area VI (120 and 180°W) (Dawbin 1966). Although today the exact migratory destinations of whales moving south from Oceania breeding grounds are not fully understood, recent satellite telemetry (Riekkola *et al.*, 2018), genotype and photo-identification matching (Robbins *et al.*, 2011; Constantine *et al.*, 2014; Steel *et al.*, 2017), and mixed-stock analyses (Albertson *et al.*, 2018) have confirmed the wide range of their feeding areas. They extend over 115° of longitude, from the Balleny Islands west of the Ross Sea, to the Bellinghousen Sea located in feeding Area I (Fig. 1.17).

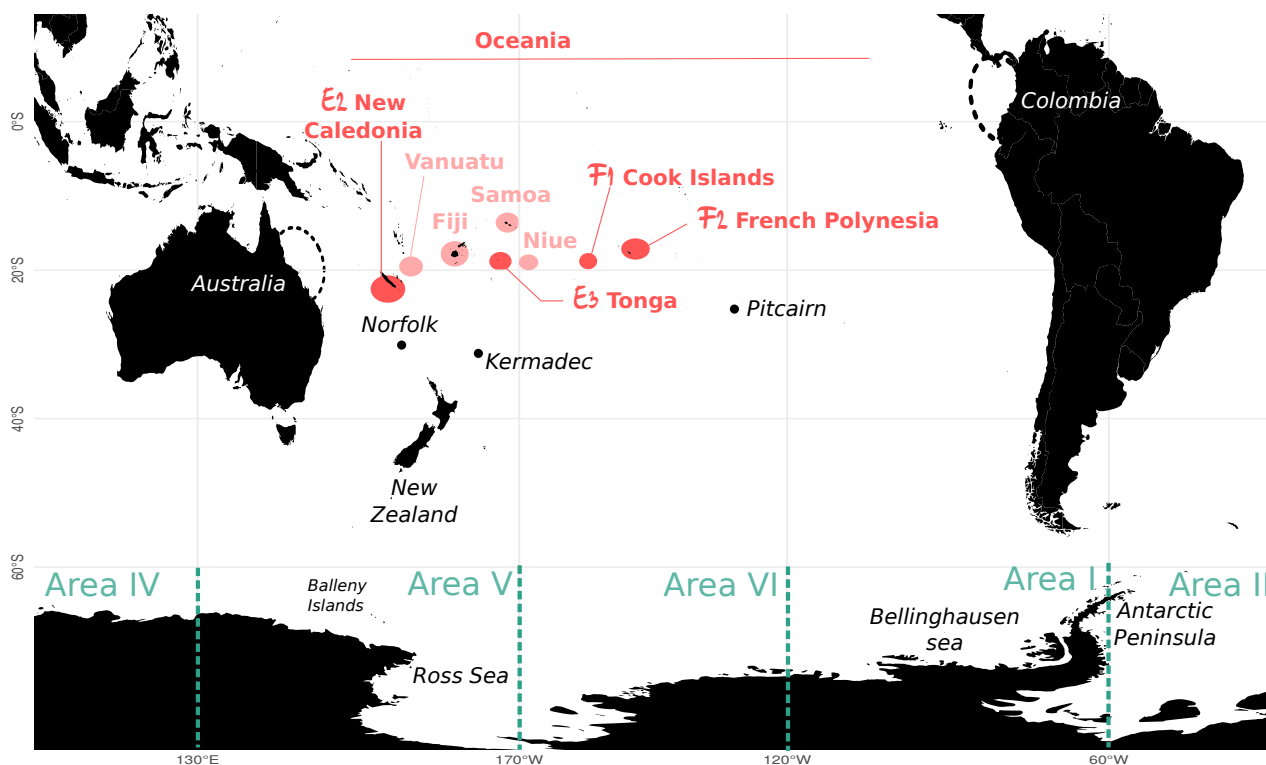


Figure 1.17 Oceania breeding grounds and related Antarctic feeding areas, as defined by the IWC. Oceania breeding sub-stocks currently recognized by the IWC are shown in red, while other known breeding grounds not yet affiliated to IWC are shown in pink. Samoa includes, American Samoa and the Independent State of Samoa. Migratory corridors are shown with black points. The migratory status for Pitcairn is uncertain. F1 is currently classified as a breeding sub-stock but recent evidence suggest that it might better be considered as a migratory corridor.

Migratory corridors

Dawbin (1966) identified a clear segregation in the migratory patterns of whales leaving the Antarctic feeding area V: on one hand the eastern Australia stream that would migrate along the coast towards the Coral Sea breeding grounds, and on the other hand the New Zealand stream that later separates into various South Pacific islands (Tonga, Fiji). New Zealand was identified as an important corridor for whales migrating to and from Oceania (Dawbin, 1956). It is now recognized that some of the islands and reefs of the southern Oceanian region also play the role of migratory corridors, where whales stop during northward and southward migrations. Migratory corridors include areas such as the Kermadec Islands (Riekkola *et al.*, 2018), and the Norfolk Island (Constantine *et al.*, 2007, Fig. 1.17). Although humpback whales mostly seem to transit through these areas and stop for short time periods along the migration, breeding and nursing activities appear to occur there to some extent too. Cook Islands are currently classified as an IWC breeding sub-stock but could be considered a migratory corridor given the transient pattern observed there (Hauser *et al.*, 2000, 2010). Moreover, humpback whale presence in Pitcairn Island has only recently been described and the status of the island is not yet defined (Horswill and Jackson, 2012).

Population structure among breeding grounds

The humpback whale population of Oceania is structured into geographically separated sub-populations² (Olavarria *et al.*, 2007; Childerhouse *et al.*, 2009; Garland *et al.*, 2015), with limited exchanges (Garland *et al.*, 2011; Garrigue *et al.*, 2011a; Steel *et al.*, 2017). The IWC recognizes several breeding stocks and sub-stocks in Oceania (IWC, 2005; Jackson *et al.*, 2015; Fig. 1.17) including **BSE2** (New Caledonia), **BSE3** (Tonga), **BSF1** (Cook Islands, potential migratory corridor) and **BSF2** (French Polynesia). The humpback whale population of Oceania is bordered to the west by BSE1 (Australia) and to the east by BSG (Colombia and Central America, Fig. 1.17).

Other islands are known to host breeding sites, but are not yet affiliated to an IWC stock or sub-stock. **Samoa and American Samoa** lie on the geographic boundary of BSE3 and BSF, and individuals exhibit exchange to both breeding stocks (Garrigue *et al.*, 2011a; Garland *et al.*, 2015; Steel *et al.*, 2017), as well as BSE2 (Steel *et al.*, 2017). Photo-identified and genotyped individuals in **Vanuatu** (Garrigue *et al.*, 2004b) and **Niue** (South Pacific Whale Research Consortium, SPWRC, pers. com.) have also been resighted in New Caledonia or Tonga. **Fiji** was historically visited by humpback whales in great numbers but relatively few currently do so (Dawbin, 1959; Gibbs *et al.*, 2006; Miller *et al.*, 2015). A few recent connections were found between Fiji and Tonga and New Caledonia (SPWRC, pers. com.). Finally, some countries such as **Wallis and Futuna** (Garrigue pers. comm.) are known to be visited (or have been visited) by humpback whales, but their connection to either of the established Oceania stocks has not been revealed yet.

Recovery and conservation

Although at global scale humpback whales are considered a species of 'least concern' by the IUCN, the humpback whale population of Oceania have recently been classified as 'endangered' (Childerhouse *et al.*, 2009) because of its small size and slow recovery rate (Constantine *et al.*, 2012; Jackson *et al.*, 2015). Indeed, the population of Oceania is still well below its pre-exploitation numbers (47 % recovered in 2015). As a comparison, the neighboring continental stocks appear to have had a much faster recovery rate; they are now estimated to be > 90 % recovered in Central America (BSG) and > 75 % in east Australia (BSE1; Jackson *et al.*, 2015). The total abundance estimated for 2015 over the whole Oceania population is 6,404 individuals [CI: 5,491-7,595] (Jackson *et al.*, 2015). Several conservation initiatives have been supported by international institutions, local governments and non-governmental organizations in the last decades to help the recovery of humpback whales in Oceania. The cultural bond between Pacific islanders and whales, and the economic value they represent through tourism have contributed to their conservation. In 2005, more than half of the South Pacific waters had been declared whale sanctuaries (Hoyt, 2005) and more have followed since then (e.g., Tonga in 2017). A Whale and Dolphin Action Plan was developed by the countries members

²Following Jackson *et al.* (2015), the words 'stock' and 'population' are considered equivalent, as are 'sub-stock' and 'sub-population'.

of the intergovernmental Secretariat of the Pacific Regional Environment Programme (SPREP) in 2006 (SPREP, 2012). A non-binding agreement was also signed by the South Pacific countries and territories in 2006 based on the Convention on Migratory Species or Bonn convention established in 1979 and effective since 1983. As a result, the Memorandum of Understanding for the Conservation of Cetaceans and their Habitats in the Pacific Islands Region (Pacific Cetacean MoU) was launched in 2006 to coordinate regional conservation efforts and encourage member countries to implement plans to protect cetacean and their habitats (www.cms.int/pacific-cetaceans).

1.4.4 New Caledonia

The present thesis aims to describe humpback whale spatial ecology in the South Pacific using New Caledonia as a main study site. This archipelago of Oceania is part of the Melanesian region and an Overseas Territory of France going through a process of growing autonomy. The EEZ of New Caledonia covers 1,200 km from north to south, and 1,800 km from east to west. A great portion of the New Caledonian waters are part of the **Coral Sea**, which separates the mainland from the Australian East Coast.

Geography and geodiversity

The New Caledonian EEZ spans more than 1.3 million km² and is characterized by a **complex seabed topography** (Fig. 1.18). The islands and banks of the EEZ are spread over two parallel ridges. The mainland, 'Grande Terre' is boarded by smaller islands to the north (Belep Islands, Entrecasteaux Islands) and to the south (Isle of Pines), and sits on the Norfolk Ridge. To the east, the Loyalty Islands (Ouvéa, Lifou, Tiga and Maré) emerge from the Loyalty Ridge, as well as smaller islands and reefs (Walpole, Durand, Pétrie, Astrolabe). On the eastern border of the New Caledonian EEZ, the Australian plate is actively moving in subduction under the Pacific plate, forming the New Hebrides trench. Two small islands emerge east of the trench: Matthew and Hunter. To the west, the Chesterfield-Bellona coral reef complex forms the northern end of the Lord Howe seamount chain. Next to it, the Fairway-Landsdowne bank is part of the Lord Howe ridge and surfaces over the Néréus reef. Many seamounts can be found in the southern part of the EEZ across these various bathymetric features, specifically over the Lord Howe chain (e.g., Nova, Argo, Kelso, Capel), the Norfolk Ridge (e.g., Antigonina, Torch bank, Munida) and the Loyalty ridge (e.g., Orne bank, Ellet).

The New Caledonian EEZ encompasses vast coral reefs (4,500 km²). Particularly, the lagoon surrounding the mainland is delimited by the longest barrier reef in the world (1,500 km-long). The width of the lagoon varies around the island, from 1 to 70 km wide, hence creating a great variety of reef habitats. For instance, the South Lagoon forms a large shallow area (about 50 m deep) bounded by the Prony Bay and the Ouen Island to the north, and by two coral reef complexes to the southwest (Corne Sud) and the southeast (Isle of Pines) but largely open to the deep ocean.

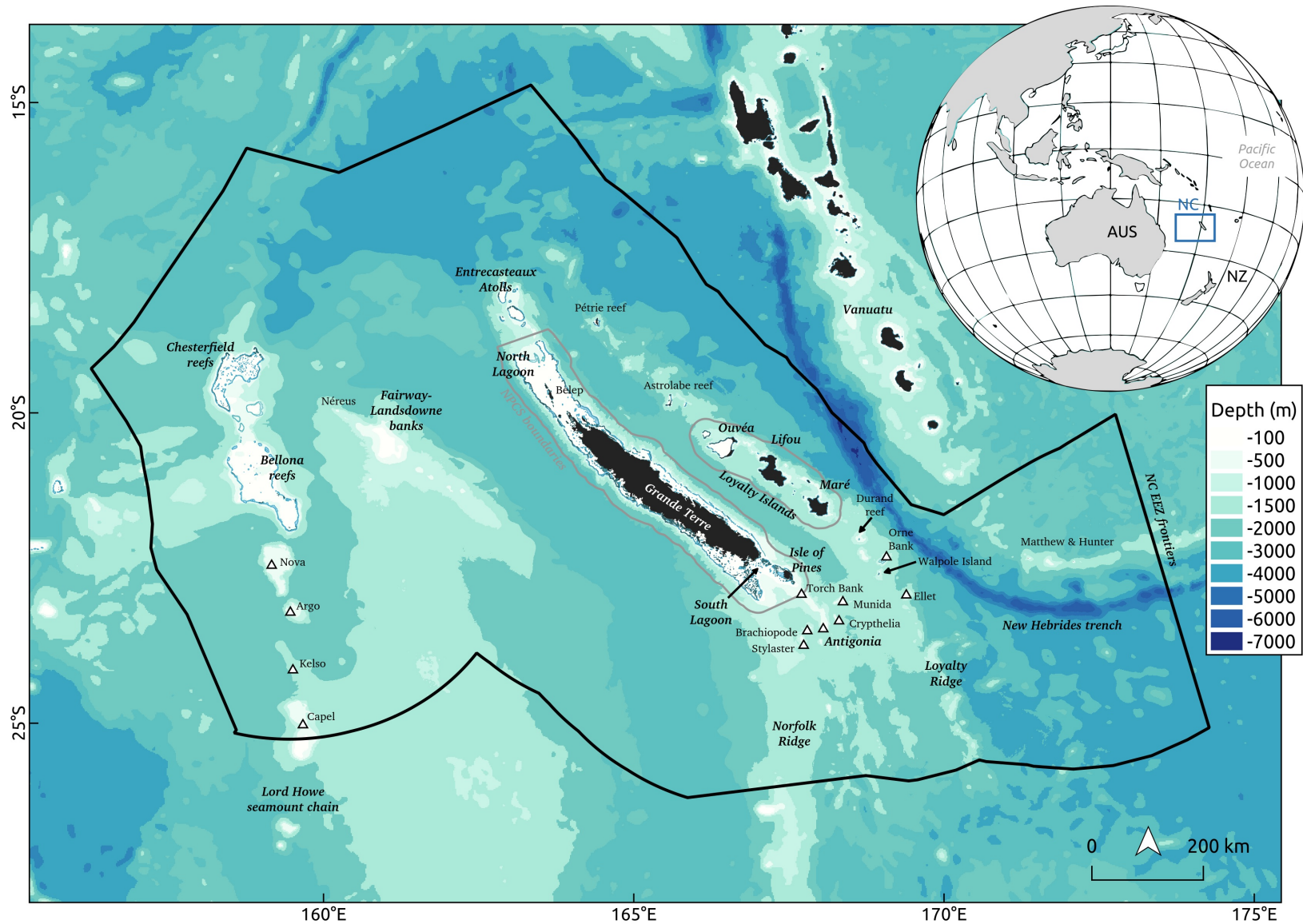


Figure 1.18 Map of the Economic Exclusive Zone of New Caledonia. The location of New Caledonia (NC) is shown on a globe, along with New Zealand (NZ) and Australia (AUS). Triangles represent the locations of seamount features mentioned in the thesis. Grey lines inside the EEZ represent the waters under provincial jurisdiction and not included in the Natural Park of the Coral Sea (NPCS).

The South Equatorial Current flowing westward across the Pacific splits into two branches when it meets the Loyalty Ridge: the **North and South Caledonian Jets** (Fig. 1.19). The SubTropical Counter Current flows from the Australian coast towards the western coast of New Caledonia. At smaller scale, the coasts of the mainland are also under the influence of two main currents. The highly unstable southeastward **Vauban Current** flows south through the Loyalty channel bringing warm waters in winter. In contrast, the southeastward **Alis Current of New Caledonia** carries colder waters into the area from the west and through an upwelling phenomenon (Marchesiello *et al.*, 2010; Cravatte *et al.*, 2015).

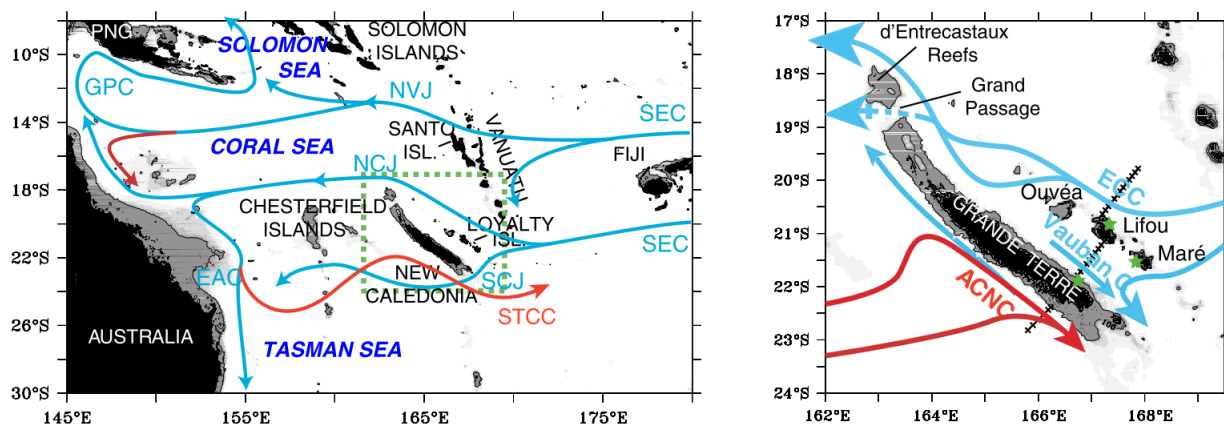


Figure 1.19 Currents of the New Caledonian region presented in Cravatte *et al.* 2015. SEC: South Equatorial Current, NCJ: North Caledonian Jet, SCJ: South Caledonian Jet, STCC: SubTropical Counter Current, ACNC: Alis Current of New Caledonia, ECC: East Caledonian Current, EAC: East Australian Current. Red lines represent surface circulation when different from thermocline circulation (blue lines).

Local conservation context

New Caledonia belongs to the world's most important hotspots for marine biodiversity (Tittensor *et al.*, 2010; Ceccarelli *et al.*, 2013), and benefits from several conservation measures, some of which specifically designed to protect cetaceans. As a French overseas collectivity, New Caledonia is bound to all international and regional agreements signed by France, including the International Convention for the Regulation of Whaling, the Convention on Migratory Species and the Convention on International Trade in Endangered Species (Schaffar, 2011). New Caledonia also participates in conventions of wider environmental scope that indirectly benefit cetaceans, such as the World Heritage Convention. Indeed, a great part the New Caledonian lagoons and coral reefs are listed as a UNESCO World Heritage Site (UNESCO, 2009).

New Caledonia is administratively organized in three provinces: **the Northern Province, the Southern Province and the Loyalty Island Province**. They are separately responsible for the conservation of the environment in their waters, extending up to 12 nautical miles off the barrier reef. Each has a separate environmental code associated with specific legislation for cetaceans (at a

very early stage for the Loyalty Island Province). Over the Northern and Southern Provinces, there are several marine parks and reserves, which forbid disturbance to animals and limit anthropogenic activities such as fishing and recreational boat traffic. The Southern Province also implements a voluntary code of conduct for whale and dolphin watching since 2008 (Schaffar *et al.*, 2013). The New Caledonian government is responsible for the management and environmental law enforcement over waters extending outside 12 nautical miles of the barrier reefs. All of this zone was declared a whale sanctuary in 2003 (Schaffar *et al.*, 2013). Furthermore, in 2014, the government created one of the most extensive marine natural park in the world: the **Natural Park of the Coral Sea** (Fig. 1.18). The Park covers all of the New Caledonian EEZ waters that are not under provincial jurisdiction. It qualifies as a giant MPA of 1.29 million km² (Pala, 2013). One of the main objectives identified in the management plan for this park is to create a network of marine protected areas to reduce anthropogenic impacts to marine megafauna, including cetaceans. Yet, the current knowledge of the preferential habitats and spatial range of these species within the park is limited.

Humpback whale sub-population

To date, 29 species of marine mammals (including 27 cetaceans) have been recorded in the New Caledonian waters (Garrigue and Poupon, 2013; Laran *et al.*, 2017) corresponding to one third of the world's cetaceans (www.marinemammalscience.org). From the many French overseas regions targeted by the REMMOA³ campaigns (Laran *et al.*, 2017), New Caledonia showed the highest marine mammal species diversity (19 taxa). Among these species, humpback whales are undoubtedly the most popular and charismatic. The knowledge of their seasonal presence in New Caledonia dates back to 1842 (Bérard, 1854; Pisier, 1975) and is also reflected in **local oral tradition** (Garrigue and Gill, 1994). On the Ouen Island located in the New Caledonian South Lagoon, people of the Ouara tribe tell stories about whales, and how their seasonal arrival sets the calendar for the harvest of a culturally important tuber, the yam.

New Caledonia is the most westerly archipelago visited by the humpback whale population of Oceania. Humpback whales found in this archipelago are **demographically isolated and genetically differentiated** from the two neighbor breeding sub-stocks of eastern Australia and Tonga (Garrigue *et al.*, 2004b; Olavarría *et al.*, 2007). Indeed, within-region return index calculated over several breeding sub-populations of Oceania have shown the highest fidelity in New Caledonia where 21 % of the identified individuals were resighted between 1999 and 2004 (Garrigue *et al.*, 2011a). The New Caledonian sub-population is relatively small as its abundance was estimated to 562 individuals (CI 95% 351-772) in 2008 (Garrigue *et al.*, 2012). However, **abundance is increasing** at a realized growth rate of 1.15 (CI 95% 1.11-1.20) equivalent to a 15% annual increase (Orgeret *et al.*, 2014), with a steep increase in 2009 (Garrigue *et al.*, 2012).

Humpback whales of New Caledonia are also known for their original migratory pattern. Indeed, satellite telemetry has shown a very large migratory corridor at the end of the breeding

³REcensement des Mammifères marins et autre Mégafaune pélagique par Observation Aérienne.

season (Garrigue *et al.*, 2015). Whales migrated in various directions: some following a southeastern direction, towards the Kermadec Islands, others moving south in the direction of Norfolk and New Zealand, and a few moving west in the direction of the Lord Howe seamount chain. Despite the proximity to **Australia**, very few exchanges have been detected between New Caledonia and the Australian migratory corridor for the breeding sub-stock E1 (Garrigue *et al.*, 2011b). On the other hand, a strong connexion has been demonstrated between New Caledonia and the main islands of **New Zealand**, as many individuals have been resighted through genetics (Steel *et al.*, 2014) and photo-identification (Constantine *et al.*, 2007; Meriot, 2016, and unpublished data from SPWRC), indicating that New Zealand is likely a major migratory corridor for sub-stock E2. More recently, humpback whales migrating past the **Kermadec Islands** have also been matched with New Caledonia using photo-identification and genetics (Garrigue *et al.*, 2016; Riekkola *et al.*, 2018).

A great part of the knowledge acquired on the humpback whale New Caledonian sub-population originates from the long-term research monitoring of the **South Lagoon** (Fig. 1.18). This long-term data set is the longest consistently recorded across all of the Oceania sub-populations. The South Lagoon is now considered one of the main breeding grounds known for this sub-population (Garrigue *et al.*, 2001). However, it must be noted that humpback whales are observed in other areas of the archipelago (Garrigue and Gill, 1994; Poupon and Garrigue, 2014). Notably, whaling logbooks (Townsend, 1935), wrecks (<http://museemaritime.nc/>) and remains of whaling stations (Guillou, 1983) suggest that humpback whales used to be present in the **Chesterfield-Bellona reef complex**. Indeed, this area has been identified as one the hotspots targeted by 19th century commercial whaling of humpback whales in the South Pacific (Townsend, 1935), but the magnitude to which humpback whales currently use the area is unknown (Gill *et al.*, 1995; Oremus and Garrigue, 2014).

Finally, recent satellite telemetry of humpback whales during the breeding season has unexpectedly revealed the intensive use of several offshore seabed features in New Caledonia, such as seamounts and banks (Garrigue *et al.*, 2015). These offshore features (e.g., Antigonie seamount, Fig. 1.18), are ecologically very different from most humpback whale breeding grounds studied around the world as they are located far from any coast and do not provide sheltered waters. Due to their relative in-accessibility, offshore waters of the open ocean are generally subject to less survey effort than coastal areas. In 2015, the **WHERE project** (Humpback Whale Habitat Exploration to improve spatial management in the natural park of the CoRal Sea) was launched in New Caledonia in order to explore remote waters of the New Caledonian EEZ. My PhD thesis falls within the scope of this project to describe and predict the habitat, distribution and movements of humpback whales at multiple scales in New Caledonia and the South Pacific, both in the nearshore and open ocean.

1.5 General objectives and thesis outline

1.5.1 Thesis research questions

The objectives of the present thesis are three folds:

1. Investigating cetacean SDM methodological approaches, using humpback whales as a study case.

How do different statistical approaches perform for describing and predicting distribution based on non-systematic research data? How can non-systematic research surveys and citizen science data be used to produce informative cetacean distribution models? What are the key constraints to studying the distribution of a wide-ranging long-lived cetacean in its breeding phase, and how do we overcome them?

2. Acquiring fundamental knowledge of humpback whale ecology during the breeding season.

What are the environmental drivers of humpback whale distribution in their breeding grounds? How do social factors influence distribution? How do environmental fluctuations and changes affect distribution at multiple temporal scales?

3. Applying spatial ecology to humpback whale conservation in the South Pacific.

What are the potential anthropogenic impacts on humpback whales in a coastal breeding ground of New Caledonia, and is current management action efficient? Based on the species-environment relationships identified at multiple spatial scales, can we predict priority conservation areas, in both coastal and offshore waters of New Caledonia? At an ocean basin scale, what is the potential for adaptation to global warming?

1.5.2 Scales of study & data overview

The present thesis primarily relies on more than two decades of research conducted in New Caledonia. Although most research has been conducted in coastal waters, survey effort since 2000 has also targeted offshore remote waters of the EEZ (Fig. 1.20). Over these many years of research, a multidisciplinary approach has been applied, combining visual observation (through non-systematic surveys at sea, from land and opportunistic), satellite tracking, acoustics, photo-identification and genetics. For the purpose of this thesis, I focus on data from non-systematic research surveys (Fig. 1.20), citizen science and satellite tracking to produce distribution models for humpback whales and describe movement patterns. Other types of data, such as individual identifications using genotyping and photo-identification, are only used punctually to complement some of the analyses reported in this thesis.

Furthermore, data recorded during boat-based non-systematic research surveys was contributed by members of the South Pacific Whale Research Consortium (SPWRC) and other colleagues to investigate humpback whale habitat and distribution at the scale of the South Pacific. Based on this large scale dataset, our study of humpback whale spatial ecology could be extended to a basin wide scale.

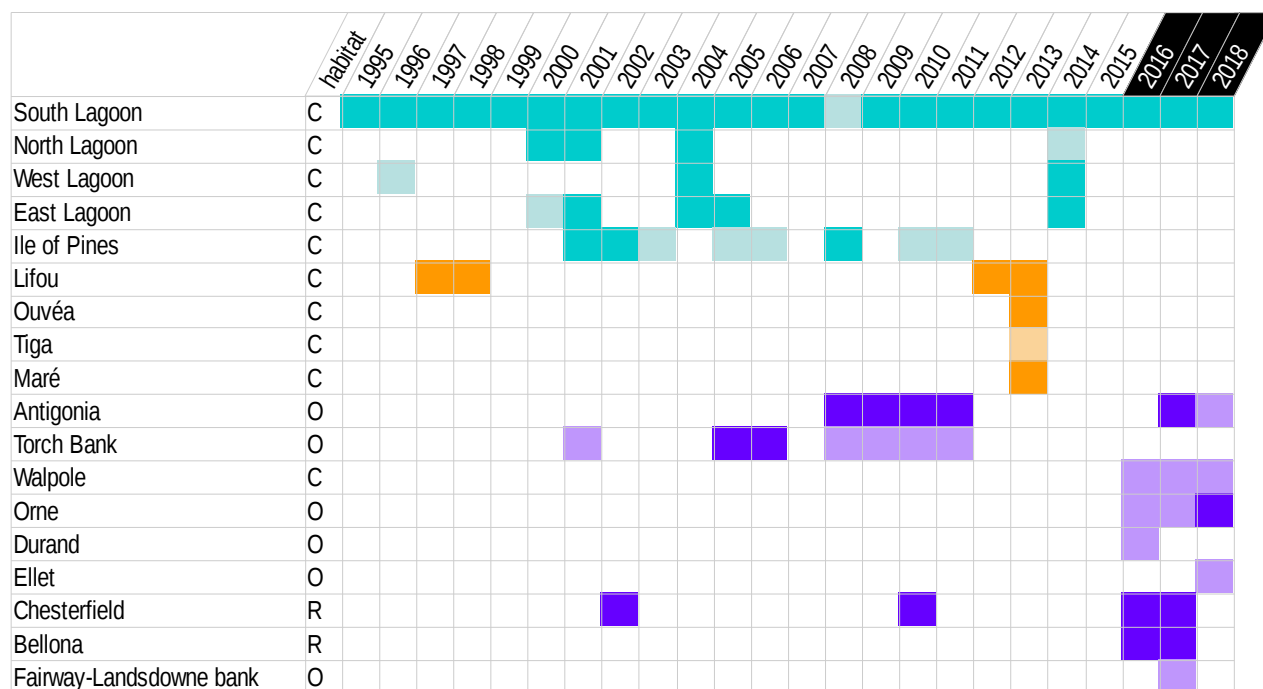


Figure 1.20 Non-systematic boat-based survey data available in the New Caledonian EEZ. Years in black represent those when the WHERE project surveys were conducted. Blue cells represent coastal surveys conducted around Grande Terre, orange cells represent coastal surveys conducted in the Loyalty Islands, and purple cells represent surveys conducted in the Natural Park of the Coral Sea. The main type of habitat per study site is indicated: C = coastal, O = offshore, and R = reef complexes. Lighter shades of color are associated with surveys that were two days or less for a given year and location.

1.5.3 Thesis outline

The outline of the thesis is based on the increasing spatial scales considered over New Caledonia and the South Pacific (Fig. 1.21). Each of the following chapter is related to an article (published, in review or in preparation).

Chapter 2 describes the long-term space use patterns of humpback whales in the main coastal breeding ground of New Caledonia, the South Lagoon. Building on more than two decades

of consistent monitoring at sea and from land, I investigate the trends in encounter rates, social composition and habitat use of whale groups at a local scale. Results are discussed in a spatial management perspective, in comparison to the current MPAs and potential anthropogenic impacts in the area.

Chapter 3 extends the study of humpback whale space use patterns into offshore waters and considers the influence of social factors on distribution. Social segregation of maternal females with a calf is compared between two sites with contrasting habitat types: a coastal lagoon site, the South Lagoon, and an offshore seamount site, the area encompassing Torch Bank and Antigonina seamount. Using individual photographs, calf age is investigated as a potential driver of the mother's habitat selection pattern.

Chapter 4 aims at describing humpback whale-habitat relationships at the regional scale of the New Caledonia EEZ and predicting habitat suitability. In this chapter, I compare the capacity of various statistical algorithms to deal with biases commonly found in non-systematic cetacean surveys and I evaluate the potential for citizen science data to improve habitat modeling and predictions.

Chapter 5 investigates humpback whale breeding habitat diversity and adaptability to climate change at the Oceania scale. In this chapter, I use non-systematic research surveys conducted in seven countries and territories of the South Pacific, whose humpback whale sub-populations belong to the endangered Oceania population. Current and future distributions are modeled with respect to topographic environmental features. Adaptability of humpback whales to climate change is discussed in relation to predicted water temperatures for the end of the 21st century.

Chapter 6 addresses the use of critical humpback whale habitats within breeding latitudes. I model horizontal and vertical movement patterns of humpback whales in relation to habitat and reproductive status using ARGOS satellite tracking and diving records from tags deployed in New Caledonia as part of the WHERE project. The use of shallow offshore features such as seamounts and banks is specifically investigated to understand why humpback whales aggregate around these bathymetric features.

Chapter 7 is a general discussion targeting methodological, fundamental and conservation aspects of the present thesis. First, I discuss various methodological aspects of cetacean distribution modeling, such as the limitations of various types of cetacean spatial data, the approaches to deal with spatial sampling bias, the choice for statistical algorithms and environmental predictors, and the importance of model transferability. Second, I summarize the findings of the thesis regarding the spatial ecology of humpback whales in their breeding grounds of New Caledonia and the South Pacific. The behavioural, demographic, and evolutionary implications of the observed patterns of distribution, habitat and movements are discussed. The role of seamounts for breeding and migrating humpback whales is specifically highlighted as an avenue for future research. Finally, the conservation perspectives brought by this thesis are presented for the local New Caledonian context, as well as the broader Pacific context. Implications for spatial management and anthropogenic impact mitigation are presented.

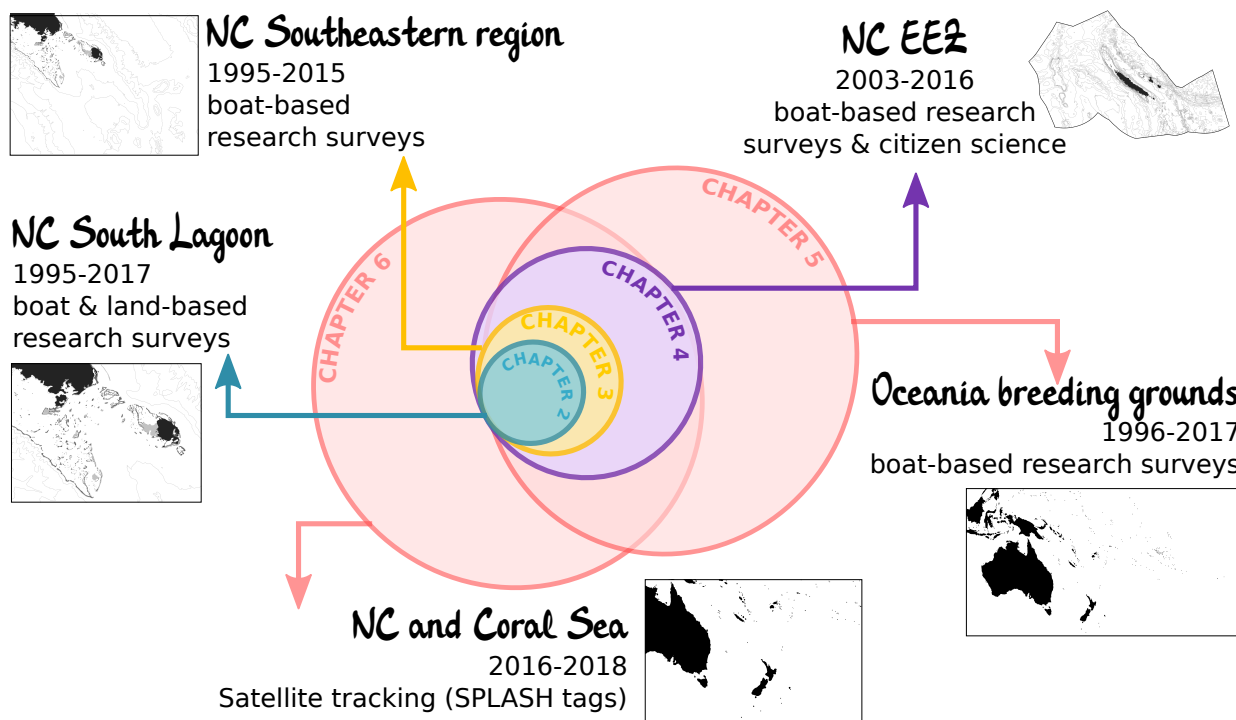


Figure 1.21 Summary of the thesis chapters, ordered by increasing spatial scale of interest. The study period and area for each chapter is indicated, along with the main type of data that was included in analyses.

Following a framework of increasing spatial scale, I will begin this thesis with the study of a New Caledonia local breeding ground: the South Lagoon. This site has been the focus of a long-term monitoring program initiated in the early 1990s. For a long time, it was considered the main breeding ground for the New Caledonian humpback whale subpopulation. Using an exceptional dataset of non systematic surveys at sea conducted over more than two decades, I investigate the inter-annual variability of humpback whale occurrence, including social composition, habitat use and encounter rates. The persistence of humpback whale presence in this area is discussed in relation to the predictability of suitable breeding and nursing environmental conditions over the years. The conservation applications of our results are emphasized in a context of growing anthropogenic activities likely to result in increased disturbance in this coastal area.

II. Long-term distribution in a coastal area

From land and sea, long-term data reveal persistent humpback whale breeding habitat in New Caledonia

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In review in Aquatic Conservation

Derville, S., Torres L. G., and Garrigue, C. (In review) From land and sea, long-term data reveal persistent humpback whale breeding habitat in New Caledonia. *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Abstract

1. Long-term monitoring is a prerequisite to understand and protect long-lived species such as cetaceans. In New Caledonia, South Pacific, an endangered sub-population of humpback whales seasonally congregates for breeding and nursing during the austral winter. For more than two decades, dedicated surveys have been conducted at sea and from land to monitor humpback whale presence in a coastal breeding site, the South Lagoon.

2. Methods were developed to investigate space use patterns and their temporal variations over the long term using a joint dataset of boat-based and land-based observations (1995 - 2017). A total of 2,651 humpback whale groups were observed, including 1,167 from land and 1,484 at sea (of which 30% were initially detected by the land-based observers).

3. Humpback whales displayed a persistent space use pattern over this 23 year period, consistent social composition over the years, and an increase of the encounter rates from land and at sea. The core area of use by humpback whales was characterized in the austral winter by stable and relatively low sea surface temperature (22°C). They consistently occupied nearshore waters from 10 to 200 m and open to the ocean. Waters surrounded by dense coral reefs were avoided.

4. Although humpback whale distribution patterns were persistent and occurrence was found to increase over two decades, a mismatch between humpback whale critical habitat and marine protected areas was revealed. In the context of growing anthropogenic pressure from tourism and industrial development, these findings should be incorporated into local management efforts to protect the endangered Oceania humpback whales in one of their main breeding sites.

Key words

Long-term monitoring, encounter rate, habitat mapping, marine protected areas, human disturbance

2.1 Introduction

Industrial whaling of the 19th and 20th century greatly impacted humpback whale populations (*Megaptera novaeangliae*) worldwide (Rocha *et al.*, 2015). Today, humpback whales are globally well below their pre-exploitation numbers although populations have undergone contrasting degrees of recovery during the past decades (13 to 97 % recovered in Southern Hemisphere stocks, Jackson *et al.*, 2015). As humpback whale populations are now facing the cumulative effects of growing anthropogenic activities from threats of pollution, vessel traffic, entanglement, noise or tourism (Schaffar *et al.*, 2013; Avila *et al.*, 2018), there is a need to monitor local population recovery. Understanding the trends in distribution, habitat use and dynamics of populations is essential to implementing appropriate local conservation measures, and ensure the species recovery as a whole. However, the slow breeding rate and long life-span of humpback whales warrants long-term datasets in order to highlight potential population trends.

Long-term datasets are rarely available in marine ecosystems, especially regarding cetaceans (Sydeman *et al.*, 2015). The high financial cost and challenging survey environment characterizing cetacean studies are obvious obstacles to the implementation of research projects over several decades (Simmonds and Elliott, 2009). Also, once actually collected, long-term datasets often constitute data processing and statistical challenges, particularly due to protocol mismatches (Ducklow *et al.*, 2009; Lindenmayer and Likens, 2010) regarding the extent of survey effort and methods used across several years or decades. However, when such challenges are overcome, great knowledge can be gained from long term monitoring programs, such as from humpback whale surveys conducted in Glacier Bay (Saracco *et al.*, 2013; Neilson *et al.*, 2017) or the Gulf of Maine (Robbins, 2007). Indeed, given the relatively long generation time (e.g., humpback whales 21.5 yr, Taylor *et al.*, 2007) and life span (e.g., humpback whales 95 yr, Chittleborough, 1965) of large whales, decade-long datasets are necessary to detect trends in distribution and population demographics.

The Oceania population of humpback whales is relatively small, has one of the slowest recovery rates (Constantine *et al.*, 2012; Jackson *et al.*, 2015) and is still listed as 'endangered' in the IUCN Red List (Childerhouse *et al.*, 2009). Humpback whales of the Oceania population feed during the austral summer in the remote waters of the Southern Ocean, from the Balleny Islands to the Antarctic peninsula (Constantine *et al.*, 2014; Steel *et al.*, 2017; Albertson *et al.*, 2018; Riekkola *et al.*, 2018). During the austral winter, they visit breeding grounds dispersed in the tropical and subtropical waters surrounding islands and reefs of the South Pacific. Various degrees of sub-population structuring has been identified across this vast area (Olavarría *et al.*, 2007; Constantine *et al.*, 2012) and the International Whaling Commission recognizes several breeding sub-stocks including BSE2 in New Caledonia, BSE3 in Tonga and BSF in French Polynesia and the Cook Islands (IWC, 1998; Jackson *et al.*, 2015). Among the widely dispersed breeding grounds found across Oceania, humpback whale research has only been carried out in a few specific study sites.

New Caledonia is the most westerly archipelago visited by the endangered humpback whale

population of Oceania. Humpback whales found in this archipelago are demographically isolated and genetically differentiated from the two neighbour breeding populations of eastern Australia and Tonga (Garrigue *et al.*, 2004a; Olavarria *et al.*, 2007). The New Caledonia South Lagoon (Fig. 2.1) is considered one of the main humpback whale breeding grounds known to date for this sub-population (Garrigue *et al.*, 2001). This sub-population of humpback whales has been the focus of a long-term research project (Garrigue *et al.*, 2001) initiated in the early nineties, which has documented humpback whale presence in the South Lagoon from the beginning of July to the end of September, with a peak of abundance after mid-August.

The New Caledonia South Lagoon also concentrates several human activities that constitute liable threats to whales. Active nickel mining industry on the mainland induces sediment runoff (Heintz *et al.*, 2015) and maritime traffic (Bourgogne *et al.*, 2018). New Caledonia also is a leading whale watching destination among the South Pacific Islands (Schaffar *et al.*, 2010, 2013). Observations guidelines have been in place since 2008, to promote responsible whale watching behaviour (Province Sud, 2018) but increasing tourism and human population density (www.isee.nc) is a cause of concern in terms of vessel traffic and collision risks. An integral marine protected area, the Merlet reserve, was created in 1970 to prevent all human activities over a 170 km² area northeast of the South Lagoon (IUCN category Ia, Fig. 2.1). A great part of the South Lagoon is also classified as a UNESCO World Heritage Zone (UNESCO, 2009), as well as a Province Park (IUCN category II, Fig. 2.1) but the level of protection provided by these zones is very low (Cleguer *et al.*, 2015). The contribution of these protected areas to the conservation of critical habitats for humpback whales has never been investigated.

This study is based on the long-term monitoring of a humpback whale sub-population occurring 30 years after commercial whaling of this species ended in the Southern Hemisphere. A dataset of simultaneous boat-based and land-based surveys was used to evaluate humpback whale occurrence, social composition, distribution and habitat use in the New Caledonia South Lagoon, over more than 20 years (a quarter of a humpback whale's maximum life span). A broadly applicable methodological approach was developed to 1) robustly combine data collected through two different observation platforms, 2) account for spatio-temporal survey effort variability, and 3) assess trends from two-decades of survey. In the context of a population recovering from industrial whaling and facing growing human pressure, this study aims to provide a baseline of the New Caledonia South Lagoon humpback whale sub-population status. The overlap between current protected areas and humpback whale space use patterns is evaluated to help the implementation of appropriate conservations measures for this endangered population.

2.2 Materials and methods

2.2.1 Study region

New Caledonia is an archipelago located in the southwest Pacific Ocean about 1,500 km northeast of Australia (Fig. 2.1). New Caledonia mainland, also called 'Grande Terre', is surrounded by a large lagoon delimited by a 1,500 km-long barrier reef. The South Lagoon is a large shallow area (about 50 m deep) located south of the mainland, bounded by the Prony Bay and the Ouen Island to the north, and by two reef complexes to the southwest ('Corne Sud') and the northeast (Isle of Pines, Fig. 2.1). The southeastern part of this lagoon is open to the ocean and is characterized by deeper waters (reaching 600 m deep). New Caledonia is under the influence of two main currents: the highly unstable southeastward Vauban current flows south through the Loyalty channel bringing warm waters in winter. In contrast, the southeastward Alis Current of New Caledonia carries colder waters into the area from the west (Fig. 2.1; Marchesiello *et al.*, 2010; Cravatte *et al.*, 2015).

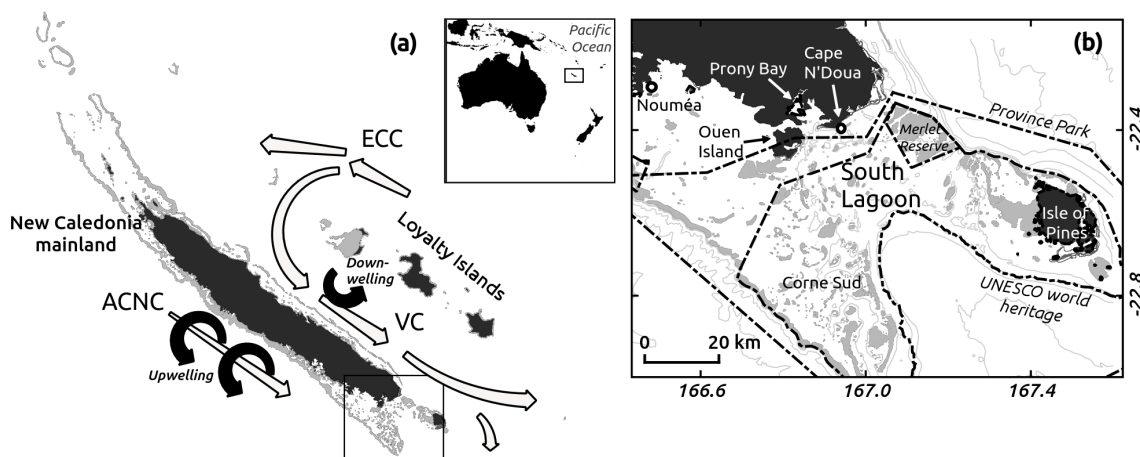


Figure 2.1 Map of New Caledonia (a) and the South Lagoon study area (b). Main currents are illustrated on the map based on Marchesiello *et al.* (2010) and Cravatte *et al.* (2015): ECC = East Caledonian Current; VC = Vauban Current; ACNC = Alis Current of New Caledonia. The ECC is a local branch of the larger scale South Equatorial Current. Upwellings and downwellings are represented with black curved arrows. Land is shown in black. Barrier and patch reef complexes in grey. Marine protected areas are shown with dashed lines.

2.2.2 Data collection

Surveys were conducted in the South Lagoon of New Caledonia from 1995 to 2017 (except for 2004 and 2008), between the beginning of July and the end of September. Surveys were conducted in Beaufort sea-states ≤ 3 (and avoiding heavy rain) and were simultaneously conducted at sea and from a land-based look-out located on top of the Cape N'Doua (altitude 189 m, $> 270^\circ$ visibility, Fig. 2.1). Both teams could communicate at all times using Very High Frequency (VHF) radios. A land-based team composed of one to five trained observers scanned the study area and detected whales up to 36 km from the cape. A few areas close to the coast and within the Prony Bay were masked from

the Cape and their extent was measured using a theodolithe (Schaffar *et al.*, 2013; Fig. 2.2b). The boat-based team was composed of three to five trained observers in a 6 m rigid-hulled inflatable boat moving at 14 km.h⁻¹ on average. Surveys followed a haphazard sampling regime (Corkeron *et al.*, 2011), with effort dependent on weather conditions and focused on waters accessible on a daily basis from the Prony Bay.

For each encounter, geographic position, time, social group type, and minimum-maximum group size were recorded. A whale group was also defined by a unique detection source, land or boat-based or from an external source, and may have been subsequently followed by both the land- and the boat-based teams. Encounters were considered independent events, as repeated observations of the same individual whale within a survey day rarely occurred (Derville *et al.*, 2018a). The geographic position of groups followed at sea was recorded in latitude-longitude using an on-board GPS, whereas groups only followed from land were located either with a precise latitude-longitude position in years where a theodolite was used (51% of observations), or using a grid of 1 nautical mile resolution (latitude-longitude was subsequently extracted as the centre of the grid-cell the whale group was located in; 32% of observations), or by a simple textual description of the location (latitude-longitude was subsequently extracted in a GIS interface based on these descriptions: <https://explorateur-carto.georep.nc/>; 17% of observations).

Data processing and statistical modelling was performed with the R software version 3.2.5 (R Core Team, 2016) and geographical data visualisation was performed using QGIS v.2.14. (QGIS Development Team, 2016).

2.2.3 Temporal trend of occurrence

Social group types observed at sea were defined as: groups of three adults, groups of four adults, competitive groups, mother with calf, mother with calf followed by a single escort, mother with calf followed by a competitive group, pairs, singletons and singers. From land, singers could not be differentiated from singletons, and groups of three or more adults were pooled in the same category.

The proportion of social group types observed from land and at sea was calculated for each year. The effect of the observation platform (land or sea) and time (breeding seasons from 1995 to 2017) on the proportion of social group types was tested with beta regressions using the *betareg* R package (version 3.1-0).

The encounter rates were calculated separately from land and at sea as the number of whales observed per hour of survey effort conducted during each breeding season. The rate of increase of encounter rates through time was estimated between the period 1995-2003 and 2012-2017. Encounter rates were averaged for these two periods, and the rate of increase was calculated between the two means.

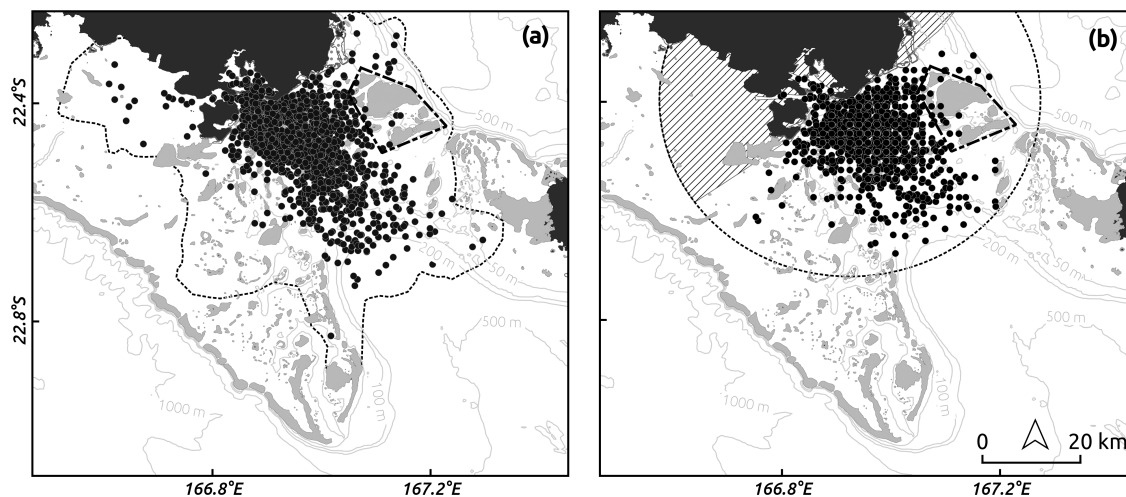


Figure 2.2 Map of humpback whale groups observed in the South Lagoon, New Caledonia, between 1995 and 2017: groups observed at sea (a; $n = 1,484$) and groups observed from land only (b; $n = 1,167$). The dotted lines represent the study area at sea and from land respectively. In panel (b), areas filled with dashes could not be observed from the land-based lookout, and represent 29% of the encircled study area. Land is shown in black, barrier and patch reef complexes in grey. Isobaths are represented with light grey lines. The Merlet integral reserve is shown with a thick dashed line.

2.2.4 Quantifying survey effort at sea

The distribution of survey effort was estimated annually and separately for boat-based and land-based teams. From 2003 to 2017, effort was estimated from boat GPS tracklines recorded at one position per minute (about one position every 230 m for a boat moving at $14 \text{ km}\cdot\text{h}^{-1}$). Tracklines were segmented into on-effort (times when the boat-based team was actively searching for whales) and off-effort sections (times when the boat was engaged in a focal follow and was not vigilant to the detection of other groups). Effort was estimated seasonally over $500 \times 500 \text{ m}$ resolution grids. Time spent on-effort per grid cell was calculated, rather than distance travelled, to account for variable boat speed. To account for detection distance spanning further than the dimensions of a grid cell (average detection distance 2 nm, Garrigue pers. obs.), a density surface of effort was derived from discrete boat GPS on-effort positions. Per breeding season, GPS tracks were projected in a UTM coordinate system and a density surface of effort was estimated with a 2-dimension Local Polynomial Regression (LOESS; span = 0.005).

From 1995 to 2002, research boats were not equipped to record GPS tracklines, a common limitation in marine surveys prior to the mid-2000s. An original method was developed to assess the distribution of survey effort for these seven years. GPS positions recorded over each day (end and start of focal follows, and acoustical sampling positions) were compiled and connected together in a chronological order, thus forming daily paths hereafter referred to as 'pseudo-tracklines'. These pseudo-tracklines were considered a subsample of the real tracklines followed by the research boat over the course of a day. Yearly maps of pseudo-effort were produced using a method similar to that applied to real GPS tracklines: they were interpolated at one position/minute, sections off-effort

were removed, and the remaining positions were smoothed with a LOESS applied with a varying bandwidth (i.e. span ranging from 0.002 and 0.02). After evaluating the quality of each smoothed trackline in comparison to maps of effort after 2003, the 0.01 bandwidth was selected to provide the most realistic estimate of pseudo-effort distribution from 1995 to 2002 (for details see Appendix 2.A).

Finally, yearly maps of pseudo-effort from 1995 to 2002 and yearly maps of effort from 2003 to 2017 were concatenated, hence generating a time series of 21 yearly maps of boat-based effort. Yearly maps were rescaled to [0-100], so that cells with maximum intensity across all years were attributed 100% intensity values.

Table 2.1 Summary of survey effort and observations of humpback whales at sea and from land in the South Lagoon, New Caledonia, from 1995 to 2017. (#) indicates the number of humpback whale groups. # unique groups observed is the sum of the groups observed at sea and the groups observed from land only.

Year	Boat-based effort (days)	Land-based effort (days)	# groups observed at sea	# groups detected from land	# groups observed from land only	# unique groups observed
1995	27	18	25	24	13	38
1996	55	48	54	82	45	99
1997	44	41	53	54	29	82
1998	50	52	42	50	21	63
1999	46	43	23	22	11	34
2000	50	43	44	25	10	54
2001	55	47	77	56	36	113
2002	33	38	20	6	4	24
2003	39	42	70	28	23	93
2005	33	25	56	35	27	83
2006	41	47	103	124	100	203
2007	48	49	124	162	140	264
2009	32	48	67	126	126	193
2010	36	38	97	138	84	181
2011	39	38	133	154	113	246
2012	29	30	96	105	81	177
2013	25	27	96	112	55	151
2014	29	23	38	28	9	47
2015	31	29	99	131	101	200
2016	26	25	61	50	41	102
2017	39	38	106	73	98	204
Total	807	789	1484	1585	1167	2651
Mean	38.4	37.6	70.7	75.5	55.6	126.2
SD	9.5	9.9	33.4	49.5	43.5	74.2

2.2.5 Quantifying survey effort from land

The effect of the number of observers on whale detectability from land was tested with a sequential Generalized Linear Model (GLM, [McCullagh and Nelder, 1989](#)). First, the number of groups detected from land per day was modelled as a Poisson variable, relative to time on effort,

year and Julian day of year. Residuals from this regression were modelled with a gaussian linear regression as a function of the number of observers, with values simplified to one for one observer, and two for several observers, based on preliminary tests.

Daily land-based effort was modelled per grid cell of coordinates (x, y) as a logistic function of distance to the coast:

$$Effort_{land}(x, y, t) = N_{obs}(t) * T_{obs}(t) * \frac{100}{1 + \exp(-\sqrt{d(x,y)-12})}$$

where $N_{obs}(t)$ reflected the number of observers on day t, $T_{obs}(t)$ was the time (in hours) spent on-effort at the Cape N'Doua on day t, and $d(x,y)$ was the distance between the grid cell of coordinates (x, y) and the land-based observatory (in km; for more details see Appendix 2.B). The logistic curve midpoint was set to 12 km to approximate the average distance from the land-based look-out from which humpback whales were observed ($11.3 \text{ km} \pm 5.9 \text{ SD}$). Effort was set to null for grid cells further than the maximum detection distance from the land-based look-out (36 km). Finally, daily maps of land-based effort were summed together per year to produce yearly maps of land-based effort, which were subsequently rescaled to [0,100], consistent with the boat-based survey effort maps.

2.2.6 Estimating humpback whale distribution

For each year of survey, the geographic positions of humpback whale groups observed at sea were combined with that of groups observed from land but not at sea. Kernel Density Estimates (KDE, Worton 1989) were applied to humpback whale group positions to model yearly areas of use in the South Lagoon. KDE were applied with weights associated to each group positions, to account for survey effort variability across breeding seasons. Values of survey effort intensity were extracted respectively from the yearly maps of sea- or land-based effort at the humpback whale group positions. These extracted values ranging from 0 to 100 were converted to weights ranging from 0 to 10 with an inverse function in order to downweight whale positions occurring in highly surveyed areas. Finally, weights at each whale group position were multiplied by group size to provide more weight to positions at which larger groups were observed. As group sizes were not always recorded precisely from land, weights were attributed as follows for land-based observations: 3 for a group of three or more individuals, 2 for a pair and 1 for singletons and unidentified social group types. KDE were calculated with plug-in bandwidth selector (Hpi) then rescaled to [0-100], either with all years of data pooled together, or separately for each breeding season. In the latter case, yearly core areas of use were calculated as the 50 % contour of the yearly probability surfaces. The overlap of yearly core areas of use was calculated from 1995 to 2017 to illustrate the persistence of the humpback whale distribution pattern through time.

2.2.7 Environmental conditions

Daily rainfall (in mm) and mean wind conditions (in knots) recorded between 1995 and 2009 were retrieved from a weather station based at the Cape N'Doua (22°23'24" 166°55'30", Meteo France). The effect of rainfall and wind strength on the number of groups observed at sea or detected from land was assessed with sequential GLM. The daily number of groups observed or detected was modelled with a Poisson GLM as a function of time on effort, year and Julian day of year. Then, the residuals from this regression were modelled as a function of rainfall (square-root transformed) and wind strength using a linear Gaussian regression.

Monthly sea surface temperature (SST) was obtained to estimate the mean thermal conditions in the area during the austral winter. SST was obtained from the National Aeronautics and Space Administration (NASA) Multi-scale Ultra-high Resolution SST (MURSST) with a 1 km resolution from 2002 to 2017 (jplMURSST41, <http://coastwatch.pfeg.noaa.gov/-erdaap/>). Average SST and associated coefficients of variation were calculated within and across seasons, and mapped over the study region.

Several topographic environmental variables were collected in the study areas to characterize habitat at a 100 m resolution. Coastline and reef shapefiles were produced by the Millennium Coral Reef Mapping Project (version 8—[Andréfouët et al., 2008](#)). Fringing reefs (in contact with the coastlines) were removed in order to focus on barrier and intermediate patch-reef complexes. Using these shapefiles, distance to the coast and distance to non-fringing reefs were calculated for each 100 × 100 m cell in the South Lagoon study area as the Euclidean distance to the closest landmass (i.e., New Caledonia mainland, Ouen Island, or the Isle of Pines) and closest barrier or patch reef complexes, respectively. Bathymetry data ([DTSI, 2016](#)) were provided at a 100 × 100 m resolution and gaps in the depth raster were subsequently filled through extrapolation of satellite and aerial composite imagery (J. Lefèvre, IRD, pers. comm.). Two terrain features were derived from the bathymetry raster: seabed slope (in degrees) and seabed aspect (the orientation of the slope, in degrees).

2.2.8 Modelling habitat use

The relationship between humpback whale distribution and environmental conditions was modelled with a Generalized Additive Model (GAM, [Hastie and Tibshirani, 1990](#)) using the *mgcv* R package (version 1.8-23). GAMs were applied to KDE values calculated for all years of survey from 1995 to 2017. The response variable was modelled with a beta-regression log link function. Explanatory variables included: depth, distance to the coast, distance to barrier and/or patch-reef complexes, slope, and aspect. Depth and slope were log-transformed to prevent an inflated influence of outliers as recommended by [Wood \(2006\)](#). Pearson coefficients were calculated between environmental variables to prevent collinearity (control that $r < 0.5$ for all variables). Smoothed effects of explanatory variables in the GAM were optimized by Restrictive Maximum likelihood (REML) and cubic smoothing

splines with basis size limited to 5 to prevent overfitting. The descriptive performance of models was assessed through the computation of the proportion of deviance explained (Guisan and Zimmermann, 2000). The deviance explained (%) is calculated from the null deviance (deviance for a model with just a constant term) minus the residual deviance (deviance of the fitted model with explanatory terms). Partial dependence plots were produced to visualize the effect of one variable while all others were held constant at their mean (Friedman, 2001).

2.3 Results

2.3.1 Survey from two platforms

Across 21 years of study from 1995 to 2017, 807 days were spent on survey at sea and 790 from land (Table 2.1). On average, seasonal surveys covered $38.4 \pm \text{SD } 9.5$ days at sea and $37.6 \pm \text{SD } 9.9$ from land. Most of the survey effort was conducted simultaneously by both teams, on land and at sea, totalling 714 days of survey in common over the study period. As a result, the team at sea was assisted by the land based observers during 88% of the days of survey.

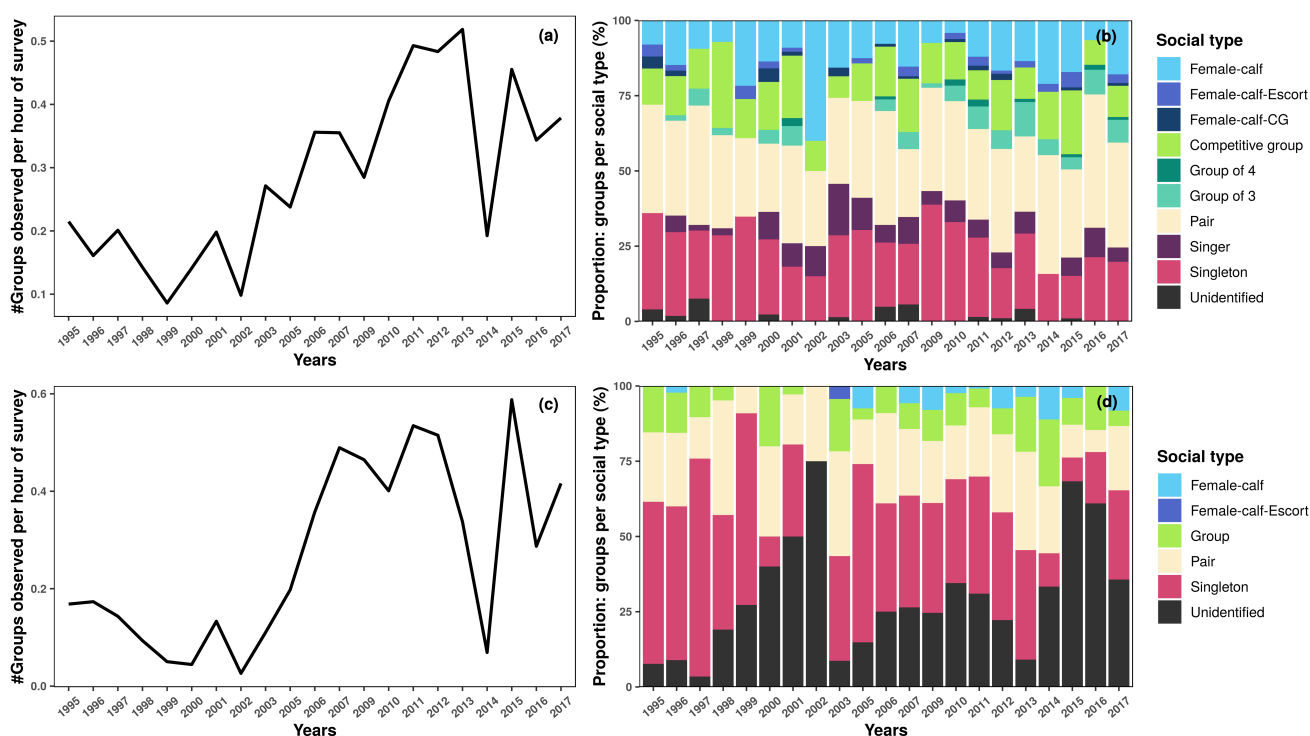


Figure 2.3 Breeding season encounter rates and social group types measured in the South Lagoon, New Caledonia, between 1995 and 2017. (a) Groups observed at sea ($n = 1,484$), and (c) from land only ($n = 1,167$), per hour of survey effort. Proportions of social group types observed per year (%) using each platform is represented in stacked colour bars: (b) at sea, and (d) from land. The breeding seasons 2004 and 2008 were removed from the analysis.

The land-based team followed 2,021 groups of humpback whales ($96.2 \pm \text{SD } 60.2$ per year)

among which 1,167 (57.8%) were not followed by the boat-based team (Fig. 2.2, Table 2.1). The boat-based team followed 1,484 groups ($70.7 \pm \text{SD } 33.4$ per year), among which 30.2 % were originally detected by the land-based team who communicated the position through VHF.

The number of observers from land varied between 1 and 5 (mean = $2.0 \pm \text{SD } 0.9$, number reported for 737 survey days out of 790), and was strictly > 1 in 64 % of survey days. The number of humpback whale groups detected from the Cape N'Doua was significantly higher when more than one observer was surveying. The residuals of the null model relating the daily number of groups detected from land to year, found Julian day of year and duration of survey effort to be significantly related to the number of observers (GLM: $t\text{-value} = 7.1$, $p < 0.001$). On average, $2.0 \pm \text{SD } 1.3$ groups were observed when one observer was present, against $2.7 \pm \text{SD } 2.6$ with several observers.

Between 1995 and 2009, wind and rainfall were measured over 453 days of survey. Wind strength varied from 4 to 27 knots (mean = $14.1 \pm \text{SD } 4.8$ knots) and daily rainfall varied from 0 to 61 mm (mean = $1.2 \pm \text{SD } 4.0$ mm). A null model was produced to relate the daily number of groups detected from land, to year, Julian day of year and duration of survey effort. The residuals of this null model were not significantly affected by rainfall (GLM: $t\text{-value} = 0.4$, $p = 0.7$) nor wind strength (GLM: $t\text{-value} = 1.6$, $p = 0.1$).

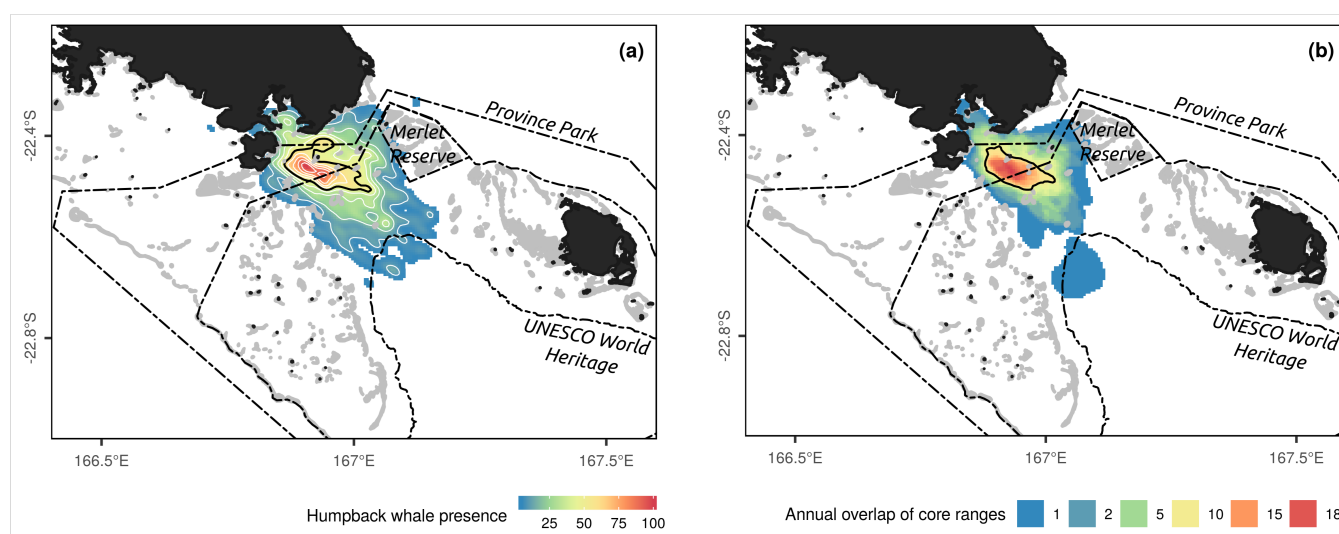


Figure 2.4 Kernel density estimates (KDE) of humpback whale distribution in the South Lagoon, New Caledonia, between 1995 and 2017. (a) KDE based on unique observations at sea and from land over the whole study period ($n = 2,651$). KDE values below 5% are not shown. White lines delineate 10% contours of the KDE from 10% to 100%. The 50 % contour, or core area of use, is represented with a black line. (b) Overlap between 50% contours of annual KDE (colours represent the numbers of years over which the grid cell was included in a 50% contour). The black line delineates the area where more than 10 years of core areas overlap (77 km^2). Observations are weighted proportionally to the number of individuals in the group and the amount of survey effort. Land is shown in black and reefs in grey. The marine protected areas are shown with a thick dashed line.

Among these 453 days, 412 days were surveyed at sea. A null model was produced to relate the daily number of groups observed at sea, to year, Julian day of year and duration of survey effort. The residuals of this null model were not significantly affected by rainfall (GLM: $t\text{-value} = 0.2$, p

= 0.8), but showed a small effect of wind strength (GLM: t-value = -2.3, p = 0.02). The number of groups observed at sea decreased with stronger winds.

2.3.2 Long-term temporal occurrence

In total, 2,651 independent whale groups were observed from land and at sea (Fig. 2.2), with a maximum number of occurrences observed in 2007 (n = 264; Table 2.1). When accounting for total survey effort per year, encounter rates showed an increasing trend from 1995 to 2017 (Fig. 2.3a, 2.3c) both at sea, and from land. Both platforms showed a very similar trend, notably with a steep increase between 2005 and 2011, as well as a low encounter rate (< 0.2 groups per hour of survey) in 2014. The growth rate between the encounter rate calculated for 1995-2003 and for 2012-2017 was equal to 1.35 at sea and 2.52 from land. Considering an 8 year interval between these two periods, these growth rates correspond to an annual increase of 16.9 % yr⁻¹ at sea and 31.5 % yr⁻¹ from land.

The average proportion of social group types observed per year at sea was 13.9 % mother-calf pairs (\pm SD 7.7 %), 1.8 % mother-calf-escort groups (\pm SD 1.6), 14.2 % competitive groups (\pm SD 5.0 %), 1.1 % mother-calf with competitive groups (\pm SD 1.3 %), 32 % adult pairs (\pm SD 5.6%), 24.5 % solitary whales (\pm SD 6.9 %) and 6.2 % singers (\pm SD 4.1; Fig. 3b). A larger proportion of group types remained unidentified by land-based observers (29.8 % \pm 20.1) compared to observers at sea (1.7 % \pm 2.3, Fig. 2.3d), as noted in a beta-regression relating the proportion of unidentified groups to platform (z-value = 7.3, p < 0.0001).

Combined together, the proportion of social group types observed from both platforms did not show any linear trends from 1995 to 2017. This analysis included groups with calf (mother-calf pairs, mother-calf pairs with escort or competitive groups; beta-regression: z-value = 1.2, p = 0.2), groups of adults (beta-regression: z-value = 1.7, p = 0.8), pairs (beta-regression: z-value = -0.2, p = 0.8), singleton (including singers; beta-regression: z-value = -1.9, p = 0.05), and unidentified social types (beta-regression: z-value = 1.9, p = 0.05).

2.3.3 Long-term spatial distribution

A core area of use for humpback whales was identified outside the Prony Bay, between the two main reef complexes of the South Lagoon, the Corne Sud to the southwest and the Merlet reserve to the northeast (Fig. 2.4a). Humpback whales were also found to display a noteworthy use of the inner waters of the Prony Bay. Yearly core areas of use showed a strong overlap, in a zone located at the centre of the study area (Fig. 2.4b). Persistent use was found over a 77 km² zone that was included in yearly core areas of use for at least 10 years (Fig. 2.4b). Overall, there was little overlap between the core area of use and the Merlet reserve, nor the UNESCO World Heritage zone. On the other hand, the Province Park included the core area of humpback whale use.

2.3.4 Habitat characterization

Depth (edf = 3.8, $\text{Chi}^2 = 575.7$, $p < 0.001$), distance to coast (edf = 2.0, $\text{Chi}^2 = 1081.2$, $p < 0.001$), distance to barrier and patch reef complexes (edf = 1.9, $\text{Chi}^2 = 63.3$, $p < 0.001$), and seabed slope (edf = 2.0, $\text{Chi}^2 = 145.3$, $p < 0.001$) were significant predictors of humpback whale habitat in the South Lagoon (GAM, deviance explained = 36.6%, Fig. 2.5).

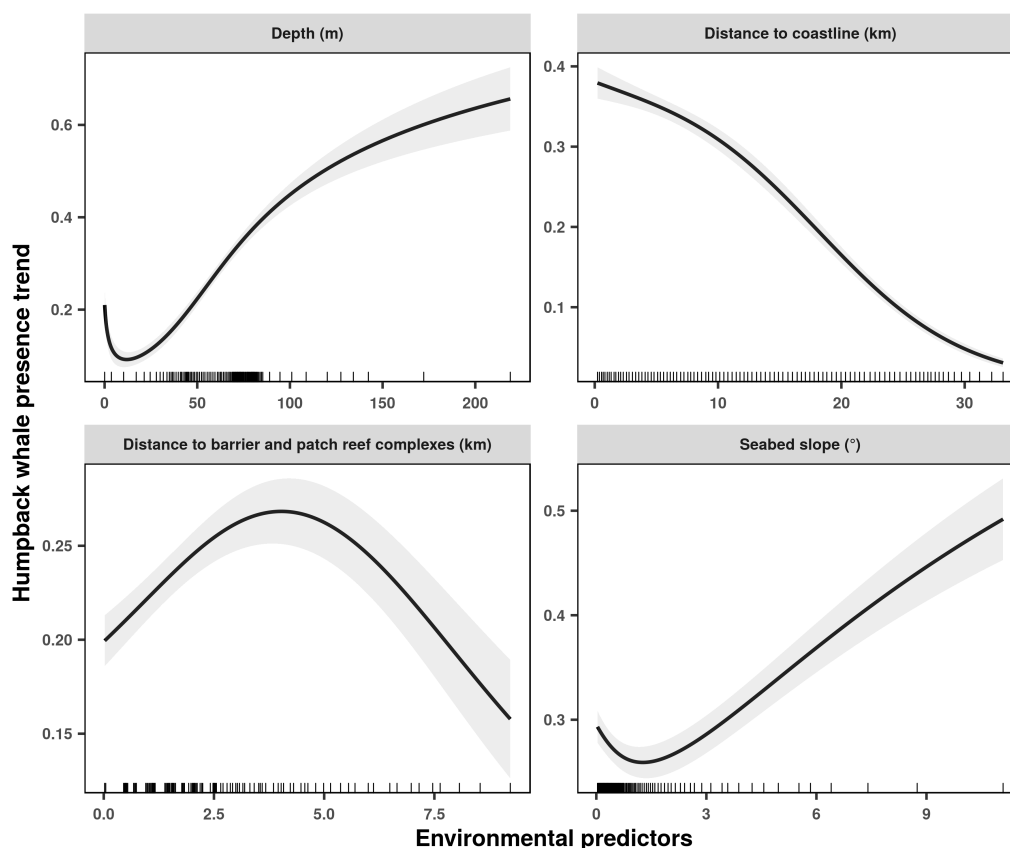


Figure 2.5 Partial dependence plots modelling habitat selection of humpback whales from combined boat- and land-based surveys in the South Lagoon, New Caledonia between 1995 and 2017. Predicted habitat suitability is shown on the y-axis with varying scales. Rug plots illustrate the distribution of values in the modelled dataset in percentiles.

The occurrence of humpback whales increased with proximity to coast in the South Lagoon. Humpback whales were found in the vicinity of coral reef complexes (about 3 km from a reef) rather than in close contact to them. Seabed slopes of more than 2° were favoured, though there are few high values of slope in the dataset. Humpback whale occurrence patterns displayed a complex relationship with respect to depth: both very shallow waters (10 m) and relatively deep waters (50 - 100 m) were predicted to be suitable habitats. The modelled probability of presence reached a plateau when depth increased past 100 m deep indicating that deeper waters may also be suitable, although there was little data collected at such depth within the South Lagoon, as revealed by the rug plot associated to this variable (Fig. 2.5).

SST patterns averaged over the study area from 2002 to 2017 revealed that waters located in the north-western limit of the study area near Ouen Island were consistently colder during the winter (Fig. 2.6). The core area of use for humpback whales was characterized by average temperatures between 22°C and 22.4°C. Moreover, SST in this zone was the most stable in the winter (within and between breeding seasons), in contrast with the eastern coast of New Caledonia and the Isle of Pines under influence of the Vauban current (Fig. 2.1). Indeed, standard deviation of the MURSST in winter was highest in the north-eastern part of the study area (Fig. 2.6).

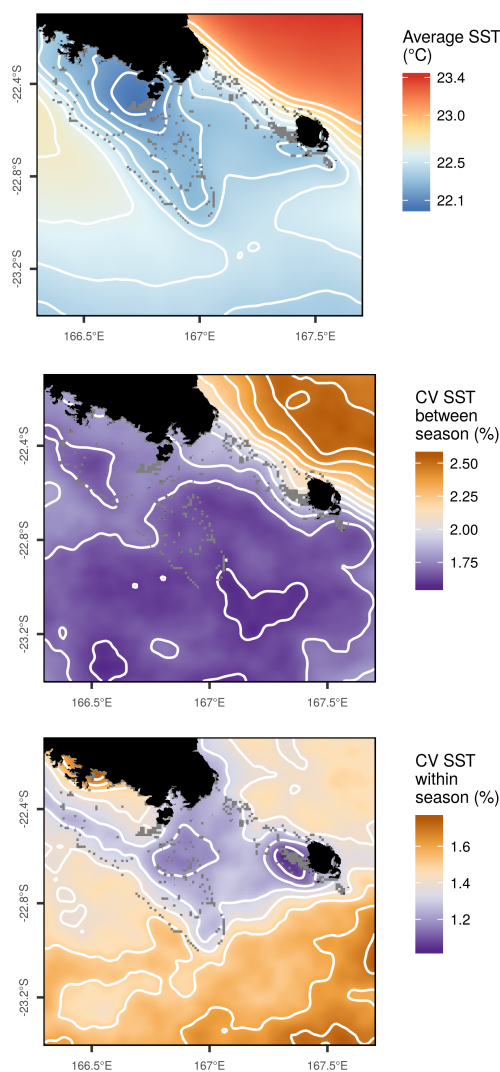


Figure 2.6 Sea Surface Temperature (SST) in the South Lagoon, New Caledonia, averaged from MURSST (jplMURSST41, <http://coastwatch.pfeg.noaa.gov/erdaap/>) between July and August, 2002-2017. (a) Mean austral winter SST averaged across 16 years. (b) Coefficient of variation of SST calculated across 16 years. (c) Coefficient of variation of SST calculated across 3 months of austral winter and averaged over 16 years. Land is shown in black and reefs in grey. White lines delineate contours of the SST patterns.

2.4 Discussion

This study provides information on the long-term occurrence patterns of an endangered population of humpback whales seasonally present in the New Caledonia South Lagoon. Occurrence of humpback whales in the South Lagoon was found to increase between 1995 and 2017. The distribution and social composition of the population visiting the area in the austral winter, between July and September, was stable across years. Humpback whales were persistently found in a coastal

and relatively shallow habitat that is typical of breeding grounds. However, a mismatch was found between habitats favoured by humpback whales and currently existing marine protected areas in the South Lagoon. Persistent habitat use patterns were robustly modelled using two complementary long-term datasets extending over more than two decades.

Although many of the most studied cetacean species live in coastal waters, the use of land-based lookouts for the purpose of scientific research is uncommon. Indeed, many cetacean studies favour the collection of biological samples and photographs that cannot be collected from land but that provide valuable information on individuals (e.g., [Garrigue *et al.*, 2004a](#)) for studying behaviour, life history and demography. In addition, unless the cetaceans are very close to shore (e.g., [Stockin *et al.*, 2006](#)), group sizes and behaviours are generally more accurately measured during focal follows at sea than from land. Here, many of the groups observed only from land did not describe social type, and groups of more than three individuals were all pooled in the same category, with no distinction of group size, competitive behaviour or singing activity. On the other hand, compared to surveys at sea, land-based surveys have the great advantages of being cheaper, less technically challenging and not impactful for animals ([Aragones *et al.*, 1997](#); [Giacoma *et al.*, 2013](#)). They have been successfully applied to monitor the impact of whale watching and maritime traffic (e.g., [Stamation *et al.*, 2010](#); [Schaffar *et al.*, 2013](#); [Avila *et al.*, 2015](#); [Sullivan and Torres, 2018](#)). Here, the land-based team had a greater spatial and temporal whale detectability than the boat-based team as it could survey a larger extent, and was capable of following several groups at the same time. For instance, the Merlet integral reserve was consistently surveyed by the land-based team all over the study period, whereas the research boat was only permitted to enter the perimeter over half of the study years. Land-based lookouts have been used in support of boat-based survey teams to detect smaller cetacean species in other parts of the world (e.g., Risso dolphin, *Grampus griseus*, [Hartman *et al.*, 2014](#)). Considering the relatively low cost of adding a team on land when a boat-based monitoring program is already in place, this study supports the synergic advantages of combining these two platforms of observation when a land-based look-out is available in the study area.

In recent decades, ecological research methods have undergone tremendous technological advances. One indirect drawback is the potential to alter the consistency of survey protocols used in long-term studies. In the South Lagoon humpback whale monitoring program, as in many marine long-term studies, the incorporation of onboard GPS tracking has greatly improved the quality of spatial data collected. Indeed, tracklines represent an essential piece of information to spatially quantify survey effort ([Derville *et al.*, 2018b](#)), but were only recorded from 2003 onward in this study. In order to maintain the integrity of the 20-year long dataset collected in the South Lagoon, survey effort at sea was approximated using 'pseudo-tracklines' (see Appendix 2.A). This method was based on acoustic sampling and group locations, but it may be applied to any 'location data' recorded during a day of survey at sea (e.g. environmental sampling locations). Using this approach on this long-term dataset, a general trend of increasing encounter rates was identified throughout the study period, both at sea and from land. Anomalous years in the trend may be explained by slight changes in

the seasonality of survey effort, such as in 2014 when the mid-August breeding season peak was exceptionally not surveyed. Interestingly, the increase of encounter rate of 16.9% yr⁻¹ measured at sea from 1995-2003 to 2012-2017 is consistent with the realized growth rate of 15% yr⁻¹ estimated from robust photo-identification capture-recapture models covering the period 1996 to 2012 (Orgeret *et al.*, 2014). The increase was strongest between 2005 and 2011, which also confirms the anomalous increase detected between 2008 and 2011 by capture-recapture (Garrigue *et al.*, 2012). Combining several lines of evidence, this study supports the ongoing recovery of the New Caledonia endangered humpback whale sub-population.

The presence of numerous maternal females and competitive groups was constant across breeding seasons, reflecting consistent breeding and nursing activity in the South Lagoon. The core area of humpback whale distribution was located at the centre of the study area, bounded by the coast and two large reef complexes. Although humpback whales are observed sporadically in coastal waters and lagoons all over the New Caledonian archipelago (Garrigue and Gill, 1994; Derville *et al.*, 2018b), the South Lagoon appears to be the most visited coastal breeding and nursing site (Garrigue *et al.*, 2001). This aggregation is likely to be at least partially driven by social factors (Clapham and Zerbini, 2015), but it may also be linked to environmental conditions specific to this area. In the core area of humpback whale distribution, SST averaged 22 - 22.5°C in the austral winter, a temperature that is well within the preferential SST range identified by Rasmussen *et al.* (2007). The SST in the core area of use was also relatively stable both within and between years, compared to the surrounding open ocean. Spatio-temporal predictability of resources, or suitable environmental conditions, is an important driver of spatial distribution in the ocean (Scales *et al.*, 2014; Lambert *et al.*, 2018). The persistence of temperature conditions in the South Lagoon could contribute to its attractiveness for maternal females that can rely on this area to provide suitable habitat to their calf.

Habitat models suggest a preference for nearshore shallow waters in accordance with other humpback whale breeding grounds around the world (Martins *et al.*, 2001; Oviedo and Solís, 2008; Cartwright *et al.*, 2012; Smith *et al.*, 2012; Lindsay *et al.*, 2016; Bortolotto *et al.*, 2017; Trudelle *et al.*, 2018). However, the modelled habitat relationships also suggested that whales may be found in the relatively deep waters south of the study area (about 200 m deep). The modelled occurrence was relatively high in these conditions but was associated with a strong uncertainty. Nevertheless, this result is consistent with satellite tracking of individuals humpback whales from this region that moved between the South Lagoon and several seamounts located south of the Isle of Pines (i.e. Torch Bank and Antigonía seamount, Garrigue *et al.*, 2015). Antigonía seamount is now known as an important breeding ground (Garrigue *et al.*, 2017; Derville *et al.*, 2018a). Frequent movements between these hotspots (Orgeret *et al.*, 2014; Garrigue *et al.*, 2017) may explain the relatively high occurrence of whales in the southernmost part of the South Lagoon.

The relationship to coral reef complexes was not linear and showed that humpback whales occurred in waters neighbouring reefs (3-4 km) but not directly next to them. In contrast, distance to coral reef was not identified as a primary factor influencing humpback whale distribution in other

breeding grounds that include large reef extents (Great Barrier Reef, [Smith *et al.*, 2012](#)), except when considering maternal females only (Vava'u, Tonga, [Lindsay *et al.*, 2016](#)). In Vava'u, females with a calf preferentially used the sheltered waters inside the reef complexes, whereas groups with no calf occupied deeper waters on the external slope. In the South Lagoon, groups with and without a calf do not segregate with respect to reef habitats but rather relative to proximity to the coastline ([Derville *et al.*, 2018a](#)). Dense reef complexes of the South Lagoon appeared to be avoided by all social group types. Indeed, dense and shallow reef areas form intricate networks that have the potential to trap large whales. Also, seabed terrain and depth are known to affect sound propagation ([Mercado III and Frazer, 1999](#)), hence potentially constraining the spatial distribution of singing males. Rugged ([Pack *et al.*, 2017](#)) and/or shallow habitats ([Mercado III and Frazer, 1999](#)), such as that of the South Lagoon reef complexes could be less suitable for acoustic communication, and therefore less attractive for singers and their audience. Based on these distributional preferences, the Merlet integral reserve (IUCN category Ia) was rarely used by humpback whales in the New Caledonia South Lagoon. The UNESCO World Heritage Zone was also mostly in mismatch with the humpback whale core area of use. The Province Park did include the area of humpback whale use but only offers a very low level of protection with respect to human activities. There is no marine protected area specifically dedicated to the mitigation of anthropogenic impacts on cetaceans in New Caledonia. Moreover, it appears that the existing conservation areas with high levels of protection in the South Lagoon do not overlap with critical habitats of this endangered sub-population of humpback whales.

Encounter rates measured per year from both platforms of observations support the increase in the population sizes that was independently estimated from capture-recapture ([Garrigue *et al.*, 2012](#); [Orgeret *et al.*, 2014](#); [Jackson *et al.*, 2015](#)). However, this encouraging sign of recovery of a humpback whale sub-population in Oceania should be put in perspective with emerging threats in the region. Coastal breeding grounds are particularly exposed to increasing anthropogenic activities such as vessel traffic, increased noise, or pollution. Whale watching activities are growing in popularity ([O'Connor *et al.*, 2009](#)), and are an increasing source of income in the Pacific Islands. Although observation guidelines exist for the region ([Province Sud, 2018](#)), the ever increasing number of boats in the area during the winter is a current cause of concern. Land-based whale watching exist in a few regions of the world (e.g., Cook Islands, South Africa, Australia, [O'Connor *et al.*, 2009](#)) and could be promoted in New Caledonia as an alternative to boat-based tours. By using a long-term monitoring approach, this study provides important information for the protection of an endangered sub-population of humpback whales. Furthermore, this work provides a baseline to detect potential shifts of distribution, changes of social composition or habitat degradation as a result of growing anthropogenic activities or environmental change in a major breeding ground of Oceania.

Acknowledgments

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Appendix 2.A. Estimating boat-based survey effort without GPS tracklines

In this appendix, we describe the method to estimate the spatial extent of survey effort during non-systematic cetacean surveys at sea where boat GPS tracklines were not recorded. When GPS tracks are not available, survey effort extent may be estimated from various latitude-longitude positions recorded along the day. Here, we used the locations for acoustic samplings, and the start/end of focal follows. Locations were linked together through time to reconstruct daily "pseudo-tracklines" (Fig. 2.A.1).

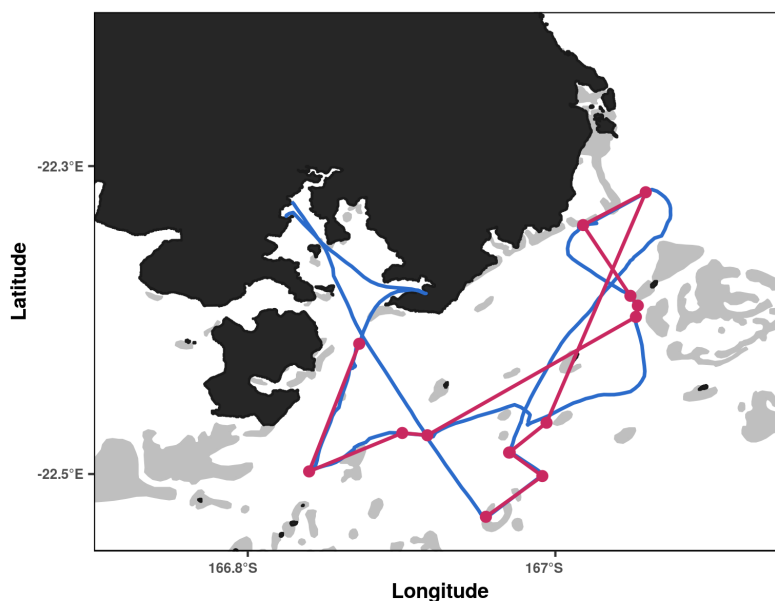


Figure 2.A.1. GPS trackline (blue) and pseudo-trackline (pink) reconstructed for a day of survey in the South Lagoon of New Caledonia (2012-08-20). Locations along the pseudo-trackline are represented with pink points.

Pseudo-tracklines were considered a subsample of the real tracklines followed by the research boat over the course of a day. Seasonal maps of pseudo-effort were produced using a method similar to that applied to real GPS tracklines: they were interpolated at one position/min, sections off-effort were removed, and the remaining positions were smoothed with a LOESS applied with a varying bandwidth (i.e. span ranging from 0.002 and 0.02). Seasonal maps of pseudo-effort were created with various spans using the LOESS approach. In order to assess the best parametrization for this smoothing, we calculated the surface area covered by the pseudo-effort density contour and the real effort density contour per breeding season. The difference between these two surface areas (at a given contour of the density surface) is expected to converge towards zero when the pseudo-effort map is most similar to the real effort map (Fig. 2.A.2). The 0.01 bandwidth was selected to provide the most realistic estimate of pseudo-effort distribution from 1995 to 2002. The pseudo-tracklines and pseudo-effort maps were comparable in shape and extent to the real effort maps (e.g., Fig. 2.A.3).

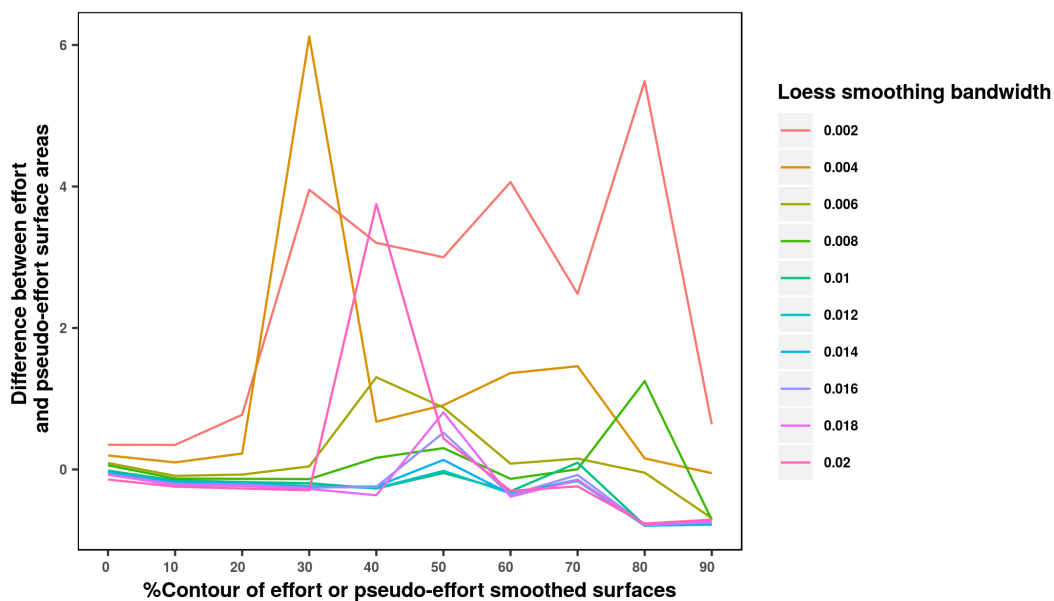


Figure 2.A.2 Difference between real effort and pseudo-effort surface areas for different bandwidth and at different % contours of the density surface.

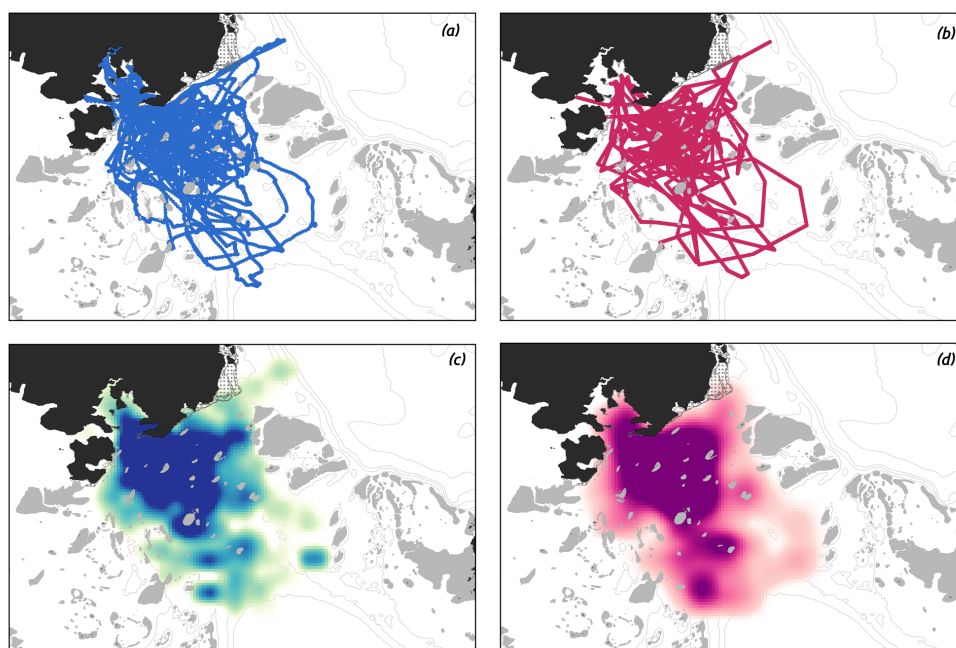


Figure 2.A.3 Comparative maps of GPS tracklines (a) with reconstructed pseudo-tracklines (b) for the humpback whale breeding season 2012 in the South Lagoon of New Caledonia. Maps of effort (c) and pseudo-effort (d) show the density surface of search effort intensity over a colour scale (darker shades indicate more effort).

From 2003 to 2017, the pseudo-effort maps could be compared to the real effort maps obtained from GPS tracklines recorded in the field. On average, the 95% contour of pseudo-effort density surfaces overlapped with 59 % of the 95% contour of real effort density surfaces (Fig. 2.A.4).

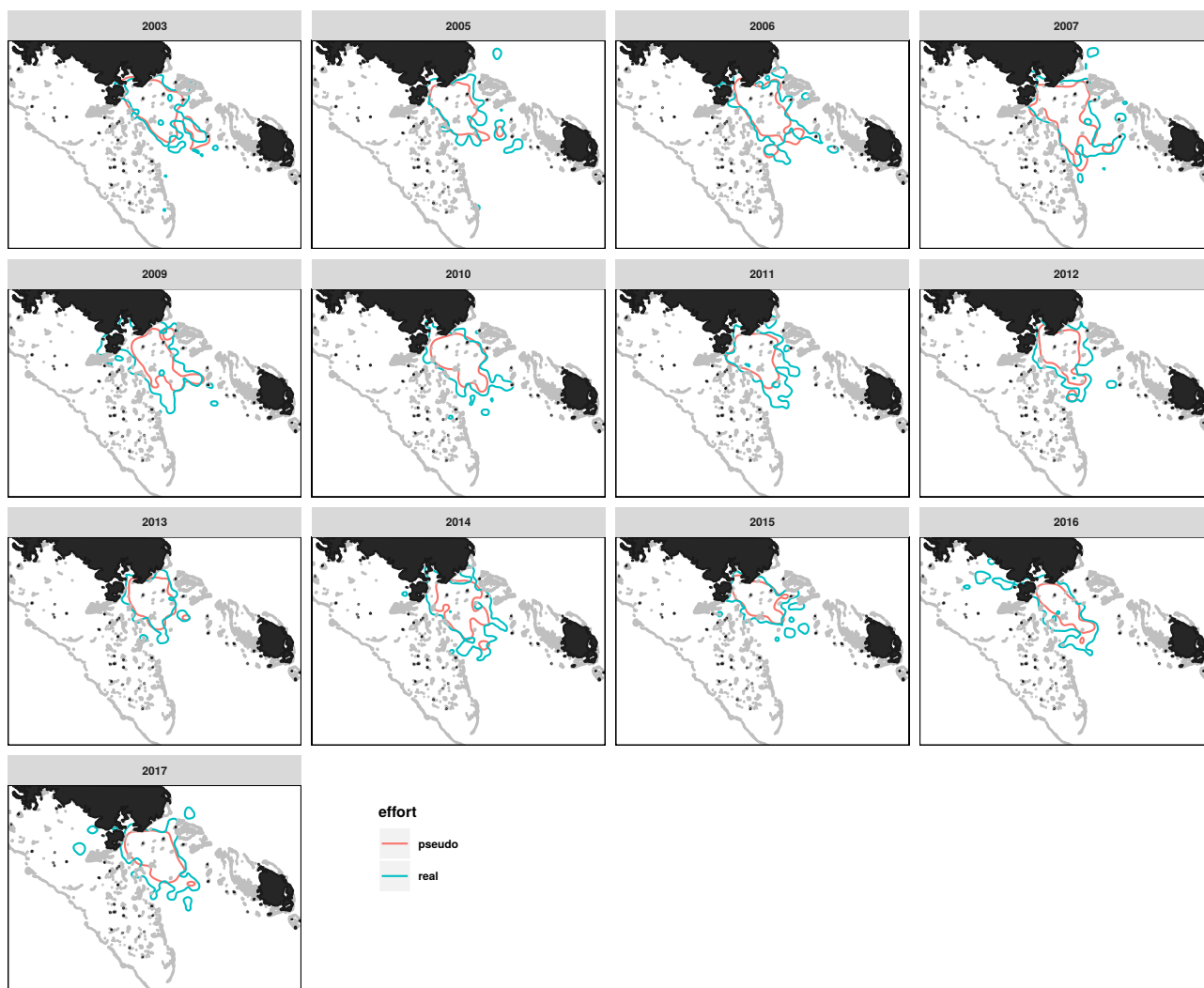


Figure 2.A.4 Contours of the 95% density surface calculated from real effort (GPS tracklines, blue) and pseudo-effort (acoustic sampling/focal follow positions, pink) from 2003 to 2017 in the South Lagoon of New Caledonia.

Appendix 2.B. Estimating land-based survey effort

A logistic function was used to model the survey effort from the land-based look-out as a function of distance from the look-out (Fig. 2.B.1). This function was selected as it reflects the strong detectability of whales in the immediate vicinity of the look-out, and the rapid decrease of detectability as distance from the observer increases. The logistic function was parametrized based on the average and maximum distances at which whales were detected (11.3 km and 36 km respectively).

Using the logistic function above, survey effort was calculated over a raster grid covering the study area. This raster represents land-based survey effort from an average survey day (Fig. 2.B.2).

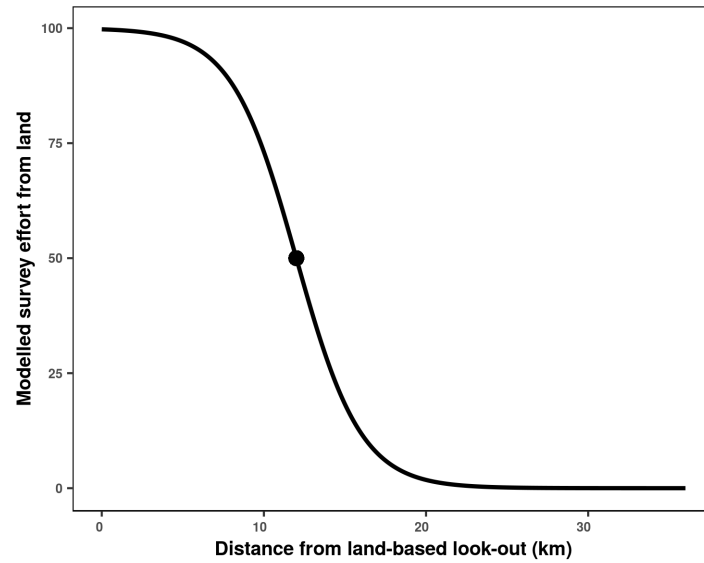


Figure 2.B.2 Logistic detection function from the land-based look-out. The mid-point of the curve was set at 12 km and the maximum detection distance at 36 km.

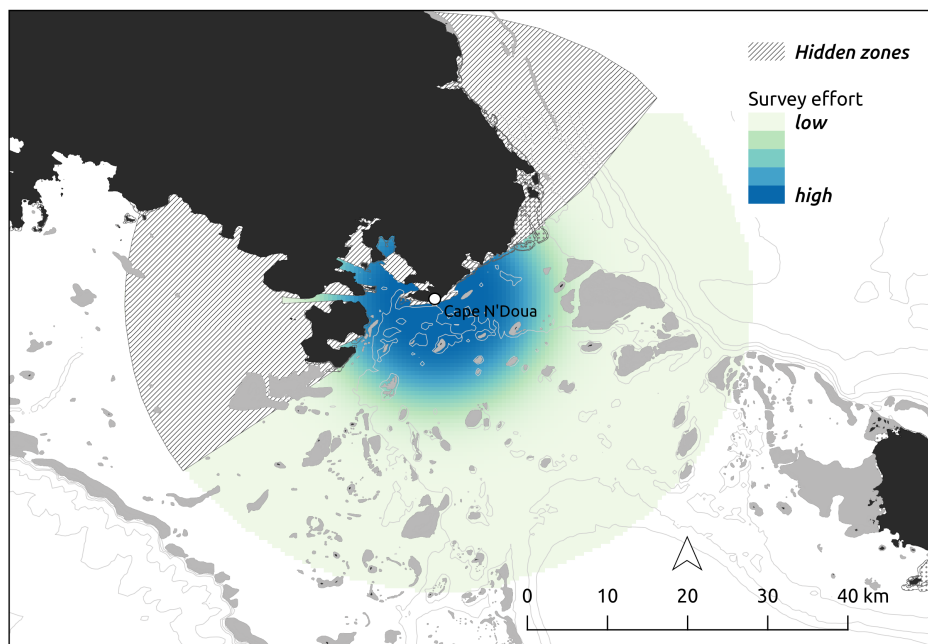


Figure 2.B.2 Map of daily survey effort from land showing the relative density of effort on a colour scale. Dashed areas are hidden from the observers at the land-based look-out of Cape N'Doua.

Chapter 2 characterized the social composition of humpback whale groups observed in the South Lagoon over more than twenty years. The consistent presence of maternal females with a calf is typical of humpback whale breeding grounds. Several studies have shown that these social groups have specific habitat requirements and seek sheltered and shallow waters away from other whales. However, most studies of humpback whale distribution have been conducted in coastal breeding grounds. In New Caledonia, there is evidence of humpback whale presence over offshore shallow seamounts, such as the Antigonina seamount and Torch bank located south of the Isle of Pines. In chapter 3, I therefore seek to 1) test the hypothesis that maternal females spatially segregate from other social groups in the South Lagoon coastal breeding ground, and 2) investigate social interactions and space use patterns of maternal females in a contrasting offshore and unsheltered environment, the Southern Seamounts. From the coast to the high seas, this chapter questions how social and habitat factors affect humpback whale distribution within two connected breeding areas.

III. Social drivers of distribution

Social segregation of humpback whales in contrasted coastal and oceanic breeding habitats

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Abstract

Maternal habitat preferences of humpback whales (*Megaptera novaeangliae*) are well documented from decades of coastal research but oceanic areas have received less attention. Whales breeding in New Caledonia occupy both ecosystems: a coastal reef complex (South Lagoon) and oceanic seamounts (Southern Seamounts). Generalized Additive Models were applied to 20 years of boat-based whale observations ($n = 1,526$) to describe habitat preferences and Permissive Home Range Estimations were used to explicitly model spatial segregation in relation to social context. Groups with calves ($n = 206$) preferred shallow coastal waters throughout the season in the South Lagoon, whereas no habitat segregation was observed between groups with ($n = 74$) and without calves ($n = 140$) in the Southern Seamounts. As a result, spatial overlap between groups with and without calves was more common in the Southern Seamounts than the South Lagoon. Despite a lack of social segregation around seamounts, mother-calf pairs were proportionally more frequent in the Southern Seamounts (27%) than in the South Lagoon (16%). Photographs of the calves' dorsal flanks were analyzed to compare age and ecological markers across sites. Calves appeared older in the Southern Seamounts than in the South Lagoon but no difference in scarring nor shark bites was found across sites, suggesting that calves experienced similar lifestyles and may move between off-shore and coastal waters during the breeding season. This study highlights the flexible habitat use patterns of breeding humpback whales and raises new questions about the environmental and social drivers of their presence in off-shore breeding grounds.

Key words

Breeding ground, Habitat use, Humpback whales, Pacific Ocean, Seamounts, Social interactions

3.1 Introduction

Space-use dynamics and habitat selection of mobile animals are driven by multiple ecological demands such as feeding, mating, or avoiding predators. The concept of 'ecological niche' relies on the notion that individual fitness depends on space-use strategies and access to optimal habitats. Yet, biological needs vary throughout an individual's lifetime, causing changes in space-use patterns. These changes are very patent in migrating species, such as humpback whales (*Megaptera novaeangliae*) whose habitat varies drastically during annual migrations between polar and tropical waters (Clapham, 2000a). Though still subject to an ongoing debate, the primary driver explaining the evolutionary persistence of this behavior appears to be calf development and survival. The warm waters in tropical and sub-tropical breeding grounds (Clapham, 2000b), and reduced risk of killer whale (*Orcinus orca*) predation in these regions (Corkeron and Connor, 1999), assumedly contribute to greater calf survival. Yet, even within breeding grounds, survival is not guaranteed. Due to the higher energetic demand of calving, lactation, and care for the young calf, mothers have a tighter energetic balance than other individuals (Lockyer, 1981) and are considered more at risk from environmental stressors, including human disturbance (Lammers *et al.*, 2007; Cartwright *et al.*, 2012).

In several coastal and island breeding grounds across the oceans, female humpback whales with calves have been shown to avoid their con-specifics. This behavior results in a spatial segregation of social groups, with mother-calf pairs preferentially occupying waters shallower than 50 m (Martins *et al.*, 2001; Ersts and Rosenbaum, 2003; Zerbini *et al.*, 2004; Oviedo and Solís, 2008; Craig *et al.*, 2014; Félix and Botero-Acosta, 2011; Guidino *et al.*, 2014; Lindsay *et al.*, 2016) and closer to shore (within 1 to 2 km of islands with steep seabed slopes: Hawaiï, Frankel and Clark, 2002; Antongil Bay, Madagascar, Ersts and Rosenbaum, 2003; Osa Peninsula, Costa Rica, Oviedo and Solís, 2008; and within 10 km of low islands with gradual slopes: Abrolhos Bank, Brazil, Martins *et al.*, 2001; Ecuador, Félix and Botero-Acosta, 2011) compared to other social groups.

However, less scientific exploration has been dedicated to oceanic habitats where coastlines and or reefs do not constrain space-use. Satellite tracking has recently uncovered that humpback whales also occupy the high seas during the breeding season (Kennedy *et al.*, 2014b; Garrigue *et al.*, 2015; Dulau *et al.*, 2017), but these offshore areas have rarely been directly surveyed. In the Coral Sea, an oceanic breeding ground has been identified south of New Caledonia around Torch Bank and Antigonia Seamount (hereafter referred to as the 'Southern Seamounts'; Fig. 3.1). These 2 seabed features are respectively located at 25 and 100 km from the closest land (the Isle of Pines) along the Norfolk Ridge. These features are totally submerged and characterized by shallow depths (30–60 m) and rough sea state due to the lack of shelter from wind and currents. In austral winter, a population of humpback whales congregates in the New Caledonian breeding grounds such as these Southern Seamounts and the well-known breeding ground of the South Lagoon (Orgeret *et al.*, 2014; Garrigue *et al.*, 2015). These whales have been monitored for more than 2 decades (Garrigue *et al.*, 2001, 2015) and photo-identification of individual whales has revealed evidence of connectivity

between the Southern Seamounts and South Lagoon (Garrigue and Poupon, 2013; Orgeret *et al.*, 2014). Humpback whales breeding in this region belong to the Oceanian population, classified as 'Endangered' in the IUCN Red List (Childerhouse *et al.*, 2009).

In this study, we examined the space-use of humpback whale females with a calf in two connected breeding grounds (Garrigue *et al.*, 2013) characterized by contrasting environmental conditions (coastal versus oceanic). We explored the patterns of geographical and environmental social segregation in the South Lagoon and in the Southern Seamounts throughout several breeding seasons using statistical habitat modeling. We predicted that social segregation will differ in these two breeding grounds based on age of calf and time of the season.

3.2 Material and methods

3.2.1 Study area

New Caledonia is located in the southwest Pacific Ocean about 1,500 km northeast of Australia, on the Norfolk Ridge (Fig. 3.1A). This area displays original terrain and oceanographic features, including many banks and seamounts (e.g., Antigonía seamount, Torch Bank). New Caledonia's mainland, 'Grande Terre', is surrounded by a large lagoon delimited by 1,600 km of barrier reef. Since 2014, 92% of the New Caledonian waters are included in the Natural Park of the Coral Sea.

New Caledonia South Lagoon

Located south of the mainland, the South Lagoon is a large shallow area (mean depth about 50 m), including the Prony Bay and the Ouen Island to the north and bounded by 2 reef complexes to the southwest and the northeast (Fig. 3.1B). The southeastern part of the lagoon is open to the ocean and is characterized by deeper waters (reaching 600 m deep below 22°54'S). The South Lagoon constitutes the main humpback whale breeding ground known to date in New Caledonia (Garrigue *et al.*, 2001). These whales belong to the breeding stock E, as defined by the Scientific Committee of the International Whaling Commission, and more specifically to the breeding sub-stock E2, which is demographically isolated and genetically differentiated from the 2 neighboring breeding sub-stocks of eastern Australia (E1) and Tonga (E3) (Garrigue *et al.*, 2004a; Olavarría *et al.*, 2007). Humpback whales visit the South Lagoon in austral winter with a peak of abundance in mid-August (Garrigue *et al.*, 2001, 2011a).

Antigonía Seamount and Torch Bank

Antigonía seamount is located 170 km from the mainland, on the Norfolk Ridge, south of the South Lagoon, the Isle of Pines and Torch Bank (Fig. 3.1B). Torch Bank (167°41'W 22°51'S) and Antigonía (168°4'W 23°24'S) respectively culminate at 30 and 60 m deep, span about 48 km²

and 98 km² (Gardes *et al.*, 2014), and are surrounded by waters about 1,500 m deep. Presence of humpback whales in this area was first discovered using satellite monitoring: most whales tagged in the South Lagoon between August and September visited the Southern Seamounts (males and females, including maternal females) and remained there from several days to several weeks (see Garrigue *et al.*, 2015, for further details). Boat-based surveys conducted subsequently in the area at the end of the breeding season confirmed the high density of humpback whales, compared to the South Lagoon (Garrigue *et al.*, 2013; Orgeret *et al.*, 2014; Garrigue *et al.*, 2017).

3.2.2 Data collection

Surveys were conducted from 1995 to 2015 in the South Lagoon and between 2001 and 2011 in the Southern Seamounts (Table 3.1). Surveys took place between July and September in the South Lagoon and from the end of August to the end of September in the Southern Seamounts (with the exception of 5 days of survey in Torch Bank in July). For the purpose of this study, breeding seasons were divided into 2 periods: the 'beginning of the season' from July to mid-August (calendar week 25 to week 32) and the 'end of the season' from mid-August to end of September (calendar week 33 to week 40).

Surveys did not follow a systematic or explicitly randomized sampling technique but rather a haphazard sampling regime (Corkeron *et al.*, 2011) to maximize encounters with whales (see maps of survey effort, Appendix 3.A). Surveys were only initiated in Beaufort sea-states ≤ 3 . In the South Lagoon, the search effort primarily focused on waters that could be accessed with a 6-m rigid-hulled inflatable boat. The team at sea was supported by a land-based team located at the Cape N'Doua, a 189-m-high cape overlooking the study area (Fig. 3.1B). Teams could communicate continuously using Very High Frequency (VHF) radios and whale groups could therefore be detected at sea or from the land, and subsequently approached by boat. In the Southern Seamounts, surveys were only boat-based and were conducted with a sailing or motor catamaran. Field surveys conformed to the guidelines of the American Society of Mammalogists on use of live animals in research (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016).

A group was defined as a spatial aggregation of whales characterized by a social group type following the definitions of Clapham *et al.* (1992): groups of 3 or more individuals, involved in competitive behavior or not (R); mother with calf pair (MC); mother with calf followed by a single escort (MC-E); mother with calf followed by a competitive group (MC-R); pair of adults (P); and singletons (S). For each encounter, GPS position, time, social group type, minimum group size, and maximum group size were recorded. Due to the fluid social structure typically displayed by humpback whales in their breeding grounds (Clapham, 1996), a few individuals may have been encountered more than once per survey day, if they moved to a new group with a different social type (for instance, a maternal female observed as a MC on one occasion, and later on the same day as a MC-E or a MC-R).

Table 3.1 Survey effort and number (#) of groups of humpback whales (*Megaptera novaeangliae*) observed in the South Lagoon and the Southern Seamounts, New Caledonia. Gnocalf: groups without a calf, Gcalf: groups with a calf. SD = standard deviation.

	South Lagoon			Southern Seamounts		
	Days at sea	#Gnocalf	#Gcalf	Days at sea	#Gnocalf	#Gcalf
1995	27	20	4			
1996	55	46	10			
1997	44	46	5			
1998	50	41	3			
1999	46	18	8			
2000	45	34	8			
2001	40	47	3	1	2	0
2002	27	12	6			
2003	39	59	14			
2004	5	21	0			
2005	33	53	10	6	17	12
2006	41	92	9	3	14	0
2007	47	96	25			
2008				7	19	19
2009	32	65	5	5	22	9
2010	34	85	7	6	31	15
2011	38	110	22	6	35	19
2012	29	77	20			
2013	25	78	15			
2014	28	31	9			
2015	31	75	23			
Total	716	1106	206	34	140	74
Mean	35.8	55.3	10.3	4.5	20.0	10.6
SD	11.2	28.6	7.2	2.1	11.0	8.1

In the past decade, individuals were photographed with digital cameras (CANON EOS 40D and 50D; Canon Inc., Courbevoie, France) equipped with 70 X 300 mm lenses. For adults, photo-identification of individuals is typically conducted using the unique markings on the ventral surface of the tail fluke (Katona *et al.*, 1979). Calves on the other hand rarely show their fluke when diving. Calves were therefore individually identified using the shape and markings of their dorsal fin, or of their mother's fluke and dorsal fin. Insofar as possible, calves were photographed on both sides of their dorsal fin, with their body oriented perpendicular to the photographer. Tissue samples were collected from both adult and calf whales using a crossbow with a specially adapted bolt (Lambertsen *et al.*, 1994), or a modified .22 caliber capture veterinary rifle (Krutzen, 2002). Genomic DNA was extracted from these biopsy samples to identify sex (Gilson and Syvanen, 1998) and individuals (see Garrigue *et al.*, 2004a, for further details). Photo-identification and genotyping allowed individual identification of whales in each group encountered, allowing the estimation of daily resighting rates as the mean number of times a given individual was observed during a given day of survey. Daily resighting rates were compared between study sites and between group types to ensure that group

encounters did not suffer from spatial auto-correlation.

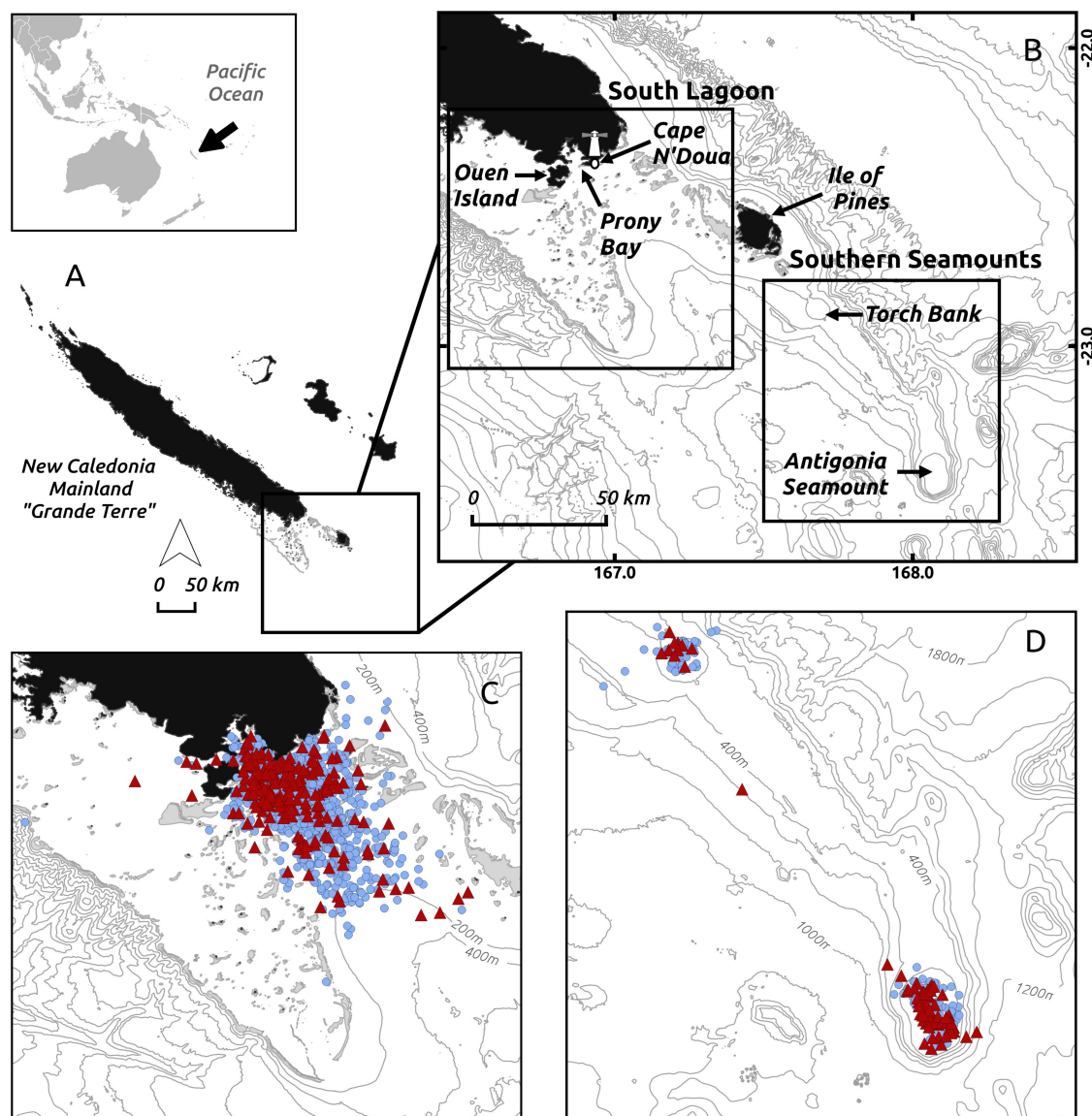


Figure 3.1 Map of New Caledonia (A), study areas (B), and positions of humpback whale (*Megaptera novaeangliae*) encounters in the South Lagoon (C) and Southern Seamounts (D). Groups with a calf are shown with triangles and groups without a calf are shown with circles. Light gray lines represent 200-m isobaths. Land is shown in black and reefs in gray.

Several environmental variables were collected in the study areas to characterize habitat at a 500-m resolution. Coastline and reef shapefiles were produced by the Millennium Coral Reef Mapping Project (version 8, [Andréfouët et al., 2008](#)). Using these shapefiles, distance to the coast and distance to reefs were calculated for each 500 x 500 m cell in the South Lagoon study area as the euclidean distance to the closest landmass (i.e., New Caledonia mainland, Ouen Island, or the Isle of Pines) and closest reef, respectively. Bathymetry data ([DTSI, 2016](#)) was provided at a 100 x 100 m resolution over both study areas. Raster gaps were filled through extrapolation of satellite and

aerial composite imagery (Lefèvre, French National Research Institute for Sustainable Development, pers. comm., February, 2016). Two terrain features were derived from the bathymetry raster: slope over both study areas, and shading only at the Southern Seamounts, which is a metric combining orientation and inclination of the slope with respect to a southeast axis that represents the dominant wind direction (Horn, 1981). Finally, distance to the center of the seamounts was calculated for the Southern Seamount study area.

3.2.3 Space use analysis

Groups were classified into 2 categories: groups with a calf (Gcalf) including MC, MC-E, and MC-R social types, and groups without a calf (Gnocalf) including R, P, and S social types. Group encounters were georeferenced and their positions were projected in a UTM coordinate system (UTM zone 58S). For this analysis, group encounters were considered statistically independent within each study area at a daily scale.

Pairwise distance analysis

For this analysis, a metric was developed to estimate the spatio-temporal closeness between group encounters that was then used to assess potential patterns of attraction or avoidance between whale groups. Euclidean distance was calculated between whale groups observed each day in the South Lagoon. The distributions of distance values were compared between groups with a calf and groups belonging to other social types. Subsequently, these distances were divided by the time interval between each group encounter. This metric, hereafter referred to as the spatio-temporal closeness, was calculated per social type and compared using Kruskal-Wallis rank sum tests.

Habitat preferences

The probability of encountering a calf in a group was modeled with Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990). First, the GAM was applied only to groups observed at the end of the season in the South Lagoon to assess the effect of distance to the coast, distance to reefs, bathymetry, and seabed slope (see Supplementary Data S1, for more detail on predictor selection). Second, all observations recorded in the South Lagoon were combined to test for a potential effect of the time of season (included in the model as calendar week of the year) on the space-use pattern of groups with a calf. A GAM was built over all observations of groups with or without a calf and including distance to the coast, week, and a linear interaction term between these 2 variables as predictors. Finally, encounter rate per week of the year and per social types (Gnocalf, MC, MC-E, and MC-R) was calculated by dividing the number of groups observed by the number of hours spent on-effort for each week (sum of daily survey durations: from start to end of observations), all years pooled together.

In the Southern Seamounts, time of season was not tested because the great majority of the data was collected at the end of the season. Distance to the coast and to the reefs were also excluded and replaced by other environmental factors thought to be more relevant in this off-shore area: bathymetry, seabed slope, distance to the center of the seamounts, and shading.

GAMs were applied with a binomial response type (presence or absence of a calf in a group), logit link function and maximum likelihood (ML) smoothing selector. Several models of decreasing complexity were fitted to our dataset and model selection was performed with a stepwise approach using the Bayesian Information Criterion (BIC; Schwarz, 1978). BIC is a variant of the more commonly applied Akaike Information Criterion (AIC). It takes in account the number of observations included in the model and penalizes model complexity more heavily than AIC. The Receiver Operating Characteristic (ROC) curves were also calculated for each model and the corresponding Area Under the Curve (AUC) was reported in order to compare descriptive and predictive performance across models. AUC evaluates the model's capacity for binary classification: a random model has an AUC of 0.5 and a perfect model an AUC of 1 (Swets, 1988). DeLong's Z-test was applied to compare models to the AUC of the null model (DeLong *et al.*, 2016).

Spatial overlap

Differences in habitat preferences between social types may result in distinct patterns of spatial distribution. The core area of use for groups with or without a calf was estimated using the Permissive Home Range Estimation (PHRE) method developed by Tarjan and Tinker (2016). This method was initially developed to assess home ranges of individual animals based on satellite tracking data. Here, it was applied to the positions of group encounters, so that the term "home range" actually refers to the range of the overall population. Instead of calculating home ranges using a Kernel Density Estimate (KDE, Worton, 1989) in geographical space, the PHRE applies a KDE to the positions in a multidimensional environmental space and then reprojects the niche estimate to a 2-dimensions geographical surface. The same environmental variables applied in the GAM analysis were considered. Similar to a traditional KDE, PHRE can be calculated with different smoothing parameters. Three methods were tested to optimize the KDE bandwidth: the plug-in bandwidth selector (Hpi), the least-square cross validation (Hlscv), and the smoothed cross-validation (Hscv) described in Duong (2007). Once the environmental hypervolume occupied by observations was identified, it was reprojected to latitude-longitude to create a map of relative probability of presence. The 50% contour of the probability surface was outlined and considered as the core area of use. Then, the overlap of these areas was calculated between groups with or without a calf.

All data manipulation and spatial analysis was conducted using R statistical software v.3.2.5 (R Core Team, 2016) and QGIS v.2.14. (QGIS Development Team, 2016). More specifically, GAMs were modeled using the mgcv R package and PHRE was based on a modified version of a custom code by Tarjan and Tinker (2016).

3.2.4 Photographic analysis

Photographs of calves were used to evaluate age and ecological markers between the 2 breeding sites. Indeed, the approximate age of humpback whale calves may be assessed from the degree of unfurling of the dorsal fin (Cartwright and Sullivan, 2009b). A pale flank pigmentation (Chittleborough, 1953) and a furled dorsal fin (Cartwright and Sullivan, 2009b) are known traits of neonatal humpback whales. As the calf grows, pigmentation darkens and the dorsal fin unfurls. These phenotypic changes may be recorded within a breeding season (Cartwright and Sullivan, 2009b). Also, scarring patterns are important ecological markers for cetaceans: they have been analyzed in several species to study intra-specific interactions, predation, habitat use, and migratory patterns (Heithaus *et al.*, 2016; Wenzel and Suárez, 2012; Marley *et al.*, 2013; Towers *et al.*, 2013; Elwen *et al.*, 2014; Best and Photopoulou, 2016). In particular, Cookiecutter sharks (*Isistius spp.*) primarily live in tropical oceanic waters and are known to attack cetaceans, leaving distinctive crater-like wounds on their body (Dwyer and Visser, 2011; Best and Photopoulou, 2016). Prevalence of Cookiecutter shark bites on individual whales may therefore be interpreted as a rough indicator of pelagic habitat use (Wenzel and Suárez, 2012; Towers *et al.*, 2013; Best and Photopoulou, 2016). Finally, scars, and occasionally observed fresh wounds, are assumed to be partially due to prolonged antagonist interactions with competitive males as the barnacles on the fluke and pectoral fins of the latter can injure the calf during contact.

Photographic analysis was performed on pictures of the dorsal fins of calves encountered at the end of the season in the South Lagoon and in the Southern Seamounts, between 2007 and 2015. Only pictures with fair or better quality were retained in the analysis (quality assessment was based on focus, lighting conditions, proportion of the frame occupied by the animal, and angle of the animal relative to the sensor plane; following Towers *et al.*, 2013). If a calf was encountered on several occasions, only the earliest encounter among those including good-quality pictures was retained.

For each calf encounter at the end of the season, the following physical characteristics were recorded: flank pigmentation (very light, light, medium, dark), unfurling of the dorsal fin measured by the angle between the dorsal fin and the flank (furled = 45-80°, medium = 15-45°, almost unfurled = 0-15°, unfurled = 0°), scarring (none, few scars, medium, many scars), presence or absence of fresh wounds, presence or absence of Cookiecutter shark bites, and number of visible Cookiecutter shark bites over the left and right flanks (for more details on rating criteria, see Appendix 3.B). A manual that described and illustrated these characteristic was produced prior to the analysis and was used as a reference throughout the rating process. These physical characteristics were qualitatively rated visually by a single researcher blind to the exact date of the encounter and to the identity of the calf in order to avoid observer bias (Coomber *et al.*, 2016). Physical characteristics were compared between South Lagoon and Southern Seamounts calves using Pearson's Chi-square tests with simulated P-values (based on 2,000 Monte-Carlo replicates). Finally, the independence between scarring and social group type in which the calf was found (MC, MC-E, or MC-R) was tested over both study sites

pooled together using the same statistical test.

3.3 Results

In the South Lagoon, a total of 1,312 whale groups were encountered over 20 years of surveys (equivalent to 716 days of effort), of which 206 included a calf (16%, Fig 3.1C). A total of 646 groups were observed at the end of the season (517 without a calf versus 129 with a calf). In the Southern Seamounts, 214 groups were observed over 7 years of surveys (equivalent to 34 days of effort), from which 74 included a calf (35%, Table 3.1, Fig 3.1D).

The number of daily resightings of an individual was close to 1 on average. Individuals in groups without a calf were observed 1.19 times (\pm SD 0.48) in the South Lagoon and 1.15 times (\pm SD 0.41) in the Southern Seamounts. Maternal females were resighted 1.07 times (\pm SD 0.28) per day on average in the South Lagoon and 1.17 times (\pm SD 0.42) in the Southern Seamounts. Resights were significantly lower for maternal females than adults from groups without a calf (2-way ANOVA: $F_{1, 2664} = 7.3$, $P = 0.007$), but did not vary across study sites (2-way ANOVA: $F_{1, 2664} = 0.8$, $P = 0.4$).

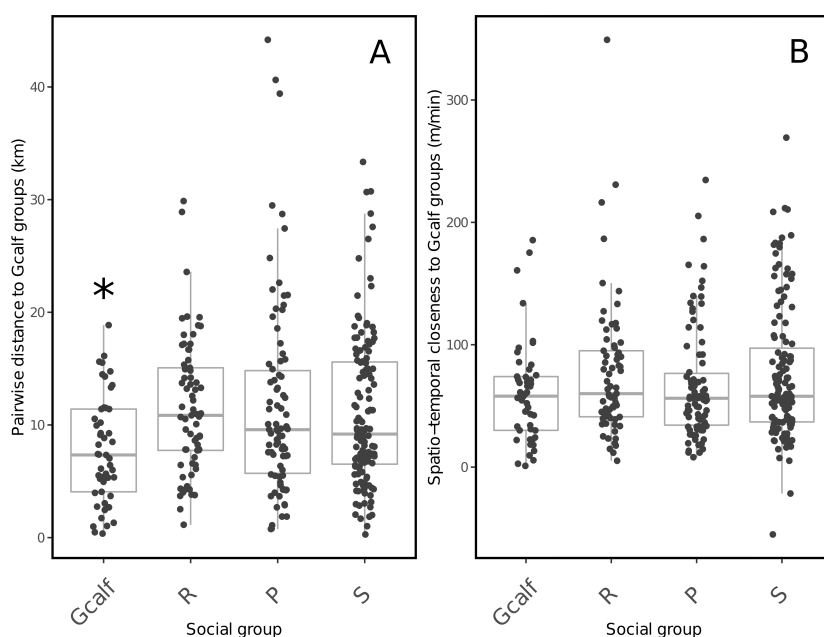


Figure 3.2 Daily pairwise distances (A) and spatio-temporal closeness (B) between humpback whale (*Megaptera novaeangliae*) groups with a calf and other social group types in the South Lagoon, New Caledonia ($n = 335$). Gcalf: groups with a calf, R: Competitive groups, P: Pairs of adults, S: Singletons. Raw distances are represented with jittered points directly on the boxes. Kruskal-Wallis tests show a significant difference across groups in (A) $X^2_3 = 12.4$, $P = 0.01$ but not in (B) $X^2_3 = 3.5$, $P = 0.32$.

Space use in the South Lagoon

In the South Lagoon, the daily pairwise distances ($n = 335$ distance values in total) between groups with a calf was significantly lower than between groups with a calf and all other social group types without a calf (Kruskal-Wallis test: $X^2_3 = 12.4$, $P = 0.01$, Fig. 3.2A). Indeed, Dunn's post-hoc test with a Bonferroni correction showed significant differences between Gcalf and R ($Z = -3.36$, $P = 0.02$), Gcalf and P ($Z = -2.74$, $P = 0.02$), Gcalf and S ($Z = -2.91$, $P = 0.01$), but not between R, P, and S. Yet, when balancing these pairwise distances with the duration of the time interval between each

observation, groups with a calf no longer distinguished themselves from the rest of the population. The spatio-temporal closeness between groups with a calf was not significantly different from that between groups with a calf and all other social group types without a calf (Kruskal-Wallis test: $X^2_3 = 3.5$, $P = 0.32$, Fig. 3.2B). Therefore, groups with a calf were observed in the same geographical areas as groups without a calf, but rarely at the same time of the day. Groups with a calf avoided all other groups, including other groups with a calf.

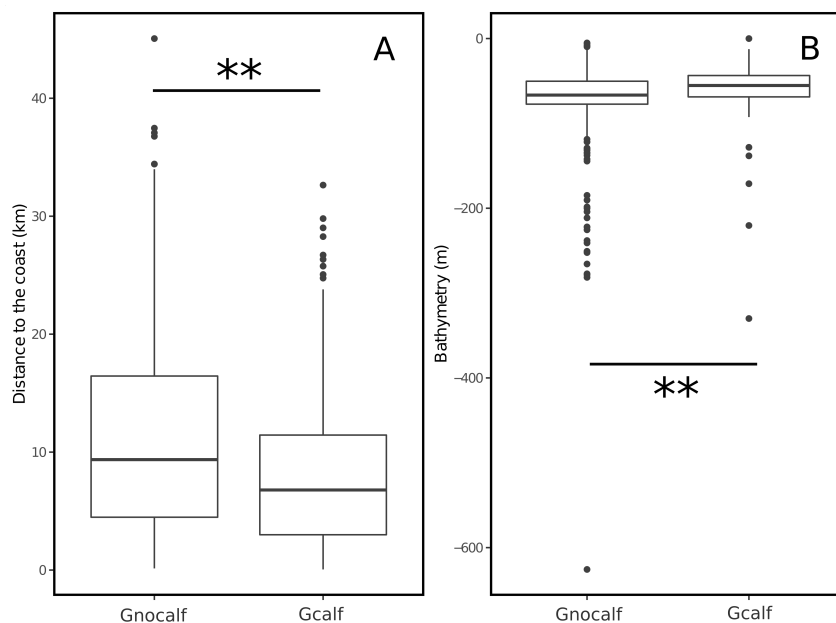


Figure 3.3 Distance to the coast (A) and bathymetry (B) extracted at the humpback whale (*Megaptera novaeangliae*) group positions in the South Lagoon, New Caledonia, at the end of the season ($n = 646$) Gcalf: groups with a calf, Gnocalf: groups without a calf. Kruskal-Wallis tests show significant differences between groups in (A) $X^2_2 = 13.2$, $P < 0.001$ and (B) $X^2_2 = 16.5$, $P < 0.001$.

In the South Lagoon, groups with a calf observed at the end of the season were observed closer to the coast (Kruskal-Wallis test: $X^2_2 = 13.2$, $P < 0.001$) and in shallower waters (Kruskal-Wallis test: $X^2_2 = 16.5$, $P < 0.001$) compared to groups without calves (Fig. 3.3). This habitat-use relationship relative to distance to the coast was also detected through the GAM analysis of group encounters ($n = 646$) at the end of the season. The simplest model including only distance to the coast as a predictor of calf presence was selected as the best model based on BIC (Table 3.2). Interestingly, this model did not maximize AUC compared to other models including more predictors, but it provided the best trade-off between performance and complexity. The predictive performance of this model measured through AUC was significantly higher than that of a random model (DeLong's Z-test: $Z = -3.7$, $P < 0.001$). None of the GAM models included a significant effect of depth (Table 3.2), which can be attributed to the strong correlation between distance to the coast and bathymetry (Spearman coeff = -0.71 , calculated on the full season sample of sightings, $n = 1,312$).

The overall encounter rate peaked in the last week of August in the South Lagoon, but the proportion of groups with a calf, and particularly of MC groups, increased throughout the season and peaked in September (Fig. 3.4). Additionally, in our 3-term GAM analysis of group encounters over the whole season ($n = 1,312$, see Supplementary Data S1), distance to the coast (approximate significance of smooth terms: $s(\text{dist_coast})$ edf = 1, $X^2 = 19.54$, $P < 0.001$) and week (approximate significance of smooth terms: $s(\text{week})$ edf = 1, $X^2 = 39.35$, $P < 0.001$) were significant predictors of

calf presence. Yet, the interaction between distance to the coast and week had no significant effect on the probability of encountering a group with a calf (approximate significance of smooth terms: $s(\text{dist_coast}, \text{week})$ edf = 2.07e-05, $X^2 = 0$, $P = 0.38$), suggesting that despite the change in calf abundance throughout the breeding season, their habitat preferences remain the same.

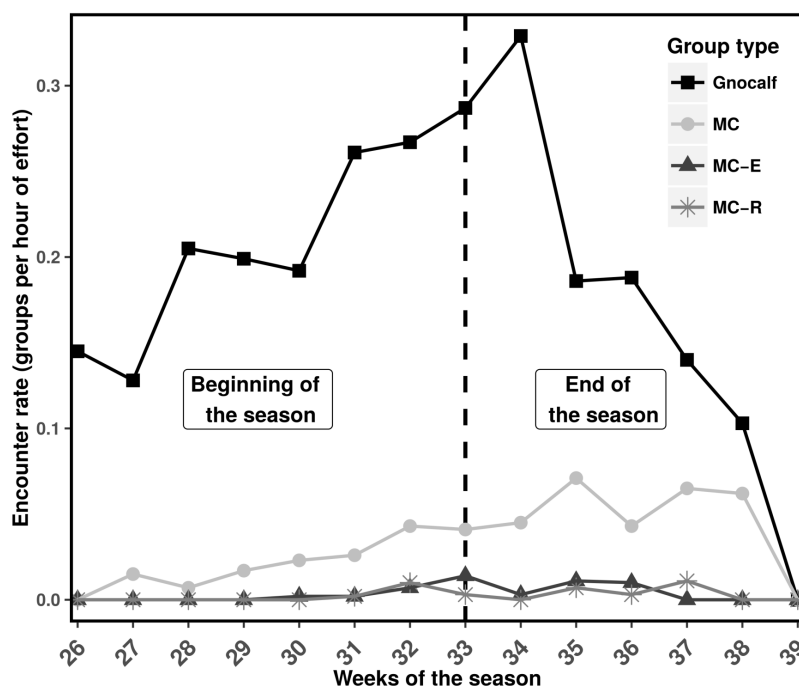


Figure 3.4 Encounter rate (number of groups observed per hour of survey at sea, all years pooled together) by humpback whale (*Megaptera novaeangliae*) social group type in the South Lagoon, New Caledonia, across the breeding season. Calendar weeks are shown on the x-axis: August starts on week 31 and September starts on week 35.

Table 3.2 Summary of the Generalized Additive Models describing presence of calves of humpback whales (*Megaptera novaeangliae*) in the South Lagoon (SL) and Southern Seamounts (SS), New Caledonia, at the end of the season. BIC: Bayesian Information Criterion, Resid deviance = residual deviance, AUC = Area Under the ROC Curve, Z-stat = Delong's Z-test statistic. Based on BIC, model 5 was selected as best model in the South Lagoon. In the Southern Seamounts, no model outperformed the null model based on BIC.

Study site	Model	Predictors ^a	BIC	Res.dev	AUC	Delong's test Z-stat	Delong's test p-value
SL	Null	~1	652	646	0.500	0	1
	1	dist_coast + dist_reef + bathy + slope	657	627	0.622	-4.49	< 0.001
	2	dist_coast + dist_reef + bathy	654	628	0.620	-4.41	< 0.001
	3	dist_coast + dist_reef	650	630	0.150	-4.20	< 0.001
	4	dist_coast + bathy	653	633	0.610	-3.98	< 0.001
	5	dist_coast	647	634	0.603	-3.71	< 0.001
SS	Null	~1	281	276	0.500	0	1
	1	bathy + dist_mount + slope + shading	297	274	0.510	0.23	0.82
	2	bathy + dist_mount + slope	299	269	0.607	-2.06	0.01
	3	bathy + dist_mount	299	269	0.607	-2.06	0.01

^a dist_coast = distance to the coast, dist_reef = distance to the reef, bathy = bathymetric measure of depth, dist_mount = distance to the center of the seamount, slope = seabed slope.

Comparative habitat analysis between study sites

In the GAM analysis of calf presence on the Southern Seamounts, none of the 5 models built with different combinations of environmental predictors outperformed the null model (lowest BIC = 281.3, Table 3.2). This indicates that there was no habitat segregation between groups with and without calf in the Southern Seamounts with respect to bathymetry, slope, distance to the center of seamounts, and shading.

After graphically comparing the maps of relative probability of presence generated by the PHRE set at different bandwidths, the unconstrained Hscv method was selected as the best candidate for our PHRE analysis. The relative probability of whale presence was mapped in a geographical coordinate system and the 50% probability contours were separately retrieved for each social type: Gcalf and Gnocalf (Fig. 3.5). The overlap of the PHRE core area between groups with and without a calf was higher in the Southern Seamounts (75%) than in the South Lagoon (59%). The core area of use for groups with a calf also was more than twice as small in the Southern Seamounts (63 km²) than in the South Lagoon (139 km²).

On average, groups with a calf were proportionally more common in the Southern Seamounts (26.9% ± SD 19.5) than in the South Lagoon (16.0% ± SD 8.5) at the end of the season (Pearson's Chi-square test with 2,000 Monte-Carlo simulations: $X^2 = 19.0$, $P < 0.001$; Table 3.3). The breeding site significantly affected the social group type of groups with a calf (Pearson's Chi-square test with 2,000 Monte-Carlo simulations: $X^2 = 49.3$, $P < 0.001$). Groups with a calf were predominantly MC pairs in the South Lagoon whereas in the Southern Seamounts, MC-E and MC-R groups were more frequent (Table 3.3). Molecular analysis of tissue samples confirmed that all escorts biopsied in MC-E groups were males.

Table 3.3 Mean proportions of social group types of humpback whales (*Megaptera novaeangliae*) encountered in the South Lagoon and in the Southern Seamounts, New Caledonia, at the end of the season. Gcalf: MC = mother-calf, MC-E = mother-calf-escort, MC-R = mother-calf-competitive group. Gnocalf: groups with no calf (R, P, and S groups). Mean proportions and the associated standard deviation (SD) are calculated on a sample of 20 years in the South Lagoon and 7 years in the Southern Seamounts.

	South Lagoon		Southern Seamounts	
	Mean %	SD	Mean %	SD
Gcalf	16.0	8.5	26.9	19.5
MC	17.3	10.2	10.0	9.8
MC-E	3.2	4.1	7.4	7.4
MC-R	0.9	1.6	9.3	7.3
Gnocalf	84.1	8.5	73.1	19.5

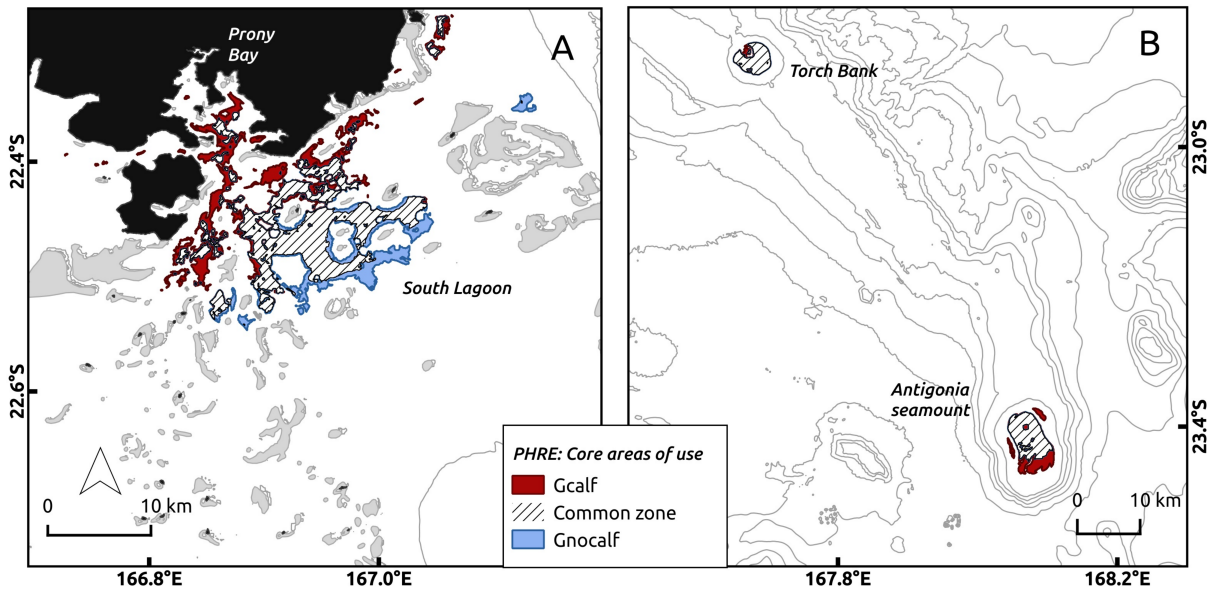


Figure 3.5 Permissive Home Range Estimate (PHRE) calculated for humpback whale (*Megaptera novaeangliae*) groups with and without a calf in the South Lagoon (A) and the Southern Seamounds (B), New Caledonia. 50% contours of the PHRE are represented. The area of overlap between the 2 social group types is represented with black dashes. Light gray lines represent 200-m isobaths. Land is shown in black and reefs in gray.

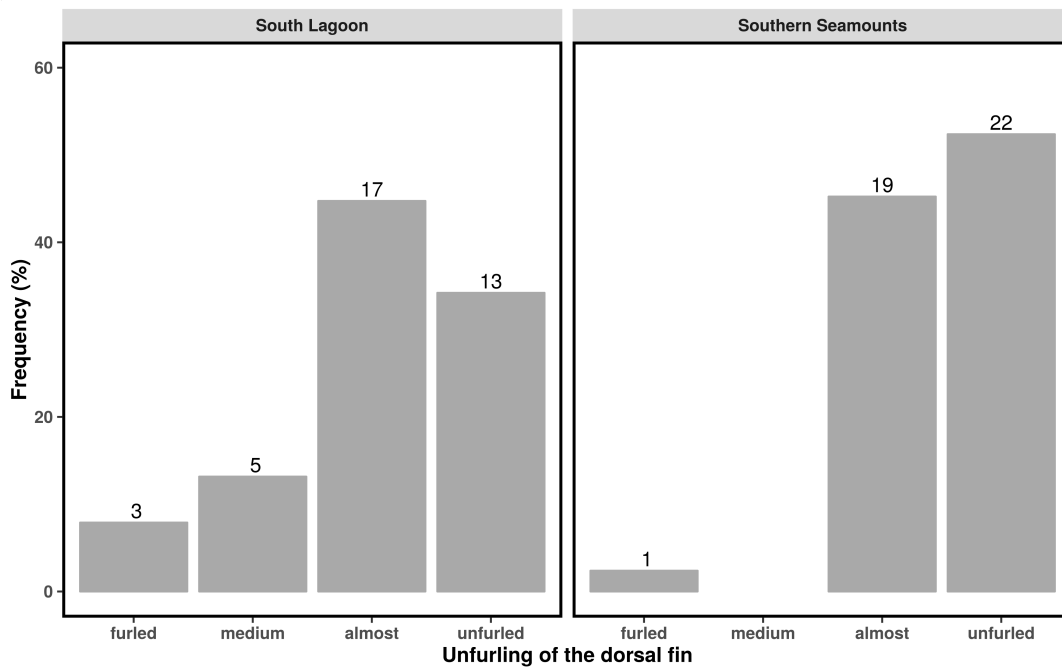


Figure 3.6 Degree of unfurling of the dorsal fin for calves of humpback whales (*Megaptera novaeangliae*) observed in the South Lagoon (n = 40) and the Southern Seamounds (n = 47), New Caledonia, at the end of the season. Sample sizes are indicated on top of the bars. Dorsal fins are classified in an increasing order of unfurling from left to right. Pearson's Chi-square test shows significantly more advanced unfurling in the Southern Seamounds: $X^2 = 8.25$, $P = 0.03$.

Comparative photographic analysis between study sites

From a total of 180 encounters with groups with a calf between 2007 and 2015, a subset of 116 encounters that occurred at the end of the season for which pictures were available was selected for analysis. After deleting resights and poor pictures, the dataset was composed of 40 calves in the South Lagoon and 47 in the Southern Seamounds. No significant difference in scarring, presence of fresh wounds, number of Cookiecutter shark bites, or flank pigmentation was found between calves observed in the South Lagoon and the Southern Seamounds. Calf scarring also was not related to its social group type (MC, MC-E, or MC-R; Pearson's Chi-square test with 2,000 Monte-Carlo simulations: $X^2 = 6.0$, $P = 0.44$). A significant difference was found in the degree of unfurling of the dorsal fin, which was on average more advanced in the Southern Seamounds (Pearson's Chi-square test with 2000 Monte-Carlo simulations: $X^2 = 8.25$, $P = 0.03$; Fig. 3.6).

3.4 Discussion

In this study, maternal female humpback whales displayed different space-use patterns with respect to other whales depending on whether they occupied coastal or oceanic habitat. In the South Lagoon, groups with a calf avoided contact with other con-specifics and occurred in higher proportion in waters nearest to the coast. This pattern of social segregation is consistent with studies in other humpback whale breeding grounds of the world that also found that mothers with a calf favor shallow coastal waters close to the coast or to reefs (Smultea, 1994; Martins *et al.*, 2001; Ersts and Rosenbaum, 2003; Oviedo and Solís, 2008; Félix and Botero-Acosta, 2011; Craig *et al.*, 2014; Guidino *et al.*, 2014; Lindsay *et al.*, 2016). This pattern has been observed in other cetaceans (i.e., southern right whale, *Eubalaena australis*— Rayment *et al.*, 2015; Risso's dolphin, *Grampus griseus*— Hartman *et al.*, 2014) and is thought to result from a need to 1) shelter from wind and currents (Félix and Botero-Acosta, 2011; Rayment *et al.*, 2015), and 2) avoid male harassment (Elwen and Best, 2004; Craig *et al.*, 2014). Indeed, lactating females and their offspring are constrained by a tight energy balance on their breeding ground and during the migration towards polar feeding grounds (Chittleborough, 1958). Spatial segregation from other whales and sheltering are thought to be energy-saving strategies for females with a calf. Yet, in this study we show that females with a calf also occupy areas where neither of these 2 needs are fulfilled. In the Southern Seamounds, groups with a calf were found in greater proportion than in the South Lagoon, despite this area's lack of shelter or the possibility to spatially avoid adult males. In the Southern Seamound site, the core area used by groups with a calf strongly overlapped with the area occupied by the other whale groups.

Our photographic analysis suggested that calves observed in the Southern Seamounds at the end of the season were older than the calves observed in the South Lagoon during the same period. It is not known precisely how long it takes the dorsal fin of humpback whale calves to unfurl completely, and the rate of unfurling is likely to vary between individuals (Cartwright and Sullivan, 2009b). Our

picture database also is part of a long-term monitoring program and was not collected specifically for this purpose (Cartwright and Sullivan, 2009b). Thus, caution is warranted in the interpretation of these results. Nonetheless, maternal females have been shown to use deeper waters as their calf grows larger during the breeding season (Hawaii, Pack *et al.*, 2017). Females could be more reluctant to visit unsheltered oceanic habitats such as the Southern Seamounts until their calf grows large enough that the risk of exposure to harsh environmental conditions and separation decreases, as suggested by Trudelle (2016).

Photographic analysis showed that scarring and prevalence of wounds was not significantly different between calves from the 2 sites. Injuries to newborns are inflicted by males during reproduction in many species (Palombit, 2015). Direct deadly injuring is rarely observed in humpback whales, but there is proof for increased energy expenditure by calves in the presence of adult males (Darling *et al.*, 2006; Cartwright and Sullivan, 2009a) and increased strandings of calves in areas where the density of males is high (southern right whales, Elwen and Best, 2004). In New Caledonia, males have been observed trying to separate calves from their mother in the South Lagoon and in the Southern Seamounts (C. Garrigue, personal observation). Despite the high density of whales in the Southern Seamounts, calves did not bear more scars there than in the South Lagoon. Interestingly, more females with a calf were observed with a single escort in the Southern Seamounts than in the South Lagoon. Females in oceanic habitats could therefore be avoiding male harassment and injuries to their calf by seeking the protection of an escort as suggested in the 'bodyguard hypothesis' (Mesnick, 1997). However, the presence of a competitive group (MC-R) or an escort (MC-E) with the maternal female did not seem to have an effect on the scarring of calves. As it is not possible to tell whether the calves acquired scars from contacts with escorts, competitive males, or even potentially from their mother, this study cannot provide further support in favor or against the bodyguard hypothesis. Previous studies have demonstrated increased distance to the coast of escorted mother-calf groups in several breeding grounds (Craig *et al.*, 2014; Trudelle, 2016). Selecting a single escort (MC-E groups) in some contexts instead of remaining alone with her calf (MC groups) could therefore be interpreted as an alternative strategy that allows the mother to protect her calf from harmful interactions when the density of whales is high or the environment does not include natural barriers to allow spatial avoidance of males (Cartwright *et al.*, 2012).

Prevalence of cookiecutter shark bites was not significantly different between the two study sites. Cookiecutter sharks are primarily found in tropical, deep off-shore waters (*Isistius brasiliensis*—Jahn and Haedrich, 1988), though they may migrate vertically at night, moving to the surface with the deep scattering layers (Heithaus, 2001). Despite the lack of ecological data regarding the distribution of this ectoparasite, their predominant preference for waters >1,000 m deep (Heithaus, 2001) has led to cookiecutter shark bites on cetacean being used as proxies for time spent offshore (Wenzel and Suárez, 2012; Best and Photopoulou, 2016). Hence, a higher prevalence of these marks is expected on calves that spent more time in oceanic habitats during their ontogeny. The fact that this ecological marker was similar between our 2 sites suggests a similar life-history for calves observed in the South

Lagoon and the Southern Seamounts. Photo-identification has indicated individual re-sights ($n > 30$) between these 2 breeding grounds within and between seasons (site fidelity indices, [Garrigue *et al.*, 2013](#); probability of transitions, [Orgeret *et al.*, 2014](#)). Satellite tracking also demonstrated that toward the end of the breeding season many individuals (68% of tagged whales), including mothers with a calf (50% of tagged maternal females), visited both the South Lagoon and Antigonina seamount ([Garrigue *et al.*, 2015](#)). These concordant results confirm that the humpback whales observed in the South Lagoon and on the Southern Seamounts breeding grounds are part of the same population.

Mothers with a calf must derive some form of benefit from using this relatively inhospitable oceanic habitat. The Southern Seamounts are ecologically very different from most humpback whale breeding grounds studied around the world ([Garrigue *et al.*, 2015](#)). Similar oceanic unsheltered breeding grounds have been described, namely Penguin Banks (Hawaii: [Baker and Herman, 1981](#); [Mobley *et al.*, 1999](#)) or Navidad Bank (Dominican Republic: [Winn *et al.*, 1975](#); [Mattila *et al.*, 1989](#)), but have been subject to less research due to their relative inaccessibility. This peculiar habitat might provide unexpected advantages for maternal females, at least towards the end of the breeding season. While predation is often considered a major driver of species distributions, there is a paucity of data concerning the potential predators of humpback whales in the area. Killer whales are known to attack calves of humpback whales ([Pitman *et al.*, 2015](#)), but the past and present intensity of this predation in breeding grounds is debated ([Clapham, 2000b](#)). Killer whales have been reported outside the New Caledonian lagoon on 15 occasions since 1995 ([Poupon, 2010](#)), and [Mehta *et al.* \(2007\)](#) have estimated that 31% of flukes photographed in New Caledonia bore killer whale rake marks. Killer whales have never been observed in the South Lagoon nor in the Southern Seamounts, however, and never in interaction with humpback whales. Avoidance of predation is therefore unlikely to be the main factor driving the intense use of offshore seamounts by maternal females in New Caledonia. Alternatively, 2 hypotheses may explain this space-use pattern: opportunistic feeding grounds and staging grounds. Seamounts are known to be sites of large vertical water excursions due to internal waves, together with vigorous turbulences and mixing, which in turn leads to nutrient export or stimulation of biological production ?. These enriched and dynamic waters trigger local trophic cascades ([Morato *et al.*, 2010](#)) that humpback whales could be using as opportunistic feeding spots ([Stockin and Burgess, 2005](#); [Hann *et al.*, 2016](#)). Neither humpback whale feeding behavior nor defecation has ever been directly observed in the Southern Seamounts to date, however (C. Garrigue, personal observation). Alternatively, eddies and currents around these seamounts might provide navigational cues connecting the South Lagoon to the southward migration routes. The Southern Seamounts could constitute a staging ground before departure southward, where maternal females may congregate with the rest of the population before initiating their migration south. In this scenario, fewer whales would be found in the Southern Seamounts at the beginning of the season than at the end. However, knowledge of use of the Southern Seamounts in the early season is limited. Over the few days of survey conducted on the Southern Seamounts at the beginning of July ($n = 5$), no females with a calf were observed (in 2001 and 2006, Table 3.1). Additionally, as most whales were

tagged in August and September, satellite tracking over the Southern Seamounts only occurred at the end of the season (Garrigue *et al.*, 2015). Though this tracking showed movements in both directions between the South Lagoon and the Southern Seamounts, it is not known whether females with a calf stop on the seamounts on their way to the other breeding grounds, such as the South Lagoon, at the beginning of the austral winter. Surveying the Southern Seamounts early in the breeding season is required to fill this data gap in occurrence patterns of whales throughout the season, and acquire a more complete perspective on use of these oceanic habitats by humpback whales.

Satellite tracking showed a marked preference by humpback whales for Antigonina seamount and Torch Bank compared to other similar neighboring seabed structures (Garrigue *et al.*, 2015). Social interactions might partially drive this distribution (Clapham and Zerbini, 2015) and the selection of the Southern Seamounts as congregation areas. Indeed, social aggregation is commonly observed independently from surrounding environmental conditions. The organization of humpback whales within their winter grounds has long been attributed to a lekking system (Herman and Tavorga, 1980), defined as a gathering of males engaged in competitive or vocal and visual display to attract females. This concept has been elaborated on by Clapham (1996) who suggested the term of a "floating lek" to reflect the absence of territoriality in leks of humpback whales. There also can be more than one congregation spot (referred to as "arenas") for humpback whales within a given breeding ground (Herman, 2017), as observed in the New Caledonian region (Garrigue *et al.*, 2017). However, the lek hypothesis fails to explain why gravid and maternal females would also join the arenas, including the South Lagoon and the Southern Seamounts. Natal philopatry has been put forward as an explanation for movements of maternal females (Baker *et al.*, 2013; Herman, 2017), but the spatial scale of this process is unknown: does it function across the arenas, such as the Southern Seamounts versus South Lagoon, or the whole wintering ground, such as the New Caledonian region? Furthermore, Dulau *et al.* (2017) suggested that the wandering behavior of maternal females, who sometimes travel extensive distances with their newborn calf to visit several arenas, may serve the maternal cultural transmission of breeding area geography. It is unlikely that this reason alone could explain the large amount of time spent in the Southern Seamounts (Garrigue *et al.*, 2015) but it could partially drive transits between the South Lagoon and other breeding locations in New Caledonian waters.

In conclusion, maternal female humpback whales displayed alternative and non-exclusive space-use patterns: in coastal breeding grounds such as the South Lagoon, they actively avoided other whales and specifically used shallow waters closer to the coast, whereas in the oceanic habitat of the Southern Seamounts, they congregated with the rest of the population and had no sheltered habitat available. Thus, maternal humpback whales demonstrate flexible patterns of habitat use on their breeding grounds, contradicting the paradigm that females obligatorily seek shelter from rough seas and males when nursing a newborn calf. This finding has important conservation implications for spatial management within the Natural Park of the Coral Sea, a large protected area covering most of New Caledonia's economic exclusive zone. Further research into the mechanisms underlying mother-calf presence around off-shore seamounts and shallow banks is needed to advise efforts to

protect these sensitive hot-spots.

Acknowledgements

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Appendix 3.A. Habitat modeling in the South Lagoon and Southern Seamounds

The spatial distribution of survey effort (Fig. 3.A.1) was not accounted for in this study, but is simply reported here, to provide an overview of the extent and intensity of effort in the two study sites. Survey effort maps were produced using the GPS tracks of the survey boat pooled from 2003 to 2015 (GPS tracks were not available for years prior to 2003). Only the portions "on-effort" (when observers were searching for whales or following whales) were conserved for this calculation. On-effort GPS tracks were binned over a grid with 1 x 1 km resolution.

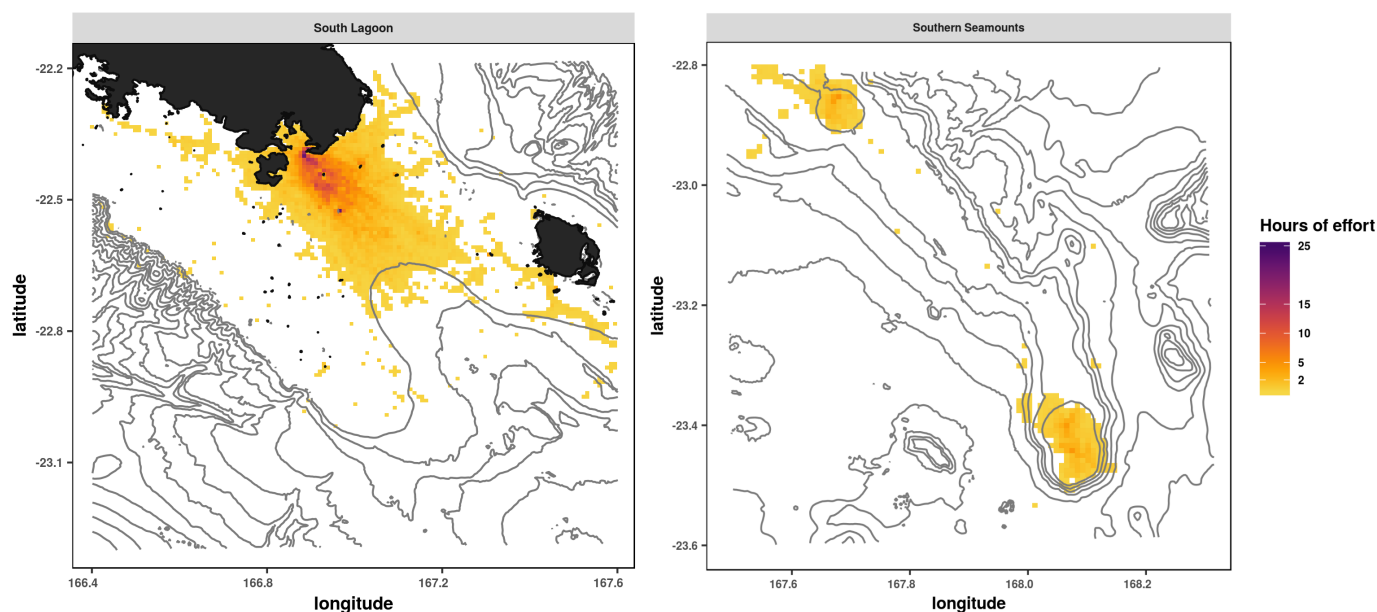


Figure 3.A.1. Spatial distribution of survey effort in the South Lagoon (left) and the Southern Seamounds (right), calculated from GPS tracks of the boat from 2003 to 2015. Light grey lines represent 200 m isobaths.

In the South Lagoon we modeled calf presence (binomial response type) as a function of time of the season (as calendar week) and distance to the coast. The aim of this analysis was to explore the potential changes in habitat selection throughout a breeding season (Fig 3.A.2 & 3.A.3).

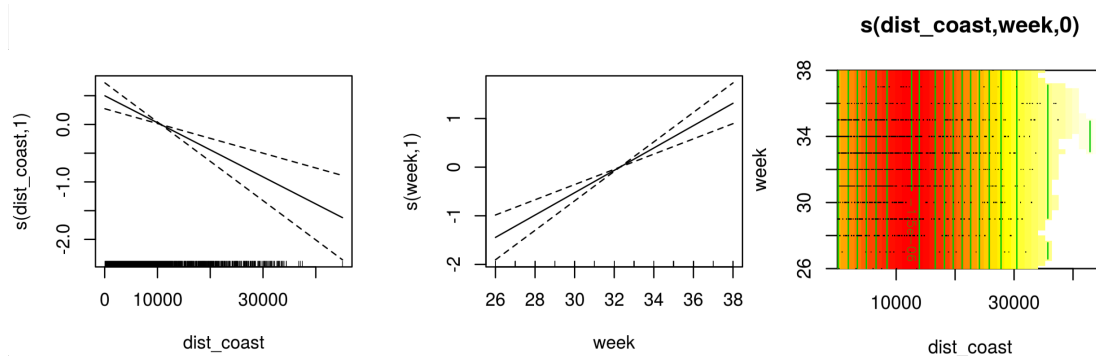


Figure 3.A.2 Partial response for a GAM of calf presence relative to distance to the coast, week of the year and an interaction term. Probability of calf presence increases along the season and decreases with distance to the coast. The interaction plot shows no cross-effect of these two predictors on calf presence (dist_coast in meters). Y-axis is on the logit scale.

```
##
## Family: binomial
## Link function: logit
##
## Formula:
## cat ~ s(dist_coast) + s(week) + s(dist_coast, week)
##
## Parametric coefficients:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.81599    0.08532  -21.29  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##             edf Ref.df Chi.sq p-value
## s(dist_coast)    1.000e+00     1  19.54 9.84e-06 ***
## s(week)          1.000e+00     1  39.35 3.55e-10 ***
## s(dist_coast,week) 2.068e-05    27   0.00  0.378
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.0483   Deviance explained =  5.3%
## -ML = 540.07   Scale est. = 1         n = 1312
```

Figure 3.A.3 Model output for a GAM of calf presence relative to distance to the coast, week of the year and an interaction term. "Cat" is the binomial response variable of presence/absence of a calf in a group.

Appendix 3.B. Photographic analysis of humpback whale calves

In the analysis of photographs we distinguish two types of parameters: characteristics used for age estimation (flank pigmentation and degree of unfurling of the dorsal fin) and characteristics used to assess habitat use and social interactions (scarring, presence of fresh wounds and presence of Cookiecutter shark bites). Presence of wounds and presence of Cookiecutter shark bites were only assessed if both flanks of the calf had been photographed. Rating criteria are described below.

- Flank pigmentation
 - dark: flanks are entirely black or dark grey
 - medium: light grey patches are visible
 - light: flanks are entirely light grey or partially covered with white patches
 - very light: flanks are entirely white or light grey with white patches
- Unfurling of the dorsal fin
 - unfurled: angle 0°
 - almost unfurled: between 0° and 15°
 - medium: between 15° and 45°
 - furled: between 45° and 80°
- Cookie-cutter shark bites
 - present / absent
 - number of bites: only counted if both flanks have been photographed
- Wounds: contrary to scars, wounds are still fresh and are deeper: noted present / absent
- Scarring
 - none: no visible scars on either flank
 - few: <10 and superficial
 - medium: >10 and <20 , some scars are deeper
 - many: >20 , both flanks are covered with scars, both superficial and deep



Figure 3.B.1 Examples for unfurling of the dorsal fin rating on four calf pictures.

Chapter 3 demonstrated the importance of seamounts for maternal females as well as for the rest of the humpback whale population during the breeding season. However, surveying offshore seamounts is technically challenging and costly, as it requires large ships and good weather conditions. As a result, many potentially suitable habitats for humpback whales might have gone undetected in the New Caledonian region due to their remoteness. SDMs allow the prediction of suitable habitats over vast extents and represent a useful tool to identify critical habitats for conservation. In chapter 4, I apply SDM to several datasets in order to describe the environmental drivers of humpback whale distribution and predict suitable habitats at the scale of the Natural Park of the Coral Sea encompassing the majority of the New Caledonian EEZ. This chapter constitutes an opportunity to investigate the performance of various statistical approaches to model cetacean distribution based on non-systematic survey designs. Moreover, I evaluate the potential for citizen science data to describe cetacean habitats in a conservation perspective.

IV. Distribution at the New Caledonian scale

Finding the right fit: Comparative cetacean distribution models using multiple data sources and statistical approaches.

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Abstract

Aim. Accurate predictions of cetacean distributions are essential to their conservation but are limited by statistical challenges and a paucity of data. This study aims at comparing the capacity of various statistical algorithms to deal with biases commonly found in non-systematic cetacean surveys and to evaluate the potential for citizen science data to improve habitat modelling and predictions. An endangered population of humpback whales (*Megaptera novaeangliae*) in their breeding ground was used as a case study.

Location. New Caledonia, Oceania.

Methods. Five statistical algorithms were used to model the habitat preferences of humpback whales from 1,360 sightings collected over 14 years of non-systematic research surveys. Three different background sampling approaches were tested when developing models from 625 crowdsourced sightings to assess methods accounting for citizen science spatial sampling bias. Model evaluation was conducted through cross-validation and prediction to an independent satellite tracking dataset.

Results. Algorithms differed in complexity of the environmental relationships modelled, ecological interpretability, and transferability. While parameter tuning had a great effect on model performances, GLMs generally had low predictive performance, SVMs were particularly hard to interpret, and BRTs had high descriptive power but showed signs of overfitting. MAXENT and especially GAMs provided a valuable complexity trade-off, accurate predictions and were ecologically intelligible. Models showed that humpback whales favoured cool (22-23°C) and shallow waters (0-100 m deep) in coastal as well as offshore areas. Citizen science models converged with research survey models, specifically when accounting for spatial sampling bias.

Main conclusions. Marine megafauna distribution models present specific challenges that may be addressed through integrative evaluation, independent testing and appropriately tuned statistical algorithms. Specifically, controlling overfitting is a priority when predicting cetacean distributions for large-scale conservation perspectives. Citizen science data appears to be a powerful tool to describe cetacean habitat.

Key words

Citizen science, Generalized regression, Humpback whales, Machine learning, Species Distribution Models, Support vector machines.

4.1 Introduction

Species Distribution Models (SDMs) have become an indispensable tool for ecologists and conservationists to describe the complex ecological relationships between species and their environment, and to predict distributions over multiple spatial (e.g., [Mannocci *et al.*, 2015](#)) and temporal scales (e.g., [Legrand *et al.*, 2016](#); [Morán-Ordóñez *et al.*, 2017](#)). Correlative SDMs rely on statistical algorithms to fit empirical observations of species occurrence to environmental conditions ([Austin, 2007](#); [Elith and Leathwick, 2009](#); [Guisan *et al.*, 2013](#); [Guisan and Zimmermann, 2000](#)). Considering the great potential for SDMs to inform conservation, a growing field of research has emerged to develop applicable models and improve their predictive performance. A multitude of statistical algorithms are now available to build SDMs: profile models (e.g., Ecological Niche Factor Analysis ENFA, [Hirzel *et al.*, 2002](#)), regression models (e.g., Generalized Linear Models GLMs, Generalized Additive Models GAMs, [Hastie and Tibshirani, 1990](#)); Multivariate Adaptive Regression Splines MARS, [Friedman, 1991](#)), machine learning (e.g., Maximum Entropy MAXENT, [Phillips *et al.*, 2006](#); Boosted Regression Trees BRTs, [Friedman, 2001](#); Random Forests RF, [Breiman, 2001](#); Support Vector Machines SVMs, [Boser *et al.*, 1992](#)) and Bayesian approaches (Occupancy models, [MacKenzie, 2006](#)), among others. These methods have been compared empirically ([Aguirre-Gutiérrez *et al.*, 2013](#); [Elith *et al.*, 2006](#); [Oppel *et al.*, 2012](#); [Phillips *et al.*, 2009](#)) and with simulated data ([Elith and Graham, 2009](#); [García-Callejas and Araújo, 2016](#); [Qiao *et al.*, 2015](#)) in various contexts. Most studies have stressed the existing trade-off between the descriptive and predictive performance of all models, hence emphasizing the fact that model evaluation and transferability are data- and study-specific ([Qiao *et al.*, 2015](#)).

The descriptive and predictive power of SDMs has proved particularly useful to understanding the spatial patterns of rare species or species living in ecosystems that are technically challenging to survey ([Dunn *et al.*, 2015](#); [Engler *et al.*, 2004](#); [Stirling *et al.*, 2016](#)). Given their wide-ranging behaviour, their rarity, and the remote habitats they live in, cetaceans fall in this category ([Redfern *et al.*, 2006](#)), with added observational challenges due to the high proportion of time they spend below the surface. Also, as many cetacean species are in need of protection from emerging anthropogenic threats ([Avila *et al.*, 2018](#)), SDMs are greatly valued for their ability to predict probabilities of presence in unsurveyed locations where spatial management is needed ([Breen *et al.*, 2017](#); [Gomez *et al.*, 2017](#); [Mannocci *et al.*, 2017b](#); [Redfern *et al.*, 2017](#)). However, cetacean distribution models have unique statistical challenges that warrant specific methodological exploration. Robust predictions have been derived from Density Surface Models ([Miller *et al.*, 2013](#)) but a large proportion of cetacean research efforts worldwide is not designed to collect data compatible with this approach (e.g., distance measurements, systematic effort). Indeed, non-systematic cetacean surveys conducted at-sea are often characterized by a heterogeneous spatio-temporal distribution of effort, which can be biased towards easily accessible habitats, areas and times with better weather, or known areas of use ([Corkeron *et al.*, 2011](#)). As a result, cetacean habitat datasets tend to display patterns of spatial autocorrelation

(Dormann *et al.*, 2007), hierarchical structures (Roberts *et al.*, 2017), and unmeasured confounding effects (e.g., detection distance depending on vessel type, weather, etc.) that can affect SDMs.

Many of the technical challenges of data collection in marine ecosystems can be overcome by combining data from multiple sources (Pacifiçi *et al.*, 2016). To this extent, citizen science may be a promising opportunity to increase the quantity and spatial extent of cetacean observations for habitat modelling efforts (Tiago *et al.*, 2017). Citizen science, as a form of crowdsourcing, can be broadly defined as 'the engagement of non-professionals in scientific research' (Miller-Rushing *et al.*, 2012) and the method may vary from fully trained and equipped volunteers operating in well-defined study areas, to anecdotal reports of observations by members of the general public. In cetacean research, sighting data may be gained from the general public, fishing operators, ferries, oil and gas platforms, cargo ships, or whale-watching operators. Citizen science geographical data have been used successfully to study cetacean behaviour and ecology on several occasions (Bruce *et al.*, 2014; Thorne *et al.*, 2012; Tobeña *et al.*, 2016; Torres *et al.*, 2013), but their application to SDMs is fraught with an array of statistical challenges (Bird *et al.*, 2014). Indeed, the probability of recording a species at a given site is always based on both the probability of species occurrence and of an observer recording the data. In citizen science, the sampling effort is rarely recorded and as a result, it is often hard to determine whether a higher encounter rate at a site is due to high habitat suitability or simply to a higher observer effort (Bird *et al.*, 2014). The correct implementation of methods to account for uneven survey effort, particularly when it was not explicitly quantified, is crucial for cetacean SDMs because highly mobile species are thought to be especially sensitive to background sampling (Brotons *et al.*, 2004).

This study investigates the distribution of an emblematic species, the humpback whale *Megaptera novaeangliae*, in New Caledonia, Southwestern Pacific Ocean. Humpback whales that spend the austral winter in New Caledonian waters are part of the Oceanian breeding population, and are classified as endangered by the IUCN (Childerhouse *et al.*, 2009). Furthermore, the recently created Natural Park of the Coral Sea (Decree GNC:2014-1063), requires in-depth knowledge of the spatial distribution and habitats of migratory megafauna to support large-scale management in the region. Fourteen years of whale observations recorded through boat-based non-systematic research surveys and crowdsourcing are used to model the habitat preferences of humpback whales in the New Caledonian Economic Exclusive Zone (EEZ) through a presence-background SDM approach. The aim of this study is to 1) compare the performance of different SDMs statistical algorithms using a typical cetacean survey dataset, and 2) evaluate the potential for crowdsourced cetacean observations to describe and predict habitat preferences using various background sampling techniques that account for sampling bias. An independent humpback whale satellite tracking dataset is tested for robust validation of the modelling approaches.

4.2 Material and methods

4.2.1 Study area

Located in Southwestern Pacific Ocean (Fig. 4.1) the New Caledonian EEZ spans more than 1.3 million km² and is characterized by a complex seabed topography. The area includes a main island, 'Grande Terre', as well as remote reef complexes such as the Chesterfield-Bellona plateaus (60 m deep on average), seamounts such as Antigoniam seamount (60 m deep), and shallow banks such as the Fairway-Landsdowne banks (200 to 0 m deep). The mainland is surrounded by a barrier reef that delineates large lagoons. Shallow waters are therefore found both nearshore and offshore (defined here as waters at least 10 km away from any reef or land). New Caledonia is visited every austral winter by a humpback whale breeding sub-stock that is part of the endangered Oceanian population (Childerhouse *et al.*, 2009).

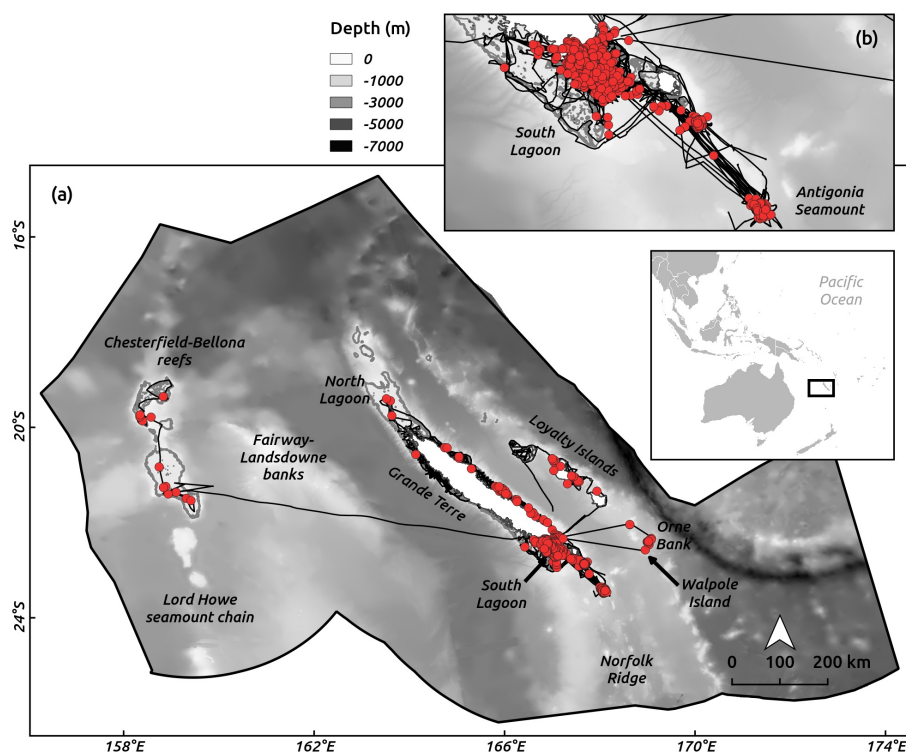


Figure 4.1 Research surveys and humpback whale observations (2003-2016) in New Caledonian waters (a). Shallow reefs are shown in grey over a depth raster. GPS tracklines of the boat are shown in black, with most of the survey effort concentrated in the South lagoon (b). Humpback whale observations are represented with red points (n=1,360).

4.2.2 Data Collection

Data processing and statistical analysis were performed with *r* (version 3.3.2, R Core Team, 2016), *qgis* (version 2.18.3, QGIS Development Team, 2016), and *arcmap* (version 10.3, Environmental Systems Research Institute (ESRI), 2016).

Research surveys dataset

At-sea humpback whale surveys were conducted from June to October, over 14 years between 2003 and 2016 (Appendix 4.A). The survey effort was non-systematic as it did not follow transect lines (see 'haphazard' surveys in [Corkeron *et al.*, 2011](#)) and was conducted in closing mode (cetaceans were approached after detection). The location of survey effort was determined to maximize chances of whale encounter while accounting for common cetacean survey limitations: weather conditions, harbour proximity and vessel capacity (e.g., [Derville *et al.*, 2016](#)). As a result, effort and observations were spatially biased towards coastal and reef areas, a data clustering pattern commonly found in cetacean sea survey datasets ([Kaschner *et al.*, 2012](#)). Most of the surveys (65%) were conducted in the South Lagoon (Fig. 4.1). Small semi-rigid hulled inflatable boats were typically used (76% survey days), with three to five trained observers aboard (see [Garrigue *et al.*, 2001](#)). To a lesser extent (24% survey days), larger vessels such as catamarans and oceanographic vessels were used to survey other areas of the New Caledonian EEZ (Fig. 4.1). Cetaceans were searched for by naked eye in Beaufort sea states ≤ 3 . All GPS boat tracklines were standardized to display one position per minute (initial resolution ranging from 1 position/30 sec to 1/min). Presence locations were recorded as the position of the vessel for each whale group encounter. Encounters are considered independent events, as repeated observations of the same individual whale within a survey day rarely occurred ([Derville *et al.*, 2018a](#)).

Citizen science dataset

Crowdsourced sightings of marine mammals included in this analysis were recorded from June to October 2003-2016 (Appendix 4.A) through a marine mammal observation network coordinated by NGO Option C since 1991 (<http://umr-entropie.ird.nc/index.php/home/ressources/ressource-observation-de-mammiferes-marins>). Sightings were conserved when: 1) the volunteer provided a picture allowing an accurate identification of the species, 2) the volunteer had advanced cetacean species identification skills, or 3) enough description was provided to perform species identification with little doubt (e.g., shape of the fluke/dorsal, specific surface activities). Precise GPS positions were recorded in 50% of cases. Other sightings were positioned within 2 km confidence in 82 % cases (up to 5 km max) using the description of the locations (usually referencing small reefs/bays) projected in a GIS website (<https://explorateur-carto.georep.nc/>).

ARGOS tracking dataset

Adult humpback whales were tagged in coastal and offshore waters around New Caledonia from 2007 to 2016, in August and September ($n = 43$, for more details see [Garrigue *et al.*, 2015](#)) with implantable transmitters (SPOT5, SPLASH-10 ©Wildlife Computers). Whales of both sexes were equally sampled (21 females, 21 males and 1 unknown), including females with a calf ($n = 14$).

ARGOS locations of lowest quality (classes 'B' and 'Z'; [Nicholls et al., 2007](#)), overlapping with land or implying unrealistic speeds (> 12 km/h) were removed.

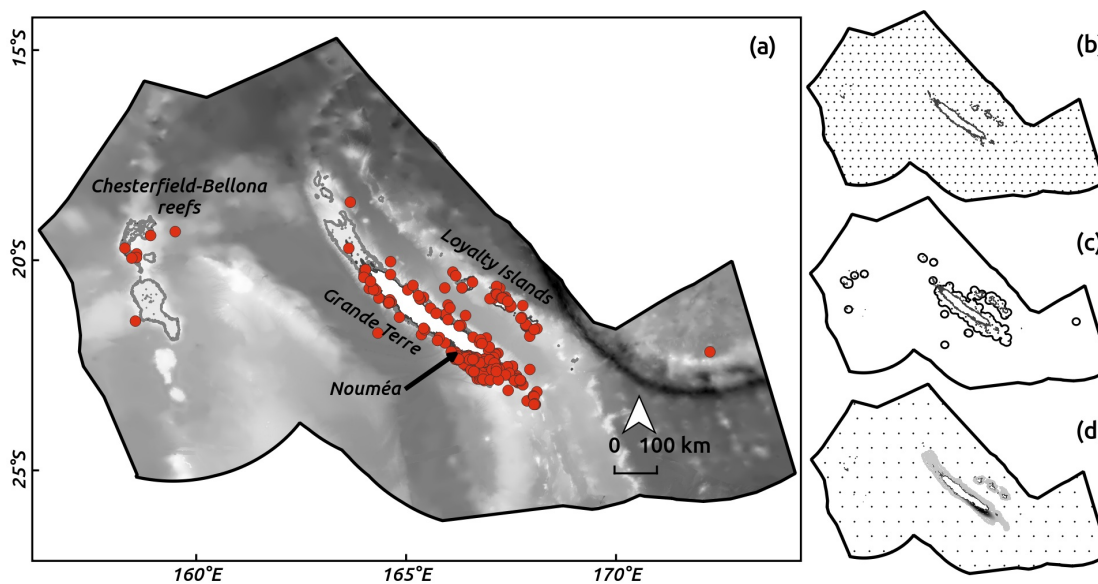


Figure 4.2 Citizen science observations of humpback whale groups (2003-2016) in New Caledonian waters (a). Observations are represented with red points ($n=625$). Schematics of the three background sampling methods are provided: the UNIFORM sampling (b), the TARGET sampling restricted to areas surrounding sightings (c), and the POP sampling weighted in proportion to human densities (d). In the last approach, darker shades of grey represent a higher probability of sampling.

Environmental data

Dynamic environmental conditions averaged at a monthly temporal scale were included in this analysis based on hypothesized humpback whale preferences. A monthly scale was considered a good temporal trade-off to capture coarse scale intra and inter-annual oceanographic processes (e.g., El Niño Southern Oscillation phenomenon) that could affect whales in their tropical breeding latitudes ([Fernandez et al., 2017](#); [Mannocci et al., 2017a](#)), while allowing for almost gap-free remotely sensed maps. Sea Surface Temperature (SST) and Diffuse Attenuation at 490 nm (K490) were extracted from remotely sensed data sources at weekly resolutions and averaged per month from June to October of each year (Table 4.1). SST has frequently been correlated with many top predator distributions ([Scales et al., 2014](#)) and specifically breeding humpback whales ([Bortolotto et al., 2017](#); [Rasmussen et al., 2007](#); [Smith et al., 2012](#)). K490, which is a measure of turbidity, has also been linked with cetacean distribution ([Mendez et al., 2010](#)). K490 tends to be systematically higher inside the tropical lagoon environment, and was therefore included as a proxy of suitable humpback whale habitat in shallow lagoons ([Lindsay et al., 2016](#)).

Depth (DEPTH) was primarily extracted from a 500 m resolution bathymetric chart, and small gaps were filled with the ETOPO 1 maps (Table 4.1). Several topographic variables were derived from bathymetry in order to best capture the seabed topographic complexity ([Bouchet et al., 2015](#)) of the unique New Caledonian region. Mean slope (S.AVG), coefficient of variation of the slope (S.COV),

and mean aspect (A.AVG, orientation of the slope) were calculated using a 5 x 5 km moving window. Euclidean distance to the closest land or shallow reef (DISSURF) was calculated from coastline and reef shapefiles (Andréfouët *et al.*, 2008). Finally, profile curvature (C.PRO) was calculated using the arcmap '3D Analyst Tool' and averaged over a 5 x 5 km moving window to estimate the convexity of the slope and reveal terracing of seabed structures such as seamounts (Table 4.1).

To ensure consistency across statistical algorithms, all environmental variables were scaled and centred, by subtracting the mean and dividing by the standard deviation calculated over the full presence-background dataset. Finally, Pearson coefficients were calculated between environmental variables in the presence-background dataset to prevent collinearity (control that $r < 0.5$ for all variables).

Table 4.1 Predictor variables implemented in the habitat preference models for humpback whales in New Caledonian waters.

Predictor	Description	Unit	Resolution	Source
SST	Sea Surface Temperature	°C	0.04° monthly	NOAA ^a SWFSC (MODIS) ^b
K490	Diffuse attenuation at 490 nm	-	0.04° monthly	NASA ^c GSFC (MODIS) ^d
DEPTH	Depth	m	500 m	DTSI ^e +NOAA ETOPO Composit
DISSURF	Distance to closest land/reef	km	500 m	https://imars.marine.usf.edu/MC/
S.AVG	Mean slope	rad	5 km mw ^f	
S.COV	Coefficient of variation of the slope	-	5 km mw	
A.AVG	Mean aspect (slope orientation)	rad	5 km mw	
C.PRO	Profile curvature	-	5 km mw	

^a National Oceanographic and Atmospheric Agency www.ngdc.noaa.gov/

^b Moderate Resolution Imaging Spectroradiometer, dataset reference: *erdMH1sst8day*

^c National Aeronautics and Space Administration, <https://oceancolor.gsfc.nasa.gov/>

^d Dataset reference: *erdMH1kd4908day*

^e Direction des Technologies et des Services de l'Information

^f mw: moving window

4.2.3 Modelling habitat preferences

Using research survey data

Humpback whale occurrence data collected during research surveys was modelled relative to environmental conditions with five algorithms: GLM, GAM, BRT, MAXENT and SVM. While non-systematic cetacean surveys are generally not designed to record data as presence-absence, they often include some sort of sampling effort estimation, through the recording of times on effort and boat GPS tracklines. Here, the areas surrounding boat tracklines were used to characterize available environmental conditions between sighting locations (presence) and area surveyed (background, e.g., Torres *et al.*, 2008; Derville *et al.*, 2016). Tracklines were segmented into on- and off-effort sections. A set of points, denoted background points (a.k.a 'pseudo-absences'), was sampled within the on-effort survey track strip-width, spanning 4 km to each side of the tracklines to reflect the average detection distance of the semi-inflatable boat used in most surveys (pers. comm. Garrigue), though detection distance might have been larger with the bigger research vessels. Daily samples of background points

were generated with a minimum distance of 1 km from each other, but independent of presence locations. The number of background points was proportional to the time on effort per survey day (on average 35 points per 5 hour survey, Appendix 4.B.1). Combined background and presence points constituted a binomial dataset of 18,046 data points. Cross-validation is a common model evaluation procedure and a powerful tool to account for hierarchical structures within the dataset, such as spatial autocorrelation (Roberts *et al.*, 2017). Here, Monte-Carlo cross-validation accounted for dependencies in the observation data, namely, the daily autocorrelation resulting from daily clusters in the extent and intensity of the survey effort. The dataset was divided into 638 blocks containing presence and background points for each day of survey. Fifty training datasets containing 90% of randomly selected days of survey were sampled without replacement. As a result, each training dataset of the cross-validation contained many blocks (each block is a survey day) and was paired with an evaluation dataset containing the remaining blocks. Presence and background points were weighted to control for prevalence, so that the sum of weights on presences was equal to the sum of weights on background points in each training dataset (Elith *et al.*, 2010).

BRTs, SVMs, and MAXENT models were subject to a preliminary tuning stage ensuring optimal performance within the scope of our training datasets (see Appendix 4.D). In the GLMs, each predictor was included as a cubic orthogonal polynomial. In the GAMs, restricted maximum likelihood was used to optimize parameter estimates for the thin plate regression splines. All models were first tested using a set of 9 predictors, including 8 environmental variables plus Julian day, then run using a smaller set of predictors after removing the ones that contributed the least (See Appendix 4.D). Julian day was added to the set of predictors to account for the seasonal phenology of humpback whales in breeding areas that results in a peak of prevalence in August. The contribution of each predictor was directly provided in the *r* summaries for BRTs and MAXENT models, but assessed using the *caret R package* (version 6.0) for GLMs/GAMs. For SVMs, the Recursive Feature Elimination algorithm (Guyon *et al.*, 2002) was applied for linear kernels only (as this method is not available for radial kernel SVMs), and the resulting ranking criteria were rescaled to sum to 100. For GLMs, the contribution of the three orthogonal polynomial terms were summed per predictor. All contributions were averaged over the 50 cross-validation runs.

Partial dependence plots were produced for each predictor variable and averaged over the 50 cross-validation runs of each statistical algorithm. These plots allow the graphical visualization of the marginal effect of a given variable on the response while all other predictors are held constant at their mean sampled value (Friedman, 2001). They provide a useful ecological interpretation of SDMs, though should be regarded with caution when strong interactions exist between the predictors (Goldstein *et al.*, 2015).

Using citizen data

Three different sampling approaches were tested to generate background points, hereon referred to as 'UNIFORM', 'TARGET', and 'POP'. The number of background points was set separately

for each approach to generate the same background density as in the research survey models (estimated to a minimum of 0.02 point/km²). In the UNIFORM sampling approach, 36,300 background points (equivalent to 605 per month) were randomly sampled over the entire New Caledonian EEZ (covering 1.6 M km², Fig. 4.2b). The TARGET sampling is based on a popular method developed by Phillips *et al.* (2009) in which the spatial bias in the sightings data is transferred to the background data by approximating areas where the probability of detection is non-zero. In practice, the areas of background sampling may be limited to those where sightings of species within the same taxonomic group have been reported by the public. Here, 2,340 background points (equivalent to 39 per month) were sampled in 25 km buffers surrounding all marine mammal observations in the citizen science New Caledonian dataset (n = 818 sightings across 15 marine mammal species including humpback whales, background area covering 0.1 M km², Fig. 4.2c). Finally, the POP sampling approach was designed to correct the spatial bias in crowdsourced sightings by including a proxy of human densities in the background data (Fig. 4.2d). This approach relies on the assumption that sampling is biased towards waters that are more accessible/closer to human settlements or that are more attractive to people. In New Caledonia, most of the population concentrates in the mainland 'Grande Terre', specifically in the capital Noumea (Fig. 4.2a). Also, lagoons and waters surrounding the reef's outer edge are popular sites for recreational activities. The POP background sampling was designed to sample 36,300 background points over the EEZ proportionally to local human density (see Appendix 4.B.2).

The relationship between the observations of humpback whale groups by citizens and environmental conditions was modelled using GAMs with the same settings as the research survey GAMs. Monte Carlo cross-validation was applied over 50 randomly sampled training and evaluation datasets representing respectively 90% and 10% of the total datasets stratified by months. Weights for presence and background points were applied similarly to the research survey models. GAMs were applied to 7 predictors: DEPTH, DISSURF, S.AVG, S.COV, K490, SST, and month to account for humpback whale migratory phenology.

4.2.4 Validation and prediction

The descriptive power of each model was assessed by calculating the Area Under the ROC Curve (AUC) of the training datasets ('int.AUC'). AUC measures the capacity of the models to classify between presence and background points and ranges between 0 and 1 (Swets, 1988). This metric allows a 'threshold-independent' evaluation of model performance, a useful characteristic for model comparison. Predictive performance was assessed by calculating AUC over the evaluation datasets ('ext.AUC'), which is the withheld data portion in each cross-validation iteration. The absolute value of the difference between ext.AUC and int.AUC was also calculated in order to assess the degree of overfitting in the model ('diff.AUC', Warren and Seifert, 2010). A threshold to convert continuous predicted probabilities into a binomial output was estimated for each model run, using the threshold value that maximized specificity (true negative rate) and sensitivity (true positive

rate) over the evaluation dataset predictions (Liu *et al.*, 2016). Using this threshold, two metrics of predictive performance were derived: the sensitivity of models when predicting ARGOS tracking locations ('sensitivity.ARGOS', in % correctly classified as presences), and the True Statistic Skill when predicting the evaluation datasets ('TSS'; Allouche *et al.*, 2006). Following the tuning of BRTs, SVMs and MAXENT models, two different settings were selected for each approach: the model with highest ext.AUC was considered the best predictive model (annotated '.pred'), while the model with the lowest diff.AUC was considered the most stable model (annotated '.stable'). Finally, the predictive performance of the citizen science models was tested relative to the 50 research survey evaluation datasets, hence allowing the estimation of AUC values ('comp.AUC') comparable to the research survey ext.AUC.

Humpback whale habitat suitability was predicted on a grid with 500 x 500 m cells covering the EEZ. For this purpose, SST and K490 were averaged beforehand over June to October, from 2003 to 2016. Julian day and month were fixed to the date of the peak of humpback whale presence for the research survey and citizen science models respectively, on August 28th. Predicted layers for each model were averaged over the 50 cross-validation runs (Roberts *et al.*, 2017) and the standard deviations of predictions were mapped to report uncertainty (see Appendix 4.C). The similarity between average predicted maps was assessed using Pearson coefficients. Environmental extrapolation was not limited in the predictions per se, but the areas where environmental conditions strayed outside their training ranges were highlighted in the final maps of habitat suitability to be interpreted with caution (e.g., Mannocci *et al.*, 2017b).

4.3 Results

Dedicated research surveys covered 49,843 km across 14 years and 638 days of effort (see Appendix 4.A). Survey effort covered 21% of the EEZ waters, and encountered a total of 1,360 humpback whale groups (annual mean = $97 \pm \text{SD } 40$ groups). A total of 625 humpback whale group encounters were recorded opportunistically by citizen scientists (annual mean = $45 \pm \text{SD } 28$). Sightings were recorded predominantly by park rangers (29%) and whale-watching operators (22%). After filtering the 43 raw ARGOS tracks, 1,539 locations out of 4,180 were conserved.

4.3.1 Modelling habitat preferences from research survey data

All models were first applied to the set of 9 predictors; then the predictors that contributed the least, CPRO and A.AVG, were removed for further analysis (Appendix 4.D). The comparison of parameter tunings for BRTs, SVMs and MAXENT models showed a trade-off between diff.AUC and ext.AUC/TSS (Table 4.2). For a given algorithm, the impact of tuning on all evaluation metrics was large, for instance MAXENT models showed a 9% increase in ext.AUC when applied with hinge features in comparison to linear features only. Models selected for their 'predictive performance' (high ext.AUC and TSS), were less 'stable' from training to evaluation (larger diff.AUC).

Table 4.2 Parameters and validation metrics of habitat preference models for humpback whales in New Caledonian waters. The mean and (\pm) standard deviation of each metric is calculated over 50 runs of the cross-validation. For SVMs, BRTs and MAXENT models, metrics for the parametrization that led to the best diff.AUC ('stable model') and ext.AUC ('predictive model') are reported.

	Tuning	int.AUC	ext.AUC	diff.AUC	TSS	sensitivity.argos %
Research survey models						
GLM		0.724 \pm 0.003	0.714 \pm 0.032	0.011 \pm 0.035	0.349 \pm 0.053	61.8 \pm 6.3
GAM		0.736 \pm 0.003	0.727 \pm 0.031	0.009 \pm 0.034	0.373 \pm 0.05	42.7 \pm 4.9
MAXENTstable	linear, beta 1 ^a	0.675 \pm 0.005	0.675 \pm 0.041	0 \pm 0.046	0.274 \pm 0.063	53.3 \pm 9.8
MAXENTpredictive	hinge, beta 1 ^a	0.747 \pm 0.004	0.736 \pm 0.031	0.011 \pm 0.034	0.364 \pm 0.055	46.1 \pm 6.2
SVMstable	linear, cost 0.01 ^b	0.669 \pm 0.005	0.669 \pm 0.041	0 \pm 0.046	0.27 \pm 0.062	70.9 \pm 14.5
SVMpredictive	radial, cost 10 ^b	0.772 \pm 0.003	0.744 \pm 0.029	0.028 \pm 0.032	0.39 \pm 0.047	42.8 \pm 7.0
BRTstable	lr 0.005, tc 1 ^c	0.767 \pm 0.004	0.738 \pm 0.033	0.029 \pm 0.036	0.364 \pm 0.056	43.9 \pm 7.8
BRTpredictive	lr 0.005, tc 3 ^c	0.843 \pm 0.004	0.775 \pm 0.027	0.069 \pm 0.029	0.425 \pm 0.045	40.8 \pm 5.9
Citizen science models						
UNIFORM		0.990 \pm 0.001	0.990 \pm 0.005	0.001 \pm 0.006	0.936 \pm 0.021	47.0 \pm 6.8
POP		0.947 \pm 0.003	0.937 \pm 0.017	0.010 \pm 0.02	0.754 \pm 0.041	46.0 \pm 10.1
TARGET		0.927 \pm 0.004	0.919 \pm 0.027	0.009 \pm 0.031	0.733 \pm 0.075	43.9 \pm 12.3

^a MAXENT were applied with a linear or hinge feature and beta parameter equal to 1.

^b SVM are applied with linear or radial kernel type and cost of constraint violation equal to 0.01 or 10.

^c BRT were applied with a learning rate of 0.005 and a tree complexity of 1 or 3.

The same trade-off was present in the broad comparison of the five statistical algorithms. Diff.AUC was highest for BRTs, and the SVM.pred model, reflecting increased overfitting of the relationships. Statistical algorithms can be ranked in increasing diff.AUC: SVM.stable – MAXENT.stable, GAM, GLM - MAXENT.pred, SVM.pred, BRT.stable, BRT.pred; and in decreasing ext.AUC: BRT.pred, SVM.pred, BRT.stable, MAXENT.pred, GAM, GLM, MAXENT.stable, SVM.stable. TSS was correlated to ext.AUC ($n = 8$, Pearson $r = 0.98$) and was surprisingly high for GAMs considering its

medium ext.AUC. Sensitivity calculated over the ARGOS data tended to be lower in more complex models that had high ext.AUC (BRTs, SVM.pred, GAMs).

The five statistical algorithms mostly agreed on the relative contribution of the main variables. DEPTH, DISSURF, and SST were the major contributors, together accounting for 54% to 96% of the contributions (Table 4.3). Yet, both algorithm type and tuning impacted the predictor's contributions. Contrary to GLMs and GAMs where DISSURF was preponderant, BRTs found that DEPTH was the most important predictor, with very little effect of DISSURF. Interestingly, K490 had a relatively high contribution in BRTs and GLMs. Tuning affected contributions: MAXENT.stable favoured SST, while MAXENT.pred favoured DEPTH.

Table 4.3 Mean contribution of environmental variables to habitat preference models for humpback whales in New Caledonian waters. Values are ranked and scaled to 100 separately for each algorithm (greatest influence in bold). Coefficients of variation (%) of the mean contribution calculated over 50 cross-validation runs is indicated by \pm . For SVMs, BRTs and MAXENT models, contributions for the parametrization that led to the best diff.AUC ('stable model') and ext.AUC ('predictive model') are reported.

^a	S.AVG	S.COV	JULIAN / MONTH	K490	SST	DISSURF	DEPTH
Research survey models							
GLM	5.5 \pm 17.7%	11.0 \pm 8.8%	9.9 \pm 11.1%	19.4 \pm9.7%	19.0 \pm8.8%	21.6 \pm13.5%	13.6 \pm 13.0%
GAM	2.2 \pm 27.3%	2.3 \pm 21.7%	9.8 \pm 11.2%	10.7 \pm 23.4%	22.9 \pm8.7%	28.4 \pm10.2%	23.7 \pm9.7%
MAXENTstable	7.7 \pm 34.7%	0.4 \pm 54.6%	0.2 \pm 127.2%	0.9 \pm 28.6%	40.8 \pm7.4%	28.9 \pm10.0%	21.2 \pm13.6%
MAXENTpredictive	1.2 \pm 30.0%	1.4 \pm 60.9%	4.1 \pm 17.4%	2.4 \pm 20.5%	23.8 \pm9.6%	20.4 \pm6.6%	46.6 \pm4.4%
SVMstable	2.5 \pm 32.4%	0.4 \pm 38.4%	0.3 \pm 89.5%	0.6 \pm 36.8%	75.1 \pm1.7%	12.9 \pm6.4%	8.2 \pm22.3%
BRTstable	6.1 \pm 8.6%	5.6 \pm 13.6%	2.4 \pm 13.4%	20.9 \pm5.5%	27.0 \pm6.8%	2.6 \pm 12.8%	35.5 \pm4.3%
BRTpredictive	6.9 \pm 6.5%	17.4 \pm5.1%	4.6 \pm 7.0%	16.5 \pm 5.5%	23.9 \pm6.5%	5.2 \pm 6.3%	25.6 \pm4.5%
Citizen science models							
UNIFORM	0.6 \pm 66.7%	1.9 \pm 21.1%	1.3 \pm 46.2%	13.8 \pm12.3%	9.4 \pm 17.0%	37.2 \pm7.8%	35.7 \pm12.6%
POP	1.7 \pm 35.3%	1 \pm 30.0%	11.1 \pm17.1%	55 \pm 5.5%	6.2 \pm 14.5%	7.7 \pm 15.6%	17.4 \pm16.1%
TARGET	1.6 \pm 37.5%	2.1 \pm 33.3%	4.4 \pm 38.6%	39.9 \pm7.8%	20.7 \pm16.9%	1.7 \pm 88.2%	29.5 \pm20.7%

^a Average slope (S.AVG,) julian date (JULIAN) for research survey models or month of year (MONTH) for citizen science models, coefficient of variation of the slope (S.COV), diffuse attenuation as turbidity index (K490), sea surface temperature (SST), distance to closest reef or land (DISSURF) and depth (DEPTH).

Ecological relationships between humpback whale occurrence and environmental conditions (Fig. 4.3) showed different trends across the five statistical algorithms and varying complexity. In relation to overfitting trends revealed by high diff.AUC and ext.AUC in Table 2, BRTs showed noisy response curves. On the contrary, GLMs, SVMs and MAXENT models captured the general trends in the relationships but missed some specific features. For instance, habitat suitability globally increased with increasing DISSURF in BRTs, GLMs and MAXENT models, whereas SVMs predicted high suitability only for small DISSURF values (around 20 km). GAMs predicted a bimodal relationship to DISSURF, with a high suitability around 35 km, then between 130 and 200 km, and a decrease for larger distances. Overall, humpback whales favoured shallow waters about 0-100 m deep, and relatively cold water temperatures, between 22°C and 23°C. Models demonstrated that whales had a preference for relatively flat seabeds (low S.AVG), of medium to relatively high topographic complexity (S.COV 1 - 2% and above), which could represent the top of banks, seamounts, or reef lagoons. Finally,

the probability of occurrence increased with lower values of K490, but most models demonstrated a peak between 0.1 and 0.2, denoting a preference for medium turbidity.

The algorithms differed in their predictions over certain zones (Fig. 4.4 & Appendix 4.C), such as the Loyalty Islands, which were suitable in GAMs and SVMs but not in the other approaches. GAMs, BRTs and MAXENT models predicted smoother gradients over the study area, while GLMs predicted low suitability in most lagoons and SVMs had strong cut-offs in the predicted values. The algorithms also differed in their predictions into unsampled environmental space (dashed areas, Fig. 4.4): BRTs and MAXENT models predicted a high suitability for the whole southern part of the study area, while GLMs predicted high suitability everywhere in the extrapolation zone. The extrapolations from GAMs appeared to be mostly driven by the bathymetric pattern. In general, spatial overlap between ARGOS tracking locations and areas of high habitat suitability was high for all models (e.g., Fig. 4.4e), especially South of the mainland. Excluding areas of extrapolation, the five models agreed on humpback whale preference for shallow waters, which resulted in high habitat suitability predictions for reef complexes (Chesterfield-Bellona, North Lagoon, South Lagoon), banks (Fairway-Landsdowne, Orne bank), coastal waters (Loyalty Islands), and shallow seamounts of the Lord Howe seamount chain and Norfolk Ridge.

4.3.2 Modelling habitat preferences from citizen science data

The three citizen science models had high AUC (> 0.90 , Table 4.2). The UNIFORM model had the best predictive performance (highest ext.AUC and sensitivity.argos), followed by the POP and TARGET models. Most importantly, the TARGET model and to a lesser extent the POP model better predicted research survey occurrences (comp.AUC = 0.573 ± 0.006 and 0.541 ± 0.003 respectively) than the UNIFORM models (comp.AUC = 0.538 ± 0.004).

The three citizen science models differed in the relative contribution of predictors (Table 4.3). The TARGET model was the most similar to the research survey models, with SST and DEPTH having a great influence. DISSURF was a major contributor to the UNIFORM model only. Finally, in all three models, K490 was among the most influential predictors.

Predicted maps of habitat suitability (Fig. 4.5) were very similar between the UNIFORM and POP models (Fig. 4.5a, 4.5c, Pearson $r = 0.98$). Despite being affected by environmental extrapolation over part of the study area (Fig. 4.5b), the TARGET models prediction maps fitted more closely with the research survey maps (Fig. 4.5b, 4.4e, Pearson coefficient: $r = 0.74$), with offshore shallow waters such as the Fairway-Landsdowne bank showing particularly high suitability. The three citizen science models predicted all waters located in reef or coastal habitats to be suitable.

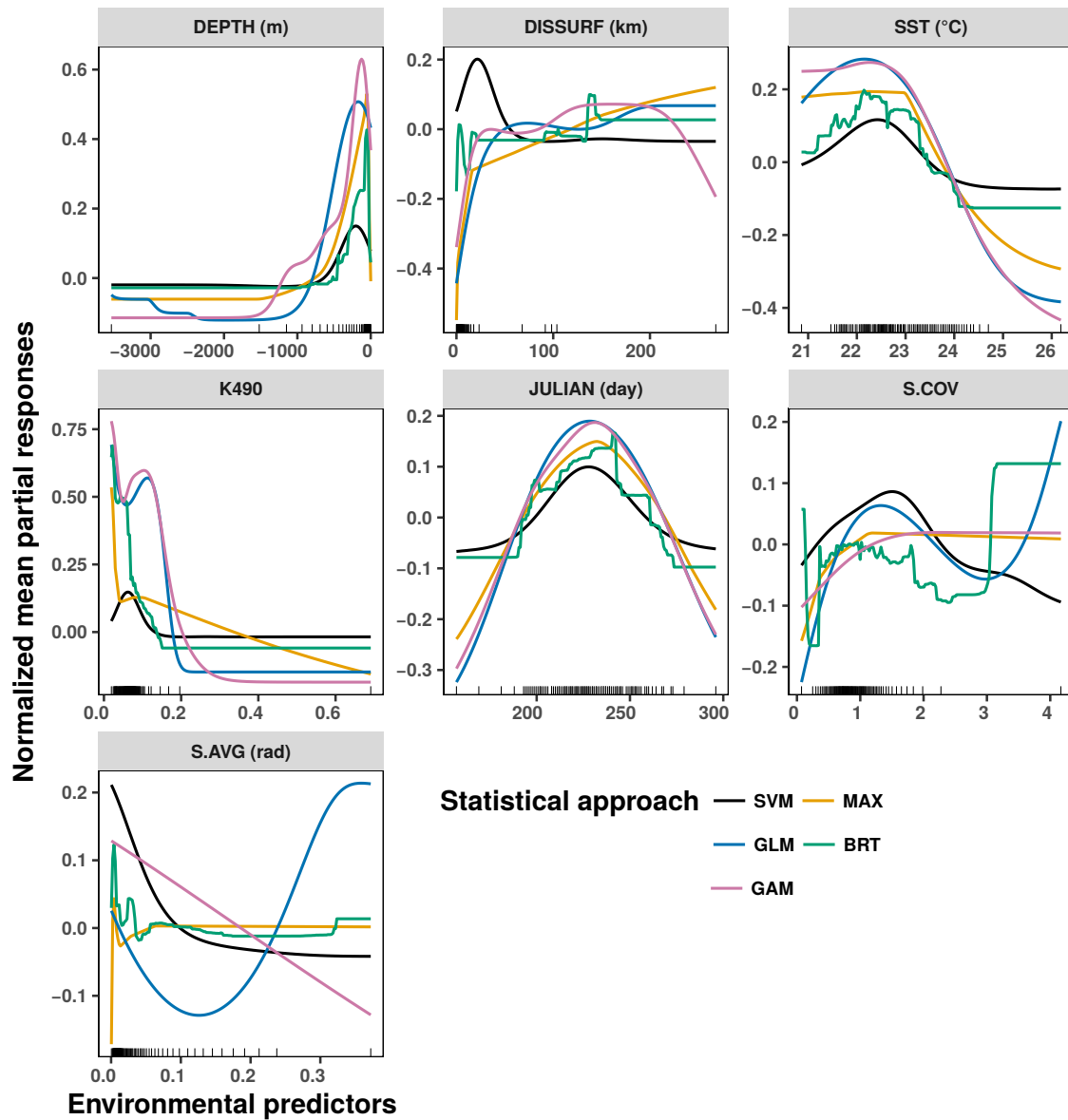


Figure 4.3 Mean partial dependence plots obtained by five statistical algorithms to model humpback whale occurrence from research survey data with respect to environmental variables: DEPTH = depth, DISSURF = distance to closest reef or land, S.AVG = mean slope, S.COV = coefficient of variation of the slope, SST = sea surface temperature, and K490 = Diffuse attenuation at 490 nm (turbidity). Solid lines represent the mean marginal effect of each variable relative to the probability of presence, over 50 cross-validation runs. Probabilities on the y axis originally ranging from 0 to 1 were normalized per model to be centered on zero. Rug plots show the distribution of values in the full presence-background research survey dataset, in percentiles, and provide a measure of confidence on the fitted responses. For SVMs, BRTs and MAXENT models, only the plots obtained with the 'predictive' tuning (highest ext.AUC) are reported.

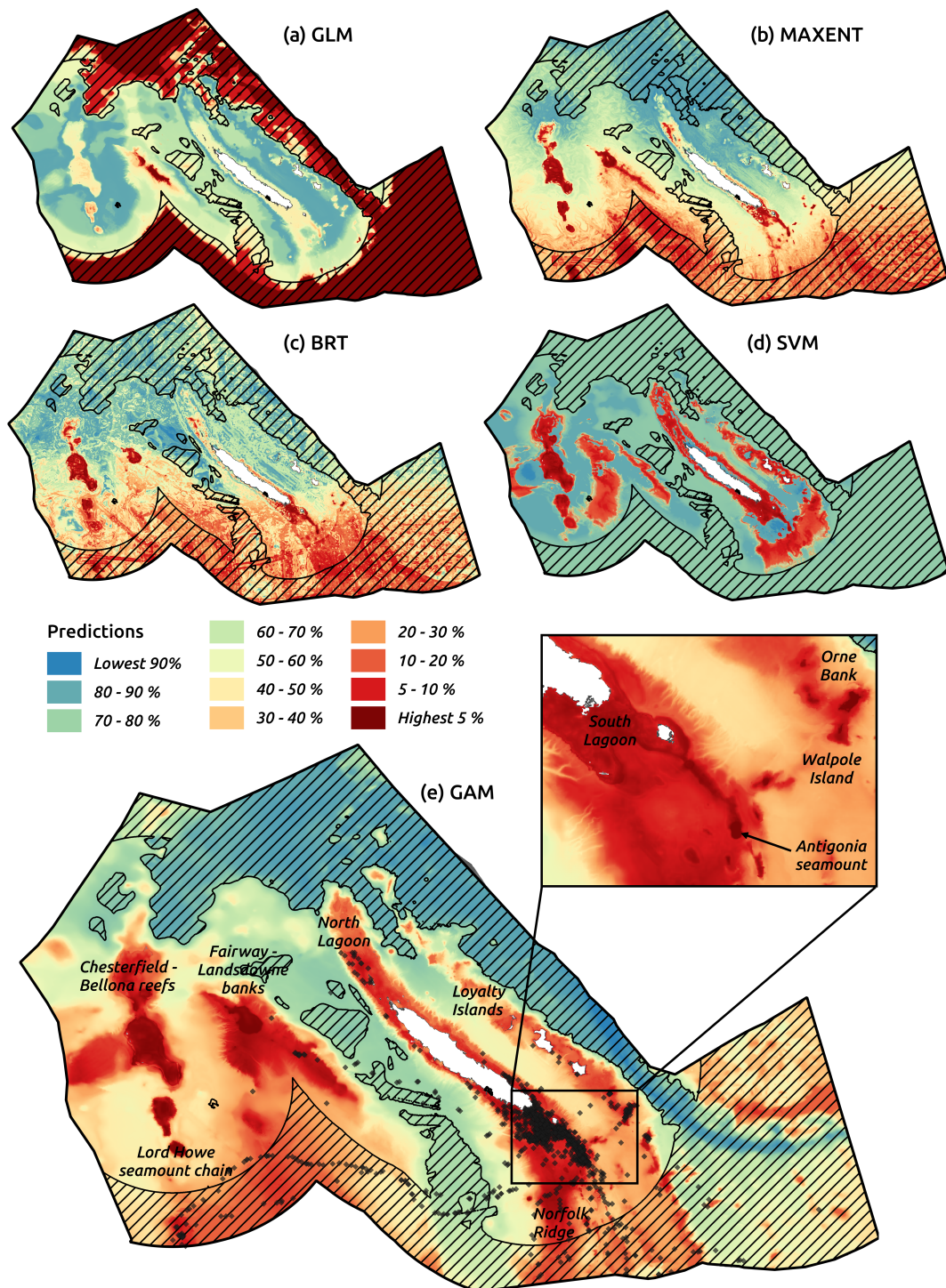


Figure 4.4 Maps of mean predicted humpback whale habitat suitability from research survey models. Habitat suitability was averaged over 50 cross validation runs for each statistical algorithm and a colored log-scale was applied to values ranging from 0 to 1. Colors represent fixed percentages of probability distributions of the suitability predicted values (e.g., the highest 10% corresponds to the decile with highest values over each map). Areas of extrapolation where at least one environmental variable expanded outside the range observed in the training dataset are dashed. Filtered positions from satellite tags deployed in the region are shown with black squares in panel (e). For SVMs, BRTs and MAXENT models, only the plots obtained with the 'predictive' tuning (highest ext.AUC) are reported.

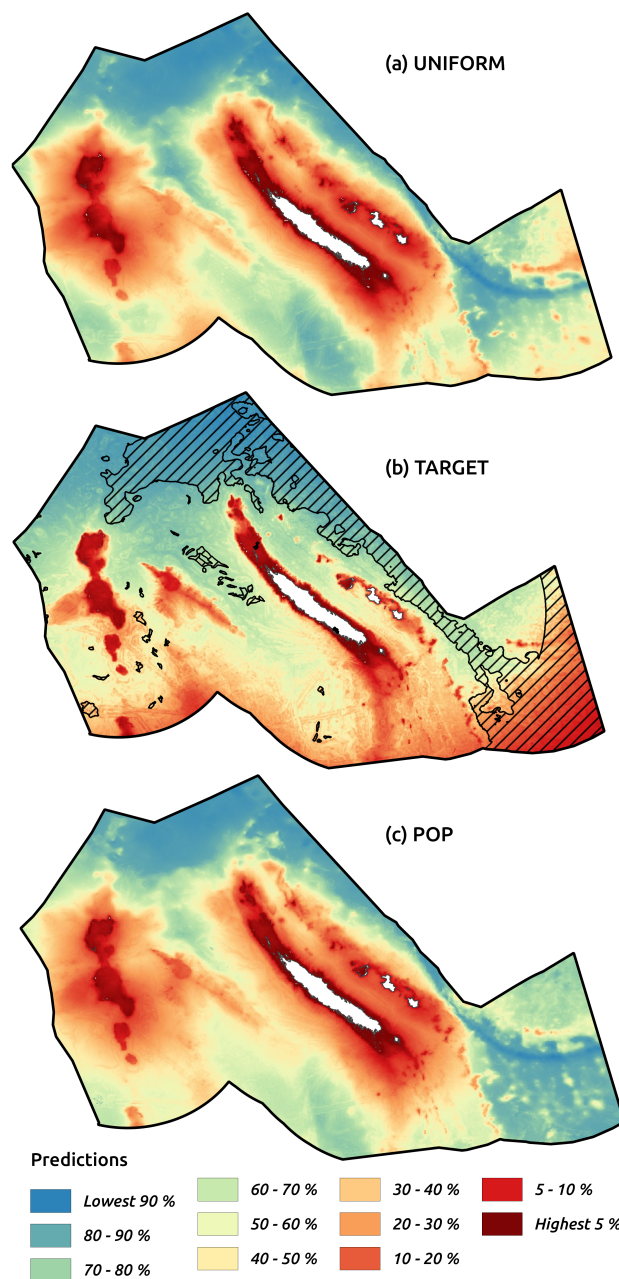


Figure 4.5 Maps of mean predicted humpback whale habitat suitability from citizen science models. Habitat suitability was averaged over 50 cross validation runs for each statistical algorithm and a colored log-scale was applied to values ranging from 0 to 1. Colors represent fixed percentages of probability distributions of the suitability values (e.g., the highest 5% corresponds to the half-of-decile with highest values over each map). Areas of extrapolation where at least one environmental variables expanded outside the range observed in the training dataset are dashed.

4.4 Discussion

The multi-source New Caledonian humpback whale dataset allowed an in-depth methodological investigation of practices (background sampling, statistical algorithms, model tuning, evaluation and predictions) to generate informative SDMs using non-systematic and citizen science data for

cetacean species. Derived results are broadly applicable to other marine megafauna modelling efforts as observations collected during non-systematic surveys and through citizen science are representative of worldwide research efforts to study marine mammals. Statistical algorithm comparisons performed on the research survey dataset revealed differences in the complexity of the environmental relationships modelled, the ecological interpretability of outputs, and model transferability across large geographical scales. Although citizen science models did not perform as well as the research survey models, they predicted similar humpback whale suitable habitats and benefited from specifically tuned background sampling approaches that account for spatial bias of effort.

In non-systematic closing mode surveys, covariates affecting detection may not be precisely recorded (e.g., sea state, vessel type/height, number of observers), and may vary within and between surveys days. While presence-background approaches should not be considered a solution to imperfect detection (Monk, 2014), they can be applied safely as long as detection probability is not directly correlated to the habitat variables of interest. Such correlation may exist if a cetacean species spends more time at the surface when resting/feeding in specific habitats for instance. A general balance between model complexity and generality was observed, in concordance with the conceptual framework detailed by Guisan and Zimmermann (2000). Models that more closely fit the relationships in the training data were less efficient at model extrapolation to new data, a relationship found both when comparing different statistical algorithms and different tunings of a given statistical algorithm. Whatever the parametrization, BRTs systematically suffered from overfitting and as a result displayed noisy partial dependence plots and predicted maps. The complexity of SVMs and MAXENT models strongly depended on tuning, for instance radial kernel SVMs were overfitted whereas the linear kernel version ranked the lowest in explanatory power, along with GLMs, and MAXENT models applied with linear features. The performances of MAXENT models applied with hinge features and of GAMs were intermediate in terms of predictive performance and stability, as measured by ext.AUC and diff.AUC. While GLMs and GAMs were not tested with different parameterizations in this study, it must be noted that tuning may also affect regression-based methods (e.g., through polynomial degree or smoothing basis size).

Considering that many marine SDMs are applied in a spatial conservation planning context (Cleguer *et al.*, 2015; Gomez *et al.*, 2017; La Manna *et al.*, 2016; Pérez-Jorge *et al.*, 2015; Robinson *et al.*, 2011), it appears that statistical algorithms that intrinsically limit overfitting should be prioritized. Indeed, managers are confronted with extrapolation needs, and SDMs are often implemented to predict the presence of a species in a place/time in which data are not available (Mannocci *et al.*, 2015; Redfern *et al.*, 2017). For instance, with proper tuning, all algorithms predicted the Fairway-Landsdowne banks to be a favourable area for humpback whales. The discovery of this new potential area of humpback whale use is supported by the satellite tracking of two humpback whales (Garrigue *et al.*, 2015), and will help target future research efforts and inform conservation policy. Furthermore, given their wide ranges and mobility, migratory cetacean species are likely to have broad fundamental ecological niches (Guisan and Zimmermann, 2000). Yet, broad niches are generally more difficult to

model than narrow ones (Morán-Ordóñez *et al.*, 2017), specifically with MAXENT (Qiao *et al.*, 2015). In this context, overfitting the species-environment relationships in a given study area is likely to strongly affect the transferability of the models (Torres *et al.*, 2015) and underestimate the breadth of the species' niches. On the contrary, approaches such as GAMs and MAXENT with hinge features were capable of modelling humpback whale habitats with a relatively high level of complexity, while conserving a good transferability to novel geographical areas. While using the restricted maximum likelihood method successfully penalized overfitting in this case study, the complexity of the GAM fitted responses may be further controlled by tuning the basis size for smoothing (e.g., Mannocci *et al.*, 2017b), hence also providing the opportunity to include explicit knowledge regarding the species' response to environmental gradients (Austin, 2007).

Ultimately, our statistical comparison underlines that there is no such thing as a universally 'best' SDM approach (Qiao *et al.*, 2015). The study goal should be clearly identified upfront, whether it is to produce accurate and/or precise spatial predictions or description of local species-environment relationships. Then, model selection depends on two main issues: the use of evaluation metrics and critical ecological thinking. This study confirms that model evaluation should rely on metrics that promote the best predictive performance while minimizing overfitting. AUC is advantageous because of its threshold-independent nature but its interpretation in a presence-background context is not straightforward (Jiménez-Valverde, 2012; Phillips *et al.*, 2006). Diff.AUC cannot be interpreted as easily as in Warren and Seifert (2010) when prevalence and presence-background overlap vary between the training and the evaluation dataset. However, diff.AUC may be used to relatively compare transferability between models as long as it is averaged over consistent cross-validation runs. Finally, the combination of diff.AUC with TSS and ext.AUC appeared like a good trade-off to reveal both stability and predictive performance of the models. Moreover, using a truly independent validation dataset can be challenging (Roberts *et al.*, 2017) but ensures the robust estimation of predictive error. Tracking data may constitute such independent data to evaluate or supplement habitat models (e.g., Louzao *et al.*, 2009; Pinto *et al.*, 2016) though it is inherently limited to measuring model sensitivity (i.e. capacity of the model to predict tracking locations as presences), unless other metrics are derived from tracking locations (Pinto *et al.*, 2016). The tracking data has to be contemporaneous to the model calibration dataset and unbiased by sex, social class or tagging location. In this study, most tags were deployed in the South Lagoon ($n = 34$, 76%), hence 30% of the track positions were located in this area. As a result, model predictive performance was relatively high for any model that predicted high suitability in the South Lagoon. Finally, ARGOS location error tends to be relatively high when tracking large whales (most locations are of quality 'B' with precision > 50 km; Nicholls *et al.*, 2007). Hence, prior to using these locations for validation of a habitat model, variables could be averaged in the vicinity of the location, or imprecise positions could be filtered out (as was the case in this study). Ultimately, the visual inspection of predicted maps overlapped with the tracks actually proved more useful than the quantification of predictions to this dataset.

Also model evaluation must include the close examination of the variables' relative contri-

butions, partial dependence plots, and spatially projected predictions. Indeed, models with similar performances have been found to predict distributions differently because of different functional relationships (Elith and Graham, 2009) and/or because the relative contribution of variables differed (Zanardo *et al.*, 2017). Here, SVMs seem to have deserved their 'black-box' reputation (Goldstein *et al.*, 2015) as their ecological interpretation was arduous. For instance, contributions of the predictor variables could only be assessed when using linear kernels, whereas the radial kernels that provided the best predictive performance could not be interpreted as easily. On the contrary, although showing signs of overfitting, BRTs are more interpretable machine learning approaches that were the only models to identify DEPTH as the dominant variable over DISSURF. In line with this trend, though they relied more on DISSURF than DEPTH, GAMs captured a multi-modal relationship relative to DISSURF, revealing preferences for coastal as well as remote waters more than 100 km from shore. While this relationship should be regarded with caution considering the spatially skewed survey effort (favouring specific study areas, such as Antigonnia or the South Lagoon), it also shows that complex environmental relationships might be revealed with increased effort in offshore waters. The preference for coastal waters has been extensively documented in humpback whale breeding grounds (Bortolotto *et al.*, 2017; Cartwright *et al.*, 2012; Guidino *et al.*, 2014; Smith *et al.*, 2012; Trudelle *et al.*, 2016) but only recently has satellite telemetry revealed the use of waters far from any coast or reef (Dulau *et al.*, 2017; Garrigue *et al.*, 2015; Trudelle *et al.*, 2016). Through robust and independent niche modelling, this study confirms that humpback whales are not constrained by proximity to sheltered shorelines, but rather by depth, as whales appear to be preferentially found in shallow waters, both in coastal and offshore areas – a pattern clearly captured by BRTs and GAMs.

Citizen science models aligned with the main ecological relationships highlighted in the research survey models. K490 was particularly influential compared to the research survey models, which could be explained by the high proportion of whales observed by the general public in the lagoons surrounding the main land that are characterized by relatively high turbidity compared to the open ocean. When sampling bias was corrected in the TARGET method, ecological relationships converged with the research survey model and SST was also found to be particularly influent. The preferred SST range in research survey models (22°C-23°C) was similar to ranges found in neighbouring breeding grounds (GBR, Smith *et al.*, 2012) but relatively low compared to worldwide breeding temperatures reported by Rasmussen *et al.* (2007). However, as recurrently highlighted in cetacean SDMs (Becker *et al.*, 2017; Redfern *et al.*, 2006) it is hard to differentiate the direct effect of a variable such as SST, from indirect effects due to a correlation with other unmeasured variables, including competition, prey distribution and social interaction.

Finally, citizen science models of humpback whale habitat preferences showed promising predictive capacities compared to the research survey models, yet were contingent upon background sampling. Given the wider distribution of background points compared to the research survey dataset, int.AUC and ext.AUC metrics appeared to be inflated (Barve *et al.*, 2011), and the use of comp.AUC was crucial to a robust model evaluation. The TARGET model, which accounted for spatial bias,

performed better than the simple UNIFORM model to predict new independent data (comp.AUC) and showed the best ecological match to research survey predictions. However, it is also detrimentally restricted by environmental extrapolation and the background sampling buffer size is likely to have an impact on predictive performance (Barve *et al.*, 2011; Fourcade *et al.*, 2014). With smaller sample sizes, the predictive capacity of the TARGET model to large areas is likely to decrease. The POP model appears like an interesting alternative in such cases, as it does not restrict the environmental space in which background is sampled, but still accounts for sampling bias. Conceptually, the POP model reflects the assumption that human activity concentrates in coastal areas in the vicinity of cities (Halpern *et al.*, 2015). This assumption is similar in essence to using distance to roads (Phillips *et al.*, 2009) or distance to the coastline (Fithian *et al.*, 2014) as a proxy for land-based observation density. Indeed, the issue of accessibility of study sites to volunteers has been addressed in land-based datasets (e.g., Tulloch *et al.*, 2013) but less so in marine studies (Robinson *et al.*, 2011). A variety of other methods have been developed to account for spatial bias in presence-only SDMs. For instance, spatial filtering has been shown to improve predictive performance in several land-based study cases (resampling presence points Boria *et al.*, 2014; Fourcade *et al.*, 2014; Kramer-Schadt *et al.*, 2013) but was not tested here because it was not considered adapted to the generally small sample sizes recorded in cetacean citizen science programs. We found that using the TARGET (based on Phillips *et al.*, 2009) and POP sampling methods provided simple and adaptable solutions to account for sampling bias in a cetacean citizen science context.

Conclusion

This study provides an in-depth investigation of statistical approaches to highlight the technical challenges associated with cetacean habitat modelling. All algorithms suggested that the endangered New Caledonian population of humpback whales displays a preference for relatively cool and shallow waters regardless of distance to reefs or coasts. Algorithms displayed a range of predictive and descriptive capacity that depended on parameter tuning. BRTs generally characterized ecologically meaningful species-environment relationships but predictions were fraught with overfitting. SVMs fitted the data closely when using radial kernels, but lacked interpretability and transferability. GAMs stood out as an interesting trade-off with ecologically interpretable results that maintained complexity at a reasonable level to allow good predictive performance over unsampled areas, which is a crucial characteristic in a conservation planning perspective. Considering the wide breadth of migratory cetacean fundamental niches, we conclude that cetacean SDMs produced for conservation purposes should specifically prevent overfitting in order to conserve some transferability to novel geographical areas. Overfitting may be prevented by using stratified cross-validation, evaluation with an independent dataset, and an appropriate statistical algorithm and parameter tuning. Finally, this study also emphasized the role of citizen science to study wide-ranging species such as cetaceans over large spatial scales. Habitat preference models based on citizen science observations converged with models based on research survey when spatial sampling bias was accounted for in the

models. The development of citizen science programs in marine environments and their application to species distribution models therefore appears like a low-cost and socially valuable research tool and contributor to marine policy.

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Appendix 4.A. Research and citizen science datasets

Table 4.A.1 Sample sizes by year used in the crowdsourced and research surveys models of humpback whale distribution in New Caledonia. Estimates of survey effort are provided for the later as number of days and distance covered.

Year	Citizen science models		Research surveys models		
	Presence	Presence	Survey effort (days)	Distance covered on-effort (km)	Control points
2003	27	71	39	2,720	1,142
2004	26	38	46	3,714	1,413
2005	33	83	47	3,744	1,479
2006	47	117	44	3,309	1,445
2007	29	123	47	3,307	1,438
2008	40	44	61	5,928	1,962
2009	26	102	45	4,053	1,450
2010	122	140	51 ^a	3,465	1,630
2011	33	187	45	2,805	1,529
2012	45	117	44	3,487	1,183
2013	36	97	49	3,672	1,524
2014	17	47	48	3,875	1,404
2015	54	99	31	1,939	961
2016	90	95	41	3,825	1,710
Total	625	1,360	638	49,843	20,270
Mean	45	97	46	3,560	1,448
SD	28	40	7	883	246

^a including three days over which two surveys were taking place simultaneously in two separate locations.

Appendix 4.B. Background sampling

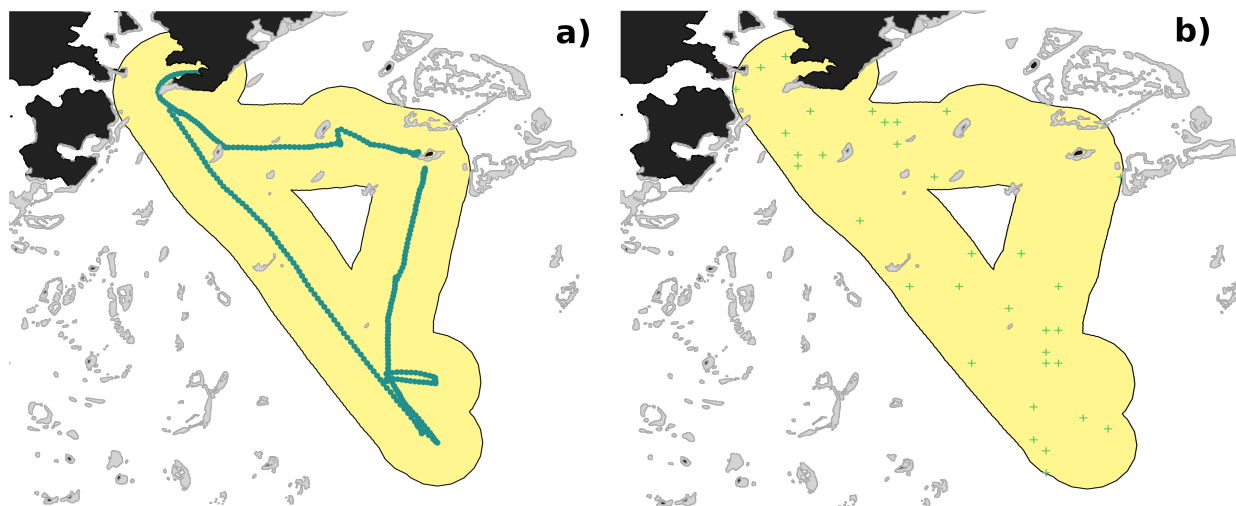


Figure 4.B.1 Background sampling for non-systematic research survey model example. a) Vessel GPS trackline in green, and 4 km stripwidth in yellow. b) Area surveyed and background samples represented with green crosses. Background samples are generated at random, with a minimum distance of 1 km between each point.



Figure 4.B.2 Background sampling for citizen science model (POP approach). a) Map of New Caledonian nearshore waters, representing the 500 m isobath in black and a 15 km buffer in blue. This buffer includes Fish Aggregation Devices represented with black stars. The main cities are represented with white points. b) Map of the New Caledonian EEZ, showing the probability of background sampling on a coloured scale. Purple areas are assumed to be the most populated / used waters and are most densely represented in the POP background sample.

Appendix 4.C. Additional maps of habitat suitability and associated uncertainty

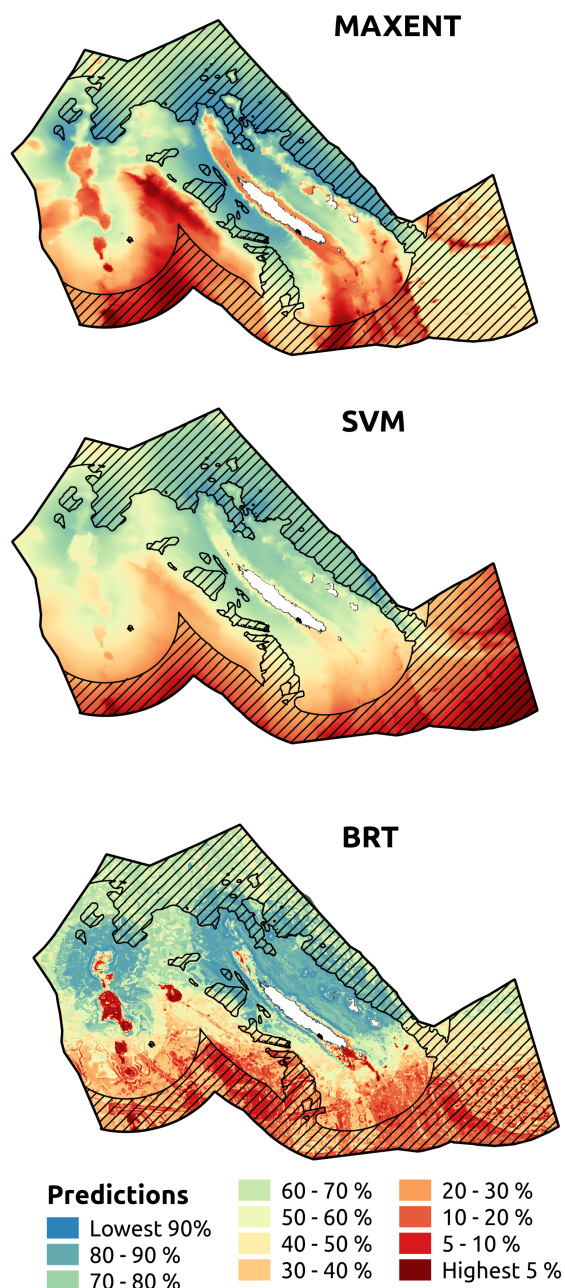


Figure 4.C.1 Maps of mean predicted humpback whale habitat suitability from research survey models: SVM.stable, BRT.stable and MAXENT.stable (models selected with best diff.AUC). Habitat suitability was averaged over 50 cross validation runs for each statistical algorithm and a colored log-scale was applied to values ranging from 0 to 1. Colors represent fixed percentages of probability distributions of the suitability predicted values (e.g., the highest 10% corresponds to the decile with highest values over each map). Areas of extrapolation where at least one environmental variable expanded outside the range observed in the training dataset are dashed.

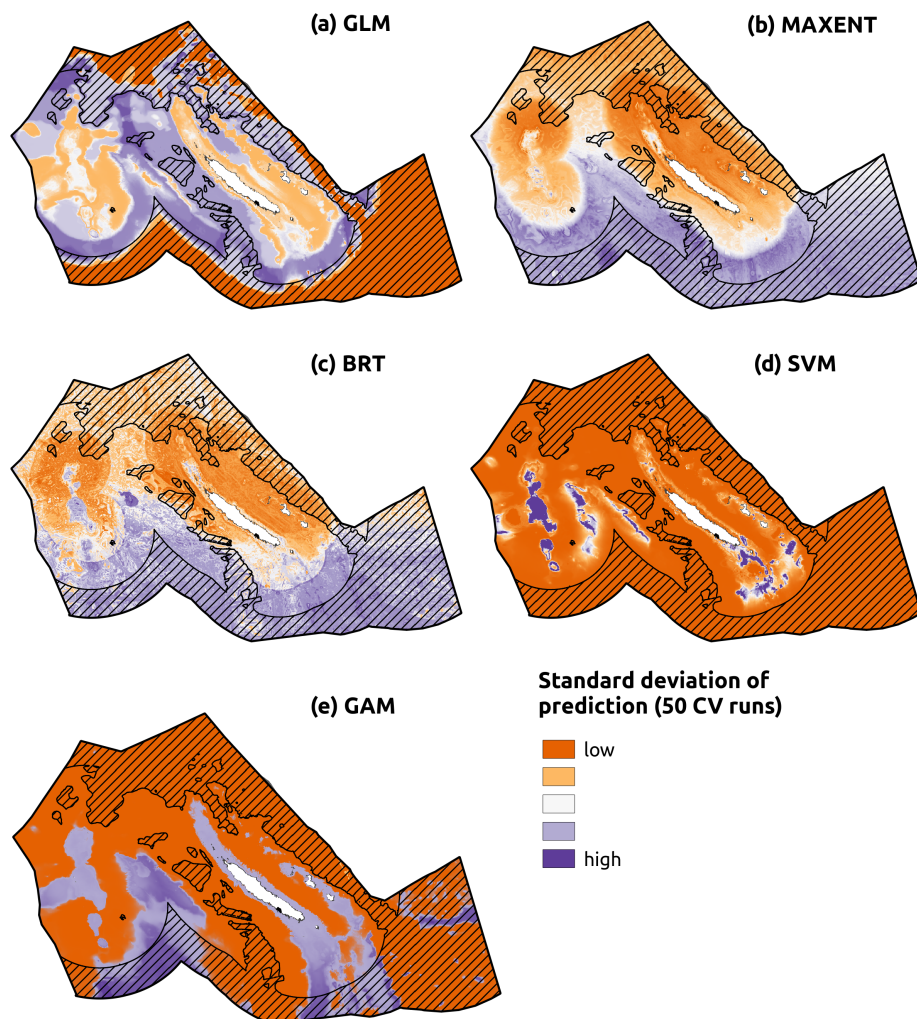


Figure 4.C.2 Maps of standard deviation of the predicted humpback whale habitat suitability from research survey models (with '.pred' settings). Standard deviation was calculated over 50 cross validation runs for each statistical algorithm. Color scales are not standardized across maps. Areas of extrapolation where at least one environmental variable expanded outside the range observed in the training dataset are dashed.

Appendix 4.D. Additional tables summarizing model outputs

Additional tables summarizing model outputs

BRTs, MAXENT and SVMs were subject to a preliminary tuning stage ensuring optimal performance within the scope of our training datasets. For BRTs, different combinations of learning rates (0.005, 0.01, 0.05) and tree complexity (1, 2, 3) were tested. Folds were set at random and other parameters were left as default in the gbm R package (version 2.1.1). MAXENT models were built with the dismo R package (version 1.1-1): the regularization parameter beta was tested over 4 values (1, 4, 7, 10) and the features type was allowed to be linear only, linear or quadratic, and linear or quadratic or hinge. Finally, 2-class SVMs were built with the e1071 R package (version 1.6-7) using the C-classification algorithm with gamma equal to the inverse of data dimension, and differential class-weighting. Linear, polynomial (degree 2 and 3) and RBF (radial) kernels were tested, with cost (i.e. constant of regularization) ranging 1e-5, 1e-2, 1 and 10. GLMs and GAMs were fitted using the glm2 (version 1.1.2) and mgcv (version 1.8-12) R packages respectively, using a clog-log link function to account for zero-inflation. In the GLMs, each predictor was included as a cubic orthogonal polynomial with function poly(). In the GAMs, restricted maximum likelihood (REML) was used to optimize parameter estimates for the thin plate regression splines. Weights were applied in each statistical approach to account for differences in prevalence in each training dataset of the cross-validation (so that the sum of weights on presences equals the sum of weights on background points).

Table 4.D.1 Model tuning of MAXENT models with 9 predictors of humpback whale habitat preferences in New Caledonian waters. 'thresh' is the threshold used to calculate TSS and sensitivity.argos.

features	beta	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity.argos	value
hinge	1	0.748	0.737	0.011	0.42	0.368	44.716	mean
		0.004	0.031	0.034	0.05	0.057	5.029	sd
hinge	4	0.738	0.733	0.005	0.431	0.361	46.937	mean
		0.004	0.031	0.035	0.048	0.056	5.757	sd
hinge	7	0.733	0.729	0.003	0.442	0.355	45.785	mean
		0.003	0.032	0.035	0.049	0.057	6.23	sd
hinge	10	0.73	0.726	0.004	0.448	0.352	46.117	mean
		0.003	0.033	0.036	0.044	0.058	5.99	sd
quadratic	1	0.707	0.702	0.004	0.45	0.312	53.579	mean
		0.004	0.037	0.04	0.039	0.057	7.943	sd
quadratic	4	0.707	0.702	0.004	0.45	0.312	53.587	mean
		0.004	0.037	0.04	0.039	0.058	7.95	sd
quadratic	7	0.706	0.702	0.004	0.45	0.312	53.663	mean
		0.004	0.037	0.041	0.038	0.057	8.165	sd
quadratic	10	0.706	0.701	0.004	0.455	0.311	52.735	mean
		0.004	0.037	0.041	0.037	0.057	8.14	sd
linear	1	0.676	0.676	0	0.427	0.276	53.84	mean
		0.005	0.041	0.046	0.046	0.061	9.961	sd
linear	4	0.676	0.676	0	0.427	0.276	53.837	mean
		0.005	0.041	0.046	0.046	0.061	9.955	sd
linear	7	0.676	0.676	0	0.426	0.275	54.192	mean
		0.005	0.041	0.046	0.047	0.061	10.174	sd
linear	10	0.676	0.676	0	0.428	0.275	54.158	mean
		0.005	0.04	0.045	0.045	0.061	9.954	sd

Table 4.D.2 Model tuning of BRT models with 9 predictors of humpback whale habitat preferences in New Caledonian waters. 'thresh' is the threshold used to calculate TSS and sensitivity.argos.

learning rate	tree complexity	trees	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity.argos	value
0.005	1	5326	0.769	0.738	0.031	0.507	0.365	42.76	mean
		309.417	0.004	0.033	0.036	0.054	0.058	6.447	sd
0.005	2	5542	0.83	0.771	0.059	0.502	0.418	41.035	mean
		321.248	0.004	0.028	0.03	0.056	0.047	5.302	sd
0.005	3	4566	0.852	0.776	0.076	0.498	0.426	39.643	mean
		295.966	0.004	0.027	0.028	0.061	0.045	5.115	sd
0.01	1	3559	0.775	0.74	0.035	0.501	0.372	43.3	mean
		231.827	0.004	0.033	0.036	0.057	0.058	6.614	sd
0.01	2	3646	0.842	0.773	0.069	0.488	0.422	41.55	mean
		267.04	0.005	0.028	0.03	0.062	0.047	5.43	sd
0.01	3	2778	0.863	0.776	0.086	0.47	0.427	41.316	mean
		267.673	0.006	0.027	0.028	0.074	0.046	6.129	sd
0.05	1	1092	0.783	0.74	0.043	0.489	0.369	43.842	mean
		233.946	0.006	0.033	0.037	0.071	0.056	6.923	sd
0.05	2	808	0.846	0.773	0.073	0.483	0.42	41.802	mean
		128.317	0.009	0.027	0.032	0.067	0.047	6.078	sd
0.05	3	537	0.859	0.776	0.083	0.47	0.425	41.354	mean
		74.1	0.009	0.028	0.029	0.075	0.046	6.23	sd

Table 4.D.3 Model tuning of SVM models with 9 predictors of humpback whale habitat preferences in New Caledonian waters. 'polynomial2' indicate second-order polynomials and 'polynomial3' indicate third-order polynomials. 'thresh' is the threshold used to calculate TSS and sensitivity. argos.

kernel type	cost	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity. argos	value
linear	0.00001	0.668	0.67	-0.002	0.002	0	99.184	mean
		0.004	0.039	0.043	0.011	0.001	5.771	sd
linear	0.01	0.67	0.67	0.001	0.066	0.27	70.616	mean
		0.005	0.041	0.046	0.019	0.062	14.472	sd
linear	1	0.672	0.669	0.003	0.066	0.272	61.418	mean
		0.005	0.042	0.046	0.018	0.061	13.951	sd
linear	10	0.672	0.669	0.003	0.066	0.272	61.397	mean
		0.005	0.042	0.046	0.018	0.062	14.163	sd
polynomial2	0.00001	0.644	0.638	0.006	0.003	0	99.544	mean
		0.004	0.036	0.037	0.015	0.003	2.367	sd
polynomial2	0.01	0.69	0.682	0.009	0.079	0.276	45.137	mean
		0.004	0.033	0.036	0.005	0.049	8.681	sd
polynomial2	1	0.738	0.726	0.012	0.085	0.351	41.618	mean
		0.003	0.032	0.034	0.013	0.049	5.071	sd
polynomial2	10	0.746	0.732	0.014	0.088	0.365	40.545	mean
		0.004	0.031	0.034	0.011	0.052	4.504	sd
polynomial3	0.00001	0.663	0.661	0.002	0.003	0.001	99.488	mean
		0.004	0.038	0.042	0.014	0.005	2.552	sd
polynomial3	0.01	0.672	0.665	0.007	0.077	0.265	61.02	mean
		0.004	0.041	0.045	0.004	0.063	6.666	sd
polynomial3	1	0.711	0.684	0.027	0.083	0.301	41.765	mean
		0.004	0.038	0.042	0.005	0.06	5.929	sd
polynomial3	10	0.738	0.699	0.039	0.086	0.324	34.606	mean
		0.004	0.032	0.034	0.005	0.054	4.732	sd
radial	0.00001	0.65	0.643	0.008	0	0	100	mean
		0.004	0.04	0.041	0	0	0	sd
radial	0.01	0.65	0.643	0.008	0.071	0.25	36.88	mean
		0.004	0.04	0.041	0.01	0.059	12.305	sd
radial	1	0.758	0.735	0.023	0.074	0.375	44.529	mean
		0.003	0.029	0.032	0.02	0.051	8.104	sd
radial	10	0.797	0.752	0.044	0.082	0.411	38.052	mean
		0.003	0.028	0.03	0.018	0.047	5.62	sd

Table 4.D.4 Model tuning of MAXENT models with 7 predictors of humpback whale habitat preferences in New Caledonian waters. The selected model is shown in bold. 'thresh' is the threshold used to calculate TSS and sensitivity.argos.

features	beta	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity.argos	value
hinge	1	0.747	0.736	0.011	0.413	0.364	46.083	mean
		0.004	0.031	0.034	0.052	0.055	6.198	sd
hinge	4	0.737	0.731	0.006	0.434	0.355	47.575	mean
		0.004	0.032	0.035	0.044	0.056	5.875	sd
hinge	7	0.731	0.728	0.003	0.445	0.351	46.659	mean
		0.003	0.032	0.036	0.049	0.054	6.201	sd
hinge	10	0.729	0.725	0.004	0.45	0.348	46.824	mean
		0.004	0.033	0.037	0.05	0.055	6.919	sd
quadratic	1	0.703	0.699	0.004	0.455	0.304	52.445	mean
		0.004	0.038	0.042	0.042	0.06	10.784	sd
quadratic	4	0.703	0.699	0.004	0.455	0.304	52.417	mean
		0.004	0.038	0.042	0.042	0.06	10.789	sd
quadratic	7	0.703	0.698	0.004	0.457	0.304	52.117	mean
		0.004	0.038	0.042	0.041	0.059	10.592	sd
quadratic	10	0.702	0.698	0.004	0.456	0.303	52.564	mean
		0.004	0.038	0.042	0.041	0.059	10.379	sd
linear	1	0.675	0.675	0	0.426	0.274	53.259	mean
		0.005	0.041	0.046	0.046	0.063	9.771	sd
linear	4	0.675	0.675	0	0.426	0.274	53.269	mean
		0.005	0.041	0.046	0.046	0.063	9.785	sd
linear	7	0.675	0.675	0	0.426	0.274	53.32	mean
		0.005	0.041	0.046	0.044	0.063	9.687	sd
linear	10	0.675	0.675	0	0.427	0.274	53.374	mean
		0.005	0.041	0.046	0.043	0.063	9.455	sd

Table 4.D.5 Model tuning of BRT models with 7 predictors of humpback whale habitat preferences in New Caledonian waters. The selected model is shown in bold. 'thresh' is the threshold used to calculate TSS and sensitivity. argos.

learning rate	tree complexity	trees	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity. argos	value
0.005	1	5206	0.767	0.738	0.029	0.507	0.364	43.895	mean
		255.479	0.004	0.033	0.036	0.056	0.056	7.785	sd
0.005	2	5245	0.823	0.77	0.053	0.506	0.416	41.762	mean
		374.063	0.004	0.029	0.031	0.062	0.048	5.839	sd
0.005	3	4361	0.843	0.775	0.069	0.496	0.425	40.832	mean
		301.745	0.004	0.027	0.029	0.066	0.045	5.934	sd
0.01	1	3378	0.771	0.739	0.032	0.501	0.369	44.239	mean
		199.274	0.004	0.033	0.037	0.063	0.056	7.917	sd
0.01	2	3356	0.833	0.772	0.061	0.499	0.42	41.742	mean
		286.364	0.005	0.028	0.031	0.063	0.048	5.363	sd
0.01	3	2668	0.854	0.775	0.079	0.485	0.425	41.244	mean
		235.554	0.006	0.027	0.03	0.072	0.045	5.974	sd
0.05	1	895	0.776	0.739	0.036	0.495	0.369	44.667	mean
		181.617	0.005	0.034	0.038	0.058	0.056	6.773	sd
0.05	2	745	0.837	0.772	0.065	0.484	0.417	43.058	mean
		118.343	0.008	0.028	0.031	0.078	0.047	7.35	sd
0.05	3	542	0.853	0.775	0.079	0.48	0.424	41.576	mean
		76.505	0.009	0.027	0.031	0.078	0.047	6.177	sd

Table 4.D.6 Model tuning of SVM models with 7 predictors of humpback whale habitat preferences in New Caledonian waters. 'polynomial2' indicate second-order polynomials and 'polynomial3' indicate third-order polynomials. The selected model is shown in bold. 'thresh' is the threshold used to calculate TSS and sensitivity.argos.

kernel type	cost	int.AUC	ext.AUC	diff.AUC	thresh	TSS	sensitivity.argos	value
linear	0.00001	0.669	0.669	-0.001	0	0	100	mean
		0.004	0.04	0.044	0	0	0	sd
linear	0.01	0.669	0.669	0	0.066	0.27	70.908	mean
		0.005	0.041	0.046	0.019	0.062	14.521	sd
linear	1	0.671	0.668	0.003	0.066	0.27	60.728	mean
		0.005	0.042	0.047	0.018	0.062	13.318	sd
linear	10	0.671	0.668	0.003	0.066	0.271	60.384	mean
		0.005	0.042	0.047	0.018	0.062	13.257	sd
polynomial2	0.00001	0.638	0.631	0.006	0.001	0	99.724	mean
		0.003	0.037	0.04	0.01	0.003	1.949	sd
polynomial2	0.01	0.674	0.666	0.008	0.073	0.249	53.07	mean
		0.004	0.035	0.038	0.003	0.05	6.875	sd
polynomial2	1	0.722	0.712	0.01	0.093	0.33	41.161	mean
		0.004	0.034	0.037	0.016	0.053	5.992	sd
polynomial2	10	0.732	0.719	0.012	0.087	0.347	40.434	mean
		0.004	0.032	0.035	0.014	0.053	4.835	sd
polynomial3	0.00001	0.662	0.66	0.002	0.001	0.001	99.783	mean
		0.004	0.039	0.043	0.009	0.004	1.534	sd
polynomial3	0.01	0.669	0.665	0.005	0.073	0.254	65.208	mean
		0.004	0.04	0.044	0.004	0.061	7.459	sd
polynomial3	1	0.688	0.674	0.014	0.076	0.288	54.5	mean
		0.0041)	0.04	0.043	0.005	0.058	6.692	sd
polynomial3	10	0.711	0.687	0.024	0.081	0.3	46.517	mean
		0.005	0.037	0.04	0.006	0.058	7.196	sd
radial	0.00001	0.667	0.658	0.008	0	0	100	mean
		0.006	0.039	0.041	0	0	0	sd
radial	0.01	0.667	0.658	0.008	0.074	0.276	43.471	mean
		0.006	0.039	0.041	0.011	0.055	13.977	sd
radial	1	0.742	0.725	0.017	0.073	0.357	48.948	mean
		0.003	0.031	0.034	0.02	0.053	7.972	sd
radial	10	0.772	0.744	0.028	0.08	0.39	42.779	mean
		0.003	0.029	0.032	0.02	0.047	7.042	sd

Table 4.D.7 Mean contribution of environmental variables* to habitat preference models for humpback whales in New Caledonian waters with 9 predictors. Coefficients of variation of the mean contribution calculated over 50 cross-validation runs indicated. Variables in grey were removed in the models presented in the main manuscript. For BRTs, SVMs, and MAXENT models results are reported for the 'stable model' tuning with best diff.AUC, and for the 'predictive model' tuning with best ext.AUC (except SVM for which contributions were only evaluated in the linear kernel case).

variables	BRT				GAM		MAXENT				GLM		SVM	
	best diff.AUC		best ext.AUC		mean	CV %	best diff.AUC		best ext.AUC		mean	CV %	best diff.AUC	
	mean	CV %	mean	CV%			mean	CV %	mean	CV%			mean	CV %
A.AVG	2.9	14.0	5.4	8.9	2.9	20.7	0.0	156.3	1.1	28.9	8.5	11.6	0.1	85.9
DEPTH	34.4	4.4	22.7	4.7	24.4	9.8	21.1	13.6	45.9	4.6	12.9	9.4	7.2	21.8
CPRO	0.4	41.0	3.9	11.8	1.1	36.4	0.3	83.3	0.0	76.3	3.5	17.7	0.4	50.7
DISSURF	2.5	13.3	4.6	7.8	26.6	10.5	28.7	10.2	20.1	7.1	18.6	13.7	11.3	8.3
JULIAN	2.2	14.3	4.5	8.1	10.6	10.4	0.2	135.3	4.2	17.3	9.4	10.1	0.2	104.4
K490	20.2	5.5	14.7	5.3	10.5	23.8	0.9	27.0	2.4	20.7	17.7	9.0	0.6	35.0
S.AVG	5.9	8.5	6.2	7.5	1.1	45.5	7.7	34.3	1.1	27.7	3.6	20.1	3.5	28.4
S.COV	5.2	14.8	16.6	4.6	2.2	22.7	0.4	55.0	1.4	65.5	9.2	9.6	0.3	47.4
SST	26.3	6.8	21.5	6.6	20.7	10.1	40.7	7.5	23.6	9.9	16.5	9.0	76.5	1.5

* average slope (S.AVG), profile curvature (CPRO), average aspect (A.AVG), julian date (JULIAN), coefficient of variation of the slope (S.COV), sea surface temperature (SST), distance to closest reef or land (DISSURF), depth (DEPTH) and diffuse attenuation (K490).

Table 4.D.8 Mean contribution of environmental variables* to habitat preference models for humpback whales in New Caledonian waters with 7 predictors. Coefficients of variation of the mean contribution calculated over 50 cross-validation runs indicated. For BRTs, SVMs, and MAXENT models results are reported for the 'stable model' tuning with best diff.AUC, and for the 'predictive model' tuning with best ext.AUC (except SVM for which contributions were only evaluated in the linear kernel case).

variables	BRT				GAM		MAXENT				GLM		SVM	
	best diff.AUC		best ext.AUC		mean	CV %	best diff.AUC		best ext.AUC		mean	CV %	best diff.AUC	
	mean	CV %	mean	CV%			mean	CV %	mean	CV%			mean	CV %
DEPTH	35.5	4.3	25.6	4.5	23.7	9.7	21.2	13.6	46.6	4.4	13.6	13.0	8.2	22.3
DISSURF	2.6	12.8	5.2	6.3	28.4	10.2	28.9	10.0	20.4	6.6	21.6	13.5	12.9	6.4
JULIAN	2.4	13.4	4.6	7.0	9.8	11.2	0.2	127.2	4.1	17.4	9.9	11.1	0.3	89.5
K490	20.9	5.5	16.5	5.5	10.7	23.4	0.9	28.6	2.4	20.5	19.4	9.7	0.6	36.8
S.AVG	6.1	8.6	6.9	6.5	2.2	27.3	7.7	34.7	1.2	30.0	5.5	17.7	2.5	32.4
S.COV	5.6	13.6	17.4	5.1	2.3	21.7	0.4	54.6	1.4	60.9	11.0	8.8	0.4	38.4
SST	27.0	6.8	23.9	6.5	22.9	8.7	40.8	7.4	23.8	9.6	19.0	8.8	75.1	1.7

* average slope (S.AVG), profile curvature (CPRO), average aspect (A.AVG), julian date (JULIAN), coefficient of variation of the slope (S.COV), sea surface temperature (SST), distance to closest reef or land (DISSURF), depth (DEPTH) and diffuse attenuation (K490).

Chapter 4 demonstrated that seabed topography is a major driver of humpback whale distribution during the breeding season. Over the New Caledonian EEZ, offshore shallow features (seamounts and banks) were specifically predicted as critical habitats for the species. In addition to these static variables, temperature was also identified as an important driver. Although the mechanisms by which sea surface temperature can restrict humpback whale distribution remain unclear, these results suggest that global warming could impact whales during the breeding season. Using the modeling approach that provided the best results in the Chapter 4, I expand the study of humpback whale habitat relationships to the South Pacific breeding grounds of the Oceania population. In Chapter 5, I apply GAMs to model suitable habitats over 7 countries and territories of Oceania, which include a great diversity of topographic features such as seamounts, banks, atolls and islands. The availability of suitable habitats is predicted for present and future temperature conditions in order to assess the potential effect of global warming on humpback whales within their breeding grounds.

V. Distribution at ocean basin scale

Whales in warming water: assessing breeding habitat diversity and adaptability in Oceania's changing climate

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In review in Global Change Biology

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Abstract

In the context of a changing climate, understanding the environmental drivers of marine megafauna distribution is important for conservation success. Humpback whales undertake some of the longest distance seasonal migrations of any mammalian species, yet the full extent of their migratory range and breeding habitats is not known. We used 19 years of dedicated survey data from 7 countries and territories of Oceania (1,376 survey days), to investigate humpback whale breeding habitat diversity and adaptability to climate change. At a fine scale, seabed topography was identified as an important influence on humpback whale distribution. The shallowest waters close to shore or in lagoons were favoured by all social group types, although humpback whales also showed flexible habitat use patterns with respect to shallow offshore features such as seamounts. At coarse scale, humpback whale breeding habitats in Oceania spanned a thermal range of 22.3 to 27.8 °C in August, with inter-annual variation up to 2.0 °C. The most detailed dataset was available from New Caledonia (774 survey days, 1996 - 2017), where encounter rates showed a negative relationship to Sea Surface Temperature, but were not related to the El Niño Southern Oscillation and the Antarctic Oscillation from previous summer. Most breeding sites that are currently occupied are predicted to become potentially unsuitably warm for this species (> 28 °C) by the end of the 21st century. Based on modelled ecological relationships, there are suitable habitats for relocation in archipelagos and seamounts of southern Oceania. Although distribution shifts might be restrained by philopatry, the apparent plasticity of humpback whale habitat use patterns and the extent of suitable habitats support an adaptive capacity to ocean warming in Oceania.

Keywords

Humpback whales, climate change, habitat modelling, species distribution, prediction, seamounts, sea surface temperature, Oceania

5.1 Introduction

In recent decades, evidence for global climate change has spurred ecologists and conservationists to increase research efforts to better understand species-climate relationships. In marine ecosystems, changes in average temperatures around the world are affecting species throughout all trophic levels (Doney *et al.*, 2012; Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al.*, 2013; Sydeman *et al.*, 2015), yet much remains unknown about the mechanisms driving these organismal responses, and whether they influence phenology, demography or distribution. In particular, the impact of climate change on marine megafauna, including cetaceans, is considered a 'big unknown' (Thomas *et al.*, 2015; Clapham, 2016). Distribution shifts are expected to occur at various geographic scales (Kaschner *et al.*, 2006; Macleod, 2009; Hazen *et al.*, 2013) and resulting population impacts are expected to vary across species, depending notably on the vulnerability and extent of their critical habitats (Macleod, 2009; Simmonds and Elliott, 2009; Sydeman *et al.*, 2015). Cetacean distribution shifts have already been recorded in response to climate-related changes (Benson *et al.*, 2002; Henderson *et al.*, 2014; Pardo *et al.*, 2015; Zerbini *et al.*, 2015; Clapham, 2016; Sprogis *et al.*, 2017) or simply in response to seasonal environmental variations (Tynan *et al.*, 2005; Di Tullio *et al.*, 2016; Gilles *et al.*, 2016). Yet, current knowledge remains insufficient to estimate the adaptive plasticity of most species to thermal changes, which is one of the key elements needed to predict the impact of climate change on marine ecosystems at large (Macleod, 2009; Sydeman *et al.*, 2015; Silber *et al.*, 2017). In recent years, Species Distribution Models (SDMs) have become a popular tool to predict distribution changes in response to climate change (Hazen *et al.*, 2013; Torres *et al.*, 2013; Legrand *et al.*, 2016; Morán-Ordóñez *et al.*, 2017), but limited long-term empirical evidence exist to validate these predictions in long-lived marine species such as cetaceans (Silber *et al.*, 2017).

Humpback whales (*Megaptera novaeangliae*) undertake some of the longest distance seasonal migrations of any mammalian species (Robbins *et al.*, 2011). They may be impacted by global ocean warming in both polar and tropical ecosystems, as they spend summers feeding in polar areas and seasonally migrate toward tropical breeding grounds where they fast during winter (Chittleborough, 1958). The reasons for such extensive migrations are still debated but could be linked to increased calf fitness in warmer waters of the tropical and subtropical breeding grounds (Clapham, 2000a). Although this hypothesis suggests a direct link between humpback whale life history and water temperature, it remains unclear how sea surface temperature (SST) drives distributions within breeding latitudes, as studies have shown both strong relationships (Brazil: Bortolotto *et al.*, 2017; Central America: Guidino *et al.*, 2014; Rasmussen *et al.*, 2007; Great Barrier Reef: Smith *et al.*, 2012) and weak or no effects (Madagascar: Trudelle *et al.*, 2016; Reunion Island: Dulau *et al.*, 2017) of this variable. SST displays complex dynamic changes through time as it fluctuates on multiple temporal scales (monthly, seasonally, annually) and follows patterns that may be stochastic, cyclic (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation, Antarctic Oscillation) or continuous (climate change). Models studying the effect of temperature on species' distribution need to explicitly reflect

these variations [Fernandez *et al.*, 2017](#); [Mannocci *et al.*, 2017a](#); [Scales *et al.*, 2017](#). Hence, datasets collected over large temporal and spatial scales are necessary to understand the effect of SST on the distribution of migratory and long-lived species such as humpback whales.

Industrial whaling of humpback whales took its greatest toll on Southern Hemisphere stocks, with more than 215,000 humpbacks killed during the 20th century ([Rocha *et al.*, 2015](#)). Following the enactment of the moratorium on commercial whaling in 1986, humpback whales have shown encouraging signs of recovery leading to the reclassification of most populations by the IUCN from 'vulnerable' to a species of 'least concern' at a global scale. However, some populations are lagging behind in recovery. In the Pacific, the Oceania humpback whale population is still classified as 'endangered' ([Childerhouse *et al.*, 2009](#)) because of its small size and slow recovery rate ([Constantine *et al.*, 2012](#); [Jackson *et al.*, 2015](#)). Compared to other breeding regions of the world, Oceania encompasses a remarkably large extent of suitable breeding habitat ([Valsecchi *et al.*, 2010](#)). It covers thousands of islands and reefs that offer the conditions usually regarded as preferred for humpback whale breeding and nursing behaviour: sheltered, shallow and warm waters ([Rasmussen *et al.*, 2007](#); [Cartwright *et al.*, 2012](#); [Smith *et al.*, 2012](#); [Lindsay *et al.*, 2016](#); [Trudelle *et al.*, 2016](#); [Bortolotto *et al.*, 2017](#); [Derville *et al.*, 2018b](#)). Shelter provided by proximity to coastlines is a well supported driver of humpback whale distribution, but this effect could locally be confounded by depth, as surveyed breeding grounds are often both shallow and nearshore ([Derville *et al.*, 2018b](#)).

At the scale of this ocean basin, humpback whales are structured into geographically separated sub-populations ([Olavarría *et al.*, 2007](#); [Childerhouse *et al.*, 2009](#); [Garland *et al.*, 2015](#)), that show varying degrees of connectivity ([Garland *et al.*, 2011](#); [Garrigue *et al.*, 2011a](#); [Steel *et al.*, 2017](#)). The International Whaling Commission (IWC) recognizes several breeding stocks and sub-stocks including BSE2 (New Caledonia), BSE3 (Tonga), and BSF (French Polynesia) ([IWC, 2005](#); [Jackson *et al.*, 2015](#)). Samoa and American Samoa lie on the geographic boundary of BSE3 and BSF, and individuals exhibit exchange to both breeding stocks ([Garrigue *et al.*, 2011a](#); [Garland *et al.*, 2015](#); [Steel *et al.*, 2017](#)), as well as BSE2 ([Steel *et al.*, 2017](#)). Recent data also demonstrates connectivity between humpback whales visiting the Chesterfield archipelago and the New Caledonia sub-stock ([Garrigue *et al.*, 2018b](#)). Photo-identified and genotyped individuals in Vanuatu ([Garrigue *et al.*, 2004b](#)) and Niue (South Pacific Whale Research Consortium pers. com.) have also been resighted in New Caledonia or Tonga. Across this vast area, the sizes of humpback whale subpopulations are not at equilibrium and their distributions have evolved through time. Social aggregation ([Clapham and Zerbini, 2015](#)) or rapid recovery of relic populations ([Olavarría *et al.*, 2007](#)) are proposed hypotheses to explain the rapid increase of some breeding populations over others, but the effect of environmental drivers on distribution has never been explored at a basin scale.

Using a compilation of humpback whale survey data spanning 7,600 km from west to east across the South Pacific, this study aims to describe the environmental drivers of humpback whale distribution and the influence of SST variation on breeding ground habitat use. Topographic and oceanographic conditions are hypothesized to influence humpback whale prevalence at multiple

scales, within and between breeding regions, and in conjunction with social factors. Patterns of space use in relation to SST are estimated from coarse scale encounter rates and fine scale sampling of used versus available habitats. The effect of SST on habitat availability is described to assess the implications of global ocean warming predicted in Oceania for the end of the 21st century. This study contributes to broad efforts to understand the temporal and spatial scales at which marine migratory species respond to climate change.

5.2 Material and methods

5.2.1 Study areas and data collection

A database was compiled from dedicated surveys for cetaceans conducted throughout Oceania by several research teams (Table 5.1). Surveys were conducted in austral winter and shoulder seasons months (May-December) between 1999 and 2017, at New Caledonia (including the main island, Loyalty Islands and Chesterfield archipelago), Vanuatu, Tonga, Niue, Samoa, American Samoa and French Polynesia (including the archipelagos: Austral, Gambier, Tuamotu, Society and Marquesas Islands; Fig. 5.1). The breeding grounds in this study were grouped based on their geographic location and affiliation to IWC definitions (Fig. 5.1): the 'western region' (Chesterfield, New Caledonia, Vanuatu), the 'central region' (Tonga, Niue, Samoa, American Samoa), and the 'eastern region' (French Polynesia). This grouping was specifically chosen to reflect genetically differentiated stocks or management units, while still producing relatively homogeneous samples in terms of survey effort and latitudinal SST gradients.

Non-systematic surveys were conducted in a closing-mode (cetaceans were approached after detection), as the primary objective for most research teams was to locate humpback whales for the purposes of photo-identification and/or genetic sampling. Though field protocols and equipment varied among surveys (e.g., vessel type, number of observers), a series of variables was consistently recorded by all teams: 1) whale observations, 2) duration of survey effort, and 3) spatial extent of survey effort. At each whale observation, group size, time of day, GPS position (WGS84 latitude-longitude), and social group types (Singleton, Pair, Mother-calf, Mother-calf-escort, Competitive group, Mother-calf-competitive group) were recorded.

In most surveys, the spatial extent of search effort was precisely recorded with a GPS trackline at a sampling frequency varying from 1 position.hour⁻¹ and 2 positions.min⁻¹ (84 % survey days). In the remaining 16 % of survey days, search effort was concentrated in small and well-defined areas that could be spatially bounded in georeferenced polygons drawn by the data suppliers (Appendix 5.A). Four polygons were manually produced in a QGIS graphical interface around the study areas of Hao (Gambier Islands), Huahine and Moorea (Society Islands), and Niue (covering 362 to 2,360 km²). Finally, for 93 % of the survey days, the time at the beginning and end of the effort was recorded, enabling a daily time on effort to be deduced. When this information was lacking, the time

on effort was deduced from the distance travelled along the boat GPS trackline and the average speed calculated over all surveys (estimated at $12.8 \text{ km}\cdot\text{h}^{-1}$).

Data processing and statistical analysis were performed with R (version 3.4.4, [R Core Team, 2016](#)) and QGIS (version 2.18.3, [QGIS Development Team, 2016](#)).

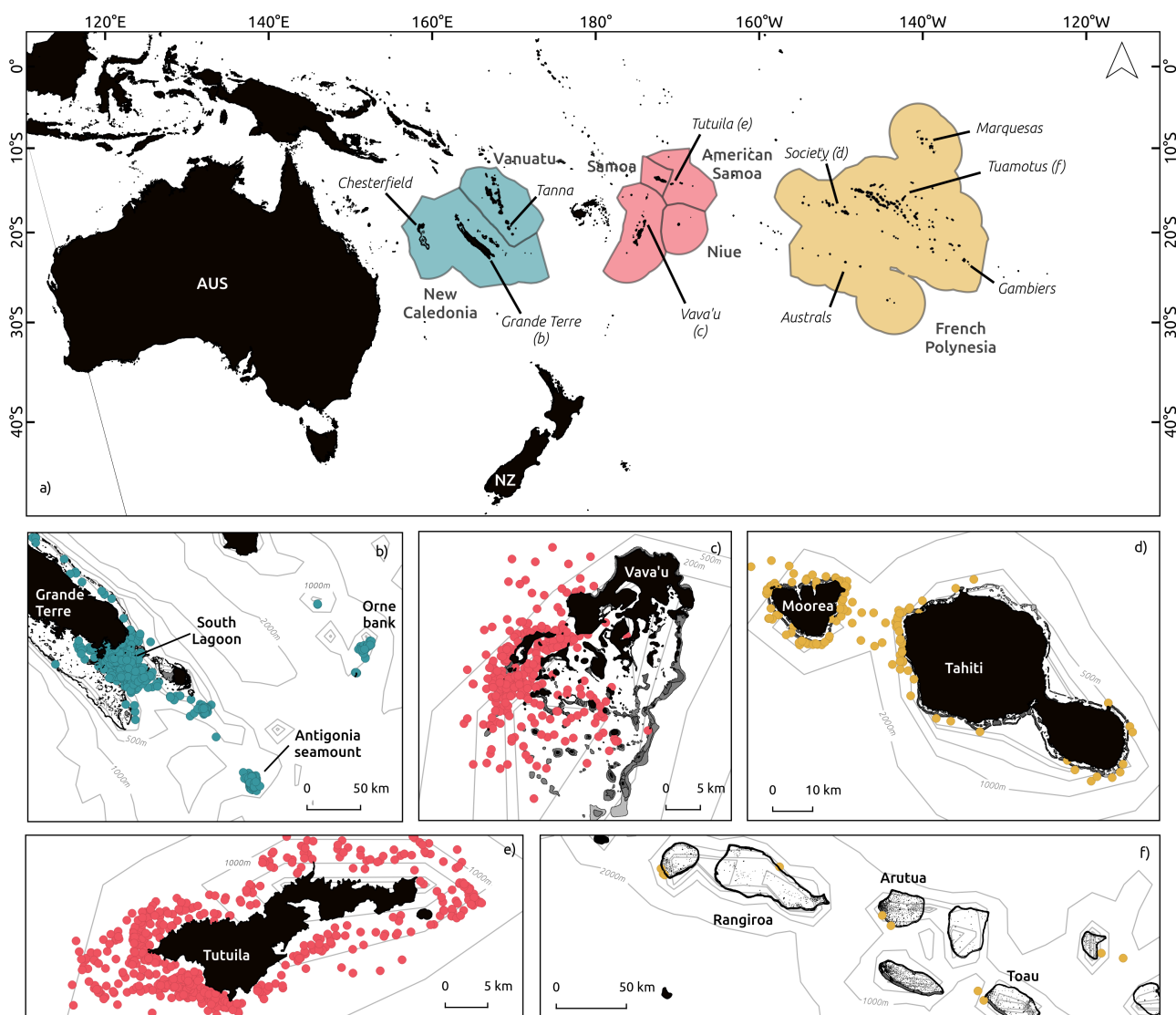


Figure 5.1 Humpback whale breeding grounds and study areas of Oceania. a) Overview of Oceania with Economic Exclusive Zones included in the study represented by coloured polygons (from left to right: western, central and eastern regions). Country names are shown in bold, localities are shown in italics. Other panels zoom in on specific study areas, with land in black, reefs in grey and presence locations in colour: b) the southern New Caledonia area; c) Vava'u archipelago in Tonga; d) Tahiti and Moorea Islands in the Society archipelago of French Polynesia; e) Tutuila island in American Samoa; f) Rangiroa atoll in the Tuamotu archipelago of French Polynesia. Isobaths are represented with grey lines.

Table 5.1 Survey effort and observations of humpback whales in Oceania between 1999 and 2017 that were used for this study. The total number of groups and number of whales observed is reported per country (#).

Region	Country	Survey years ^a	Effort (days)	Effort (hours)	#groups	#whales
Western Oceania	New Caledonia	2003 - 2017 ^b	702	5,145	1,589	3,801
	Vanuatu	2003	8	56	10	15
	Total		710	5,201	1,599	3,816
Central Oceania	Tonga	2000, 2001, 2003-2005	88	453	274	593
	Niue	2010, 2011, 2014, 2016	44	259	54	78
	American Samoa	2003-2011, 2014-2017	113	745	495	1,167
	Samoa	2012	8	77	3	4
	Total		253	1,534	826	1,842
Eastern Oceania	French Polynesia	1999-2002, 2007, 2008, 2010-2014	413	2,432	447	796

^a These numbers are not an exhaustive estimate of research in the region, but only represent the surveys that could be included in this study.

^b Additional data from 1996 to 2002 was used in the M_{NC} model of encounter rate but could not be used in the entire analysis because it lacked boat GPS tracks.

5.2.2 Coarse scale encounter rate analyses

The variations in humpback whale encounter rates were analyzed at different spatial extents, in relation to coarse scale SST patterns. To this end, the variable ' SST_{coarse} ' was obtained at daily intervals from the Reynolds NCEP Level 4 Optimally Interpolated SST with a spatial resolution of 0.25° of latitude-longitude (about 28 km resolution, <https://www.ncdc.noaa.gov/oisst>).

Current SST range over Oceania

The average SST_{coarse} from 1999 to 2017 was estimated at one specific location for each study region during the month of August to reflect SST at the peak of the breeding season (Garrigue *et al.*, 2001). August was previously used as a reference point for the Southern Hemisphere in a global review of breeding ground temperatures (Rasmussen *et al.*, 2007). However, as breeding season is reported later in some breeding sites (American Samoa, Munger *et al.*, 2012; French Polynesia, Poole, 2002), the average SST_{coarse} in October was also estimated. To this extent, SST_{coarse} was extracted and averaged at a geographic position central to the main known breeding aggregations or study sites (see Appendix 5.C for exact positions). To approximate the area of these main breeding grounds and match the rest of the coarse scale encounter rate analysis, SST_{coarse} was averaged in a 1° radius.

Present and future SST patterns

The average SST_{coarse} from 1999 to 2017 during the month of August was computed for the entire Oceania region. Using this climatology of present austral winter conditions, climate was simulated with an imposed time-invariant perturbation to assess future SST patterns under a climate change scenario (Knutson *et al.*, 2008). This method, sometimes referred to as an 'anomaly method' (e.g., Andréfouët *et al.*, 2015), is commonly used to overcome the biases found in climate model simulations such as the Coupled Model Intercomparison Project models (CMIP5; Taylor *et al.*, 2012). Indeed, CMIP5 are found to inaccurately reproduce the present-day South Pacific climate (Brown

et al., 2014), but can yield robust simulations of the change from present to future conditions (Li *et al.*, 2016). A multimodel ensemble of 31 CMIP5 models was used to predict future SST (for 2080 - 2100) conditions under the Representative Concentration Pathway 8.5 (RCP 8.5) of aerosols and greenhouse gases scenario following the methodology employed in Knutson *et al.* (2008) and Walsh (2015). The RCP 8.5 scenario corresponds to a high greenhouse gas emission pathway and is used as a pessimistic baseline if no climate change mitigation is achieved (Riahi *et al.*, 2011). Isotherms at 21 °C and 28 °C corresponding to the breeding range described in Rasmussen *et al.* (2007) were estimated from 1) the current observed August SST_{coarse} , and 2) the projected future August SST_{coarse} for the end of the 21st century.

The study area was gridded in 1° cells and total survey time per cell was calculated, summing all survey years from 1999 to 2017 (months of May to December). The encounter rate per grid cell, in number of whales per hour of survey (whales.h⁻¹) was computed by dividing the total number of whales observed (number of groups multiplied by group size) by the total time on effort per cell. The maps of mean encounter rate at 1° resolution were overlaid with present and future isotherms estimated from SST_{coarse} with a 0.25° resolution.

Local and regional coarse scale encounter rate models

Encounter rates were calculated over each survey day and modelled with a Generalized Additive Model (GAM, Hastie and Tibshirani, 1990) applied with a Gaussian log link as a function of year, day of year and SST_{coarse} . Variables were modelled with penalized thin-plate regression splines optimized with a Restricted Maximum Likelihood and basis size limited to 5 to prevent overfitting (Wood, 2017). Two separate GAMs were produced: the first, M_{OC} , estimated the effect of SST_{coarse} on encounter rate through space at the regional Oceania scale, and the second, M_{NC} , estimated the local effect of SST_{coarse} through time at a specific study site, the New Caledonia South Lagoon. This site was chosen as a case study as it provides the most consistent and prolonged survey effort in Oceania (1996 - 2017).

For the purpose of M_{OC} , SST_{coarse} was extracted at the centre of each 1° grid cell in which encounter rates were calculated. In order to account for spatial autocorrelation in this large-scale model across breeding regions, projected geographical coordinates were added as covariates in the M_{OC} model. These terms corresponded with an isotropic smoother of x- and y-coordinates at which the encounter rates were estimated. Smoothing was performed with a Gaussian process model parametrized with a power exponential correlation function of range based on Kamman and Wand (2003) and basis size 50.

In M_{NC} , SST_{coarse} was extracted at a fixed position, at the centre of the New Caledonia South Lagoon (167°E, 22.5°S). This location and the resolution of SST_{coarse} , were considered to yield a representative estimate of temperatures in the study area, which core surveyed area spans about 20 km wide. For this model, encounter rates were calculated for study days from 1996 to 2017 (Garrigue

et al., 2001, see Appendix 5.D).

Pacific Ocean conditions change in relation to periodic climatic fluctuations such as the El Niño Southern Oscillation phenomenon (ENSO, McPhaden *et al.*, 2006), the strength of which is measured by the Southern Oscillation Index (SOI). The Antarctic Oscillation (AAO) affects the Southern Ocean ecosystems and is measured by the Southern Annular Mode (SAM) index. In order to assess the effect of the conditions in the feeding grounds and migratory corridors on humpback whale presence in the South Lagoon breeding ground, SAM was obtained from the British Antarctic Survey (<http://www.nercbas.ac.uk/icd/gjma/sam.html>) and SOI was obtained from the National Oceanographic and Atmospheric Administration (NOAA, <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>). SAM and SOI monthly indexes were averaged between November and April each year to reflect the summer feeding conditions of humpback whales prior to the following breeding season in Oceania. In place of using SST_{coarse} as a predictor of encounter rate in M_{NC} , SOI and SAM were also tested.

The performance of models was assessed through the computation of the proportion of deviance explained (Guisan and Zimmermann, 2000). Partial dependence plots were produced to visualize the effect of one variable while all others were held constant at their mean (Friedman, 2001). When predicting fitted responses in the M_{OC} model, latitude and longitude were held constant to a fixed position in the South Lagoon (167°E, 22.5°S) to ensure comparability with the M_{NC} predictions.

5.2.3 Fine scale habitat use model

Habitat preferences of humpback whales were modelled based on a binomial response variable comparing 'used' to 'available' environmental conditions. Indeed, non-systematic cetacean surveys were not designed to record true presence-absence data, but included some information about the area surveyed and time on-effort. In this context, constraining the available background space is known to improve model performance (Engler *et al.*, 2004; Phillips *et al.*, 2009) and can be informed by the extent of survey effort at sea (e.g., Torres *et al.*, 2008). Following the method in Derville *et al.* (2018b), the area surrounding GPS survey tracklines was used to approximate available environment where background points were sampled. Daily survey track strip-width spanning 10 km to each side of the tracklines were generated to reflect areas surveyed and their vicinity, resulting in daily background areas of 125 to 4,460 km². The 10 km width of the background sampling area was set based on approximate maximum detection distance and distance that could be covered at sea on a daily basis. In the few cases where tracklines were not recorded, background areas were approximated in small polygons enclosing the survey areas (Appendix 5.A). Background points were sampled randomly within these areas, with a minimum distance of 2 km from each other and independently of presence locations. The number of background points was proportional to the number of hours of effort per day (on average 4 points per hour of survey).

Humpback whales in Pacific tropical breeding grounds have been shown to associate with

small seabed and reefs features ranging a few dozen meters to kilometers (model resolution: 50 m, Cartwright *et al.*, 2012; 100 - 150 m, Lindsay *et al.*, 2016; 4.8 km, Smith *et al.*, 2012). Given this potential to select habitat at very fine scale, the effect of topography and SST on habitat suitability within each region of Oceania was assessed at a kilometer spatial scale. Moreover, assuming that predictable and persistent SST conditions are a factor of attractiveness for humpback whales seeking breeding and nursing habitats, climatological estimates of SST were used in this model (Mannocci *et al.*, 2017a). Hence, the variable ' SST_{fine} ' was obtained from a climatology averaging SST from 2003 to 2014 at a 10-days scale based on the Multi-scale Ultra-high Resolution SST (MURSST) with a fine spatial resolution of 1 km (<https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>). Furthermore, bathymetric charts at 1 km resolution ('DEPTH', in meters) were obtained from the General Bathymetric Chart of the Oceans (GEBCO). Seabed slope ('SLOPE', in degrees) was calculated from bathymetry using the raster R package (version 2.6-7). Coastlines were obtained from the OpenStreetMap dataset (<http://openstreetmapdata.com/data/coastlines>) and coral reef contours were obtained from the UNEP World Conservation Monitoring Centre (UNEP-WCMC *et al.*, 2010). A raster of the distance to the closest shallow reef (emerging at low tide) or coastline ('DISSURF', in km) was calculated.

Environmental variables were extracted at presence and background locations. *DEPTH*, *SLOPE* and *DISSURF* were log-transformed to prevent an inflated influence of outliers as recommended by (Wood, 2006). *DEPTH* and *DISSURF* showed a medium to strong correlation depending on the region (Spearman coefficient > 0.7) in the presence-background dataset. Collinearity among explanatory variables is known to affect a model's stability and capacity to assess the relative influence of each variable (Dormann *et al.*, 2013). Sequential regression was used to correct for collinearity (Graham, 2003). A linear regression between *DEPTH* and *DISSURF* at the points of presence and background was developed (Appendix 5.B). The residuals of this regression (' $DISSURF_{RES}$ ') were subsequently used instead of *DISSURF* as they represent the contribution of *DISSURF* after accounting for *DEPTH*. For instance, high $DISSURF_{RES}$ values represent waters 'abnormally' shallow considering how far they are from land or reef (e.g. an offshore shallow seamount).

GAMs were used to model the presence-background response as a function of *DEPTH*, *SLOPE*, $DISSURF_{RES}$, SST_{fine} , day of year, and year. The smoothed effect of each of these variables, except for year, was assessed as an interaction with the region (i.e., western, central, or eastern Oceania, Fig. 5.1) in order to capture potentially contrasting habitat selection patterns across regions. Variables were modelled with penalized thin-plate regression splines optimized with a Restricted Maximum Likelihood and basis size limited to 5 to prevent overfitting (Wood, 2017). Finally, coarse scale differences in humpback whale prevalence were accounted for by including an isotropic Gaussian process smoother on projected latitude and longitude coordinates similar to that used in M_{OC} .

Partial dependence plots were produced for each environmental predictor/region combination. Fitted responses for each region were estimated while holding the latitude and longitude to a fixed location central to the main study site per region, namely: the New Caledonia South Lagoon for

the western region (167.24°E, 22.77°S), American Samoa for the central region (170.74°W, 14.29°S) and the Society Islands for the eastern region (149.48°W, 17.54°S). Finally, humpback whale habitat suitability with respect to *DEPTH*, *SLOPE*, *DISSURF_{RES}* and *SST_{fine}* was predicted over 1 km resolution maps. Day of year was fixed to its mean per region dataset, and year was fixed to 2017. Areas where environmental conditions strayed outside the model training ranges by region were dashed out on the final predicted maps relative to each region respectively, as they should be considered with caution (Mannocci *et al.*, 2017b).

In order to assess the effect of habitat-associated sampling bias between regions, a predicted map of habitat suitability was also produced for eastern Oceania using the western fitted habitat use trends. To ensure model transferability, *SST_{fine}* for the eastern region was fixed to 22°C (the preferred SST for humpback whales in the western region) so that predictions would only reflect seabed topography preferences. Areas where environmental conditions strayed outside the training range observed in the western region were removed from the predicted map.

5.3 Results

A total of 1,376 days of survey were compiled over years from 1999 to 2017 (for years of survey per country see Table 5.1). The majority of surveys were conducted in August (36 %), September (33 %), October (16 %) and July (12 %). Overall, 8 % of survey days were conducted more than 10 km offshore. Over all these surveys, 2,872 singletons or groups of humpback whales were observed (Table 5.1), with a cumulative total of 6,454 whales.

5.3.1 Coarse scale encounter rate and SST

The mean encounter rate per day of survey at the Oceania scale was 0.69 whales.h⁻¹ (sd ± 0.90). Averaged in 1° grid cells, the highest encounter rates were recorded southwest of New Caledonia, over the Antigonias seamount (2.4 whales.h⁻¹ ± SD 1.6) and Orne bank (2.0 whales.h⁻¹ ± SD 0.9), followed by Tutuila (American Samoa, 1.5 whales.h⁻¹ ± SD 1.1), Vava'u (Tonga, 1.3 whales.h⁻¹ ± SD 0.9) and Rurutu (Austral Islands, French Polynesia, 1.3 whales.h⁻¹ ± SD 3.1; Fig. 5.2). Antigonias showed significantly higher encounter rates than the other four top sites (Kruskal-Wallis test: $X^2 = 13.4$, $p < 0.001$). The lowest encounter rates were recorded in pelagic offshore waters (e.g., French Polynesia, Fig. 5.2) and in nearshore waters of the Marquesas, Samoas, northwestern New Caledonia, and some of the Tuamotus.

Based on current *SST_{coarse}* average isotherms for the month of August (1999 - 2017), all study sites were within the 21 - 28 °C range previously established for humpback whale breeding habitats (Rasmussen *et al.*, 2007). *SST_{coarse}* measured in each study area in August ($n = 12$, Appendix 5.C) from 1999 to 2017 varied from 22.3 to 27.8 °C. *SST_{coarse}* fluctuated by 1.1 to 2.0 °C between years at a given site, with the larger annual anomalies recorded in the Tonga (2.0 °C), Niue (1.9 °C), Vanuatu

(1.8 °C), and the Gambier islands (1.8 °C). SST_{coarse} measured in October was warmer at all sites (Appendix 5.C), even those with a breeding season peak reported later in the year (e.g., American Samoa: mean SST_{coarse} Aug = 27.67 °C vs mean SST_{coarse} Oct = 28.2 °C). Following the climate change predictions for the end of the 21st century, an average SST above 28 °C in August is expected at Tonga, Niue, Samoa, American Samoa and the northern part of French Polynesia (Society, Tuamotu and Marquesas Islands; Fig. 5.2).

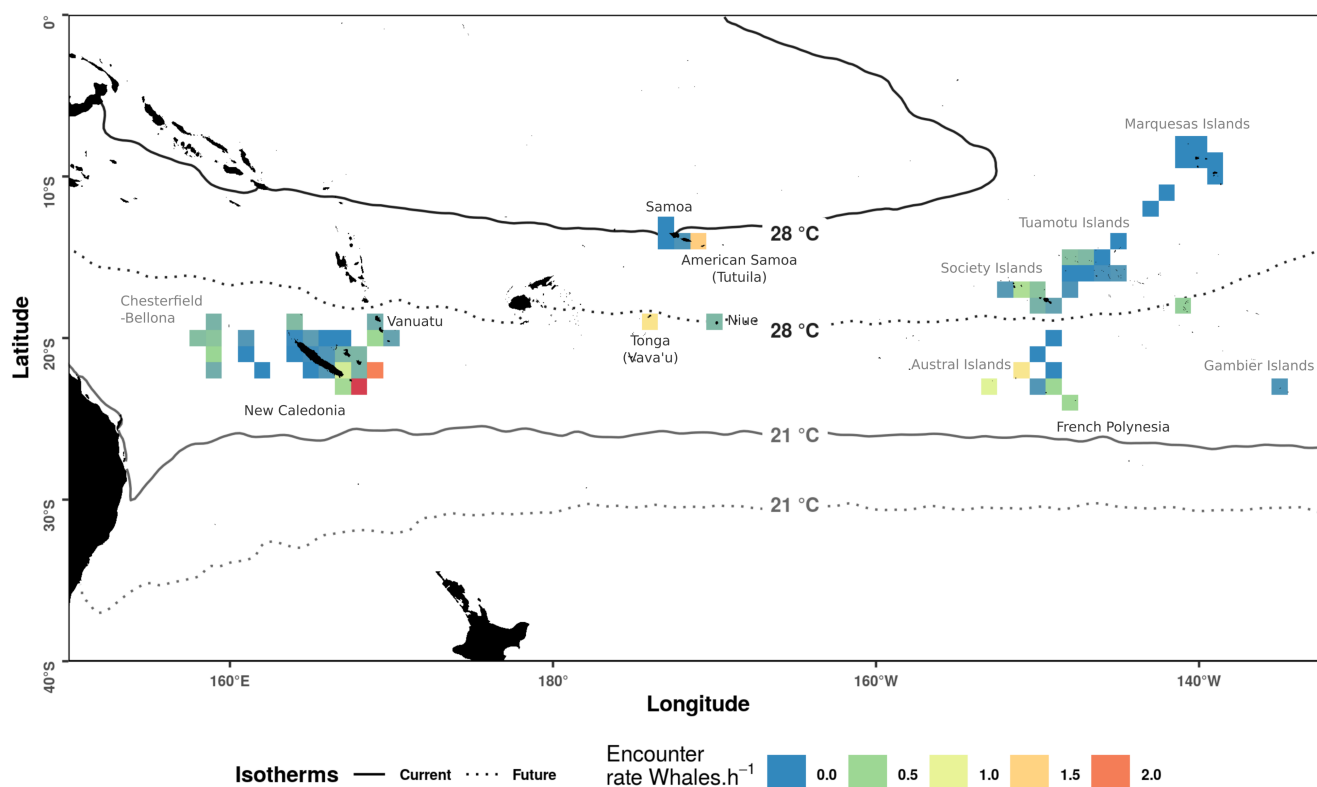


Figure 5.2 Coarse scale gridded encounter rate of humpback whales (whales.h⁻¹) at 1° resolution in Oceania between 1999 and 2017 (n = 1,376 days of survey). The map is overlaid with average August SST_{coarse} isotherms at 28 °C and 21 °C in the current (solid line: average August SST from Reynolds NCEP Level 4 Optimally Interpolated dataset, between 1999 and 2017) and future period (dashed line: 2080-2100, prediction based on CMIP5 models and RCP8.5 scenario using the method by Knutson *et al.*, 2008). Lands and islands are represented in black.

At the Oceania scale between 1999 and 2017, in the M_{OC} model, 1,376 daily encounter rates were recorded and showed a significant increase with year, particularly between 2002 and 2012 (Fig. 5.3a). The day of year also affected encounter rates, which followed a bell-shaped trend with a peak around the end of August. After accounting for spatial autocorrelation using an interaction covariate between latitude and longitude (edf = 22.8, $F = 10.6$, p -value < 0.001), encounter rate showed a decreasing trend with increasing SST_{coarse} , but the relationship was not significant ($F = 0.6$, $p = 0.06$, Fig. 5.3a). The deviance explained by the model reached 41.4 %.

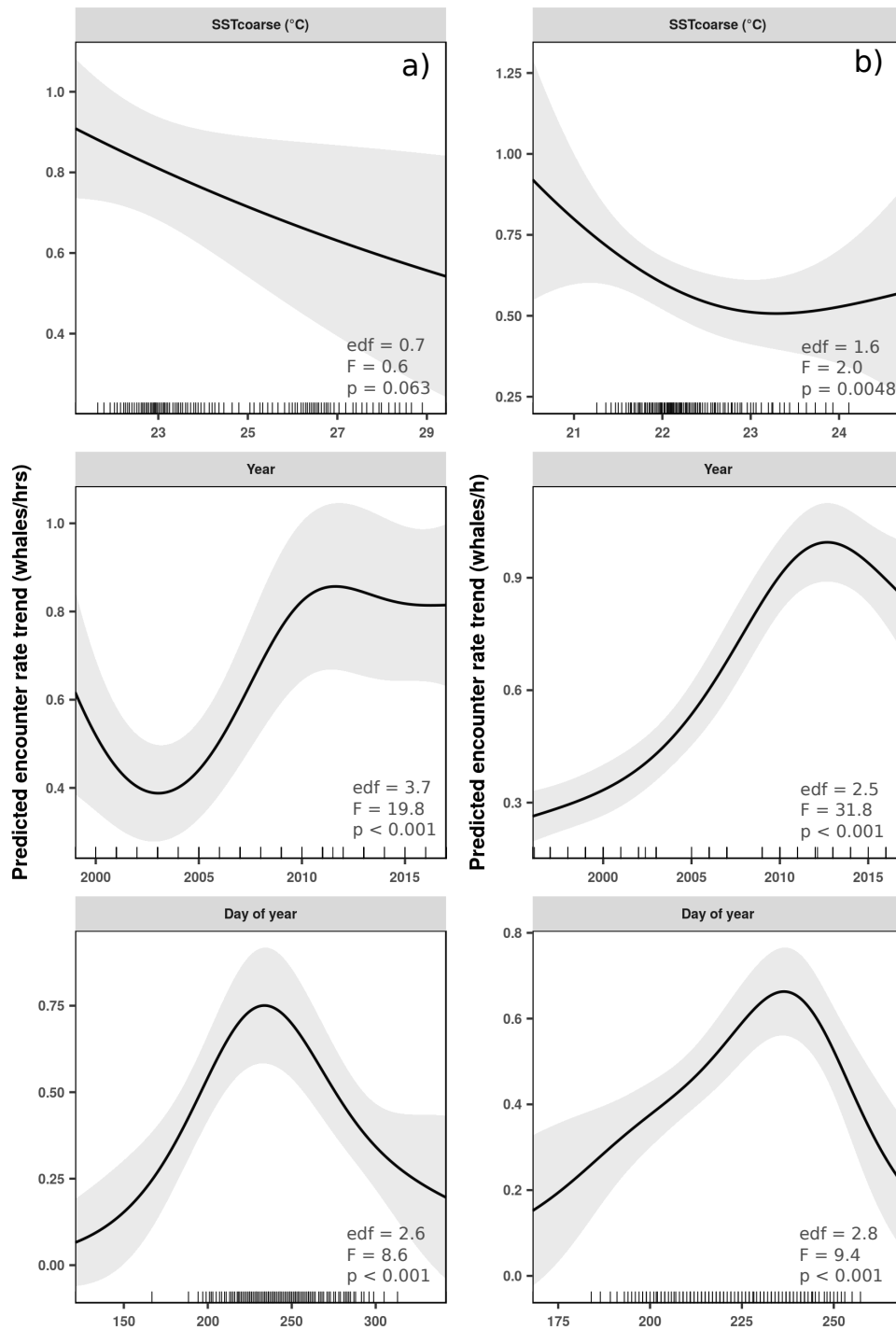


Figure 5.3 Coarse scale humpback whale encounter rate trends from, a) model M_{OC} at Oceania scale between 1999 and 2017 ($n = 1,376$), and b) model M_{NC} in the New Caledonia South Lagoon between 1996 and 2017 ($n = 774$). Solid lines represent the marginal effect of each variable relative to encounter rate. Rug plots show the distribution of values for each predictor. Shaded areas represent approximate 95% confidence intervals.

Similar trends were found in the New Caledonia South Lagoon M_{NC} model of encounter rates between 1996 and 2017 ($n = 774$ days of survey, Fig. 3B). Encounter rates showed a decreasing trend with increasing SST_{coarse} . Encounter rate also increased with year and reached a peak in 2012 -

2013. The seasonal peak was estimated to occur around the end of August. The deviance explained by the model reached 25.4 %, including 1.1 % that could be attributed to SST_{coarse} . The alternative models of M_{NC} that replaced SST_{coarse} with the SOI or SAM from the previous summer led to slightly lower deviance explained (24.7 % and 24.5 % respectively, Appendix 5.D), and both variables had no significant effect on encounter rate in the New Caledonia South Lagoon ($F = 0.5$, p -value = 0.08; $F = 0.0$, p -value = 0.86 respectively).

5.3.2 Fine scale habitat use

Fine scale humpback whale habitat preferences were modelled with a presence-background approach in a binomial GAM. The model explained 21.6 % of the deviance in the presence-background dataset counting 47,620 data points (including 2,872 presences). All predictors had a significant effect on humpback whale probability of presence (Table 5.2).

Table 5.2 Fine scale model of humpback whale habitat use in Oceania: approximate significance of smooth terms in GAM. Significance is reported for all smooth terms in interaction with region (western, central or eastern Oceania) and for smooth terms with no interaction (year and projected coordinates $X * Y$). Edf = estimated degrees of freedom.

	Western			Central			Eastern		
	edf	Chi ²	p-value	edf	Chi ²	p-value	edf	Chi ²	p-value
DEPTH	3.5	257	<0.001	3.8	419	<0.001	3.8	59	<0.001
DISSURF_{RES}	3.6	124	<0.001	1.5	14	<0.001	3.6	148	<0.001
SLOPE	3.0	30	<0.001	1.6	8	0.004	2.8	45	<0.001
<i>SST_{fine}</i>	2.9	112	<0.001	2.1	50	<0.001	1.3	4	0.047
day of year	1.9	15	<0.001	3.9	45	<0.001	2	8	0.010
year	edf = 1.9, Chi ² = 22, p-value <0.001								
X * Y	edf = 39.1, Chi ² = 811, p-value <0.001								

The relationship between humpback whale presence and depth was similar between the three regions (Fig. 5.4), though favouring deeper waters in eastern (mean depth at whale presence positions = 360 m ± SD 480) and central Oceania (mean = 198 m ± SD 296), compared to western Oceania (mean = 43 m ± SD 89; Anova: $F_{(2, 2869)} = 523$, $p < 0.001$). In contrast, the relationship with $DISSURF_{RES}$ differed between regions. The trend was positive in western Oceania, indicating a preference for shallow waters away from surfacing reefs or coasts (e.g., offshore seamounts and banks). This trend was reflected in predicted habitat suitability maps for the region, where the seamounts of the Norfolk and Loyalty Ridges were particularly suitable (Fig. 5.5b). On the contrary, in both central and eastern Oceania, the trend between humpback whale presence and $DISSURF_{RES}$ was negative, indicating that whales were found in waters closest to coasts or reefs but relatively deep. Again, this trend manifested in the predicted habitat suitability maps, which emphasized the importance of the external slope of fringing/barrier reefs and coastal waters of high islands such as Tutuila (Fig. 5.5c), Tahiti (Fig. 5.5e) or Niue (Fig. 5.5f).

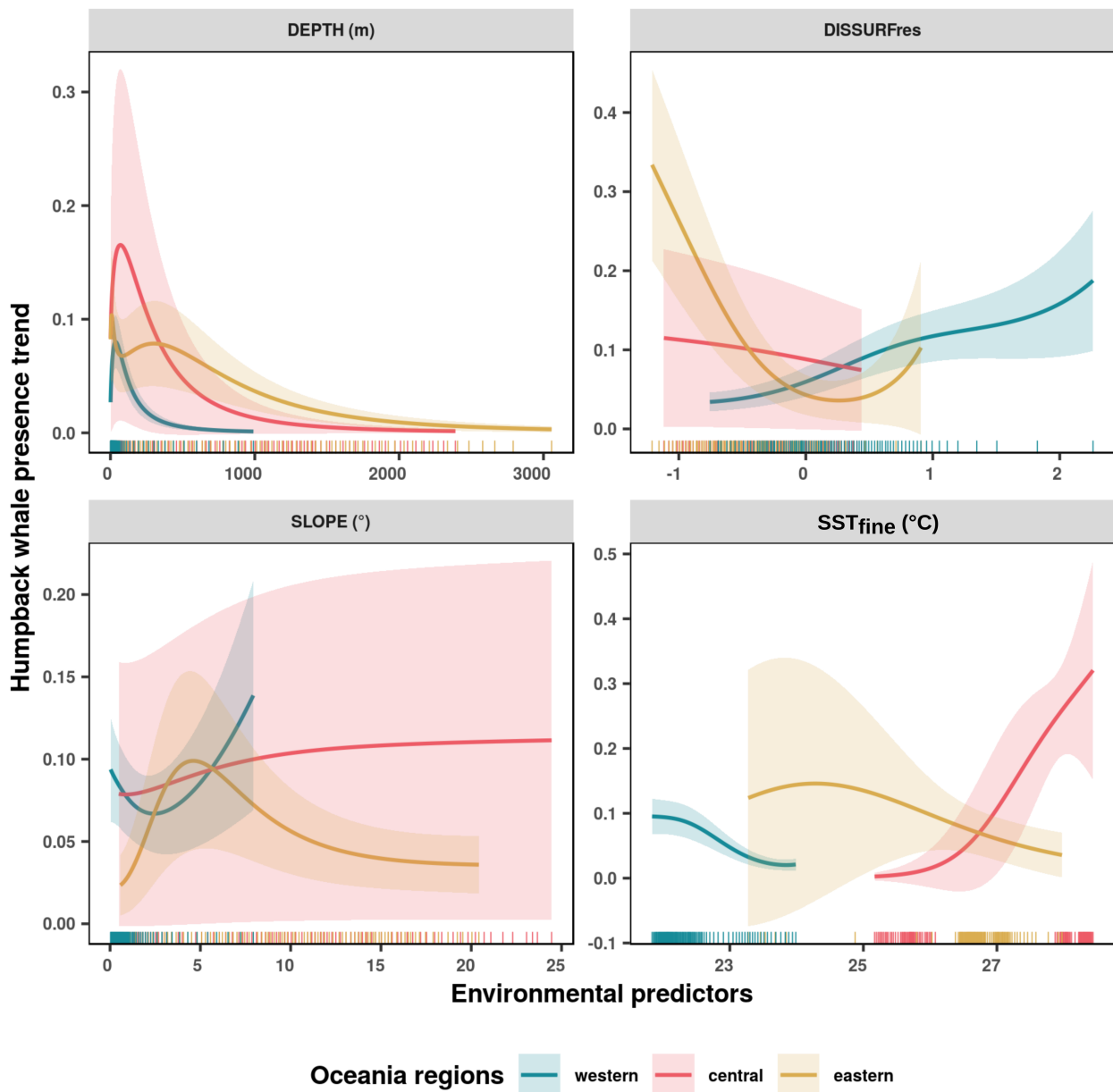


Figure 5.4 Fine scale humpback whale habitat use from a GAM relative to environmental predictors: seabed depth in meters (*DEPTH*), residual distance to coast/reef accounting for depth (*DISSURF_{RES}*: larger values indicate regions that are shallower than what would be expected considering their distance to closest coast/reef, no unit), seabed slope in ° (*SLOPE*), and climatology SST in °C (*SST_{fine}*). Predictors relative to time and space (year, day of year and spatial covariates) were held constant during predictions and are not represented. The y-axis indicates the effect of the smooth function of each predictor upon the trend in humpback whale presence; with higher values indicating increased presence. Regional smooth estimates are shown with different colours. Solid lines represent the marginal effect of each variable relative to humpback whale presence. Rug plots show the distribution of values per region for each predictor. Shaded areas represent approximate 95% confidence intervals.

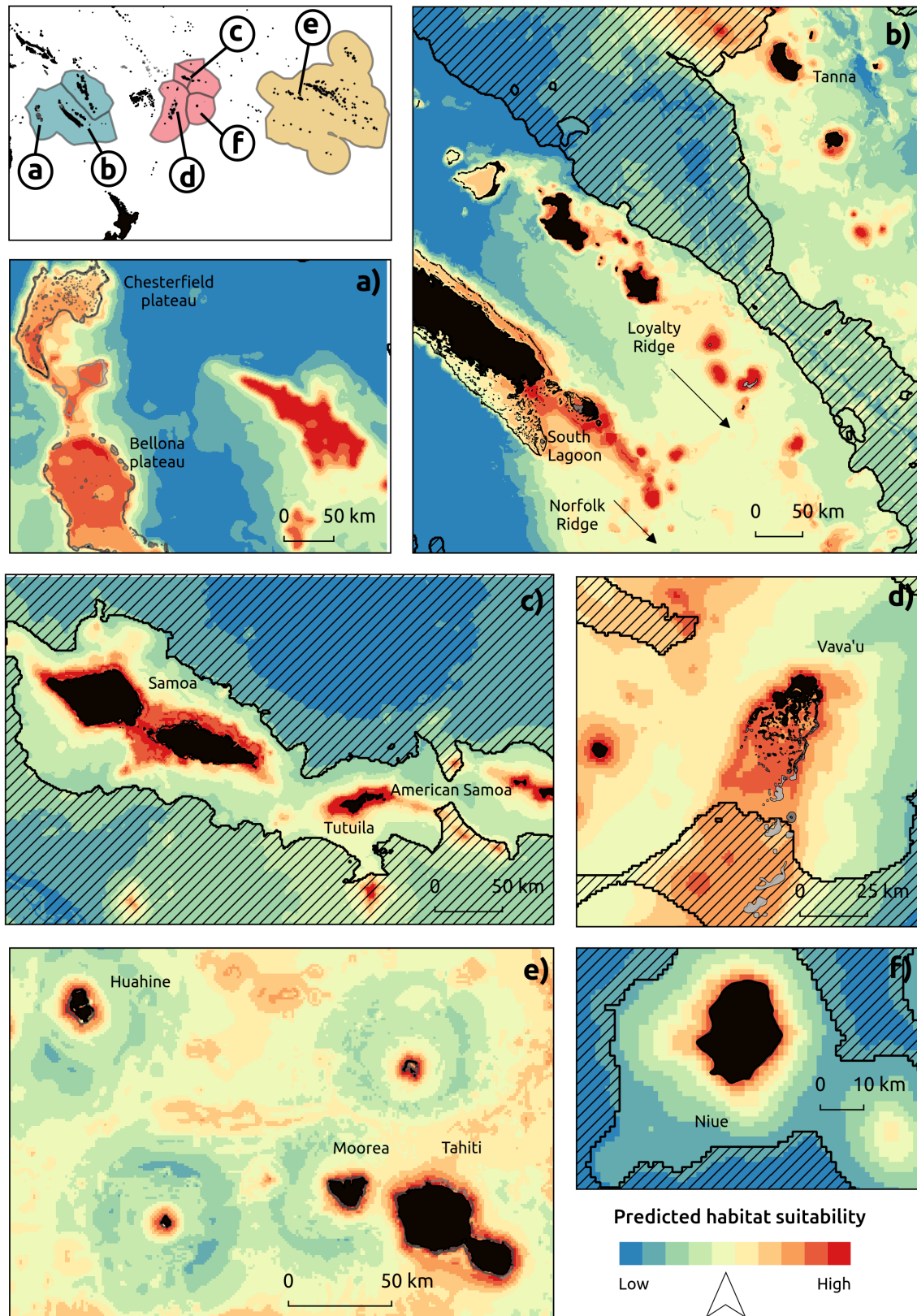


Figure 5.5 Maps of humpback whale habitat suitability predicted from a presence-background GAM based on surveys conducted in Oceania from 1999 to 2017. Habitat suitability is shown on a coloured log-scale. Dash areas represent where the model extrapolated at least one environmental variable beyond the range observed in the training datasets of that region. Land is represented in black and reefs in grey.

The western region showed the highest amount of offshore survey effort. Hence, transferring the western fitted trends to eastern Oceania revealed potentially suitable habitats in offshore seamounts located south of the Society archipelago and in the southeastern part of the Austral archipelago (Fig. 5.6). Based on these predictions, when comparing the areas of highest habitat suitability (values > 0.9 quantile) in the French Polynesian EEZ with current and predicted future 21°C and 28°C isotherms, it appeared that 91 % of the EEZ suitable habitats are currently included in this preferred SST range, against 42.7 % by the end of 21st century.

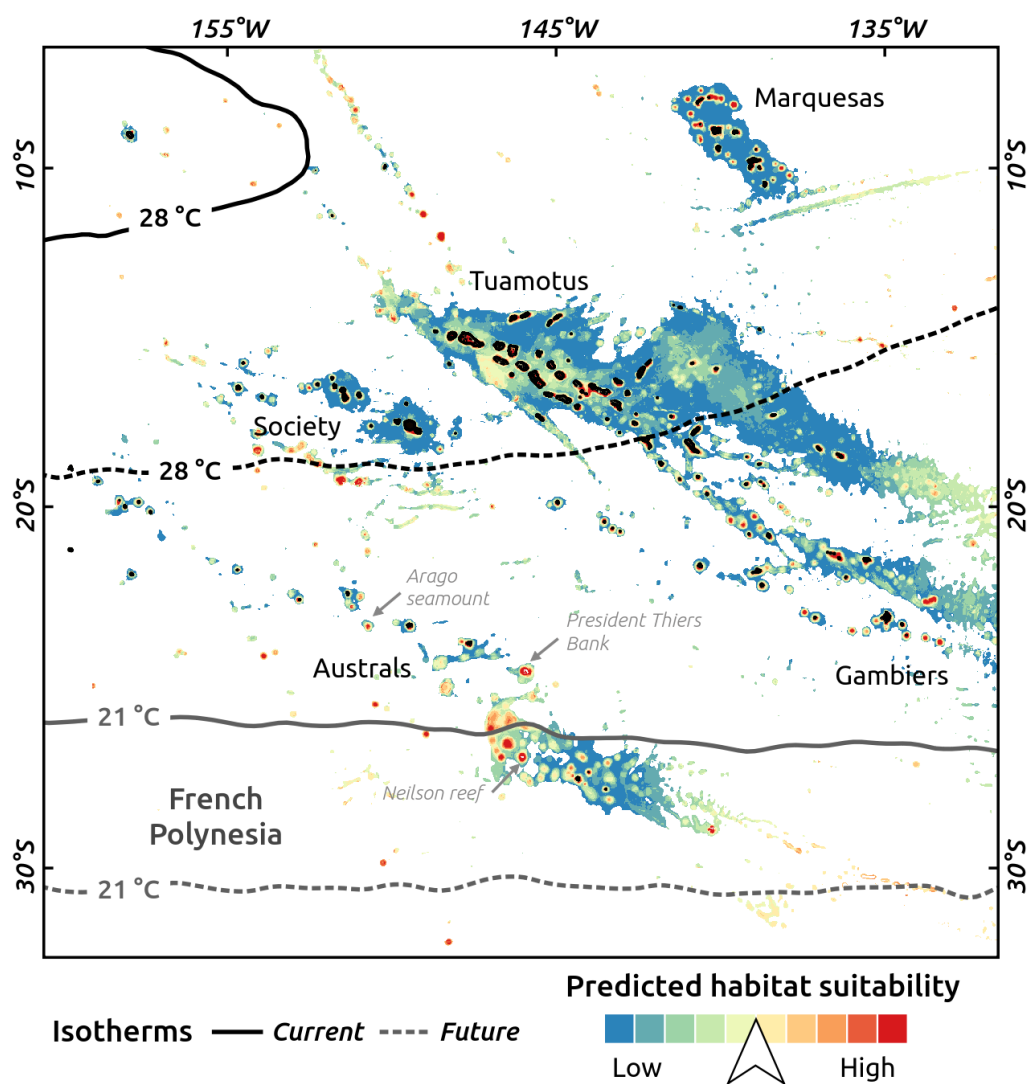


Figure 5.6 Map of humpback whale habitat suitability predicted from fitted responses for western Oceania and transferred to eastern Oceania. Predictions are based on seabed topography only (*DEPTH*, *SLOPE* and *DISSURFRES*). The map is overlaid with average August SST_{coarse} isotherms at 28 °C and 21 °C in the current (solid line: average August SST from Reynolds NCEP Level 4 Optimally Interpolated dataset, between 1999 and 2017) and future period (dashed line: 2080 - 2100 prediction based on CMIP5 models and RCP 8.5 scenario using the method by Knutson *et al.*, 2008). Habitat suitability is shown on a coloured log-scale. White areas represent where the model extrapolated at least one environmental variable beyond the range observed in western Oceania surveys. Islands and reefs are represented in black.

SST_{fine} ranges were different from one region to the other (Fig. 5.4): the western region

displayed the coldest temperatures and the central region the warmest. In central Oceania, humpback whale presence was positively correlated to SST_{fine} . Despite barely overlapping SST_{fine} ranges, humpback whale presence showed similar trends in eastern and western Oceania with respect to SST_{fine} . Cooler waters were related to higher probability of presence, and the warmest areas such as the Marquesas Islands were least suitable (Fig. 5.5).

5.4 Discussion

This study describes the habitat use of humpback whales on the breeding grounds of Oceania, using a large-scale dedicated survey dataset collected over almost two decades. At a coarse scale, humpback whales were observed on breeding grounds averaging 22.3 to 27.8 °C with up to 2.0 °C inter-annual fluctuations in August. SST influenced humpback whale presence locally, in the South Lagoon of New Caledonia, where encounter rates were higher in cooler conditions (< 22°C). In contrast, SST did not significantly affect encounter rates Oceania wide. At a fine scale, topography was an important driver of humpback whale distribution, and here again, their habitat use patterns demonstrated flexibility. The shallowest waters were favoured, but humpback whales showed geographically varying habitat use patterns with respect to islands, reefs, and seamounts.

All of the study sites in Oceania exhibited SST values within the 21 - 28°C range that has previously been established for humpback whale breeding grounds (Rasmussen *et al.*, 2007). However, this study provides the first analysis of SST in relation to whale density within established breeding grounds at a large scale. The sites with the highest encounter rates in Oceania exhibited some of the lowest and the highest average SST values for the region. The highest density site (New Caledonia) was at the lower end (22.3°C) and long-term observations suggested slightly greater encounter rates when water temperatures were cooler (< 22°C). American Samoa was also a preferred site in Oceania and yet was at the high end of the known acceptable breeding ground temperature range (27.7°C). Overall, our results suggest considerable tolerance to SST within the relatively narrow temperature range that has previously been established. However, there may also be temperature preferences both within and among breeding ground sites. The specific importance of SST for breeding is not well understood but may benefit calf thermoregulation, as these younger and smaller individuals are more susceptible to heat loss (Corkeron and Connor, 1999; Clapham, 2000b). Within the suitable environmental space occupied by the species, social factors and culture likely play a large role in humpback whale distribution (Rendell and Whitehead, 2001; Clapham and Zerbini, 2015), specifically through natal philopatry (Baker *et al.*, 2013; Herman, 2017). It therefore remains to be seen whether subpopulations lying on the 'thermal edge' will keep visiting their historical breeding grounds in the future, even if the temperature rises above what is locally optimal.

Differential local SST preferences were identified throughout Oceania. In the New Caledonia South Lagoon, where survey effort was most consistent over a long time period, temporal fluctuation of SST were also found to affect humpback whale presence. The potentially delayed impact of basin

wide climatic phenomena was investigated to explain the changes in encounter rate but these signals did not seem to covariate. The climatic fluctuations of ENSO and the Antarctic Oscillation are known to interact and affect sea-ice concentration in the Antarctic (Curran *et al.*, 2003; Meehl *et al.*, 2016), which in turn impacts biological productivity (Zhang *et al.*, 2014) and humpback whale foraging success. The exact migratory destinations of whales moving south from Oceania breeding grounds are not fully understood, but recent satellite telemetry (Riekkola *et al.*, 2018), genotype matching and photo-identification (Robbins *et al.*, 2011; Constantine *et al.*, 2014; Steel *et al.*, 2017), and mixed-stock analyses (Albertson *et al.*, 2018) have confirmed the wide range of their feeding areas, from the Balleny Islands west of the Ross Sea to the Antarctic Peninsula. The extent to which prey availability over this vast area may affect the migration of humpback whales to their breeding grounds is unknown. Bengtson Nash *et al.* (2018) reported ENSO-related changes in the lipid reserves of humpback whales migrating along the East Australian coast. Changes in migratory departure dates and destination can also be hypothesized as a result of foraging success and/or distribution shifts in the Southern Ocean. Changes in migration length, timing or path could impact humpback whale encounter rates measured at the breeding grounds. Yet, at New Caledonia no relationship was found between the encounter rate and the ENSO or the Antarctic Oscillation from the previous summer. Although varying feeding conditions in the Antarctic are likely to influence northbound migration, this study suggests that SST conditions on the breeding grounds predominantly affect humpback whale encounter rates.

Distribution shifts are considered the most likely response of large mobile cetaceans to climate change (Sydeman *et al.*, 2015; Silber *et al.*, 2017). History has shown that humpback whale distribution can change at the scale of a few decades, particularly in cases of over-exploitation and local extirpation. For instance, humpback whales historically visited Fijian waters in great numbers but relatively few currently do so (Dawbin, 1959; Paton and Clapham, 2002; Gibbs *et al.*, 2006; Miller *et al.*, 2015). By contrast, whales seem to have appeared rather recently in other breeding grounds such as Hawaii (Herman, 1979) and French Polynesia (Poole, 2002; Olavarría *et al.*, 2007). Social aggregation is thought to be a key factor influencing humpback whale breeding ground use of otherwise suitable habitats (Clapham and Zerbini, 2015). Male songs may play a role in attracting conspecifics towards breeding spots as they form (Herman, 1979; Clapham *et al.*, 2008). Although the range of humpback whale songs is likely limited to a few kilometres (~20 km; Garland *et al.*, 2015), there is potential for larger scale attraction to be exerted in cascade (Clapham and Zerbini, 2015). However, humpback whales might not disperse to areas with suitable environmental conditions that may have been erased from the cultural memory of individuals that survived the whaling era (Clapham *et al.*, 2008) or that may be too remote. For instance, the Marquesas Islands include suitable habitat, in terms of seabed topography and temperatures (mean SST_{coarse} Aug = 27.2 °C), but do not currently constitute a humpback whale breeding ground (Gannier, 2002; Poole, 2006). Indeed, during 33 days of survey included in this study that covered the Marquesas Islands, no humpback whales were sighted and no songs were heard (Gannier, 2004). Information regarding the historical presence

of species appears essential to understanding the mechanisms underlying their distribution.

To be successful, distribution shifts require the availability of suitable habitats in proximity to the previously occupied ranges. In Oceania, climate change scenarios suggest a shift of the 28°C surface isotherm by several degrees of latitude south by the end of the 21st century (in the high CO₂ emission scenario RCP 8.5; [Riahi et al., 2011](#)). Noteworthy, other more optimistic scenarios of climate change, such as the RCP 4.5 ([Thomson et al., 2011](#)), would have likely predicted a weaker southward shift of the 28°C isotherm. Nonetheless, to follow this shift and remain in a 21 - 28 °C range, humpback whales would have to relocate their breeding and nursing activities, either to shallow waters currently considered as part of the migratory corridors, such as the Kermadec Islands ([Riekkola et al., 2018](#)), Cook Islands ([Hauser et al., 2000, 2010](#)), Norfolk Island ([Constantine et al., 2007](#)), Pitcairn Island ([Horswill and Jackson, 2012](#)), or to already existing breeding grounds such as New Caledonia, Vanuatu, or the Austral Islands. Considering that these subpopulations are still well below their pre-exploitation numbers (< 50 % recovered, [Jackson et al., 2015](#)), there may be no capacity limit on the southernmost breeding grounds if sub-populations were to relocate there in response to climate change.

In fact, survey effort biased towards nearshore waters has likely underestimated the extent of suitable breeding and nursing habitat in Oceania. Offshore shallow banks and seamounts surveyed in western Oceania have revealed the highest encounter rates across the region (Antigonia seamount > 2 whales.h⁻¹). This unexpected preference for unsheltered offshore shallow waters contradicts the paradigm that humpback whales obligatorily seek shelter for breeding and nursing ([Derville et al., 2018a](#)). In central and eastern Oceania, humpback whales were mainly observed in waters closest to islands or on the external slope of fringing and barrier reefs (see also [Gannier, 2004](#); [Poole et al., 2014](#)). However, the surveys in these regions have focused on waters surrounding islands, with occasional transits through offshore deep waters separating archipelagos. Hence, presence on offshore shallow seamounts could have gone undetected. Transferred predictions using the ecological relationships fitted in western Oceania support the potential for suitable seamount habitats in French Polynesia. These predictions are sustained by anecdotal observations from a survey conducted in July 1999 on a platform of opportunity: three groups of humpback whales were sighted in the offshore shallow areas of the President Thiers Bank (19 m), Arago seamount (28 m), and Neilson Reef (3 m, [Fig. 5.6](#)) in the southeastern Austral Islands ([Gannier et al., 2000](#)). These previously undescribed suitable habitats constitute potential areas for relocation in response to climate change.

If humpback whales are not able to shift their distribution or to find suitable breeding habitat in response to SST changes, deleterious effects could be expected on their reproductive success. Breeding and birth rates have been shown to echo environmental fluctuations associated with ENSO in marine mammals (sperm whales, *Physeter microcephalus*, [Whitehead, 1997](#); southern right whales, *Eubalaena australis*, [Leaper et al., 2006](#); dugongs, *Dugong dugon*, [Fuentes et al., 2016](#)) and migratory seabird species (Laysan and black-footed albatrosses, *Phoebastria immutabilis* & *P. nigripes*, [Thorne et al., 2016](#)). Correspondingly, similar breeding success variations are postulated to occur in the

long term response to climate change (Sydeyman *et al.*, 2015). Hormone analysis (Pallin *et al.*, 2018; Riekkola *et al.*, 2018), stable isotopes (Bengtson Nash *et al.*, 2018), and aerial photogrammetry (Christiansen *et al.*, 2018) provide promising perspectives to monitor the effect of environmental changes on the reproductive success and health of large whales.

Conclusion

This study suggests that most of the currently occupied breeding sites in Oceania might become unsuitably warm for humpback whales by the end of the 21st century. The thermal tolerance displayed by humpback whales in Oceania, combined with flexible patterns of habitat use and the great extent of available suitable habitats, suggest an adaptive capacity of these subpopulations on their breeding grounds. Sensitive breeding habitats at the northern limit of the Oceania range should be the focus of future monitoring to clarify the acceptable temperature range of breeding humpback whales, and their organismal response to climate change. Finally, with growing anthropogenic pressure on both coastal and offshore habitats in Oceania and worldwide, whales are potentially facing cumulative risks (Avila *et al.*, 2018) in addition to climate change. In response to global warming, humpbacks risk relocating their breeding and nursing activities to areas where other threats are greater, e.g., vessel traffic, ocean noise, tourism, pollution or entanglement. In this context, understanding and predicting the distribution of suitable habitats for whales is an important step to support the implementation of appropriate conservation measures.

Acknowledgments

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Appendix 5.A. Effort and observation summaries per country

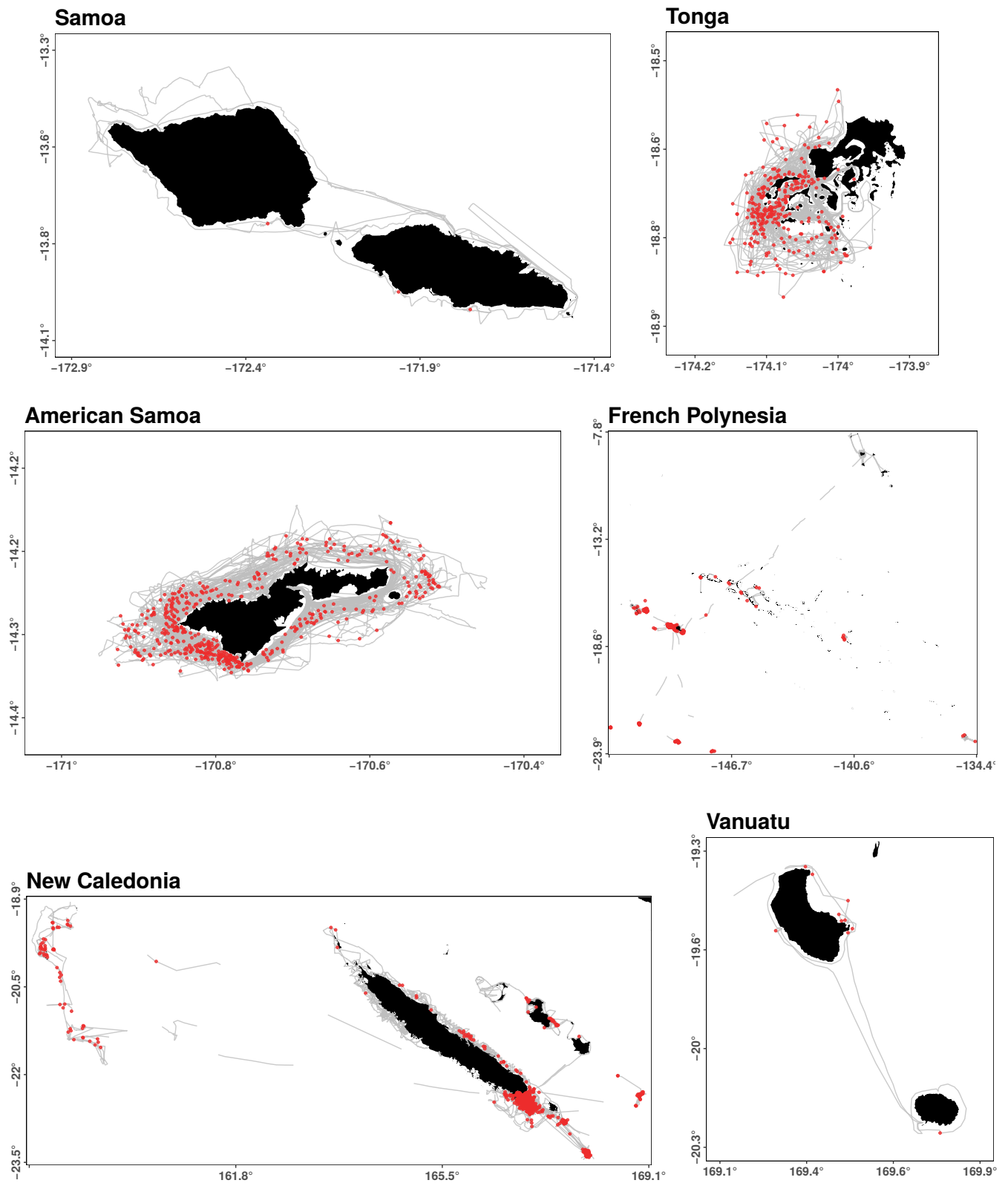


Figure 5.A.1 Maps of humpback whale observations (red dots) and survey effort (grey lines) per country for survey days where GPS tracklines were recorded.

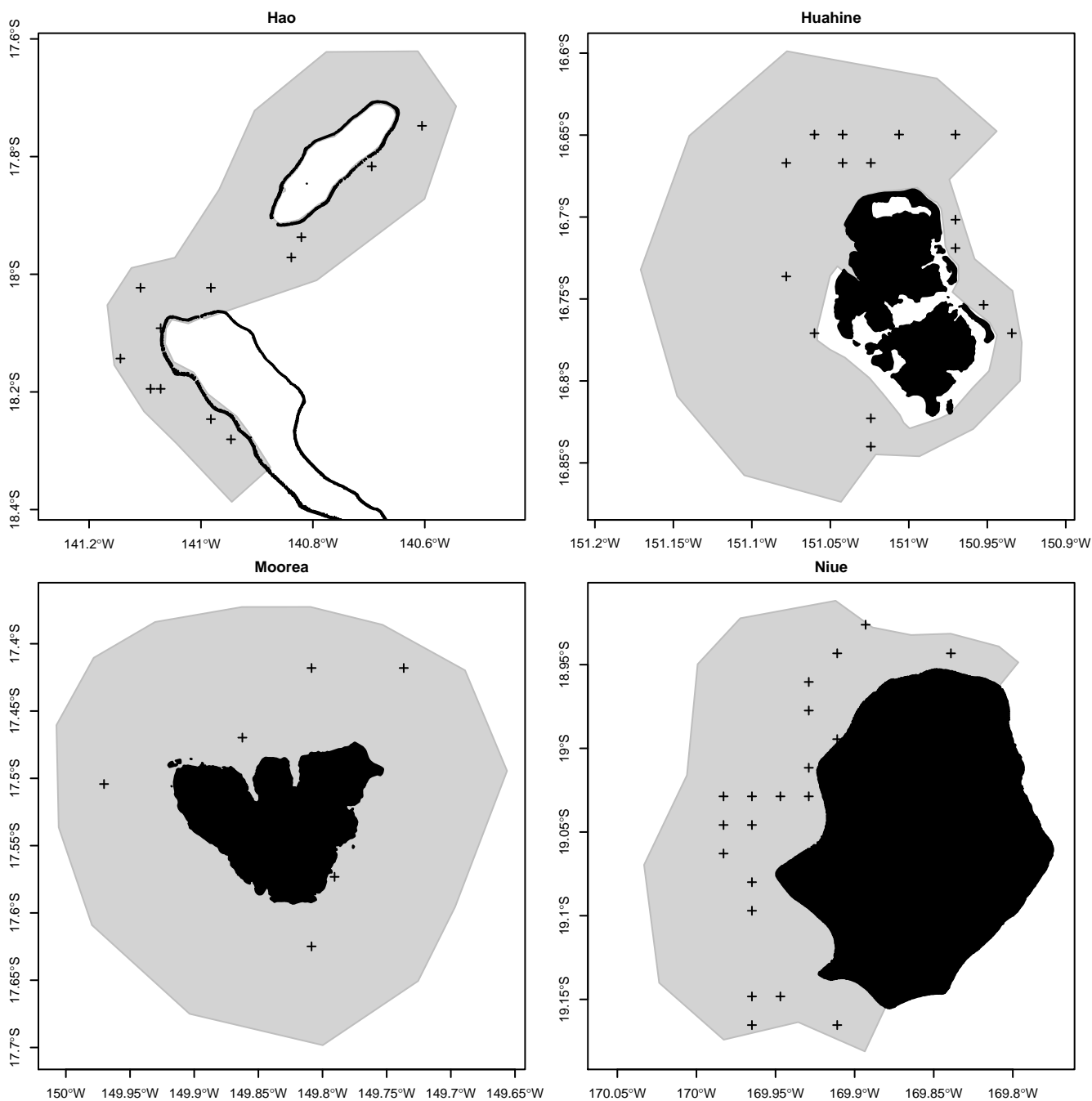


Figure 5.A.2 Expert-based survey extent estimations and background sampling. When GPS tracklines were not available (17% of survey days), the spatial extent of surveys was estimated per study area with the help of the data provider. Polygons were drawn around the survey areas with a 10-km buffer. The areas concerned are Niue ($n = 44$ days of survey), and Hao ($n = 3$ days of survey), Moorea ($n = 39$ days of survey) and Huahine ($n = 137$ days of survey) in French Polynesia. A logarithmic function was defined to describe how the probability of sampling a background point should decrease with increasing distance from the coast. This function was then used in the background sampling process and as a result more background points were sampled in the vicinity of the coast where most of the survey effort was concentrated. The probability of sampling a point was set to 3 times lower at 5 km from the coastline than at 0 km. Similarly to the surveys with GPS tracklines, for each day of survey, background points were sampled randomly within the grey polygons with a higher probability near the coasts. The number of background points was proportional to time on effort and points were separated by a minimum distance of 2 km from each other.

Table 5.A.1 Survey effort per year and per country (in hours). The number of hours of effort was estimated based on the time at start and end of observations recorded for each day of survey. Important note: opportunistic surveys might have been conducted in some years but are not represented here. This table only contains surveys that could be included in the study.

Year	AmericanSamoa	FrenchPolynesia	NewCaledonia	Niue	Samoa	Tonga	Vanuatu
1999	0	199.6	0	0	0	0	0
2000	0	456.8	0	0	0	101.5	0
2001	0	251.7	0	0	0	112.6	0
2002	0	246.6	0	0	0	0	0
2003	57.4	0	261.9	0	0	63.3	55.8
2004	73.1	0	341.8	0	0	78.8	0
2005	53.5	0	355	0	0	96.6	0
2006	55.6	0	319.7	0	0	0	0
2007	79.8	168.8	341.4	0	0	0	0
2008	62.5	63	462.1	0	0	0	0
2009	59.4	0	332.2	0	0	0	0
2010	87.5	145.8	346.6	124.2	0	0	0
2011	57.2	175.4	322.6	43.9	0	0	0
2012	0	226.5	291.4	0	76.9	0	0
2013	0	197.1	370.7	0	0	0	0
2014	53.9	300.5	338.9	26	0	0	0
2015	19.8	0	217.4	0	0	0	0
2016	34.1	0	320	65	0	0	0
2017	51.4	0	523.3	0	0	0	0
Total	745.2	2431.8	5145	259.1	76.9	452.8	55.8

Table 5.A.2 Number of groups of humpback whales observed per year and per country.

Year	AmericanSamoa	FrenchPolynesia	NewCaledonia	Niue	Samoa	Tonga	Vanuatu
1999	0	30	0	0	0	0	0
2000	0	20	0	0	0	68	0
2001	0	16	0	0	0	63	0
2002	0	31	0	0	0	0	0
2003	20	0	71	0	0	35	10
2004	30	0	38	0	0	44	0
2005	18	0	83	0	0	64	0
2006	45	0	117	0	0	0	0
2007	49	39	123	0	0	0	0
2008	53	18	44	0	0	0	0
2009	57	0	102	0	0	0	0
2010	62	11	140	11	0	0	0
2011	54	29	187	12	0	0	0
2012	0	74	117	0	3	0	0
2013	0	109	101	0	0	0	0
2014	32	70	47	4	0	0	0
2015	16	0	99	0	0	0	0
2016	23	0	95	27	0	0	0
2017	36	0	225	0	0	0	0
Total	495	447	1589	54	3	274	10

Appendix 5.B. Predictor collinearity in the fine scale habitat model

In the collinearity analysis (Table 5.B.1), DISSURF and DEPTH were found to be correlated (Spearman coefficient > 0.7) in central and eastern Oceania. SLOPE/DEPTH and yday/SST_{fine} also show some degree of correlation. We focused on DEPTH and DISSURF given the strength of the coefficients found in three regions. We performed sequential regression in order to remove collinearity from the future habitat model of humpback whale presence.

Table 5.B.1 Spearman coefficient of correlation calculated for the fine scale environmental predictors in each study region in Oceania. Correlation is estimated from 47,620 presence-background points at which environmental variables were extracted.

central	DISSURF	DEPTH	SLOPE	yday	SST _{fine}	eastern	DISSURF	DEPTH	SLOPE	yday	SST _{fine}	western	DISSURF	DEPTH	SLOPE	yday	SST _{fine}
DISSURF	-					DISSURF	-					DISSURF	-				
DEPTH	0.76	-				DEPTH	0.87	-				DEPTH	0.64	-			
SLOPE	0.19	0.47	-			SLOPE	0	0.19	-			SLOPE	0.24	0.62	-		
yday	0.26	0.13	0.06	-		yday	0.23	0.11	-0.19	-		yday	0.19	0.21	0.19	-	
SST _{fine}	0.42	0.31	0.24	0.78	-	SST _{fine}	0.11	0.05	-0.14	0.49	-	SST _{fine}	0.13	0.18	0.17	-0.07	-

Appendix 5.C. Sea Surface Temperature Oceania humpback whale breeding range

Points of reference were positioned in the geographic center of each breeding aggregations or study sites: 3 in Western Oceania, 4 in Central Oceania, and 5 in Eastern Oceania (Fig. 5.C.1).

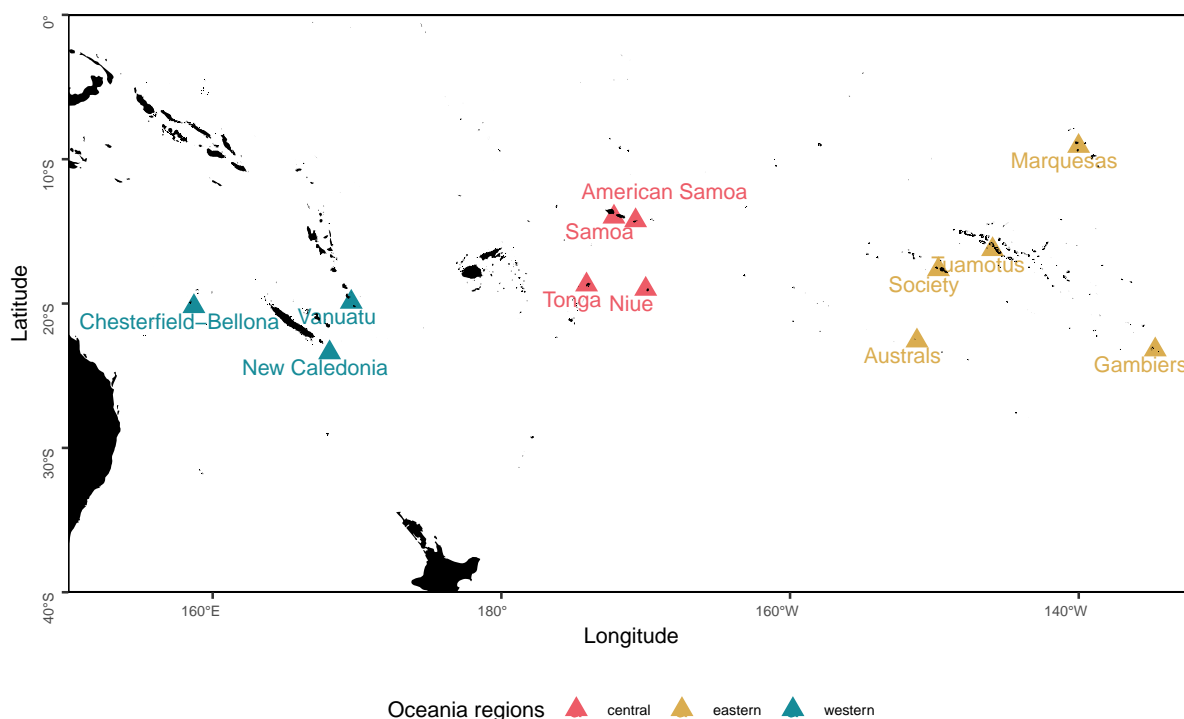


Figure 5.C.1 Points of reference at which SST_{coarse} was estimated from 1999 to 2017 to document mean, minimum and maximum temperatures in August and October.

SST_{coarse} was obtained at daily intervals from the Reynolds NCEP Level 4 Optimally Interpolated SST with a spatial resolution of 0.25° of latitude-longitude. The values were extracted from August 1st to August 31th of each year, as well as October 1st to October 31th, from 1999 to 2017 at the positions of reference (Table 5.C.1). For each study site, SST_{coarse} was averaged in a 1° radius surrounding the designated position.

Table 5.C.1 August and October mean SST_{coarse} were averaged per year and per archipelago. The mean, minimum and maximum temperatures recorded in each archipelago was calculated. From this, an inter-annual range (difference between maximum and minimum SST recorded at a given site over $n = 18$ years) was estimated per site.

Archipelago	lon	lat	August				October			
			mean	min	max	range	mean	min	max	range
American Samoa	-170.70	-14.25	27.67	26.72	28.31	1.59	28.18	27.38	29.12	1.74
Australs	-151.21	-22.58	23.56	22.67	24.20	1.53	23.93	23.39	24.95	1.56
Chesterfield-Bellona	158.70	-20.20	23.37	22.85	23.96	1.11	24.37	22.83	25.50	2.68
Gambiers	-134.70	-23.20	23.36	22.09	23.89	1.80	23.8	22.76	25.16	2.40
Marquesas	-140.01	-9.10	27.20	26.45	27.90	1.45	27.33	26.23	28.16	1.92
New Caledonia	168.10	-23.40	22.26	21.46	23.09	1.63	23.06	21.68	23.86	2.19
Niue	-170.00	-19.00	25.47	24.36	26.22	1.86	26.06	24.92	27.50	2.58
Samoa	-172.20	-14.00	27.80	27.02	28.45	1.43	28.25	27.28	29.10	1.82
Society	-149.72	-17.64	26.41	25.80	26.84	1.04	26.82	26.41	27.87	1.46
Tonga	-174.10	-18.70	25.21	24.12	26.13	2.01	26.05	25.06	27.24	2.18
Tuamotus	-145.97	-16.25	26.66	26.01	27.08	1.07	26.98	26.38	27.63	1.25
Vanuatu	169.60	-19.90	24.17	23.13	24.94	1.80	25.04	23.5	25.92	2.42

Appendix 5.D. Effect of the Southern Oscillation Index and Southern Annular Mode on Encounter rates

In this appendix we describe the M_{NC} models that relate daily encounter rates recorded in the New Caledonian South Lagoon ($n = 774$) to day of year, year and dynamic environmental conditions (SST_{coarse} , SOI or SAM: Table 5.D.1, Fig. 5.D.1). This analysis covers the period 1996 to 2017. The years 2004 and 2008 were removed from the M_{NC} as they only included 6 and 2 days of survey, respectively. The years 1996 to 2002 for New Caledonia were not included to the rest of the study since the data collected over these years did not include GPS tracklines of boat survey effort.

Monthly values of the Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) were downloaded from November to April of each year to represent summer conditions in the Austral Ocean (see: Bengtson Nash *et al.*, 2018). Daily encounter rates and yearly SAM and SOI values are merged together. The SAM/SOI values measured between November of year $y-1$ and April of year y were associated with encounter rates measured during winter of year y (July to September). As a result, encounter rates measured in austral winter were directly related to the previous summer conditions (Fig. 5.D.1).

Table 5.D.1 Generalized Additive Model M_{NC} of encounter rate ($n = 774$ survey days) related to SST_{coarse} , SOI and SAM. Parametric coefficients, approximate significance of smooth terms and deviance explained. edf = estimated degrees of freedom.

	$M_{NC} \sim SST_{coarse}$			$M_{NC} \sim SOI$			$M_{NC} \sim SAM$		
	edf	F-stat	p-value	edf	F-stat	p-value	edf	F-stat	p-value
yday	2.75	9.42	< 0.001	2.69	11.59	< 0.001	2.67	11.43	< 0.001
year	2.51	31.80	<0.001	2.47	30.87	<0.001	2.51	31.35	<0.001
SST_{coarse}	1.56	2.0	0.005						
SOI				0.78	0.52	0.08			
SAM							0	0	0.86
Deviance explained	25.4%			24.5%			24.7%		

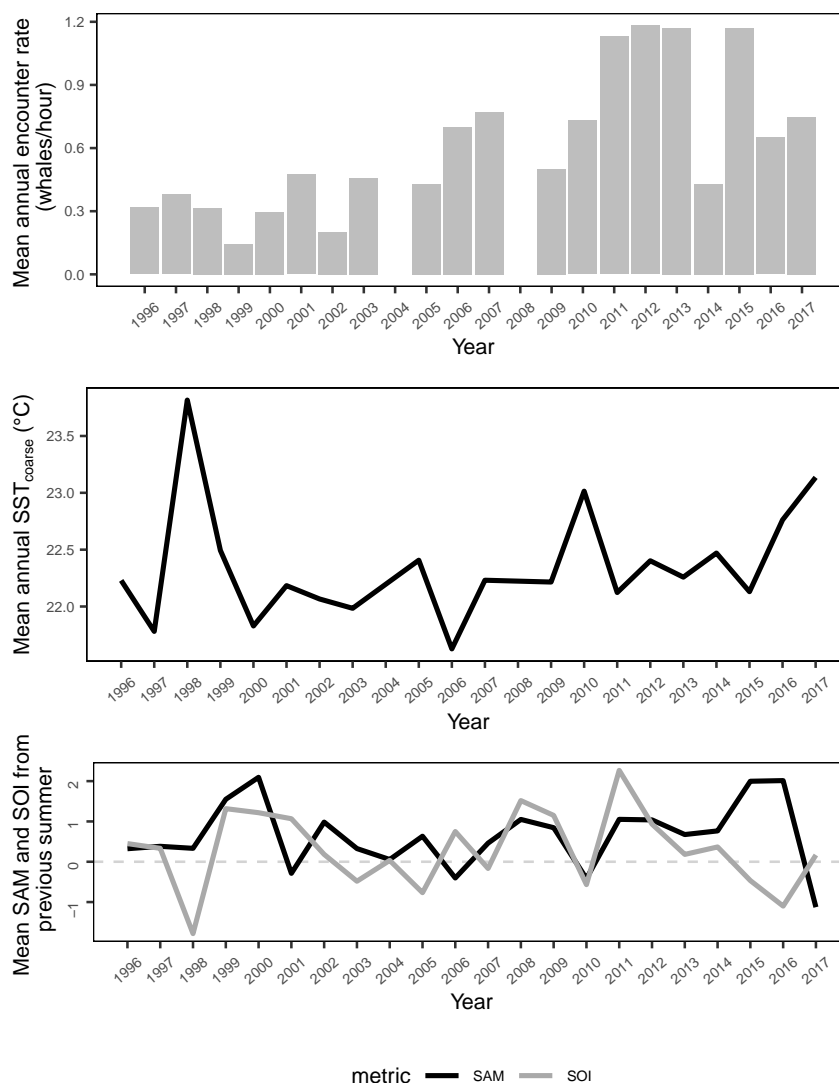


Figure 5.D.1 Encounter rates (whales.h⁻¹ of survey) recorded in the South Lagoon of New Caledonia from 1996 to 2017 and corresponding mean SST_{coarse} , SAM and SOI per year.

Chapter 2 to 5 have shown the diversity of habitats in which humpback whales gather during the breeding season, and the multiple spatial scales of these aggregations. The occurrence of humpback whales at many breeding sites, both nearshore and in the high seas, poses the question of movement between and within critical habitats. On one hand, horizontal movements between breeding grounds would result in connectivity patterns that need to be accounted for to efficiently protect this migratory species. On the other hand, analyzing both horizontal and vertical movements at fine scale would help understand the reasons why humpback whales aggregate in unsheltered offshore waters, in contrast to calm nearshore waters that appear to be favored elsewhere in the world. In Chapter 6, I investigate social and environmental drivers of horizontal and vertical movements of humpback whales based on satellite tracking and diving patterns recorded within breeding latitudes.

VI. Movements in the Coral Sea

Satellite tracking and diving of humpback whales in subtropical waters support seamounts as critical habitats for wide scale movements and breeding activities

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Abstract

Humpback whale's (*Megaptera novaeangliae*) habitat use in low-latitude breeding grounds is well documented from decades of coastal research. Yet, the use of pelagic habitats during breeding and migration has only recently been discovered. In New Caledonia, several offshore seamounts and banks are now considered important areas for humpback whales but the advantages for using these unsheltered waters remain unknown. Over 2016, 2017 and 2018, 18 satellite tags with depth recorders (SPLASH10) were deployed to shed light on environmental and social drivers of seamount association and regional movements of humpback whales during the breeding season. Individuals were tracked for 4.8 to 33.8 days within the breeding study region encompassing New Caledonian waters, the Coral Sea and part of the Australian East Coast. Local movements between shallow offshore seabed features were observed in the New Caledonia southern seamounts and banks, and over the Lord Howe seamount chain. Moreover, two whales performed long regional transits between New Caledonia and the Australian East coast. Most of the 7,986 recorded dives occurred above 80 m (88.5%) but deep dives (> 80 m, max 616 m) were also regularly recorded (11.5%), including from maternal females. Deep dives often occurred in series and were characterized by U-shapes and relatively long durations. Movement analysis in pelagic waters emphasized the influence of shallow seamounts (< 500 m deep) for humpback whale behavior during the breeding season. Residence time significantly increased with proximity to seamounts (13 % deviance explained), while dive depth moderately increased within 100 km of these seabed features. This study provides new insights into the previously disregarded use of pelagic habitats by humpback whales during the breeding season. Given increasing anthropogenic threats on deep sea habitats in New Caledonia and worldwide, this work has both fundamental and conservation implications.

Key words

Satellite tracking, diving, humpback whales, seamounts, Coral Sea, New Caledonia, Australia

6.1 Introduction

Animals are known to display multi-scale patterns of distribution and movements (Guisan and Thuiller, 2005; Benhamou, 2014) as a response to the heterogeneous and patchy spatial distribution of resources (Wiens, 1989) that are required at certain stages of the animal's life cycle. Movements scaling from several thousands kilometers to a few hundred meters have been described in the search for preys that are only available at a given time and within a given habitat. While movements resulting from the search for food resources are a well studied phenomenon, other drivers to movements must be acknowledged. Among them, the search for conspecifics and mating opportunities is a major structuring factor of animal distribution.

Humpback whales (*Megaptera novaeangliae*) undertake some of the longest distance seasonal migrations of any mammalian species (Robbins *et al.*, 2011). They spend summers feeding in polar areas and seasonally migrate toward tropical and subtropical breeding grounds where they spend the winter (Chittleborough, 1958). Humpback whales are known for occupying coastal habitats during their breeding season (e.g., Bortolotto *et al.*, 2017; Cartwright *et al.*, 2012; Guidino *et al.*, 2014; Smith *et al.*, 2012; Trudelle *et al.*, 2016). Yet, there is mounting evidence that breeding grounds may not be geographically and environmentally as restricted as coastal-based studies might have suggested (Derville *et al.*, 2018a,b). Indeed, satellite tracking has revealed the use of offshore shallow features, such as banks and seamounts located within breeding latitudes and over the migratory corridors (Kennedy *et al.*, 2014a; Garrigue *et al.*, 2015; Dulau *et al.*, 2017). Remote tracking technology has allowed to monitor whale behavior and movements in the open ocean, where regular boat-based visual surveys suffer from many logistical impairments. As a result, satellite tracking has revealed that an important part of the breeding season and early migration of humpback whales might be spent in the open ocean (Table 6.1).

In the South Pacific, humpback whales are confronted to a primarily pelagic environment, in which islands, reefs and seamounts are spread out over a vast extent (Valsecchi *et al.*, 2010). This ocean basin is visited by the endangered Oceania population of humpback whales (Childerhouse *et al.*, 2009), structured into sub-populations with varying degrees of connectivity (Childerhouse *et al.*, 2009; Garland *et al.*, 2015; Olavarría *et al.*, 2007). Although these sub-populations are considered genetically separate entities, some level of exchanges has been demonstrated across and within seasons through photo-identification and genotyping (Garrigue *et al.*, 2011a; Steel *et al.*, 2017). The New Caledonian archipelago hosts the most westerly Oceania humpback whale sub-population, the E2 sub-stock (Jackson *et al.*, 2015). This region is neighbored by the East Australian coast, between which the Coral Sea stretches over more than 1300 km. A distinct humpback whale population, the sub-stock E1 migrates along this coast to congregate in breeding grounds roughly located in the Great Barrier Reef area (Paterson and Paterson, 1984; Jackson *et al.*, 2015). Few individuals have been resighted between the New Caledonian sub-stock E2 and the Australian sub-stock E1 (Olavarría *et al.*, 2007; Garrigue *et al.*, 2011b), but genetic differentiation analysis have suggested an otherwise

stronger level of connectivity between these sub-populations (Valsecchi *et al.*, 2010).

The discovery of suitable humpback whale habitats in remote waters of the South Pacific has opened the door to a new understanding of humpback whale distribution in the region. Seamounts, banks and reefs located far from inhabited coasts constitute previously unconsidered habitats for humpback whales to congregate and move across vast distances. New satellite tracking technologies that allow the recording of diving behavior could help understand how humpback whales use pelagic habitats along the breeding season and improve estimates of metapopulation dynamics. Implanted satellite tags were deployed in offshore waters to track individuals over long durations (weeks to months) and capture their horizontal movements and diving patterns in open waters. During previous tagging conducted in the region (Garrigue *et al.*, 2015), tags were mainly deployed late in the breeding season to focus on migratory routes and feeding destinations. In this study, tags were also deployed in the early austral winter in order to capture movements during the breeding season and early migration stages. Through the study of individual horizontal and vertical movements in the New Caledonian region, the goal of this project is to describe the multi-scale aspects of humpback whale distribution and the use of diverse habitats in both coastal and pelagic waters.

6.2 Material and methods

6.2.1 Satellite tag deployment

In order to investigate horizontal and vertical movements of humpback whales in breeding latitudes, 18 SPLASH10 satellite tags (© Wildlife Computers, Redmond, WA 98052, USA) were deployed between July and September, 2016, 2017, and 2018 (Table 6.2) in New Caledonia. Tags were deployed in two oceanic shallow areas (Antigonia seamount, $n = 8$, and Orne bank, $n = 4$) and one remote reef complex (the Chesterfield-Bellona archipelago, $n = 6$), in the Natural Park of the Coral Sea encompassing most of the New Caledonian EEZ (Fig. 6.1a).

Tags were implanted on adult whales, aiming for the front of the dorsal fin, using a modified pneumatic line-thrower (ARTS, Restech, Heide-Jorgensen *et al.*, 2001) set to pressure 10 bars (Garrigue *et al.*, 2015). Tagged whales were photographed using digital camera Canon 40D and 50D equipped with lens 70 x 300 mm or 100 x 200 mm with magnifier 1.4. Both sides of the dorsal fin and the underside of the caudal fluke were photographed when possible. Tissue samples were collected with a crossbow with a specially adapted bolt (Lambertsen *et al.*, 1994). Genomic DNA was extracted from these biopsy samples to identify sex (Gilson and Syvanen, 1998) and individuals (see Garrigue *et al.*, 2004a, for further details). After comparison to the photo-identification and genotype catalogs of humpback whales observed in New Caledonia, tagged whales were individually identified.

Table 6.1 Non-exhaustive list of publications describing long-term satellite tracking of humpback whales. References include studies using implantable tags deployed in breeding grounds or migratory corridors. Depending on the trajectory of the tagged whales, the destination to feeding or breeding grounds is indicated. "OF?" signals if opportunistic feeding was suggested in this article. B, M, F stand for Breeding, Migration and Feeding regions. Crosses represent the level of description provided by each study to these three types of humpback whale habitat. Route habitat corresponds to a qualitative estimate of the main habitat type by which whales transited during migration: C = coastal, P = pelagic.

Reference	Year	Hemisphere	Ocean Basin	Deployment site	Sample size	Destination feeding	Destination breeding	ARS outside main breeding ground	OF?	Majority of tracking			Route habitat
										B	M	F	
Kennedy et al. 2014b	2008-2012	N	North Atlantic	Antillean Island chain	22	Gulf of Maine/Newfoundland/Labrador, Iceland/Norway toward upper Gulf of Alaska	-	Silver and Navidad banks		++	++	+	P
Mate et al. 1998	1995	N	North Pacific	Hawaii	6	Kamchatka Peninsula of Russia, Alaska, Aleutian Islands,	-	-		+	+		P
Mate et al. 2007	1995-2000	N	North Pacific	Hawaii	?		-	Kermit-Roosevelt seamount	+		+	+	P
Lagerquist et al. 2008	2003	N	North Pacific	Revillagigedo Archipelago	11	British Columbia, Alaska	Mexican coast	off Magdalena bay	+	+	+	+	C / P
Rosenbaum et al. 2014	2002	S	Southwest Atlantic	Gabon	13	Bouvet Island		Gulf of Guinea		++	++	+	C / P
Zerbini et al. 2011	2003-2005	S	Southwest Atlantic	Brazil	7	South Georgia, South Sandwich Islands (Area II)	-	-			++	+	P
Dulau et al. 2017	2013	S	Southwest Indian	La Réunion	15	-	Madagascar, Mascarene shelf	La Perouse seamount, Madagascar coast, St Brandon shoal		++	+		C / P
Fossette et al. 2014	2011-2012	S	Southwest Indian	Comoros archipelago	8	towards Area III	Madagascar	Juan de nova, Prince Edward Islands, French sub-Antarctic Islands	+	+	+	+	C / P
Cerchio et al. 2016	2012-2013	S	Southwest Indian	Madagascar	23	-	Mozambic	Aldabara Island, Walters Shoal seamount, Crozet Island		++	+		C / P
Trudelle et al. 2016	2012-2014	S	Southwest Indian	Madagascar	20	-	Mozambic	Walters Shoal seamount, Crozet	+	++	+		C / P
Gales et al. 2010	2009	S	Southeast Indian	Kimberley, West Australian coast	23	Area IV	-	-			+	+	C / P
Gales et al. 2010	2009	S	Southwest Pacific	Evans Head, East Australian coast	15	-	-	-		+	+		C
Garrigue et al. 2015	2007-2012	S	Southwest Pacific	New Caledonia	45	-	-	North Lagoon NC, Fairway and Lansdowne Banks, Antigonina seamount & Torch Bank, Capel seamount, Wanganella Pin seamount, Norfolk Island, Raoul Island.	+	+	+		P
Andrews-Goff et al. 2018	2008-2010	S	Southwest Pacific	Eden, East Australian coast	30	Victoria Land coast and western Ross Sea (Areas IV and V)	-	Tasmania, southern New Zealand coastline			+	++	P
Riekkola et al. 2018	2015	S	South Pacific	Kermadec Islands	18	Ross Sea to Bellinghausen Sea (Areas, V, VI and I)	-	-			+	+	P
Hauser et al. 2010	2006-2007	S	South Pacific	Cook Islands	8	Area VI (one whale)	Samoa	-		+	++	+	P
Félix and Guzmán 2014	2013	S	Southwest Pacific	Ecuador	6	Area I	-	Paracas coast of Peru	+		+	+	C / P

6.2.2 Marking the boundaries of the breeding region

As the goal of this study was primarily to describe regional movement patterns of humpback whales within and between breeding grounds, the tracking dataset was limited to the area assumed to host breeding, calving, nursing and early migration. It has been argued that water temperature mattered more than latitude to explain the distribution of breeding grounds worldwide. [Rasmussen et al. \(2007\)](#) reviewed breeding SST in both hemispheres and found that all breeding grounds were included in an average range of 21.1°C to 28.3°C. Following this assessment, the climatology of austral winter SST was calculated for the region, using monthly remotely sensed SST products acquired for the months of July to October, from 2003 to 2014 with a spatial resolution of 1 km (MURSSST, <https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>). The average isotherm at 21°C was calculated to delineate the southern boundary of the breeding study region (Fig. 6.1a).

Table 6.2 Summary of satellite tracking for the 18 humpback whales tagged with SPLASH10 tags (© Wildlife Computers) in New Caledonia. NCT = New Caledonian local time zone. # stands for 'number of'. The minimum total distance (km) is the along-the-path distance calculated from the CRW-interpolated tracks. Sex: F = Female, M = Male. Group type at the time of tagging: MC = Mother-calf, MCE = Mother calf escort, MCC = Mother calf and competitive group, C = competitive group, G3 = Group of three adults, G4 = Group of four adults, P = Pair, S = Singleton. Group type may have evolved during the focal follow (indicated by two group types, e.g., P-G4). Locality: O = Orne bank, A = Antigonias seamount, CB = Chesterfield-Bellona archipelago. Date leaving the breeding region is annotated, '-' when the tag stopped emitting before the whale left the breeding region.

Year	ID	Sex	Breeding status	Group threetype	Locality	Start (NCT)	Tag duration (days)	Date leaving the breeding region (NCT)	WITHIN BREEDING REGION				Dive profiles recorded (hrs)	
									Tag duration (days)	Minimum total distance (km)	# raw positions	# filtered positions		# dives recorded
2016	154182	F	With calf	MCE	O	23/09/2016	9.8	-	9.8	809	56	49	165	2
	154183	F	-	P	O	24/09/2016	37	07/10/2016	13.9	971	133	126	736	5
	154184	F	With calf	MCE	O	23/09/2016	15.2	30/09/2016	7.7	571	32	30	80	3
	154187	M	-	MCC	O	24/09/2016	25.8	02/10/2016	8.8	1041	42	33	25	0
2017	34215	F	-	G3	A	24/07/2017	125.3	09/08/2017	17.1	1194	123	106	184	7
	154185	M	-	G3	A	24/07/2017	29	-	29	3429	242	206	975	36
	34222	F	With calf	MC	CB	22/08/2017	33.8	-	33.8	1907	203	187	555	18
	34223	P	-	P	CB	17/08/2017	6	-	6	390	42	35	110	5
	34226	F	-	S	CB	22/08/2017	46.7	21/09/2017	30.5	2705	206	169	465	5
	34227	F	With calf	MC	CB	18/08/2017	70.5	-	70.5	4858	450	386	1188	27
	34228	F	With calf	MC	CB	20/08/2017	4.8	-	4.8	279	25	24	100	6
	34221	F	-	P	CB	12/08/2017	5.8	-	5.8	496	5	6	25	0
2018	34350	F	-	C	A	17/07/2018	32.9	24/08/2018	19.9	1552	192	157	730	18
	34354	M	-	P-G4	A	21/07/2018	45.0	12/08/2018	32.5	3915	173	87	205	6
	57535	M	-	G3	A	17/07/2018	8.8	-	8.8	500	94	81	249	7
	57536	M	-	G4	A	21/07/2018	21	-	21	1519	235	193	718	25
	57537	M	-	C	A	21/07/2018	10.8	-	10.8	617	154	131	715	24
	57538	M	-	G3-G5	A	21/07/2018	54.7	21/08/2018	32.1	2618	344	277	761	32

6.2.3 Filtering and modeling of satellite tracks

ARGOS locations were filtered to remove invalid locations of class Z, locations on land and locations implying unrealistically rapid movements (speed > 18 km/h; [Zerbini et al., 2015](#)). Whenever a track was interrupted for more than 72 hours, the track was considered to be constituted by several segments, which were subsequently modeled separately. Track segments were projected in a Pacific-centered Mercator coordinate system and were interpolated at one position every 6 hours with a Continuous-time Correlated Random Walk (CRW) model using the *crawl* R package version 2.1.1 ([Johnson et al., 2008](#)). CRW model movement as a velocity process, characterized by two parameters:

β , the velocity autocorrelation, and σ , the velocity variation. Using these models, the animal's position can subsequently be predicted at any time, from the start to the end of the original track. The error on ARGOS positions was incorporated as the ellipses semi-minor and semi-major axis error, with deployment GPS positions included with ellipses logarithmic error set to 0. The β parameter was constrained between [-3, 4] bounds and was optimized using a Normal distribution prior with mean -0.15 and standard deviation 1.5. The σ parameter was left unconstrained and was optimized from a start value of $\log(10)$.

Distance covered by each tagged whale was calculated along the crawl-interpolated track segments, within the previously identified breeding study region. In order to assess movement type along the track, residence time was calculated along the crawl interpolated tracks. This metric corresponds to the total amount of time spent, both backward and forward, within a virtual circle (of radius ρ) centered on a given location, provided the animal did not move out of the circle for more than a time threshold (τ). Residence time therefore provides an integrative measure of space use, combining both path tortuosity and speed (Barraquand and Benhamou, 2008). Residence time may reveal areas of Area Restricted Search (ARS) where animals slow down and display more sinuous paths as a result of a spatially-restricted activity such as resting, feeding, or interacting with conspecifics. ARS behavior is scale-dependent, a pattern that can easily be tested using varying radii ρ in the residence calculation. Here, residence time was calculated in a radius ρ of 1, 5, 10 or 20 km (with a time threshold τ of 12 hours) for each tagged individual. The log-transformed variance of the residence time values was averaged across individuals in order to determine the best study scale (Fauchald and Tveraa, 2003). The 10 km radius was found to maximize the variance of residence time and was therefore selected for further analysis.

6.2.4 Diving behavior analysis

Diving behavior analysis was limited to dives recorded while the humpback whales were in the breeding study region initially defined. For every dive event greater than 11 meters in depth and 1 min in duration, the SPLASH10 tags recorded three main parameters: dive depth (maximum depth reached during dive, in meters), dive duration (in minutes) and dive shape.

Dive depth is recorded by SPLASH10 tags as a confidence interval containing the depth reached at the bottom of the dive. On average, this confidence interval was equal to 0.76 m (\pm SD 1.27) and was considered negligible. Dive depth was therefore estimated as the median depth value in this interval.

Similarly, dive duration was recorded by SPLASH10 tags with a systematic 2 minutes confidence interval. Dive duration was therefore estimated as the median duration for this confidence interval. Furthermore, on very rare occasions (0.08% of dives), the wet/dry sensor did not detect the surfacing event following a dive, hence resulting in aberrant values of dive duration (max = 62 min). Based on the distribution of outliers, dives > 30 min were filtered out.

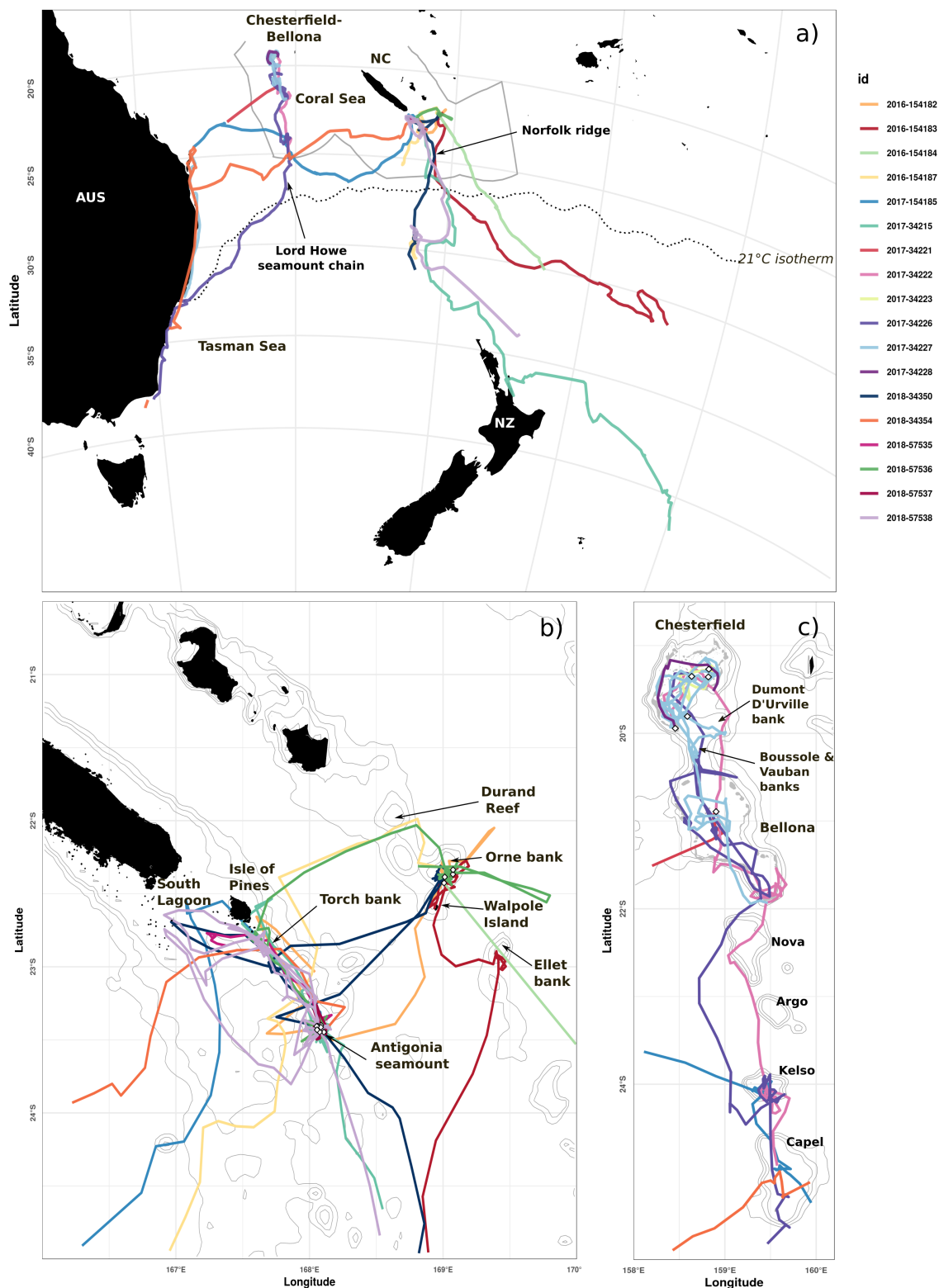


Figure 6.1 Satellite tracks recorded from 18 SPLASH10 tags deployed on humpback whales in New Caledonia. a) Regional view (with southern borders of the Natural Park of the Coral Sea in grey), b) Zoom on Southeastern New Caledonia, and c) Zoom on the Chesterfield-Bellona reef complex and Lord Howe seamount chain. Grey lines represent 500 m isobaths up to 2000 m deep. Land is shown in black. The locations of tag deployments are shown with white diamond shapes. The breeding study region is demarcated by the 21°C isotherm shown with a dotted line in a). NC = New Caledonia, NZ = Neze Zealand, AUS = Australia.

Dive shape included three categories depending on the time spent at the bottom of the dive (i.e. below 80% of the maximum dive depth reached for a given dive). During square-shaped dives, whales spent 50% of the dive duration at the bottom. In U-shaped dives, they spent between 20 and 50% of their time at the bottom. In V-shaped dives, they spent less than 20% of their time at the bottom.

Dive depth and duration were analyzed at the tagged population scale, with all tagged individuals pooled together to describe the overall vertical movement characteristics within the breeding region. Based on the relation between dive depth and duration (see Fig. 6.4), dives were categorized into two classes: deep dives > 80 m, and shallow dives between 11 and 80 m. Dive depths and durations were compared between males, females, and females with a calf, using non parametric Kruskal-Wallis tests.

Tags were also set up to record dive profiles during 24 hrs, every 7 days (in 2016) or every 3 days (in 2017 and 2018). Dive profiles record the whale's depth at a frequency of 75 s. They allowed a finer analysis of humpback whale behavior at depth such as the calculation of the time spent at the bottom of deep dives.

6.2.5 Effect of habitat on vertical and horizontal movement

The geographic positions of dives were estimated using the CRW models from each track segment. The *crwPredict* function from the R *crawl* package was applied to predict dive position in a Mercator projected coordinate system, based on the time at which the dive occurred. The predictions were associated with a standard error in projected latitude and longitude to assess the accuracy of dive positioning. Preliminary analysis showed that the error associated with predicted dive positions was positively correlated with the time elapsed between a given dive and the most recent ARGOS filtered position recorded by the tag (longitude error: Pearson's $r = 0.71$, $t = 89.2$, $df = 7984$, p -value < 0.001; latitude error: Pearson's $r = 0.76$, $t = 104.8$, $df = 7984$, p -value < 0.001). In order to remove potentially mispositioned dive events, all dives recorded more than 6 hours away from an ARGOS position were removed from further analysis. This filtering represented 3.4% of dive data, equivalent to 274 dive events removed (including 38 deep dives).

Track and dive positions occurring in 'sheltered' waters of the East Australian coast, the New Caledonian lagoons and the Chesterfield-Bellona plateaus were excluded (Appendix 6.A.1), in order to study humpback whale movements in pelagic areas. Dive depths in pelagic waters were compared between night and day time (using a 6 a.m. / 6 p.m. cut-off), using a mixed-model extension of the Wilcoxon test (*nestedRanksTest* R package, version 0.2), where diel phase was treated as a fixed effect and individual was included as a random effect.

Pelagic residence time and maximum dive depth were then averaged over individual grids of 10 km resolution. Residence time was averaged per grid cell for each tagged whale, then individual residence time grids were averaged together. The maximum dive depth was calculated per grid cell

for each tagged whale, then individual dive grids were averaged together. Gridded residence time and maximum dive depth were modeled as a function of distance to the closest shallow seamount and banks using Generalized Additive Models (GAM, [Hastie and Tibshirani, 1990](#)). Seamount positions and depths were obtained from the Pacific database in [Allain *et al.* \(2008\)](#). Shallow seamounts (< 500 m deep) were selected, following [Hann *et al.* \(2016\)](#) and [Morato *et al.* \(2008\)](#) who identified seamount depth as an important factor of attractivity for cetaceans. GAMs were applied with the *mgcv* R package (version 1.8-23). Both the mean residence time and mean maximum dive depth were modeled as Gaussian response variables with a log link function. The smoothed effect of distance to seamounts was optimized by Restrictive Maximum likelihood (REML) and cubic smoothing splines with basis size limited to 3 to prevent overfitting ([Wood, 2017](#)). The descriptive performance of models was assessed through the computation of the proportion of deviance explained ([Guisan and Zimmermann, 2000](#)). The deviance explained (%) is calculated from the null deviance (deviance for a model with just a constant term) minus the residual deviance (deviance of the fitted model with explanatory terms).

6.3 Results

6.3.1 Localized and regional movements

Among the ARGOS positions conserved after filtering, 0% to 27% recorded in the breeding study region belonged to classes 0, 1, 2 or 3 (mean = 10% \pm SD 8.4%). Tagged whales included seven males, 10 females (including 5 females with a calf at the time of tagging) and one unsexed individual. Whales were tracked for an average of 32.4 days (\pm SD 29.9, min = 4.8, max = 125.3 days), including an average of 20.2 days (\pm SD 16.3) in the predefined breeding study region (Table 6.2) and showed both localized and regional movements.

Humpback whales tagged in the New Caledonia southern seamounts and banks displayed localized movements between coastal and offshore shallow waters (Fig. 6.1b). Among the 12 whales tagged in Orne bank and Antigonie, 3 visited the South Lagoon (#154185, #34350, #57538) and 4 visited waters around the Isle of Pines (#34215, #57535, #57536, #154182). A connectivity between Orne bank and Antigonie was also revealed, as 3 whales out of 12 visited both sites (#154182, #57536, and #34350). Similar localized movements were observed for whales tagged in the Chesterfield-Bellona reef complexes. They displayed restricted movements within these plateaus before initiating their southward migration (Fig. 6.1c). While they spent some significant time in the sheltered waters of the inner reefs, they also visited shallow offshore features such as the banks located between the Chesterfield and the Bellona plateaus. Indeed, 3 of the individuals tagged in the Chesterfield visited the Dumont D'Urville, Vauban and Boussole banks (#34222, #34226, #34227).

Extensive regional movements were also observed. Humpback whales leaving the southeastern waters of New Caledonia followed two main trajectories. Six whales moved south and southeast:

three passed by Norfolk Island, one passed by New Zealand and two went in the direction of the Kermadec Islands. Two whales moved west (#154185 and #34354), stopped over the seamounts of the Lord Howe chain and finally reached the East Australian coast around 25°S (Fig. 6.1a). Interestingly, four of the six whales moving over the southeastern corridor were females, whereas the whales moving west were identified as two males (Table 6.2).

In Chesterfield-Bellona, two females (#34222 with a calf, and #34226) could be tracked south of the sheltered coral reef complexes, and they both passed by the Nova seamount, then spent time over the Kelso and Capel seamounts (10 days for #34222 and 8 days for #34226). Despite discontinuities (#34227) or early interruption (#34221) in the tracking of some individuals, three out of the six whales tagged in the Chesterfield-Bellona moved westward after leaving the plateaus. Two females (#34227 with a calf, and #34226) were tracked while migrating south along the East Australian coast in 2017, plus one male in 2018 (#34354).

6.3.2 Diving behavior in breeding latitudes

Dive depths in the breeding region were mostly concentrated between the surface and 80 m (88.5 % of dives, Table 6.3, Fig. 6.2). A minority of dives occurred below 80 m (11.5 %), with a maximum depth of 616 m reached by female #34226 east of the Bellona plateau. Deep dives below 80 m often occurred in series of several dives, as shown in the examples Fig. 6.3. Deep dives were performed by all categories of individuals (Table 6.3), including females with a calf (max depth = 336 m).

Sex and breeding status significantly influenced dive depth of individuals (Kruskal-Wallis rank sum test: $\text{Chi}^2 = 117.5$, $\text{df} = 2$, $p < 0.001$), as males dove on average deeper (mean = 51.1 m \pm SD 59.2), followed by females without a calf (mean = 50.7 m \pm SD 55.6), and females with a calf (mean = 36.2 m \pm SD 33.4). Sex and breeding status also significantly influenced dive duration of individuals (Kruskal-Wallis rank sum test: $\text{Chi}^2 = 41.5$, $\text{df} = 2$, $p < 0.001$), as females without a calf dove on average longer (mean = 6.3 min \pm SD 4.7), compared to males (mean = 5.5 min \pm SD 4.1), and females with a calf (mean = 5.2 m \pm SD 3.2).

Dive depth and duration showed a positive non linear correlation ($n = 7984$, Spearman's $\rho = 0.50$, $p < 0.001$). Based on dive shape, duration and depth, two categories of dives could be distinguished (Fig. 6.4). Deep dives below 80 m showed intermediate duration (mean = 8.3 min \pm SD 3.3, max = 24 min) and a majority of U-shapes (76 %). Shallow dives above 80 m had shorter durations on average (mean = 5.3 \pm SD 4.1, max = 26) and were primarily square-shaped (54 %). V-shapes were generally the less common (6.2 % overall), and were found both in deep and shallow dives.

Dive profiles were recorded during 226 hours, spread over 170 separate dive bouts, representing an average of 14.1 hours (\pm SD 11.4) per individual. Among these dive profiles, 48 bouts representing 66 hours of recording contained at least one deep dive below 80 m. In these profiles,

series of deep dives could be observed and time spent at depth could be evaluated (Fig. 6.5). For instance, the whale #34215 dove in a series of increasingly deep dives, from about 80 m to more than 300 m. Time spent at the bottom of the two deepest dives reached 5 minutes (Fig. 6.5).

Table 6.3 Summary of diving behavior recorded for the 18 humpback whales tagged with SPLASH10 tags (© Wildlife Computers) in New Caledonia. Sex: F = Female, F/c = Female with a calf, M = Male. Locality: O = Orne bank, A = Antigonion seamount, CB = Chesterfield-Bellona archipelago.

year	ID	Sex/Status	Locality	Dive depth (m)			% dives > 80 m	Dive duration (minutes)		
				mean	sd	max		mean	sd	max
2016	154182	F/c	O	62.5	59.7	336	24.8	6.3	3.6	16.1
	154183	F	O	47.8	52.5	288	13.9	4.8	3.5	16.4
	154184	F/c	O	43.6	57.4	240	16.2	4.2	2.4	10.6
	154187	M	O	29.2	21.2	92	4	6.6	3.4	13.1
2017	34215	F	A	44	45.1	344	11.4	6.5	4.6	22
	154185	M	A	60	69.4	392	15.9	5.3	3.8	16.7
	34222	F/c	CB	47.7	40.6	288	15	5.6	3.3	18.4
	34223	-	CB	47.1	28	188	4.5	6	4.2	22.3
	34226	F	CB	50.1	52.9	616	10.5	6.9	4.7	22.1
	34227	F/c	CB	27.4	14.7	192	0.1	4.7	3	24.3
	34228	F/c	CB	28.2	16.7	74	0	6.6	3.1	13.8
	34221	F	CB	55.5	60.6	220	12	11.5	7.8	23.7
2018	34350	F	A	55.5	61.8	448	20.1	7.2	5.2	24.2
	34354	M	A	62.2	42.6	312	25.9	6.9	4.9	23.2
	57535	M	A	38.6	34.5	296	7.2	4.4	2.9	12.2
	57536	M	A	35.2	30.4	376	4.5	6.9	4.5	26.2
	57537	M	A	38	36.8	303	4.8	4.5	3.3	19
	57538	M	A	68.8	82	520	20.9	5.3	4.5	21.9

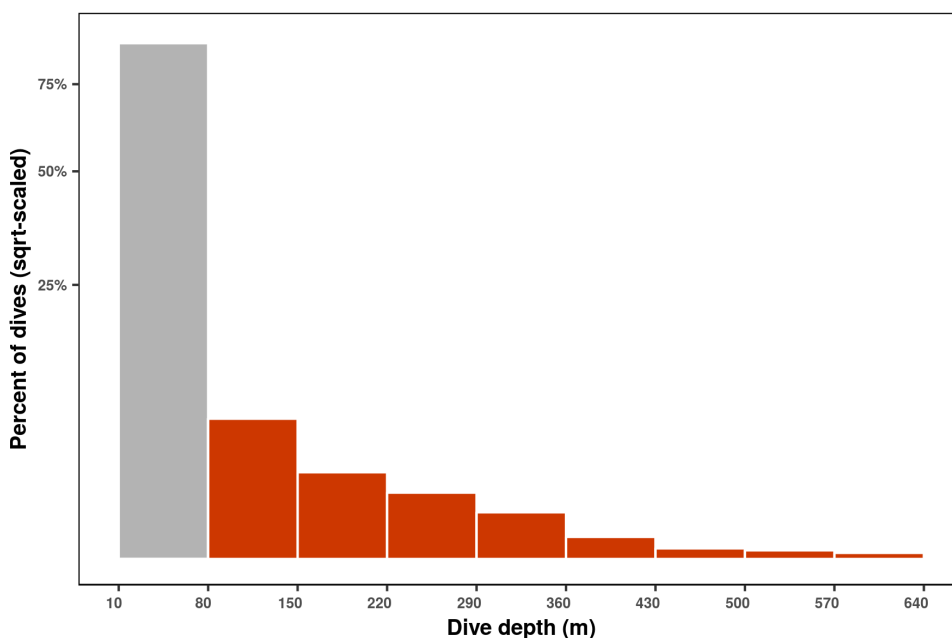


Figure 6.2 Distribution of dive depth recorded for 18 humpback whales tagged in New Caledonia ($n = 7,986$ dives). Red bars represent the deep dives recorded in the region.

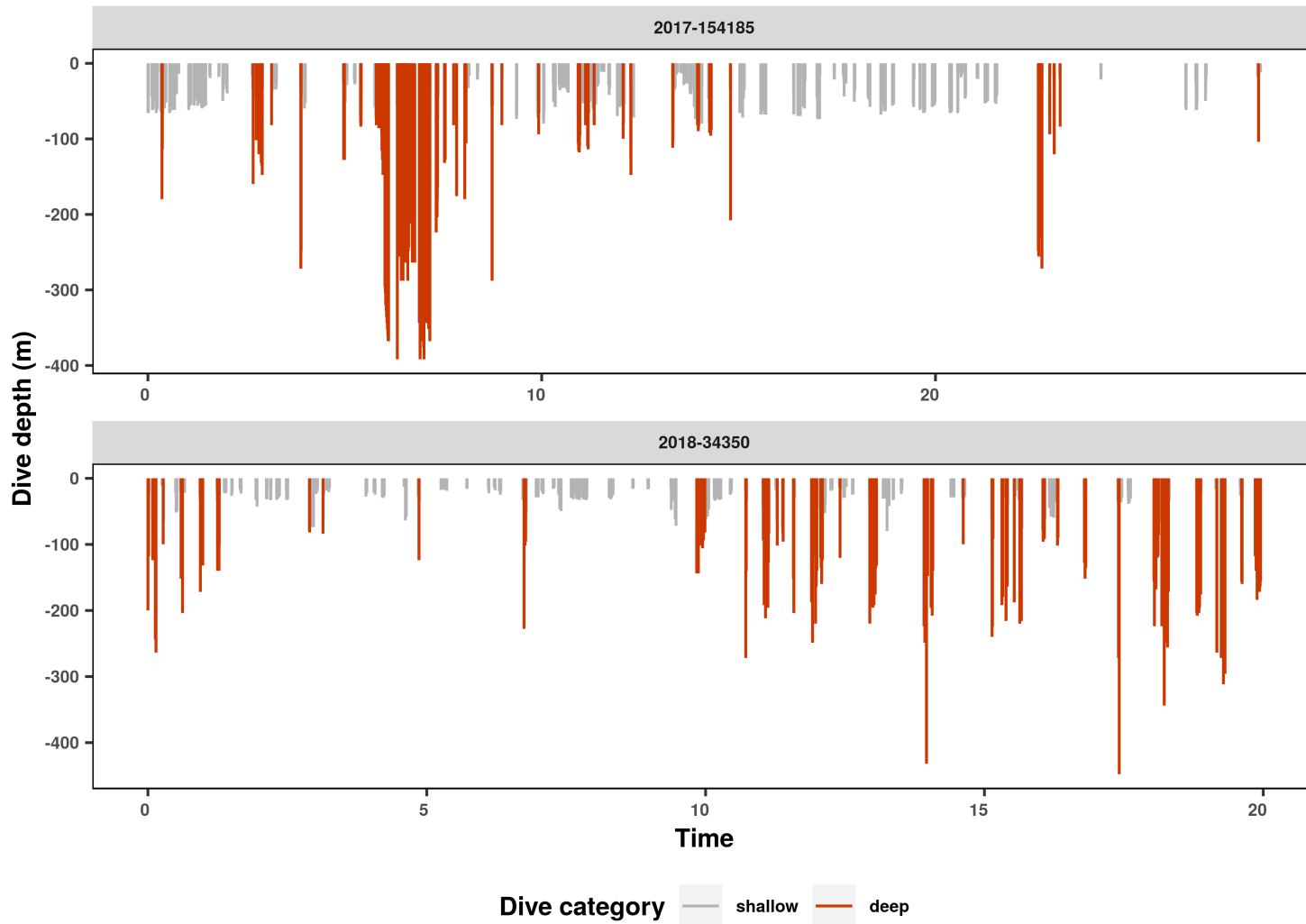


Figure 6.3 Dive depths through time for two whales tagged in New Caledonia (male #154185 and female #34350). The x-axis represents time from deployment in days. Each vertical bar represents a single dive event. Dives deeper than 80 m are shown in red.

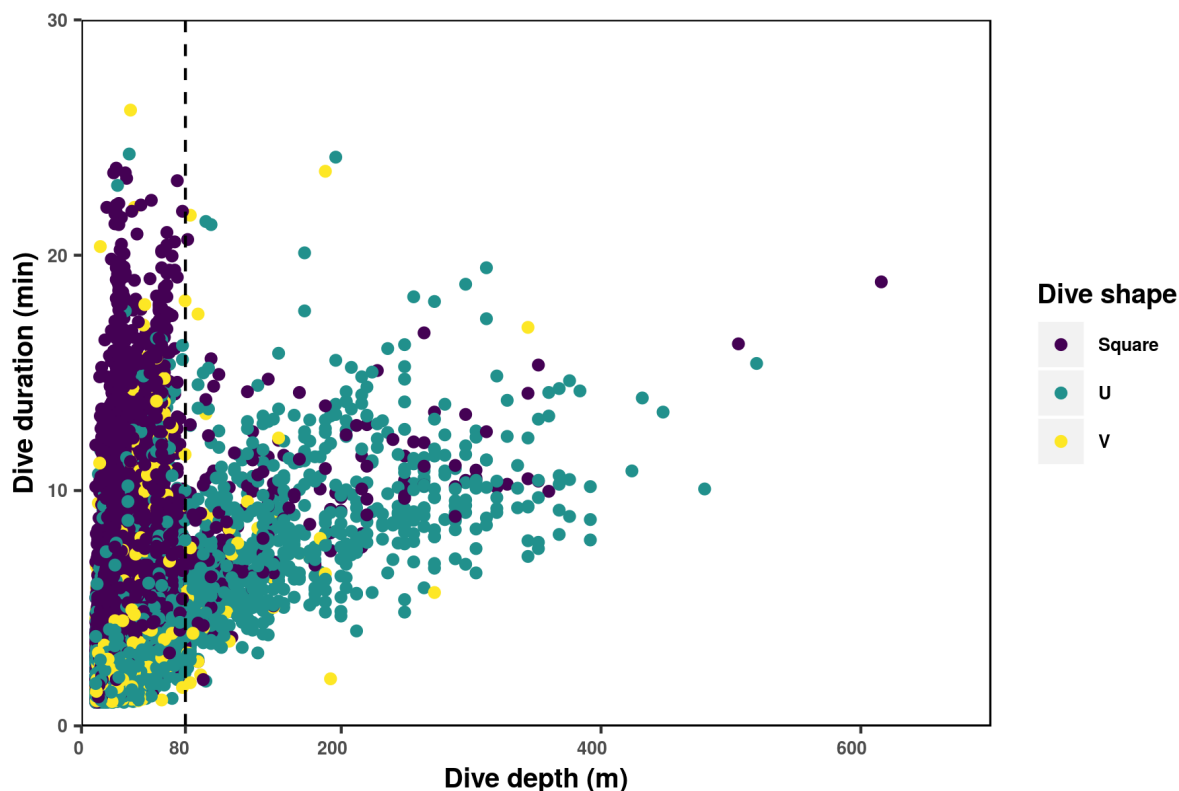


Figure 6.4 Relation between dive depth and duration for 18 whales tagged in New Caledonia ($n = 7,986$ dives). The dashed line delineates dives deeper than 80 meters. Dive shape (Square, U and V) are represented in color.

6.3.3 Pelagic movements in relation to habitat features

Out of 18 tagged whales, only 16 individuals had dive events recorded in pelagic habitats. Most of the deep dives were recorded when whales were in the vicinity of the Lord Howe seamount chain, the Norfolk Ridge and the Loyalty Ridge (Fig. 6.6). Diel phase did not significantly affect dive depth in pelagic habitats (Nested Wilcoxon test $Z = -0.18$, $p = 1$, see Appendix 6.B.1 & 6.B.2 for more details).

Gridded maps of residence time and maximum dive depth further revealed intense use of shallow seabed features such as seamounts located over these ridges (Fig. 6.7 & 6.8). Distance to shallow seamounts explained a significant part of mean residence time (GAM deviance explained = 13%). Indeed, residence time increased when whales were close to seamounts shallower than 500 m (GAM: edf = 1.9, $F = 44.07$, $p < 0.001$; Fig. 6.9). The average maximum dive depth also appeared to be related to distance to seamounts (GAM deviance explained = 3.2%), although this relation was faint. The average maximum dive depth was higher within 100 km of a shallow seamount (GAM: edf = 1.9, $F = 8.2$, $p = 0.0004$; Fig. 6.9).

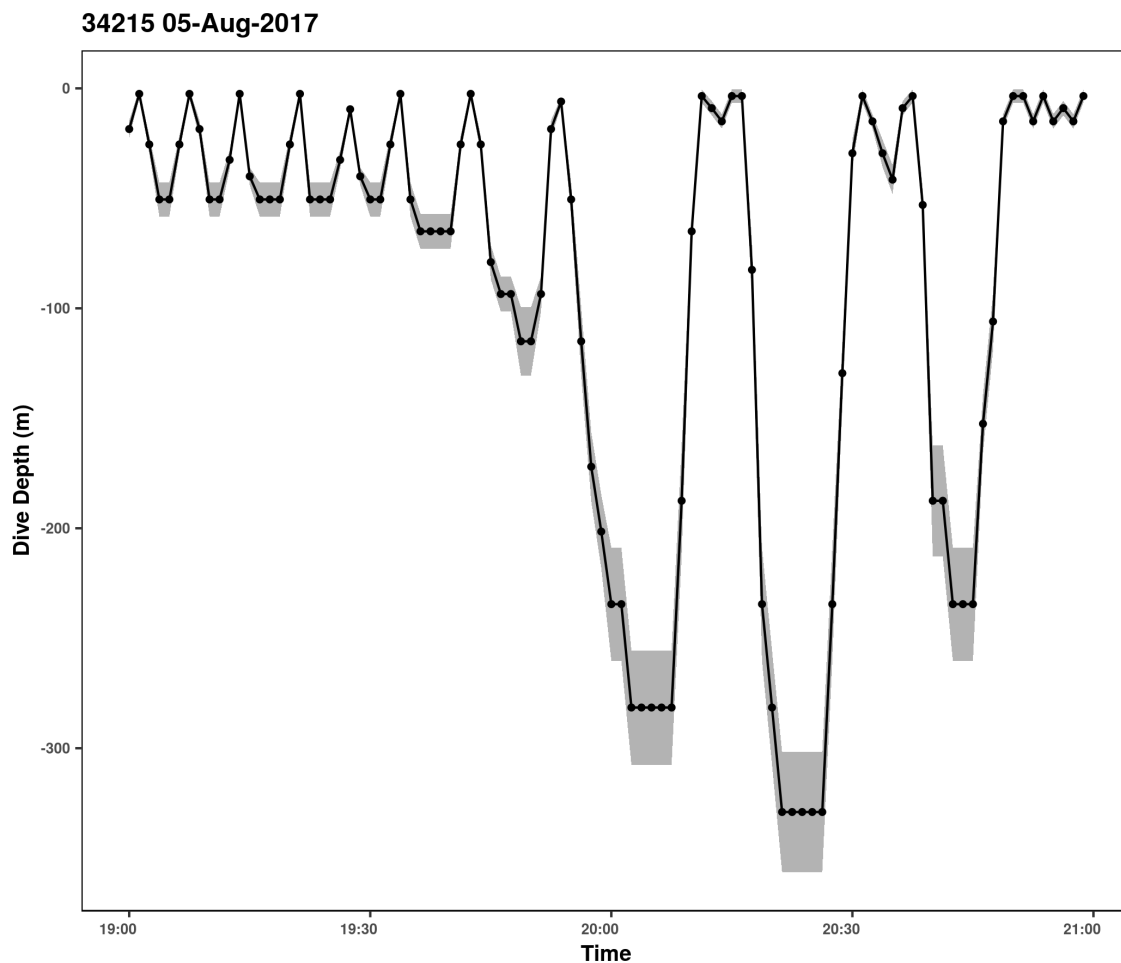


Figure 6.5 Example of a dive profile for the humpback whale #34215 (female), recorded at a frequency of one measurement every 75 seconds on August 5th, 2017. The grey ribbon shows the uncertainty of the depth measurement.

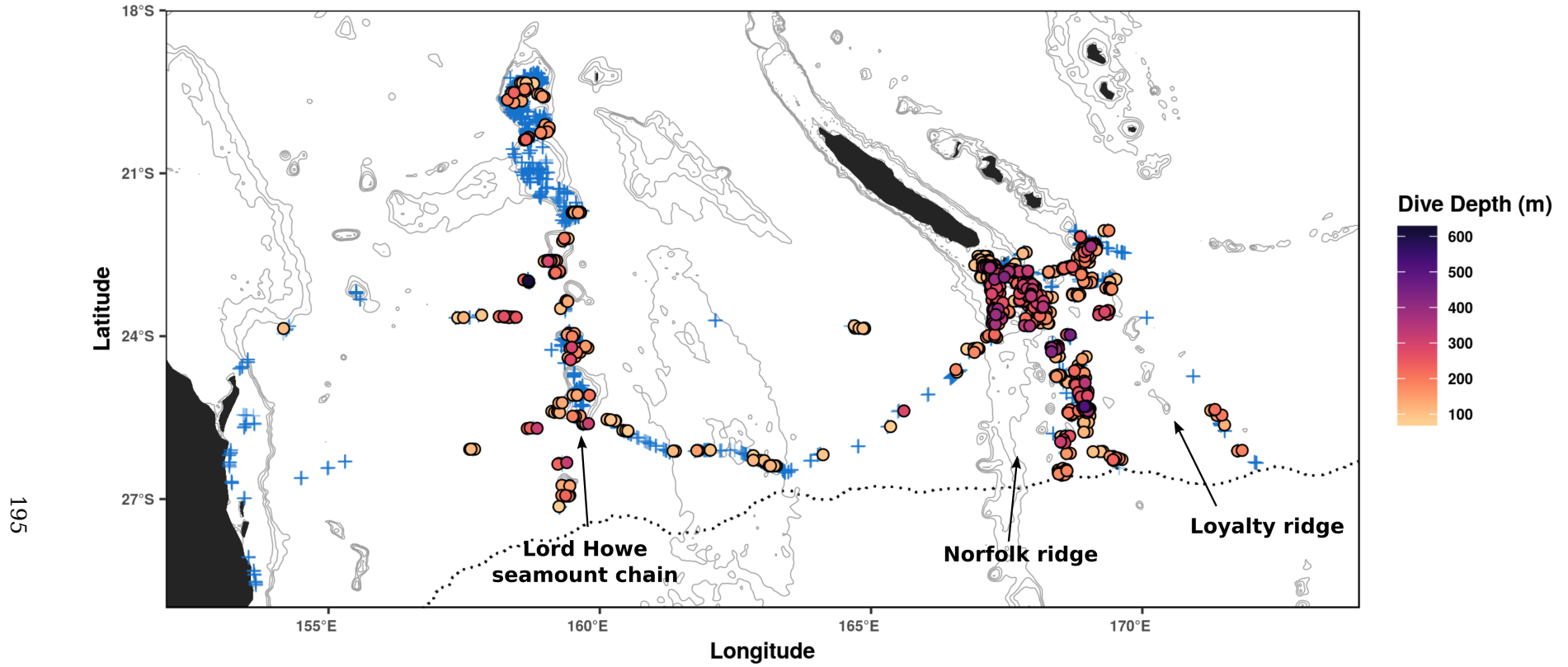


Figure 6.6 Geographic position estimated for dives recorded from 18 humpback whales tagged in New Caledonia ($n = 7,712$ dives). Dives deeper than 80 meters are represented with filled circles. Shallower dives are represented with blue crosses. Grey lines represent 500 m isobaths up to 2000 m deep. Land is shown in black. The breeding study region is demarcated by the 21°C isotherm shown with a dotted line.

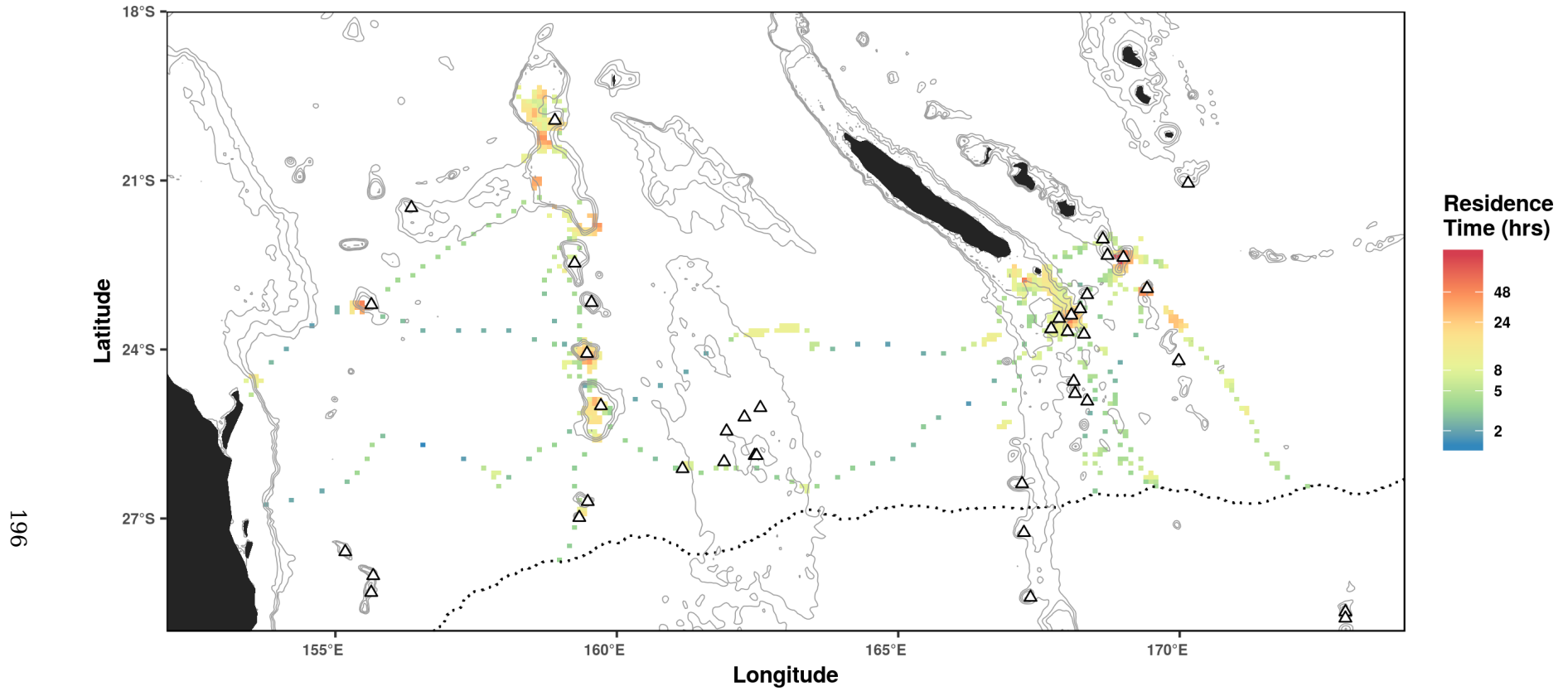


Figure 6.7 Pelagic mean Residence Time (hrs) averaged over a grid of 10 km resolution. Estimated from the CRW-interpolated tracks of 18 humpback whales. Seamounts included in the analysis (shallower than 500 m, based on [Allain et al., 2008](#)) are shown with white triangles. Grey lines represent 500 m isobaths up to 2000 m deep. Land is shown in black. The breeding study region is demarcated by the 21°C isotherm shown with a dotted line.

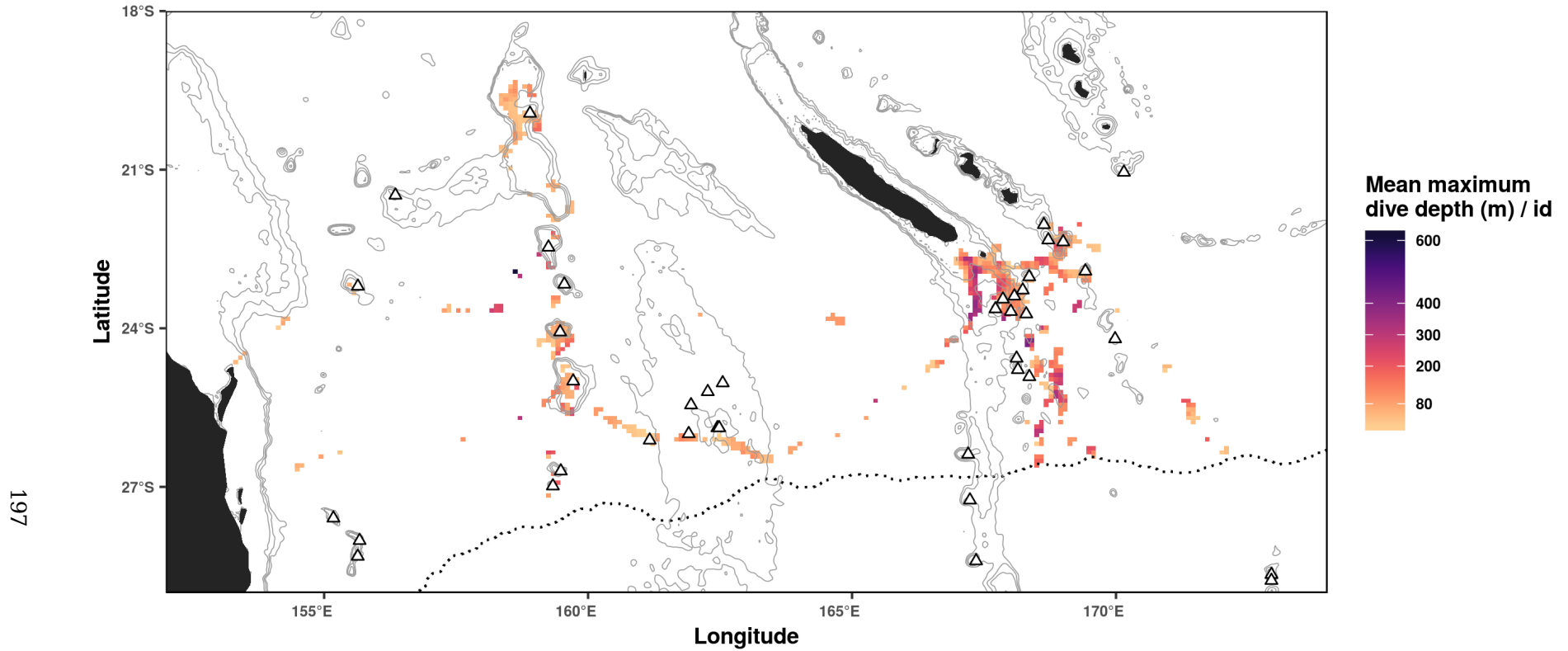


Figure 6.8 Pelagic maximum dive depths (m) averaged over a grid of 10 km resolution for 16 humpback whales. Seamounts included in the analysis (shallower than 500 m, based on [Allain *et al.*, 2008](#)) are shown with white triangles. Grey lines represent 500 m isobaths up to 2000 m deep. Land is shown in black. The breeding study region is demarcated by the 21°C isotherm shown with a dotted line.

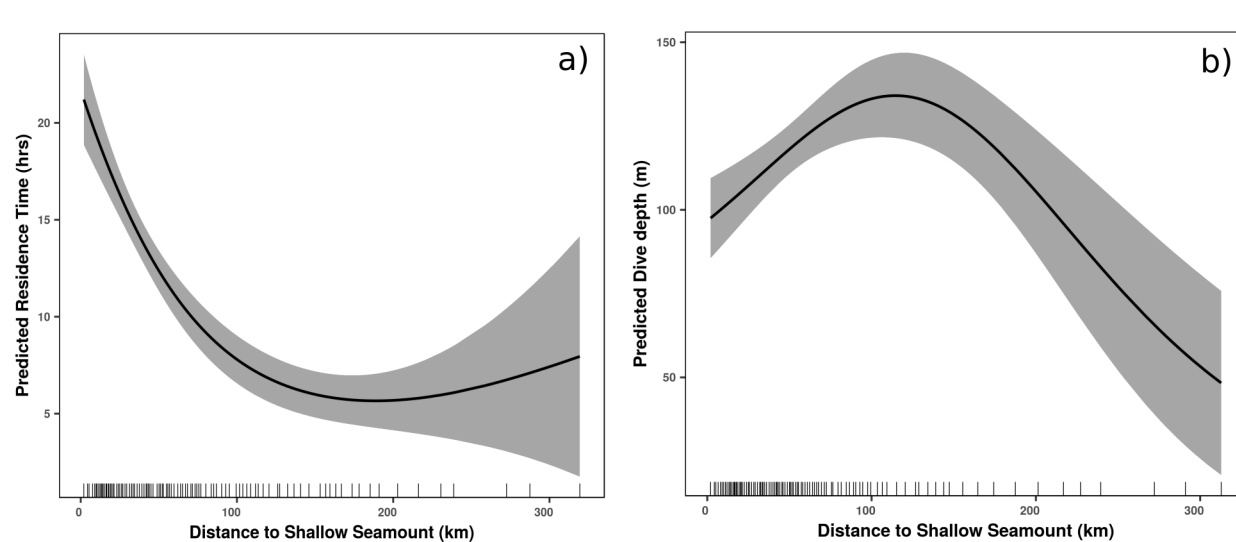


Figure 6.9 GAM predictions of horizontal and vertical movement of humpback whales in pelagic environment in response to distance to shallow seamounts. a) Predicted Residence Time (hrs) from 18 CRW-interpolated tracks, deviance explained 13.0%. b) Predicted maximum dive depth, deviance explained 3.2%. Rug plots illustrate the distribution of values in the modeled dataset in percentiles. The shaded ribbon represent approximate 95% confidence intervals.

6.4 Discussion

Using long-term satellite tracking and dive recording, this study characterized vertical and horizontal movements of humpback whales in coastal and pelagic habitats of the New Caledonian and East Australian region during the breeding season. Extensive regional movements were revealed and shed light on the spatially-structured mating system of humpback whales. Moreover, intense diving behavior in pelagic waters was recorded for whales of all social types, indicating unexpected energy expenditure during the breeding season. A strong affinity for seamount habitats was illustrated both in horizontal and vertical movements of humpback whales. The hypothesized drivers and implications of seamount associations are discussed below.

6.4.1 Diving patterns of humpback whales in breeding latitudes: unexpected energy expenditure

Most studies of humpback whale vertical movements have been conducted in feeding areas (Dolphin, 1987; Dietz *et al.*, 2002; Heide-Jorgensen and Laidre, 2007; Goldbogen *et al.*, 2008; Hazen *et al.*, 2009; Ware *et al.*, 2011; Tyson *et al.*, 2012; Friedlaender *et al.*, 2013). Dive records for breeding grounds and migration are less common, and often result from short term monitoring of less than a day (Hamilton *et al.*, 1997; Baird *et al.*, 2000; Herman *et al.*, 2007; Videsen *et al.*, 2017). In this study, long-term tracking of humpback whales at a wide spatial scale allowed for a more comprehensive description of diving patterns during the breeding season. Humpback whales displayed a relatively high proportion of deep dives in breeding latitudes. Whale #34226 was recorded to dive to 616 m,

west of the Bellona plateau. It cannot be fully excluded that this depth resulted from a dysfunction of the tag, given how outlying the value was compared to the rest of the dataset. However, other relatively deep dives have been recorded, including a dive at 520 m by whale male #57538. This dive would appear to be the deepest ever recorded for a humpback whale, as the other deepest dives in the literature were reported in the Antarctic Peninsula (388 m, [Friedlaender et al., 2013](#)), West Greenland (392 m, [Dietz et al., 2002](#) technical report) and Hawaii (396 m, [Henderson et al., 2018](#) technical report).

Deep dives were recorded for individuals of all sex and breeding status. Although on average mothers with a calf performed shallower and shorter dives than other individuals, they were found to dive as deep as 336 m. Whether the recently borne calf is capable of following its mother at these depths is unknown. Calves of a few months old have been observed following their mother down to 250 m during foraging in the Western Antarctic Peninsula ([Tyson et al., 2012](#)). In other cetacean species, mothers have been shown to adapt their vertical behavior as a function of calf age (Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, [Miketa et al., 2018](#)). The ontogeny of respiratory capacity is not well documented in mysticetes, but it is possible that prolonged hypoxia during deep dives would help develop the calf's aerobic dive capacity ([Cartwright et al., 2016](#)).

Deep dives often occurred in series, and showed U-shapes resulting in prolonged time spent at the bottom of each dive. Repeated, deep and long dives involve large energy expenditure ([Dolphin, 1987](#); [Goldbogen et al., 2008](#); [Friedlaender et al., 2013](#)). Several hypotheses can be proposed to explain why humpback whales of all social types would perform these energy-consuming deep dives in breeding regions. First, the 'scouting hypothesis' suggests that whales could be diving at depth as a mean to orientate during navigation between breeding grounds. Turbulences occurring along the slope of bathymetric features such as seamounts could constitute important cues for whales to find their suitable shallow habitats ([Haren, 2015](#)). For instance, [Rosenbaum et al. \(2014\)](#) suggested that bathymetric features such as the Walvis Ridge in the Southeast Atlantic could play a role in directing the migratory path of humpback whales. No information is currently available to describe the mechanisms by which oceanographic stimuli may be sensed by baleen whales but they have been suggested to cue on ocean stratification and currents to navigate ([Norris, 1967](#)). Oceanographic stimuli are postulated to be among the main sensory modalities used by baleen whales to locate prey at meso (10 km) to large scales (100 km; [Torres, 2017](#)). The same mechanism may be postulated in the search for shallow bathymetric features likely to host conspecifics, as whale appeared to perform deep dives at an average distance of 100 km from the shallow seamounts.

Second, the 'social hypothesis' suggests that deep dives occur as a result of interactions with other individuals during competition for mating. Indeed, humpback whales in competitive groups have been observed with Crittercams displaying competitive behavior at depth, up to 298 m ([Herman et al., 2007](#)). This hypothesis was also suggested by [Henderson et al. \(2018\)](#) who tracked humpback whales around the islands and seamounts of Hawaii. In their case, singers were also supposed to perform deep dives since tags had only been deployed on presumed males. In the present study,

singing is unlikely to be the primary driver of deep dives, given that they have been recorded for both males and females, which in the latter case do not sing. Singing hypothesis aside, this study supports the general social hypothesis as many of the deep dives were observed in the vicinity of breeding grounds where competitive activities and interactions take place.

The third hypothesis is that of 'opportunistic feeding'. The successive deep U-shaped dives observed on several occasions present the same characteristics than foraging dives of humpback whales and other rorquals (e.g. [Goldbogen et al., 2008, 2017](#)). Deep foraging dives often include a greater number of feeding lunges than during surface feeding, resulting in more time at depth ([Ware et al., 2011; Tyson et al., 2012](#)). Moreover, blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) dive deeper and longer when feeding ([Croll et al., 2001](#)). However, neither feeding nor defecation has ever been observed during visual surveys in New Caledonia offshore breeding grounds (C. Garrigue, pers. obs.). Contrary to [Henderson et al. \(2018\)](#) who found that deeper dives occurred mostly at night, the diel pattern in this study was marginal. On average, dives were deeper during daytime but this difference was not significant once accounting for the individual effect. In the western Antarctic Peninsula, humpback whales preferentially feed at night when preys are closer to the surface and more readily available ([Friedlaender et al., 2013](#)). In Stellwagen Bank, Massachusetts, humpback whales appear to switch feeding strategies (bottom or surface feeding) in function of the diel cycle of their prey ([Friedlaender et al., 2009](#)). Prey vertical migration is also observed in relatively oligotrophic tropical regions such as New Caledonia ([Menkes et al., 2015](#)). Indeed, average micronekton migrations from 500 m during the day, to 20-50 m at night have been estimated from acoustic sampling (see Appendix 6.B.3, [Receveur et al., 2018](#)). Micronekton biomass in New Caledonia is mainly composed of gelatinous organisms and fish of the myctophidae family (lantern fish; [Menkes et al., 2015](#)). Crustaceans and molluscs contribute a small fraction of the total biomass. Interestingly, *Euphausia mucronata* was reported on a few occasions ([Menkes et al., 2015](#)). This species of krill is known to play a key role in the food chain of the Humboldt Current System, where it is consumed by many top predators ([Antezana, 2010](#)), including fin whales ([Pérez et al., 2006](#)).

The fourth hypothesis is that of 'thermoregulation' as an analogy with other marine endotherm vertebrates. Indeed, vertical movements of tuna has been in part interpreted as an adaptation to diel variation of ocean temperature stratification ([Houssard et al., 2017; Williams et al., 2014](#)). Similarly, humpback whales could be diving at depth in order to cool down their body temperature and compensate overheating occasionally observed in breeding grounds (e.g. [Helweg and Herman, 1994; Videsen et al., 2017](#)). However, the vertical stratification of tropical waters results in relatively deep thermoclines. In New Caledonia, the D20 (depth of the 20°C water layer) is located between 200 m and 150 m in austral winter. The temperature decrease that whales would gain by diving below 200 m therefore appears quite marginal in comparison to the physical effort required for such dive. Physiological response to extended periods of apnea include bradycardia, peripheral vasoconstriction and metabolic suppression ([Kooyman, 2002](#)). The 'dive response' of air-breathing marine mammals

is therefore in conflict with the increased blood flow required for thermoregulation (Noren *et al.*, 1999). Finally, given that humpback whales can be found in much warmer breeding grounds (e.g. around 26-28°C in Samoa, Chapter 5), it is doubtful that overheating would be a strong driver of diving behavior in the relatively cool New Caledonian waters (22 - 24°C).

Four non-exclusive driving mechanisms have been suggested to explain the deep diving patterns observed for humpback whales tagged in New Caledonian offshore waters. Conclusions are impaired in part due to the low precision of ARGOS positioning (reaching more than 50 km for 'B' class positions, Nicholls *et al.*, 2007, the most common in this dataset), and to the relatively low frequency of data transmission (mean = 1 filtered position/ 5.8 hour \pm SD 5.8). As a result of these combined biases, the positioning of dive events was approximate, with a potential error radius sometimes larger than the diameter of seamounts of interest (e.g. Ellet about 4 km wide). Higher resolution tracking therefore might be necessary to deepen our understanding of humpback whale pelagic and seamount habitat use.

6.4.2 Humpback whale space use patterns in relation to seamounts

Most of the survey effort to describe cetacean distribution and habitats is biased towards coastal waters (Kaschner *et al.*, 2012). However, humpback whales are wide-ranging species that spend extended periods of time in the open ocean. In this study, long-term implantable satellite tags allowed to investigate their use of pelagic waters during the breeding season.

Confirming the results of Garrigue *et al.* (2015), this study emphasized the importance of shallow offshore habitat for humpback whales, whatever their sex or breeding status. It must be noted that the majority of the whales tagged in offshore waters (Antigonia or Orne bank) never got near a reef or a coast during the duration of tracking (7 out of 12). Seamounts and banks that most attracted humpback whales included: Ellet, Orne, Capel, Kelso, Antigonia and Torch (Fig. 6.1). These seabed features have in common a relatively shallow depth at their summit (Ellet 30 m deep, Derville pers. obs.; Orne 15 m, Derville pers. obs.; Capel 10 m, Gardes *et al.*, 2014; Kelso 15 m, Gardes *et al.*, 2014; Antigonia 60 m, Garrigue *et al.*, 2015; Torch 30 m, Garrigue *et al.*, 2015), surrounding seabed of 1,500 to 2,000 m deep, and guyot shapes with flat summits of a surface ranging from 17 km² (Ellet) to 1,800 km² (Capel, Gardes *et al.*, 2014). Humpback whales have been tracked during the breeding season over similar offshore features, such as Penguin Bank, in Hawaii (Mate *et al.*, 1998, 2007) or La Pérouse seamount, in the western Indian Ocean (Dulau *et al.*, 2017). Given the low latitude and proximity to known coastal breeding grounds, these seamounts were thought to host breeding activities (Dulau *et al.*, 2017). In New Caledonia, in situ visual surveys conducted over the southeastern seamount region have confirmed that humpback whales display behaviors typically observed in breeding grounds: intense singing activity, competitive behavior and nursing females (Garrigue *et al.*, 2017; Derville *et al.*, 2018a; Garrigue *et al.*, 2018a). Yet, it is intriguing to note that whales, including mothers with a calf, would prefer these unsheltered locations instead of selecting

nearby coasts and lagoons to congregate.

Several advantages of pelagic seamounts over coastal waters can be postulated to explain this habitat selection pattern. First, seamounts undoubtedly are landmarks in the open ocean. Both the shallow seabed feature itself, its geomagnetic signature (Garrigue *et al.*, 2015) and the peculiar turbulences that it triggers (Kunze and Llewellyn Smith, 2004; Pitcher *et al.*, 2008) are likely to be detected by humpback whales in search of a congregation spot. In this sense, seamounts are easily accessible and detectable areas for social aggregations during the breeding season. Along those lines, it is possible that seamounts also act as 'singing stages' for male humpback whales. These areas could be acoustically more suitable for singing males because they may be quieter than the surrounding environment and provide better sound propagation towards the open water (Frankel and Clark, 1998). As songs are likely to play a role in the spatial aggregation of individuals (Clapham and Zerbini, 2015; Herman, 2017), seamounts with dense humpback whale presence could be very acoustically attractive. Second, humpback whales could retreat over pelagic seamounts as an avoidance response to human disturbance occurring in coastal waters. As maritime traffic and whale watching activities have increased in the New Caledonian South Lagoon (Schaffar *et al.*, 2013; Bourgoigne *et al.*, 2018) it is possible that some individuals favor offshore and quieter breeding grounds.

Finally, given the enhanced primary productivity often encountered over seamount slopes (Pitcher *et al.*, 2008; Morato *et al.*, 2010; Cascão *et al.*, 2017), it is possible that seamounts act as opportunistic feeding spots for humpback whales during the breeding season or early migration. It is commonly accepted that feeding is absent or very marginal within breeding latitudes (Clapham, 2000a). However, humpback whales are also known for their highly flexible diet (Stockin and Burgess, 2005) and there is recent isotopic evidence that supplemental feeding can occur in temperate waters along their migration (Eisenmann *et al.*, 2016, 2017). Occasional feeding outside feeding grounds has been reported in a few locations: off the coast of Eden, east Australia (37°S, Andrews-Goff *et al.*, 2018), in Samana Bay, Dominican Republic (19°N, Baraff *et al.*, 1991), off the coast of Brazil based on direct observation (19.5°S, De Sá Alves *et al.*, 2009) or stomach content (Danilewicz *et al.*, 2009), and in the Gulf of California (24.5°N, Gendron and Urban, 1993). Following these observations, ARS observed in humpback whale satellite tracks after they appeared to have initiated their migration has often been interpreted as opportunistic feeding (Table 6.1). Such hypothesis was proposed by Félix and Guzmán (2014) regarding a whale that stopped for several days off the Paracas coast (15°S), in Peru, where the Humboldt Current System results in intense upwellings. Similarly, Lagerquist *et al.* (2008) suggested feeding in the Baja California Frontal System for a whale migrating past the coast of Baja California (25°N, Magdalena bay). Opportunistic feeding has also been postulated over pelagic seabed features such as the Kermit-Roosevelt seamount (39°N) for whales migrating from Hawaii to Alaska (Mate *et al.*, 2007), or the Walters Shoal seamount (33°S) for whales migrating from Madagascar (Trudelle *et al.*, 2016; Cerchio *et al.*, 2016). While a similar hypothesis could be proposed for the New Caledonian case, it remains to be identified whether seamounts located in these oligotrophic tropical waters could concentrate enough preys for humpback whales to feed on.

6.4.3 Regional longitudinal movements: migration or roaming?

Humpback whales demonstrated localized and regional movements during the breeding season. Extensive connectivity between aggregation spots within breeding latitudes moderates the longstanding view of humpback whale migration as a simple north-south migration with a single 'final destination'.

A strong connectivity was observed among breeding aggregations recently highlighted off the southeastern New Caledonian coast (Garrigue *et al.*, 2017). Many of the whales tagged in Antigonie seamount and Orne bank visited several offshore shallow features, as well as the more sheltered waters of the Isle of Pines and the South Lagoon. This pattern of connectivity is further supported by individual resights identified with genotyping and photo-identification between Antigonie, Torch bank and the South Lagoon (Garrigue *et al.*, 2013; Orgeret *et al.*, 2014). High residence time observed in these shallow waters reflects ARS that can be indicative of resting, breeding or socializing behavior (e.g., Garrigue *et al.*, 2015; Dulau *et al.*, 2017; Trudelle *et al.*, 2016). Similar medium-scale movements have been revealed by satellite tracking around the main Hawaiian islands (Mate *et al.*, 1998, 2007). Hence, the connectivity observed between several breeding grounds in southeastern New Caledonia supports the lek system proposed by Herman and Tavolga (1980). Lekking systems are defined as a gathering of males engaged in competitive or vocal and visual display to attract females. Gatherings are formed in 'arenas' that are postulated to gain in attractivity as they grow in size (Herman, 2017). Combined evidence from this study and previous work leads to the hypothesis that seamounts and banks constitute a network of breeding arenas in the region (Garrigue *et al.*, 2017). Humpback whales are therefore hypothesized to maximize their mating opportunities by visiting several arenas within a given breeding season (Dulau *et al.*, 2017). The relative proximity of diverse suitable habitats occupied by dense humpback whale aggregations supports the importance of the New Caledonian southeastern arenas as an ideal destination for breeding.

However, the spatial scale at which arenas can attract individuals is unknown. The extensive longitudinal movements observed from east to west of the Coral Sea question the scale at which the humpback whale mating system is spatially organized. Longitudinal movements were characterized by transit-like parameters, typically observed during migration: low residence time, high swimming speeds and oriented travelling (e.g., Zerbini *et al.*, 2011; Kennedy *et al.*, 2014b; Garrigue *et al.*, 2015; Andrews-Goff *et al.*, 2018; Riekkola *et al.*, 2018; Table 6.1). These movements appeared to connect the well-known breeding grounds of southeastern New Caledonia, to presumed breeding grounds of Capel and Kelso, located at a similar latitude at a distance of about 850 km. This route had previously been followed by two humpback whales tagged in 2010 (Garrigue *et al.*, 2015). Similar wide longitudinal movements between breeding grounds have been observed in the Southwestern Indian Ocean, between the Malagasy coast, the Mozambic coast, the Comoros archipelago and La Réunion (Fossette *et al.*, 2014; Trudelle *et al.*, 2016; Cerchio *et al.*, 2016; Dulau *et al.*, 2017). Here, connections were revealed between and among the breeding grounds of southeastern New Caledonia,

the Lord Howe seamount chain and the Chesterfield-Bellona reef complex. Although previously described as a 'roaming behavior' (Dulau *et al.*, 2017), we believe the movements of humpback whales between breeding arenas would be better described by the term 'stone stepping', which would reflect the straightness of paths leading from one arena to another.

In this study, two whales entirely crossed the Coral Sea to reach the East Australian coast, using the Lord Howe seamount chain as a step stone, over which they respectively stopped for 3 days (#34354) and 7 days (#154185). Three whales tagged in the Chesterfield-Bellona reef complex also moved towards the Australian coast. Whether these animals were looking for mating opportunities over the Australian breeding grounds is uncertain. All whales reached the coast further south than the E1 presumed breeding grounds of the Great Barrier Reef (Paterson and Paterson, 1984). Moreover, residence time over the coast was low, except for whale #34354 that stayed 10 days in the vicinity of Hervey bay and Moreton bay. Photo-identification and genotyping have shown limited exchanges between the New Caledonian sub-stock E2 and the Australian sub-stock E1 sampled along their migratory corridor (Olavarría *et al.*, 2007; Garrigue *et al.*, 2011b). However, Valsecchi *et al.* (2010) found no genetic differentiation between samples collected in Stradbroke Island over the East Australian coast and New Caledonia. They suggested that exchanges could result from differential migratory routes for males and females, specifically from extensive longitudinal movements of males during the breeding season. Sex and breeding status are known to affect movement characteristics, notably the proportion of ARS behavior (Trudelle *et al.*, 2016; Dulau *et al.*, 2017), and migratory destinations (Cerchio *et al.*, 2016; Riekkola *et al.*, 2018). Here, both of the two whales that crossed the Coral Sea were males. Although the small sample size must be acknowledge, these results are congruent with the hypotheses of Valsecchi *et al.* (2010). Further investigation into sex-specific population dynamics in the region is warranted to understand these exchanges and the spatial scale at which humpback whale mating system is organized.

Conclusion

Based on horizontal and vertical movement patterns recorded in the New Caledonian region and the Coral Sea, we suggest that humpback whales display hierarchical spatially structured distribution patterns as a result of their lek mating system. Multi-scale movements described in this study have implications for estimating population dynamics and exchanges between South Pacific humpback whale populations. Among other suitable breeding habitats, shallow seamounts are postulated to play a key role in the breeding arena network of Oceania humpback whales. Given worldwide anthropogenic threats related to deep sea fisheries and mining resources, these results support the importance of managing seamounts as vulnerable marine ecosystems (Clark *et al.*, 2012; Watling and Auster, 2017). Local assessments of New Caledonian seamounts to be classified as highly sensitive biodiversity hotspots (Gardes *et al.*, 2014), are reinforced by these results showing their importance for wide scale movements and breeding of an endangered population of humpback

whales.

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Appendix 6.A. Pelagic habitats in the Coral Sea

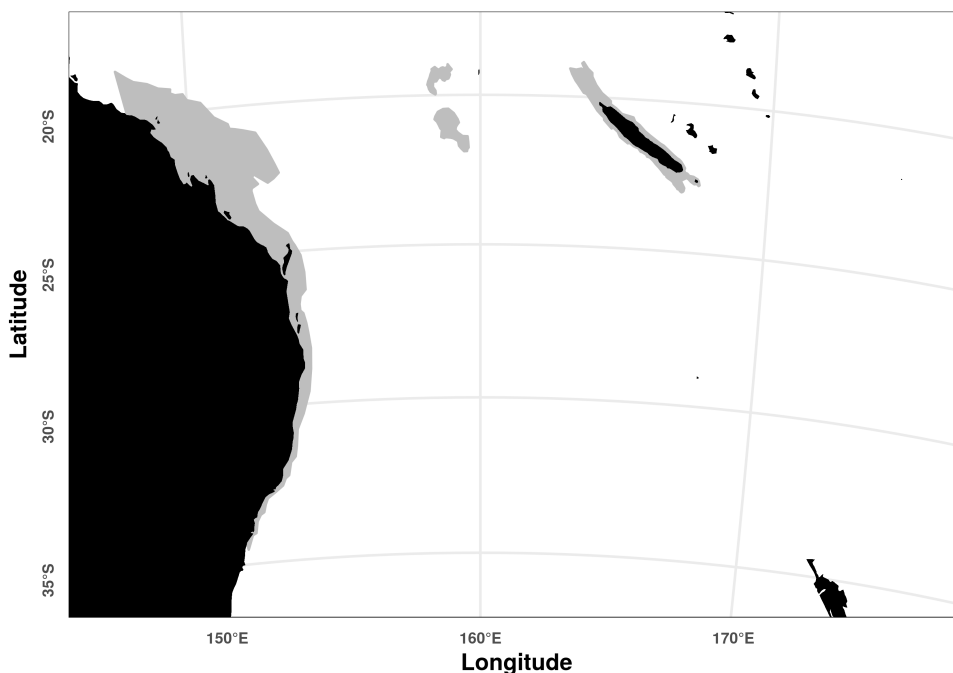


Figure 6.A.1 Map of sheltered waters excluded from the pelagic habitat movement analyses. Sheltered (coastal or lagoon) waters on the East Australian coast, New Caledonian lagoon and Chesterfield-Bellona lagoon were manually delineated (grey polygons).

Appendix 6.B. Diel vertical migration and diving patterns of humpback whales

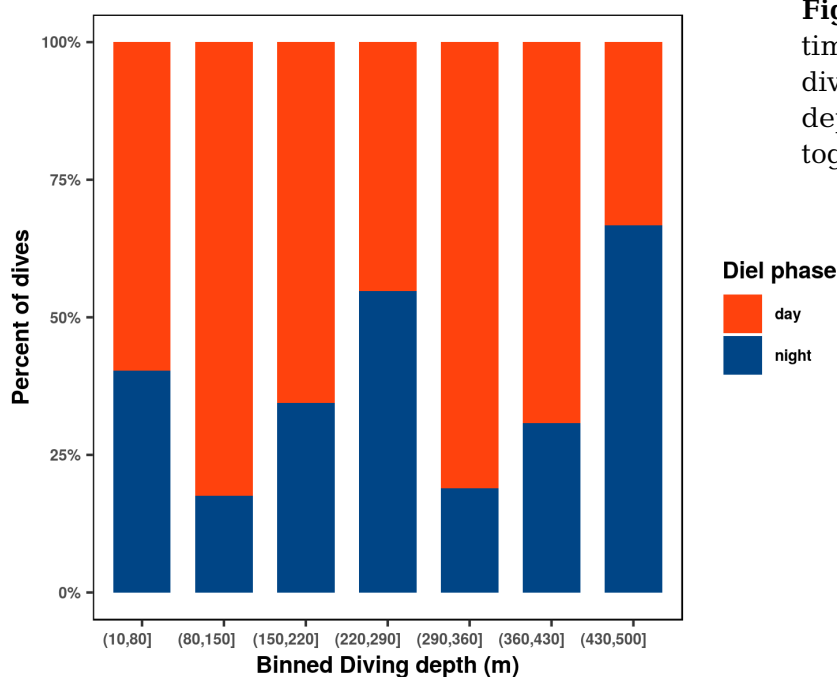


Figure 6.B.1 Percent of day-time (red) or nighttime (blue) dives recorded as a function of depth (all individuals pooled together, $n = 6,406$ dives).

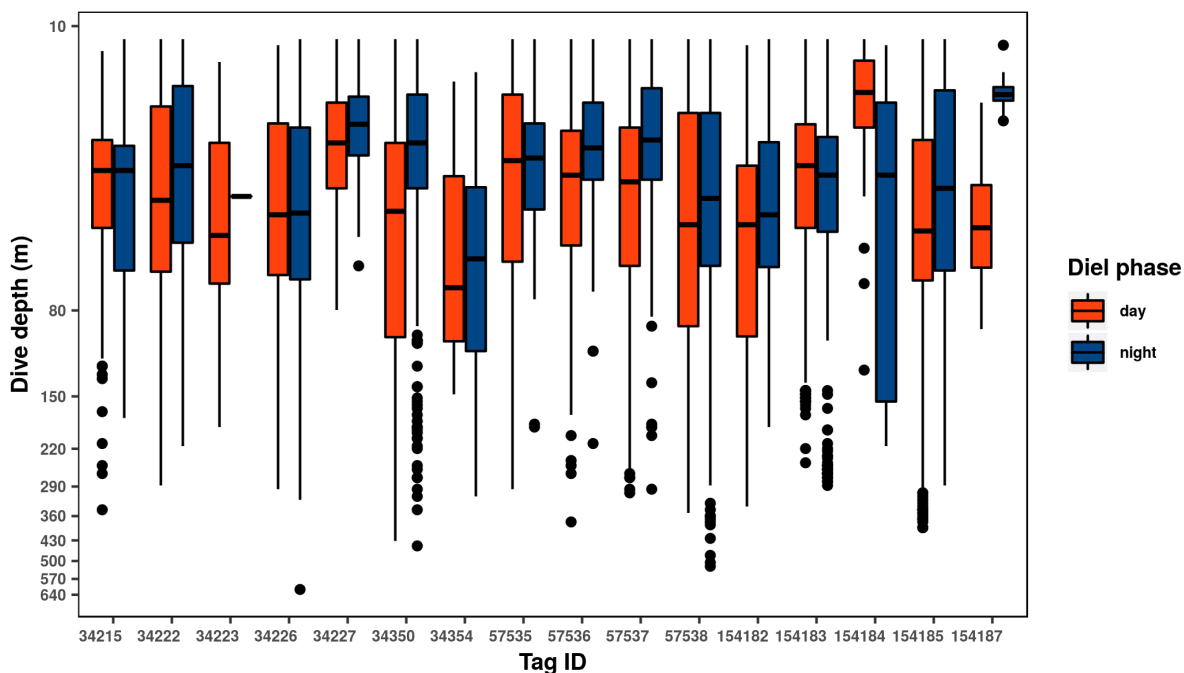


Figure 6.B.2 Dive depth of dives recorded at night (blue) or during the day (red) per individual tracked in the pelagic breeding region (n = 6,409 dives).

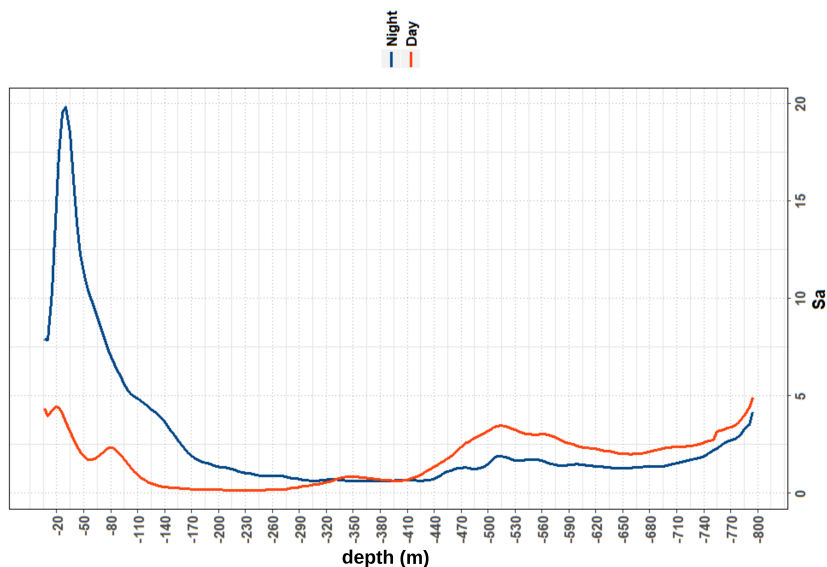


Figure 6.B.3 Mean vertical profile of the Nautical Area Scattering Coefficient (NASC, or Sa on x-axis) (similar to acoustic intensity and used as a proxy for micronekton quantity) for the 38 kHz frequency during the Day (red) and the Night (blue). These profiles are calculated on average for the zone [166.5, 169.8] [-24.5, -22] (New Caledonia southern seamounts region) and are based on cruises NECTALIS 1, NECTALIS 2, NECTALIS 3 and NECTALIS 5. Source: A. Receveur, CPS, 2018.

VII. General discussion

7.1 Cetacean SDM methodological advances

1. How do different statistical approaches perform for describing and predicting distribution based on non-systematic research data?

The statistical approaches tested differed in the complexity of the environmental relationships modelled, ecological interpretability and transferability. While no 'best algorithm' for SDMs was found, GAMs provided a valuable complexity trade-off, and the potential to include and deduce ecologically explicit knowledge. In addition to the choice of algorithm, model tuning was paramount to control for descriptive and predictive model performances.

2. How can non-systematic research surveys and citizen science data be used to produce informative cetacean distribution models?

Non-systematic research surveys, which do not rely on line transect sampling, form an advantageous low-cost field approach to acquire data both at population level (distribution, habitat) and individual level (behaviour, photo-identification, genetics). In this thesis, habitat relationships were investigated using an adapted presence-background SDM framework, and intensity of use was quantified with encounter rates. Moreover, citizen science showed promising performance to describe and predict humpback whale distribution, particularly when spatial sampling bias was accounted for. In addition to providing low-cost data over wide spatial extents, citizen science appeared like a socially valuable tool to contribute to marine policy.

3. What are the key constraints to studying the distribution of a wide-ranging long-lived cetacean in its breeding phase, and how do we overcome them?

First, the appropriate application of a presence-background SDM framework was essential to account for uneven survey effort and the seasonal pattern of humpback whale presence. Second, fine-scale indicators of topographic complexity were used as predictors, in addition to contemporaneous and climatological remotely sensed SST to predict persistent patterns of habitat suitability. Third, model overfitting was specifically addressed through integrative evaluation, cross-validation and appropriately calibrated algorithms. This approach ensured model transferability to predict the distribution of a wide-ranging species for large scale conservation perspectives.

7.1.1 Limitations of cetacean spatial data types

In this thesis, spatial and environmental cetacean relationships were estimated from a variety of data types (see Chapter 1; Fig. 1.5). Three methods of data collection were particularly represented: non-systematic research surveys visual observations, citizen science visual observations, and satellite telemetry. Here, I discuss the application of each method in this thesis, their respective limitations and potential perspective for improvement.

Non-systematic research surveys

Non-systematic surveys are a valuable research method to collect a variety of data (focal follows, biopsy sampling, photographs etc.) at relatively low cost (e.g., Corkeron *et al.*, 2011; Hartel *et al.*, 2014; Hartman *et al.*, 2014; Rayment *et al.*, 2015). These surveys do not follow explicit randomized or systematic line transects, but rather focus on presumed and accessible areas of cetacean presence. They are particularly applied in coastal regions. Hence, assumptions of typical systematic line transect surveys are not fulfilled and alternative modeling approaches have to be used to quantify habitat relationships and intensity of use.

In this thesis, non-systematic survey data were applied to model humpback whale habitat use in a **correlative SDM framework** (Chapters 2, 4 and 5). Although the method for modeling this data evolved from one chapter to the other, all chapters relied on the assumption that non-systematic survey data would be best modeled in a **presence-background** SDM framework. Considering the numerous confounding factors contributing to imperfect detection, it was admitted that the absence of sightings in a given area could not be considered as a true absence of humpback whales. Hence, modeling presence points while accounting for heterogeneous survey effort using background sampling appeared like a good compromise between presence-absence and presence-only approaches.

Density estimates cannot be derived from non-systematic visual surveys as they do not follow the assumptions relative to systematic line transect surveys (Chapter 1; Hammonds, 2010). Yet, quantifying animals is essential to prioritize spatial management and assess the effectiveness of protective actions. Hence, **encounter rates** were used as a proxy of abundance to compare the use of various breeding sites across Oceania in Chapter 5. Encounter rates can be calculated as the number of whales observed per unit of time on-effort or per unit of space surveyed (e.g., Macleod *et al.*, 2004; Garaffo *et al.*, 2011; Arcangeli *et al.*, 2015). Given that vessel speed varied substantially during a survey day, the calculation of whales.h⁻¹ was favored to whales.km⁻¹. Furthermore, encounter rates calculated from non-systematic spatial sampling can be inflated by duplicated observations of the same individuals. In this thesis, this bias was found to be limited, as the individual resight rate per day based on photographic and genetic identifications was close to zero (Chapter 3). However, in small and dense areas such as seamounts, this bias will be stronger and might need to be further considered.

Citizen science

Gaining a better understanding of the motivations and the people who contribute to citizen science can improve our capacity to model cetacean distributions from opportunistic observations. In New Caledonia, the NGO Opération Cétacés has coordinated the recording of marine mammal observations since 1991. Initially based on observation sheets distributed in marinas, touristic sites and magazines, a web platform was later created in 2016. The majority of observations was provided by people who are at sea for professional reasons and who are likely to have a good knowledge of marine life: park rangers, whale-watching operators, ferries, research vessels, fishing boats, and cargo ships. Nonetheless, almost a quarter of all marine mammal species observations were provided by members of the general public while pleasure boating (Fig. 7.1).

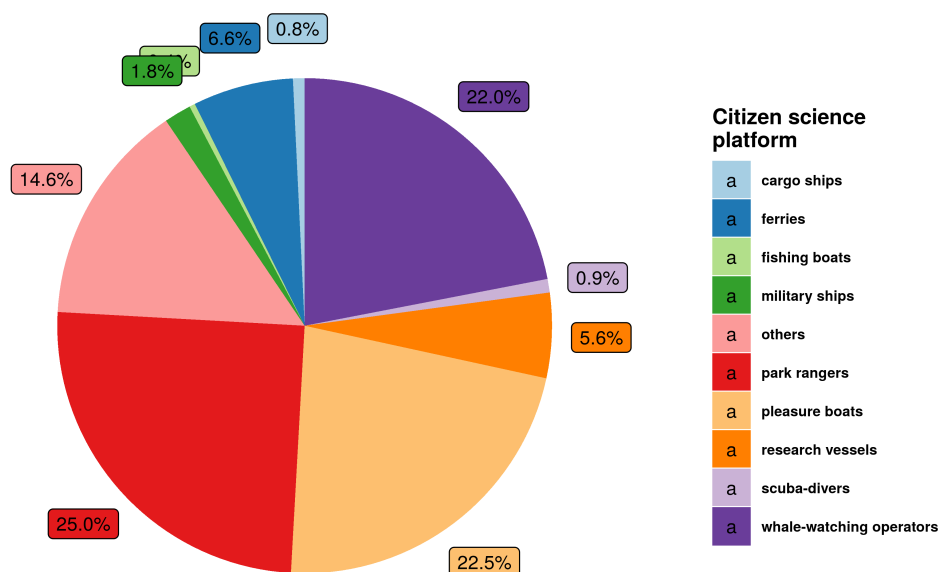


Figure 7.1 Pie chart of citizen scientists who reported sightings from 2003 to 2017 ($n = 792$ observations of marine mammals in New Caledonia, based on the dataset used in [Derville *et al.*, 2018b](#), all marine mammal species observed during this period). The category 'other' includes unknown categories as well as very rare reports such as observations from an airplane.

Like all visual surveys, records from citizen scientists are subject to perception, availability and sampling biases (see Chapter 1). We can assume that the availability bias is not impacted by the experience of the observer. In contrast, **perception bias** depended on both the experience, and the activity of the observer while at sea (how much attention was aimed at finding cetaceans). Contrary to research surveys, cetacean observation is not the primary goal of opportunistic observers, hence their attention is not focused on survey effort. Among citizen scientists, perception bias could be lower for **whale-watching operators** who are seasoned to the observation of marine wildlife. Indeed, whale-watching operators commonly contribute to semi-opportunistic surveys (e.g., [Hauser *et al.*, 2006](#); [Higby *et al.*, 2012](#); [Bruce *et al.*, 2014](#); [Trudelle *et al.*, 2018](#)) and the quality of their records (species identification, geographic location etc.) is shown to compare well with that of dedicated

research surveys (Hauser *et al.*, 2006).

Duplicated observations of the same cetacean groups over a day can also bias citizen science SDMs. In areas of highest human concentration during the austral winter (around Nouméa and in the South Lagoon) some groups of humpback whales were reported several times. Unless photographs can be used to differentiate individuals, duplicates cannot be fully excluded. Some form of filtering (Boria *et al.*, 2014) could be applied during the analysis to remove presence points observed nearby at a short time interval.

Chapter 4 focused on **spatial sampling bias** as it was considered a major issue in citizen science (Bird *et al.*, 2014; Robinson *et al.*, 2017b). Indeed, citizen scientists have their own agenda and obviously do not display an explicitly randomized nor systematic sampling. Moreover, the spatio-temporal distribution of their survey effort is generally unknown. This lack of effort quantification is problematic, as the probability of recording a species at a given site is based on both the probability of species occurrence and of an observer recording the data. It is often hard to determine whether a higher encounter rate in a site is due to a high habitat suitability or simply to a higher density of observers (Bird *et al.*, 2014). In Chapter 4, two methods were tested to model humpback whale distribution and account for spatial sampling bias. The 'target species'¹ approach (Phillips *et al.*, 2009) was the most successful at predicting humpback whale distribution at the New Caledonian EEZ scale, but may be of limited use with very small sample sizes.

An alternative approach developed in Chapter 4, the 'POP approach', provided valuable predictions by approximating citizen science sampling effort from human population densities or accessibility (Monsarrat *et al.*, 2018). This method has the potential to be improved by explicitly accounting for the spatial habits of various categories of citizen scientists. For instance, cargos and ferries always follow the same shipping routes, hence their survey effort is highly predictable. Similarly, whale-watching operators in New Caledonia concentrate in a specific area, the South Lagoon and South-Western Lagoon. The majority of boats leaves and returns to Prony Bay on a daily basis and covers limited distance away from the bay. Based on these informations, the different sampling biases of citizen scientists' categories could be better accounted in cetacean SDMs, using hierarchical models (Wikle, 2003), mixed-effects (Tonachella *et al.*, 2012) or class-conditional noise (Hutchinson *et al.*, 2017). In summary, accurate estimation of citizen science survey effort is required to ensure that models are describing the habitats of animals, rather than that of the observers (Tulloch and Szabo, 2012; Tulloch *et al.*, 2013).

Satellite tracking

Biologging, and specifically satellite tracking, has revolutionized the study of cetacean distribution and habitat use (Costa, 1993; Costa *et al.*, 2012), and especially that of elusive and wide-ranging large whales (Mate *et al.*, 2007). Satellite tracking allows the estimation of individual cetacean

¹In the 'target species sampling' the areas of background sampling are restricted to those where sightings of species within the same taxonomic group have been reported by the public.

movements, from a scale of several hours to years (Mannocci *et al.*, 2017a). In this thesis, individual positions of tracked whales were used as a validation for predicted maps of habitat suitability (Chapter 4), and to describe movements in relation to seabed topography and breeding status (Chapter 6).

The **accuracy of locations** recorded from satellite tracking devices may have a strong impact on their use and interpretation. ARGOS data is reported with several levels of position 'quality' (Chapter 6), which tend to be low when tracking marine mammals as they are invisible to satellites when underwater (Vincent *et al.*, 2002; Nicholls *et al.*, 2007). For instance, among 4,180 raw positions recorded from 2007 to 2016 in New Caledonia ($n = 43$ tags, Chapter 4), only 37 % were conserved for further analysis. In Oceania, the transmissions and quality of ARGOS positions is also affected by satellite coverage, which decreases closer to the equator (Costa, 1993). As a consequence, proper processing of the ARGOS data is essential to its unbiased ecological application. The pre-filtering of the raw data applied in Chapter 4 and 6 was based on prior studies that removed positions on land, quality 'Z' and supposing unrealistic speed (e.g., Zerbini *et al.*, 2015; Trudelle *et al.*, 2016). Movement models were then used to interpolation tracks at a regular time interval. State Space Models are popular tools for modeling and interpolating ARGOS satellite tracks as they account for ARGOS positional error, can be fitted hierarchically (with per individual effects) and automatically assess movement mode (i.e. ARS) along the track (Jonsen *et al.*, 2005). In Chapter 6, Correlated Random Walks (Johnson *et al.*, 2008) were favored as they also allowed the prediction of positions at irregular time steps when dive events were recorded.

The main advantage of satellite tracking is the capacity to **remotely and continuously** acquire data at **individual level**. Movements of individuals can otherwise only be evaluated from discrete photographic and genetic recapture, which necessitate the collection of data in situ. For cetacean species that spend significant time in hardly accessible pelagic waters, satellite tracking technology therefore is an undeniable asset (Costa *et al.*, 2012). However, individual-based data come with their own drawbacks. Due to the high cost of tracking devices, technical challenges of tagging cetaceans at sea, and animal welfare ethics, satellite tracking is usually conducted over relatively small samples (e.g., for humpback whales migration studies, 6 to 45 tags per study, Table 6.1). As a consequence, life stages, sex or breeding status of individuals are not evenly represented in samples (Hazen *et al.*, 2012). For instance, only adult whales of good size can be tagged with implantable ARGOS tags, while juveniles are systematically neglected. Moreover, the social and breeding status of a tagged individual may unknowingly change along the course of the tracking. A maternal female may loose her calf, or a pregnant female can give birth. As different patterns of vertical and horizontal movements (Chapter 6), as well as habitat preferences (Chapter 3) have been highlighted for females with a calf, such change in the course of tracking could have important consequences.

Finally, attachment and battery longevity of tags have always been major limitations of whale satellite tracking (Mate *et al.*, 2007). In New Caledonia, the average tracking duration was relatively low for all tags deployed. Garrigue *et al.* (2015) tracked whales for an average of 27 days (max = 55 days). Whales tracks presented in Chapter 6 lasted for an average of 32 days (max = 125 days).

Rather than a battery failure, tags are thought to be prematurely damaged or expelled (Robbins *et al.*, 2013), as a result of repeated contacts between individuals during interactions linked to breeding activities. As a comparison, tags deployed in the Kermadec Islands migratory corridor, where breeding activities are less intense, lasted for an average of 105 days (max = 254 days; Riekkola *et al.*, 2018). Tag attachment is a strong limitation to tracking humpback whale movements in breeding regions, but is in constant improvement (Robbins *et al.*, 2013).

7.1.2 Modeling cetacean SDMs

Integrating multiple data sources

Many of the biases presented above can be overcome by combining data from multiple sources. The improvement of such **integrated modeling** of several data types with varying biases is a current topic of research (Fletcher *et al.*, 2016; Pacifici *et al.*, 2016; Tingley *et al.*, 2016). For instance, Friedlaender *et al.* (2011) pooled together all presence locations acquired through visual surveys and satellite tracking to produce an SDM for Western Antarctic Peninsula top predators. In contrast, other authors have proceeded in multiple steps to analyze multiple data sources. Using vessel-based presence-absence observations, Louzao *et al.* (2009) modeled the distribution of foraging Cory's shearwater, *Calonectris diomedea*, in the Mediterranean Sea. Maps of feeding areas were subsequently refined with GPS satellite tracking data. Similarly, Camphuysen *et al.* (2012) conjointly analyzed GPS tracking and boat-based surveys to assess ecologically important marine areas for seabirds in separate maps.

Finally, satellite tracking positions (Smith *et al.*, 2012; Pinto *et al.*, 2016) or opportunistic sightings (Derville *et al.*, 2016) have been used to validate the predictions of research survey models. This approach was favored in Chapter 4, as satellite tracks recorded in New Caledonia from 2007 to 2016 were overlaid with predicted maps of habitat suitability based on research survey models. Although the evaluation metrics acquired from crossing these data types were not very informative, the overlapping patterns of movement and predicted habitat suitability reinforced our conclusions. The integrated pooling of multiple lines of evidence was one of the main strengths of this study.

Predictors & scales for cetacean SDMs

In Chapter 1, I presented the most common environmental predictors applied in cetacean SDM over various spatio-temporal scales (e.g., Fig. 1.8). Several categories of predictors were identified: the topographic variables and the dynamic variables, including in situ, remotely sensed or modeled data. Among these predictors, topographic variables derived from bathymetric charts, and SST from satellite remote sensing were primarily used throughout this thesis.

The available **resolution, extent and accuracy** of data was the primary practical limitation to their use. For instance, the satellite products with the highest spatial resolution (Multi-scale Ultra

high resolution SST, 1 km) could not be acquired before 2003. Datasets with lower resolution (e.g., Chapter 5, Reynolds Optimally Interpolated SST, 0.25°) had to be used instead when analyzing long time series going back to 1995. Cloud cover also limited the use satellite products at daily or weekly temporal resolution, as in [Scales *et al.* \(2017\)](#). Hence, in Chapter 4, monthly composites had to be used to limit data loss (MODIS SST and K490). Finally, bathymetric charts acquired from various sources included some discrepancies. For instance, the Kelso seamount was reported by more than 1200 m deep in the New Caledonian bathymetric atlas (map at 500 m resolution, [DTSI, 2016](#)), while it was less than 10 m deep in the NOAA ETOPO dataset, the GEBCO dataset and [Allain *et al.* \(2008\)](#) seamount database.

Predictor selection was also emphasized as a crucial step for producing meaningful SDMs. Indeed, measuring variables that are irrelevant to a species can result in erroneous habitat selection patterns ([James *et al.*, 1984](#)), and have dramatic consequences on predicted maps of habitat suitability. [Fourcade *et al.* \(2017\)](#) demonstrated that current evaluation metrics were not capable of selecting biologically significant variables and that **ecological reasoning should be prioritized**. In this thesis, the selection of environmental predictors was based on a thorough functional and ecological rationale. For instance, dynamic ocean variables such as chlorophyll-a or sea surface height were discarded a priori as potential drivers of humpback whale distribution in breeding regions. Indeed, as humpback whales are not expected to feed during the breeding season ([Clapham, 2000a](#)), there was no prior reason to include predictors of increased primary productivity.

Moreover, environmental variable choice was limited by recurrent **collinearity patterns**. Correlation among explanatory variables is known to affect a model's stability and capacity to assess the relative influence of each variable ([Dormann *et al.*, 2013](#)). For instance, topographic complexity can be estimated from a variety of variables (e.g., roughness, covariance of the slope, aspect, curvature; [Bouchet *et al.*, 2015](#)) but they are often collinear and cannot all be included in the same model (Chapter 4). Furthermore, the effects of shallow depth and proximity to coastlines have been extensively studied in humpback whale distribution (e.g., [Cartwright *et al.*, 2012](#); [Smith *et al.*, 2012](#); [Trudelle *et al.*, 2016](#); [Lindsay *et al.*, 2016](#); [Bortolotto *et al.*, 2017](#)). However, given that depth and distance to surfacing reefs or coast are often collinear, studying the effect of both variables within the same model should be done with caution. Throughout this thesis, collinearity was systematically checked, using Spearman or Pearson correlation coefficients as recommended by [Dormann *et al.* \(2013\)](#). When correlation could not be avoided by dropping a variable of lesser interest, sequential regression was applied (Chapter 5; [Graham, 2003](#)).

Background sampling and movements

Presence-only and presence-background SDMs rely on the comparison of used versus available environmental conditions. [Barve *et al.* \(2011\)](#) recommended using the **movement component M of the BAM diagram** (see Chapter 1; Fig. 1.3; [Soberón and Peterson, 2005](#)), as a conceptual

framework to calibrate the 'available area' in which to sample background points for these SDMs. This approach would require to identify the dispersal capacity of species prior to modeling their distribution. In the case of humpback whales, and generally that of all wide-ranging marine megafauna species, M is extensive and primarily restricted by land (a 'hard' boundary) and phylopatriy (a 'soft' boundary). Based on our results, the range of action of the humpback whale phylopatric bound is suggested to cover multiple breeding sites, separated by potentially great distances. Indeed, Chapter 6 has shown that humpback whales are capable of great movements in breeding regions (1500 km from New Caledonia to Australia). Altogether, the humpback whale M accessible area is likely to cover entire ocean basins during the breeding season. Hence, SDMs calibration outside the species' accessible range M (a practice that results in erroneous predictions; [Holloway and Miller, 2017](#)) was not a risk in the humpback whale case.

Nonetheless, the extent over which background data was sampled to produce presence-background SDMs had a strong impact on the model descriptive and predictive performances, as expected for highly mobile species ([Brotons *et al.*, 2004](#)). Indeed, sampling background data over large areas systematically results in higher deviance explained, as the contrast between presence and background environmental conditions overall is likely to increase when they are geographically separated by wider distances. Several studies have shown a positive correlation between AUC and the size of the model testing area ([Giovanelli *et al.*, 2010](#); [Barve *et al.*, 2011](#); [Dupin *et al.*, 2011](#)). Such effect would explain why the AUC of citizen science models was higher than that of research survey models in Chapter 4. In addition, increasing the size of the testing area tends to result in overly simplified environmental contributions of variables, with only a few dominating variables explaining most of the deviance ([VanDerWal *et al.*, 2009](#)). Oversimplified functional relationships for models fitted at large spatial scale was also demonstrated by [Paton and Matthiopoulos \(2015\)](#). For instance, distance to land/reefs and depth dominated the citizen science model with the uniform background sampling approach tested in Chapter 4. In conclusion, it appeared necessary to reasonably **limit the area over which to sample background points**. For non-systematic research surveys, the mean or maximum detection distance were used to delineate the limits of the stripwidth over which background points were sampled in the vicinity of the GPS boat trackline. For citizen science data, the POP and TARGET approaches aimed at reducing background point sampling in remote areas where human presence was low.

Finally, the **migratory behavior** of humpback whales further complicated the modeling of their distribution. [Holloway and Miller \(2017\)](#) identified the need to include a dynamic component to the BAM framework and SDMs of seasonal migratory species. Indeed, the habitat suitability of a given region may vary through time, hence driving the migratory behavior. In this thesis, temporally explicit variables were used to model the distribution at a given time of the year and account for seasonal distribution. In Chapters 4 and 5, SDMs included **julian day** as a predictor of humpback whale presence. This method allowed the models to differentiate habitats that were unoccupied because topographically or environmentally unsuitable, from habitats unoccupied simply because

they had been surveyed outside the peak of the breeding season.

Calibrating and interpreting SDMs

One of the main conclusions from this work and others (Guisan and Zimmermann, 2000; Araujo and Guisan, 2006; Qiao *et al.*, 2015) was the importance of setting a goal prior to modeling species distributions. Models with a '**descriptive goal**' primarily focus on the precise and complex modeling of species-environment relationships, whereas models with a '**predictive goal**' allow for continuous geographical projections of accurate model predictions. This primary goal contributes to the selection of a given SDM statistical algorithm. In Chapter 4, we found that some algorithms were inherently better at describing than predicting humpback whale distribution. Namely, machine learning approaches such as BRT fitted particularly complex relationships (in terms of interactions and shape of the fitted functions), which resulted in overfitting. While this level of complexity could be valuable for a purely descriptive model, it was not desirable in a predictive purpose. The comparison conducted in Chapter 4 was not exhaustive, since part of the approaches described in Chapter 1 were not tested: profile models, occupancy models and some machine learning models (RF, ANN, GP). The purpose of this comparison was not to select 'the best approach' over all existing algorithms, but rather to highlight how some popular approaches compared with respect to a typical cetacean non-systematic survey dataset.

Overfitting was identified as one of the main issues that should be prevented in cetacean SDMs produced in a conservation perspective. Other than the choice of the algorithm, overfitting was strongly affected by the calibration of the algorithm itself. Finding the right tuning for an algorithm, again relied on the choice of a proper evaluation metrics in line with the descriptive versus predictive goal identified upfront. The use of AUC and **diffAUC** (Warren and Seifert, 2010) in a presence-background framework (rather than presence-absence) was debatable (Phillips *et al.*, 2006; Jiménez-Valverde, 2012). However, diffAUC was the only metric to reflect overfitting and was therefore used to calibrate algorithms. Finally, **cross-validation** was also essential to calibrate models and limit overfitting (Roberts *et al.*, 2017). Stratified Monte-Carlo cross-validation accounted for dependencies in the observation data, namely the daily autocorrelation resulting from daily clusters in the extent and intensity of the survey effort. Cross-validation also allowed to evaluate prediction uncertainty, in maps of habitat suitability and partial dependence plots (Redfern *et al.*, 2006; Elith and Leathwick, 2009). Accounting for uncertainty levels is considered to be part of the "best practices for SDMs" (Robinson *et al.*, 2017a), and was therefore thoroughly applied throughout this thesis.

Finally, as several authors have emphasized the value of ecological thinking during the modeling process (Elith and Graham, 2009; Barve *et al.*, 2011; Fourcade *et al.*, 2017), **interpretability** of outputs was a major criteria in the comparison of statistical approaches (Chapter 4). For instance, machine learning approaches intrinsically accounted for interactions between predictors, which on one hand improved descriptive performances, but on the other hand limited their interpretability

within partial dependence plots (Goldstein *et al.*, 2015). In regression approaches, interactions have to be explicitly expressed in the model regression formula. While interactions may be technically challenging to express when there are many predictors, this approach is best to include prior knowledge of the species' ecology (Austin, 2007). For these reasons, GAMs were favored in Chapter 5, as they allowed a finer control of interactions, notably of nested regional effects.

Predictions for conservation

Anticipatory predictions have become a key application, if not the 'raison d'être', of ecological models (Yates *et al.*, 2018). Indeed, the primary purpose and application of cetacean SDMs is often to predict maps of probability of presence or habitat suitability, in a perspective of conservation (Gregor *et al.*, 2014). As a result, predictive performance and **transferability**, are paramount to many cetacean SDMs. Sequeira *et al.* (2018a) defined model transferability as the process of 'calibrating a **reference model** within a range of values for each predictor, and then projecting, or transferring, to a **target system** at some other location and/or time (and/or taxon)'. Model transfer therefore could provide predictions and inform management decisions into data-poor scenarios. Transferability applications include the study of rare endangered species in data deficient regions (e.g., Donald *et al.*, 2009; Dunn *et al.*, 2015; Stirling *et al.*, 2016; Redfern *et al.*, 2017), and range shifts caused by climate change (e.g., De Marco *et al.*, 2008; Elith *et al.*, 2010; Legrand *et al.*, 2016; Morán-Ordóñez *et al.*, 2017; Iturbide *et al.*, 2018).

Spatial transferability has been the focus of recent investigations and many have emphasized the need to 1) improve SDMs' inherent capacity to predict distribution in wider or new geographic areas (Sequeira *et al.*, 2018a; Yates *et al.*, 2018), and 2) identify and restrict extrapolation into non-analog environmental conditions (e.g., Dormann, 2007; Conn *et al.*, 2015; Petchey *et al.*, 2015; Mannocci *et al.*, 2018). Throughout this thesis, I attempted to follow both paths. First, to allow higher transferability, I purposefully used a modeling approach (GAMs) and parametrizations that would fit parsimonious relationships (smooth and mostly univariate) to a few carefully selected predictors (Wenger and Olden, 2012). Second, I systematically identified extrapolation to non-analog conditions in maps of predicted habitat suitability. Areas where at least one environmental variable expanded outside the reference range were shown with dashes or completely removed. At the New Caledonia EEZ scale, extrapolation areas represented 50 % of the predicted maps (Chapter 4), revealing the current lack of empirical reference data in pelagic ecosystems.

Temporal transferability is often impossible to validate into future times with unknown conditions. This limitation impairs the applicability of correlative SDMs to predict the impact of climate change on future species distributions (Silber *et al.*, 2017). Transferring a model into non-analog conditions (e.g., high temperatures forecasted from global warming scenarios) is a risky task in itself, and even so when empirical data is not available for validation. A solution to test for temporal transferability of models is the "space-for-time substitution" (Yates *et al.*, 2018). The environmental

gradient sampled over several contemporaneous sites spread over a wide spatial range can be used as a surrogate of temporal variability. For instance, while we do not have access to future humpback whale distribution affected by climate change at a given breeding site, we do have access to data from many humpback whale breeding sites ranging a wide temperature gradient in Oceania. Rather than blindly transferring current correlative SDM outputs to future SST conditions, we therefore estimated future habitat suitability based on the SST range currently occupied by humpback whales in Oceania (Chapter 5).

7.1.3 Perspectives

Mechanistic approaches

Correlative models of cetacean distribution, including ours, often do not satisfy the underlying **assumption of species equilibrium** with environment (Dormann, 2007). As humpback whale populations in the South Pacific have been increasing since the end of the industrial whaling era (Jackson *et al.*, 2015), their space use patterns are also likely to have evolved through time. Moreover, the effect of global warming on humpback whale distribution is indistinguishable from the population's inherent demographic change.

Mechanistic, or process-based models, offer further promise to explicitly and realistically test biological mechanisms underlying species distributions (Dormann *et al.*, 2012; Yates *et al.*, 2018). Specifically, mechanistic approaches are expected to confer higher transferability (Keith *et al.*, 2008; Yates *et al.*, 2018), but remain undertested (Kearney and Porter, 2009). Applications to marine mammals are rare (e.g., Pirodda *et al.*, 2017), perhaps as a result of the sparsity of experimental data and prior knowledge of the environmental, behavioral and physiological processes affecting these animals (Palacios *et al.*, 2014). Nonetheless, the identification of **causal processes** underlying marine mammal distribution using a mechanistic approach is advocated to predict the impact of **climate change** (Silber *et al.*, 2017).

New technologies, new challenges

Technological advances are constantly providing new tools to acquire, share and process data. In the field of spatial ecology, new trends in data collection techniques seem to favor remote approaches with minimal impact on animal and with the potential of being developed at least cost. Firstly, **satellite imagery** has recently been applied to detect and count marine mammals remotely. Southern right whales were detected from very high resolution satellite imagery off Argentina's coasts (Fretwell *et al.*, 2014) and gray seal, *Halichoerus grypus*, abundance was estimated from opportunistic observations in Google Earth imagery (Moxley *et al.*, 2017). Secondly, **Unmanned Aerial Systems** (UAS, a.k.a drones) are quickly becoming an indispensable part of the ecologists' toolbox. UAS can serve a multitude of purposes, such as recording cetacean behaviors (Torres *et al.*, 2018), estimating

their size and health (Christiansen *et al.*, 2018) or densities (Ferguson *et al.*, 2018). Both satellite imagery and drones appear like promising low-cost tools to detect and estimate densities of large whales in remote waters, such as the seamounts and reefs of the South Pacific.

Citizen science is also benefiting from digital technologies, which facilitate data collection by the general public as part of their every-day life. **Mobile applications** have been developed to help people report their observations in the field and build a better knowledge of their environment (e.g., MobI, <https://www.wwf.fr/projets/mobi-une-application-pour-recenser-les-cetaces>; Wildbook, <https://www.wildbook.org/doku.php>; Whale mAPP, Hann *et al.*, 2018). In the future, both cetacean research and conservation could benefit from the expansion of citizen science over wider scales, and accompanied by better data management systems. In New Caledonia, the existing collaboration between scientists, stakeholders and touristic operators could be further developed to favor data sharing and communication. For instance, many humpback whale photo-identifications are acquired from photos shared by the general public and whale-watching operators. Yet, this collaboration is not based on any specific numeric system to date. Marine policy in the South Pacific could greatly benefit from a better integration of scientific evidence contributed by citizen scientists and traditional monitoring over the long term (Hyder *et al.*, 2015).

7.2 Humpback whale space use patterns

This thesis aimed at acquiring fundamental knowledge of humpback whale distribution, habitat and movements during the breeding season. Three main questions were investigated throughout this thesis:

1. What are the environmental drivers of humpback whale distribution in their breeding grounds?

Seabed depth was a key determinant of humpback whale distribution at multiple spatial scales, from the South Lagoon of New Caledonia up to an ocean basin scale. Humpback whales favored shallow waters during the breeding season. A diversity of habitats were occupied, with shallow seamounts hosting some of the most important aggregations.

2. How do social factors influence distribution?

Humpback whales displayed a multi-scale hierarchical spatial distribution pattern, including localized and regional movements during the breeding season. In coastal breeding grounds, females with a calf displayed a social segregation pattern resulting from the avoidance of other conspecifics. In offshore breeding grounds, humpback whale aggregations were denser and females with a calf were more often escorted by males. Both females and males were found to move between breeding grounds, nearshore and offshore, and two tagged males performed extensive longitudinal movements to join remote breeding grounds.

3. How do environmental fluctuations and changes affect distribution at multiple temporal scales?

At a local scale, in the New Caledonian South Lagoon, the distribution was stable and the encounter rate of humpback whales increased over the years, despite fluctuations in their environment (e.g., ENSO). However, humpback whale occurrence at this local scale was found to reflect changes in SST, with colder waters being associated with higher encounter rates. At an ocean basin scale, most breeding grounds across Oceania were predicted to become unsuitably warm by the end of the 21st century.

7.2.1 Habitat diversity: a key aspect of humpback's flexible behavior

The study of humpback whale habitat preferences at multiple scales has highlighted the **diversity of habitats** occupied by this species during the breeding season. Across Oceania, humpback whales were found to occupy shallow waters, either on the **external slope of high islands**, or within the **lagoons of low islands and atolls** (Chapter 5). In New Caledonia, the use of shallow offshore seabed features such as **seamounts and banks** was particularly patent (Chapter 3 and 4). Encounter rates observed over pelagic areas such as Orne bank or Antigonina seamount were by far superior to those measured at the coast in the historical breeding ground of the South Lagoon (Chapter 5). The diversity of habitats occupied by humpback whales during the breeding season therefore reflects a certain level of **behavioral plasticity**. Interestingly, maternal humpback whales also demonstrated these flexible patterns of habitat use (Chapter 3) despite presumably higher energetic requirements and environmental constraints to maximize allocation of energy into calf growth (Lockyer, 1981; Braithwaite *et al.*, 2015).

Referring back to the ecological niche concept (Chapter 1), it is interesting to note that offshore visual survey effort and satellite tracking conducted in New Caledonia has revealed a previously unconsidered part of the **humpback whale ecological niche**. This case illustrates the dissociation between a species' fundamental niche and its modeled representation based on imperfect and uneven sampling. In French Polynesia and central Oceania, models suggested that pelagic seamounts were not favorable to humpback whale presence (Chapter 5). However, this prediction is likely to be the result of an **environmental sampling bias** (Mannocci *et al.*, 2018). If offshore surveys had never been conducted over seamounts in New Caledonia, perhaps their importance for humpback whales would never had been revealed.

The central role of shallow sheltered habitats in the humpback whale niche is well accepted (Clapham, 2000a; Rasmussen *et al.*, 2007). In this sense, the discovery of major breeding aggregations in unsheltered waters of New Caledonia is surprising and calls for a redefinition of humpback whale suitable habitats as we know them. Following the **source-sink dynamics** concepts (Fig. 1.1), I suggest the hypothesis that coastal habitats may become sink habitats when anthropogenic impacts are too intense. Indeed, the concentration of anthropogenic disturbance (from noise pollution, harassment) and threats (from boat collisions, plastic & chemical pollution) in coastal areas could cause humpback whale sub-populations using these habitats to suffer lower reproductive rates (e.g., sea lions, McHuron *et al.*, 2018). In New Caledonia, and the South Pacific Islands in general, the anthropogenic footprint is still limited due to a low human population density (e.g. New Caledonia, www.isee.nc). But human and industrial development (e.g., mining; Pascal *et al.*, 2008) are a growing source of concern for local biodiversity. It should be noted for the future that source-sink dynamics in the South Lagoon have the potential to maintain high encounter rates, even if anthropogenic impacts grow past sustainable levels. Indeed, this coastal breeding ground could be maintained only through a constant flux of animals coming from the seamount "source habitats". As a consequence, **high encounter rates should not be**

used as the only indicator of health for humpback whale populations in breeding regions.

As uncovered in Chapter 3 and 6, the reasons why humpback whales appear to strongly select for offshore unsheltered features in New Caledonia are unknown. Several hypotheses were evaluated to explain this preference for breeding aggregations to form on top of seamounts: landmarks for social aggregations, singing stages, avoidance of coastal areas impacted by human activities and opportunistic feeding sites. I reviewed the evidence supporting or refuting each of these hypotheses based on known habitat preferences described in the literature for humpback whales and other cetaceans, and on oceanographic characteristics (biotic and abiotic) presumed or described over seamounts. To date, the advantages for humpback whales to remain in pelagic seamount habitats are inconclusive and thus warrant further research.

7.2.2 Breeding and moving: drivers of multi-scale movements

The study of humpback whale distribution and movements at multiple scales has allowed a better understanding of their spatial structuring during the breeding season. Scaling up from a local to a basin spatial extent, I will discuss humpback whale distribution over three scales: the network of aggregations within a breeding sub-stock, longitudinal exchanges across sub-stocks, and basin-scale migratory movements. This hierarchical pattern is based on observations made in Oceania but warrants further investigation in other ocean basins.

Local movements: social interactions and within breeding ground distribution

In Chapters 2 and 3, I focused on local distribution pattern in southeastern New Caledonia. Humpback whales appeared to visit several breeding grounds, or 'arenas' (Herman, 2017) in this region. Within each of these breeding grounds, humpback whales displayed a **fine-scale spatial structure** based on attraction and avoidance among individuals of various sex and age class (Chapter 3). Indeed, a pattern of **social segregation** was identified in the South Lagoon where females with a calf used shallow waters closer to the coast. In offshore breeding grounds, females with a calf were not geographically or environmentally segregated from other conspecifics, and were more often accompanied by one or several male escorts (Fig. 7.2).

The reasons why **maternal females** would join breeding arenas where males display and compete are unknown (Herman, 2017), given that post-partum breeding was estimated to be rare for humpback whales (Chittleborough, 1958). If females breed every 2 to 3 years (Chittleborough, 1958; Baker *et al.*, 1987; Craig and Herman, 2000; Rankin *et al.*, 2014), they would not be expected to benefit from joining arenas when already accompanied by a calf. If anything, staying in close proximity with dense aggregations of males could be detrimental to the calf and its mother (Elwen and Best, 2004; Darling *et al.*, 2006; Cartwright and Sullivan, 2009a; Craig *et al.*, 2014). In addition, if these aggregations occur in unsheltered offshore waters where wind and swell conditions are rough,

the energetic cost to the female and her calf would be even higher (Félix and Botero-Acosta, 2011; Rayment *et al.*, 2015; Bortolotto *et al.*, 2017). Recent evidence from hormonal analyses, however, support a new hypothesis suggesting higher rates of post-partum breeding. In the Kermadec Islands, a known migratory corridor for the New Caledonian sub-population, 45.5% of females with a calf at the time of sampling were pregnant (Riekkola *et al.*, 2018). A similar rate of annual pregnancy (54.5%) was found in the Western Antarctic Peninsula (Pallin *et al.*, 2018), a region also known to host whales from Oceania's eastern breeding grounds (Albertson *et al.*, 2018). Furthermore, mark-recapture models suggest that birth intervals in New Caledonia could be shorter than expected (1.68 years, Chero, 2017), hence resulting in more frequent post-partum breeding. As a consequence of frequent annual pregnancies, it would appear less surprising that females with a calf would join arenas where mating opportunities are highest.

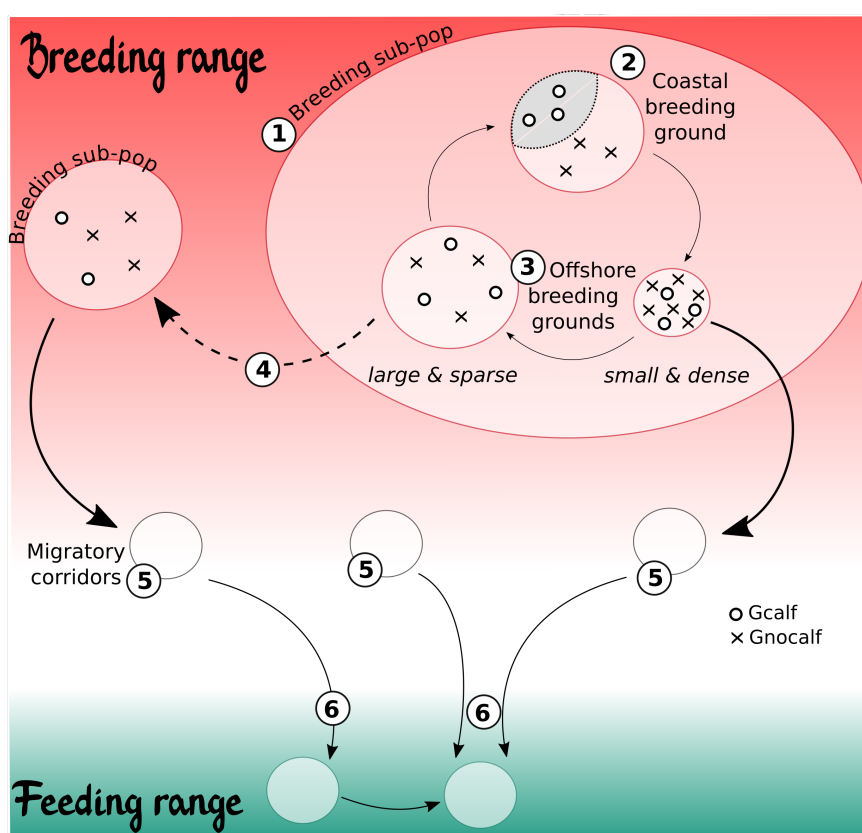


Figure 7.2 Schematic representation of hierarchical spatial structure of the humpback whale mating system and movements at an ocean basin scale. 1) Several breeding stocks or sub-stocks spread longitudinally in tropical and subtropical waters. Within these breeding stocks, several breeding grounds may exist. 2) Coastal breeding grounds can present social segregation patterns where groups with calf (Gcalf) are found in sheltered, shallow waters closer to the coast compared to groups without calf (Gnocalf). 3) Offshore breeding grounds (banks, seamounts) show no social segregation. I postulate that smaller features with higher densities are more attractive and that females with a calf are more often escorted when density increases. 4) Extensive longitudinal movements can occur between breeding sub-stocks. 5) Humpback whales migrate towards their feeding grounds and potentially stop along the migratory corridor. Opportunistic breeding probably still occurs at this stage of the migration, depending on how far south it is located. The colored gradient from red to green represents this progressive rather than clear-cut border limit feeding and breeding ranges. 6) Humpback whales appear to start feeding at variable latitudes and may move from one productive feeding ground to another.

Another noteworthy aspect of humpback whale spatial distribution within breeding grounds is that of density. **Encounter rates** were used to approximate whale density in non-systematic visual surveys. Temporal encounter rates (whales.hrs⁻¹) in the Antigonía and Orne bank offshore regions of New Caledonia were almost double those measured in the other breeding sites of Oceania (Chapter 5). A similar trend was found in spatial encounter rates (number of whales per km surveyed) calculated for the 2017 MARACAS surveys (Garrigue *et al.*, 2018a). Encounter rates of the southeastern seamounts (Antigonía 0.618 whales.km⁻¹, Orne bank 0.270 whales.km⁻¹) were by far superior to the Chesterfield (0.056 whale.km⁻¹) and Bellona plateaus (0.040 whale.km⁻¹). Despite evident differences in habitat types (pelagic seamounts versus reef plateaus), these areas present similar depths (15-60 m) but different surface areas. Antigonía is a small guyot covering 98 km², Orne bank is slightly larger (120 km²) and Chesterfield Bellona cover extensive plateaus (4,350 km² and 9,880 km² respectively). Based on terrestrial lek study cases (Lank and Smith, 1992), Herman (2017) proposed that larger leks (with more males and more acoustic activity) were more attractive to female humpback whales. Indeed, the link between lek size and attractivity is supported in several bird species (e.g., *Philomachus pugnax*, Lank and Smith, 1992; Widemo and Owens, 1995), *Tetrax tetrax* (Jiguet and Bretagnolle, 2006). Following Herman's hypothesis, I would suggest that breeding grounds offering smaller shallow surfaces (e.g., guyots such as Antigonía seamount) could result in denser and more attractive breeding aggregations. Further analyses of density in relation to the surface of available suitable shallow habitats is necessary to test this hypothesis.

Finally, satellite tracking has confirmed frequent within-season movements among neighboring breeding arenas (Chapter 6). This pattern of connectivity had already been suggested through the comparison of photo-identified and genotyped individuals in the southeastern region (Garrigue *et al.*, 2013; Orgeret *et al.*, 2014; Garrigue *et al.*, 2017). Further analysis of **individual capture histories** is required to understand the selective mating strategies underlying this connectivity.

Regional movements: connecting breeding populations

Southern Hemisphere humpback whales are managed as separate populations with varying degrees of connectivity (IWC stocks and sub-stocks; Jackson *et al.*, 2015) and the South Pacific is no exception. Based on evidence from genetic, photographic and song analysis, it is currently considered to cover several geographically separated populations and sub-populations (Olavarría *et al.*, 2007; Childerhouse *et al.*, 2009; Garland *et al.*, 2015). A form of isolation by distance appears to best explain spatial structuring at the South Pacific scale (Jackson *et al.*, 2015). However, varying degrees of geographical connectivity have been identified between and within seasons (Garland *et al.*, 2011; Garrigue *et al.*, 2011a; Steel *et al.*, 2017). In Chapter 6, I reported on the movement of two male humpback whales tagged in Antigonía seamount that crossed the Coral Sea towards the east coast of Australia. These **extensive westwards longitudinal movements** are further supported by movement data from four whales tagged in Chesterfield-Bellona (2017) and five whales tagged in the South Lagoon (2007-2011; Garrigue *et al.*, 2015; Fig. 7.3). Humpback whales could be crossing

the Coral Sea to seek more mating opportunities or simply join the East Australian migratory corridor without interbreeding. This thesis therefore suggests that the hierarchical spatial structure of breeding humpback whales covers wider geographical extents than previously thought in the South Pacific.

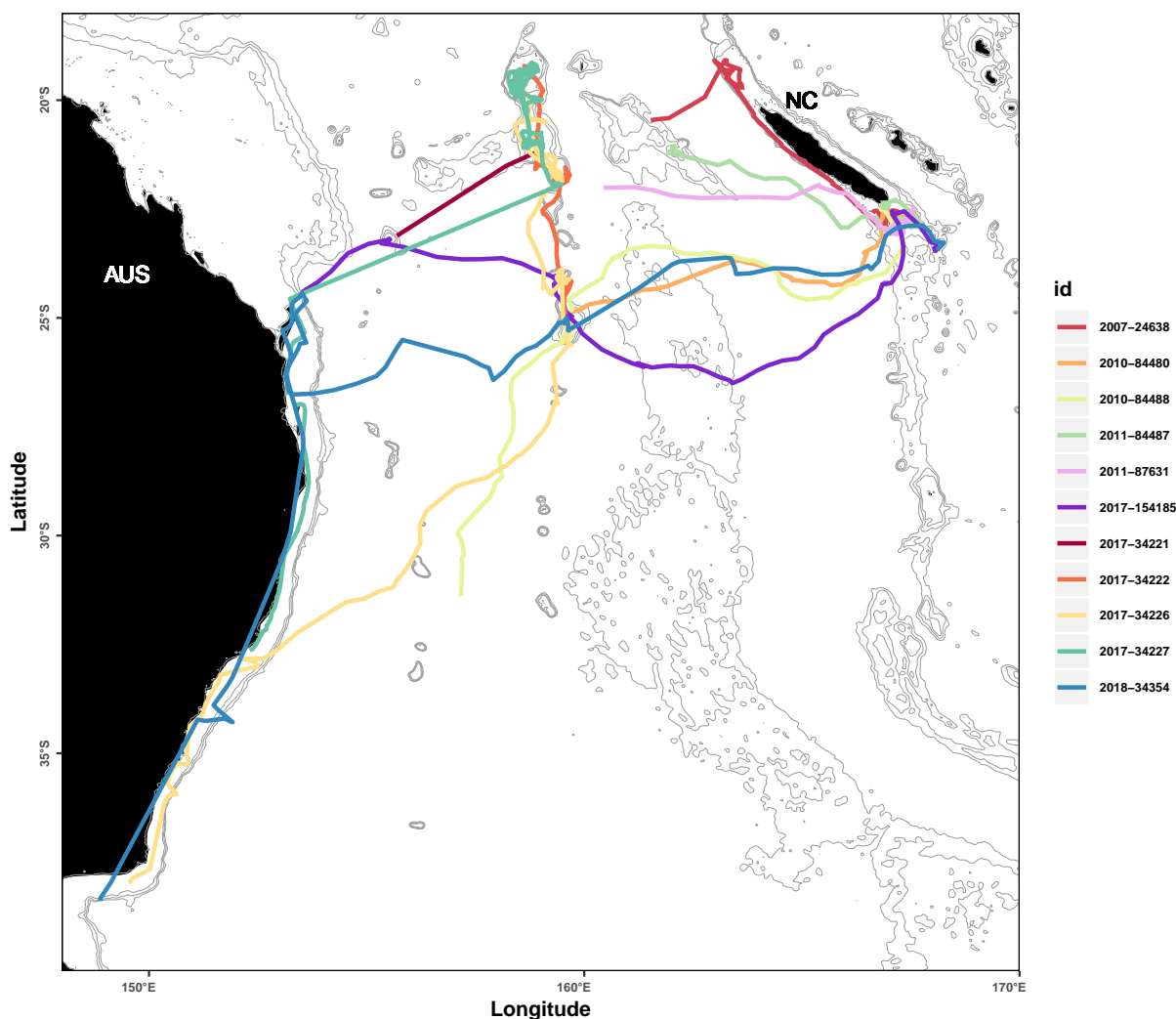


Figure 7.3 Satellite tracking of 11 humpback whales tagged: in the Chesterfield-Bellona archipelago (n=4, 2017), Antigonion seamount (n=2, 2017-2018), and the South Lagoon (n = 5, 2007-2011), suggesting longitudinal movements in the Coral Sea. Tracks from 2017-2018 were interpolated with a CRW algorithm, whereas tracks from 2007 to 2011 were only filtered to remove aberrant positions.

An interesting repercussion of westward longitudinal movements is the potential for encounters between individuals of the New Caledonian sub-population and those migrating along the east coast of Australia (Valsecchi *et al.*, 2010). These exchanges may help fill in the gap in our understanding of song exchange mechanisms. Indeed, males of the sub-populations of Oceania and East Australia produce distinct versions of a vocal sexual display, the humpback whale 'song' (Garland *et al.*, 2015). **Horizontal cultural transmission** of this song has been demonstrated over the years (Garland *et al.*, 2011). A given version of the song is systematically transmitted eastward through the South Pacific breeding grounds, from one breeding population to the next over a number

of breeding seasons. Such phenomenon requires acoustic contact between individuals of neighboring populations for the song to propagate. Shared summer feeding grounds between New Caledonia and East Australia seem to provide such opportunity (Garland *et al.*, 2013). Shared migratory routes were also proposed as an alternative, yet non-exclusive mechanism (Payne and Guinee, 1983). Our satellite tracking results support potential acoustic contact during the southward migration. Cultural exchanges could result from the movement of a few individuals from New Caledonia into the east Australian migratory corridor.

The fuzzy limit to breeding latitudes

Early studies considered coastal waters around 25 °C to be a requirement for breeding and calving activities (Dawbin, 1966). Later, Rasmussen *et al.* (2007) reviewed breeding ground water temperatures worldwide and estimated that they ranged from 21.1°C to 28.4°C, equivalent to approximately 0 to 30° of latitude. Following Rasmussen *et al.* (2007), water temperature was favored over latitude to delineate breeding regions throughout this thesis.

However, the longitudinal movements observed in the Coral Sea and stop-overs in discrete locations (seamounts, banks, islands and reefs) complicate the established pattern of humpback whale migration. In addition, neonate calves have recently been observed over what was previously considered as a **migratory corridor** in Western Australia. Irvine *et al.* (2017) demonstrated an extension of calving grounds on the west coast of Australia, from 18°S to 22.7°S in recent years. In this context, breeding grounds and stop-overs along migratory corridors become harder to distinguish (Fig. 7.2). Without direct observations in situ, locations such as Capel seamount (25°S) cannot be classified as a breeding ground or a migratory stop-over.

With the general increase in humpback whale populations in the Southern Hemisphere (Jackson *et al.*, 2015) it is possible that breeding activities have expanded south. Alternatively, the limits to breeding grounds could have been biased by a spatial sampling bias and may be revised with more data collection in the future. Specifically, the combination of multiple data types (e.g., genetics, song recordings, photo-identification, satellite tracking) is necessary to establish the use of various habitats located at the border between breeding and migratory latitudes. The Cook Islands is a good example of a location previously considered as a breeding ground (and classified as such by the IWC substock BSE1; IWC, 1998) and now rather classified as a migratory stop-over. Indeed, humpback whales have been shown to be highly transient (Hauser *et al.*, 2000) and move northward from the Cook Islands towards other breeding grounds of Oceania (e.g., Tonga, Samoa, Hauser *et al.*, 2010). In conclusion, satellite tracking should bring a better understanding of breeding region boundaries in the South Pacific.

7.2.3 Perspectives

Critical seamount habitat

This thesis provided an enhanced understanding of the patterns of habitat use and movements within breeding latitudes and early southward migration in Oceania. Seamounts were clearly identified as a critical humpback whale habitat worth further investigation.

First, the encounter rates and number of visits per tagged individual varied spatially, indicating a preference for some seamounts over others. The social and environmental drivers of this pattern of habitat selection could be investigated to understand the factors leading to the attractiveness of a specific seamount. **Systematic visual line-transect surveys** (boat-based or aerial) could be conducted over a pelagic area covering several potential breeding arenas of various sizes and environmental characteristics (depth, height, turbulences, temperature etc.). As a result, density estimates could directly be related to fine-scale variables of habitat suitability.

Second, social factors are also likely to contribute to the connectivity patterns between breeding lek arenas. Roaming behavior including visits to multiple arenas in a given season could constitute an adaptive strategy increasing **breeding success** for males as well as females. Further analysis of individual capture histories is required to understand the selective mating strategies underlying this connectivity. Paternity analysis and calving rate estimation would allow to test for individual reproductive success as a result of different breeding strategies (Garrigue *et al.*, 2017).

Migration and feeding destinations

To effectively protect a migratory species, all habitats utilized over its life cycle need to be considered. In the case of Southern Hemisphere humpback whales, “the whole picture” includes their **feeding grounds in the Southern Ocean**.

Satellite telemetry has greatly contributed to the identification of feeding destinations in the remote waters surrounding the Antarctic continent (Dalla Rosa *et al.*, 2008; Robbins *et al.*, 2011; Zerbini *et al.*, 2011; Andrews-Goff *et al.*, 2018; Riekkola *et al.*, 2018). Few of the tags deployed in New Caledonia have lasted long enough to track whales to Antarctica. (Fig. 7.4). Among those, one whale reached the Ross Sea and another was directed to the Bellinghousen Sea, east of the Antarctic Peninsula. In order to identify the full extent of South Pacific feeding grounds, such tagging information from New Caledonia need to be combined with 1) photo-identification and genotyping data from samples collected in feeding grounds (e.g., Balleny Islands or Western Antarctic Peninsula; (Constantine *et al.*, 2014; Steel *et al.*, 2017; Albertson *et al.*, 2018), and 2) tags deployed in known migratory corridors located closer to the feeding destinations (e.g., Kermadec Islands, Riekkola *et al.*, 2018).

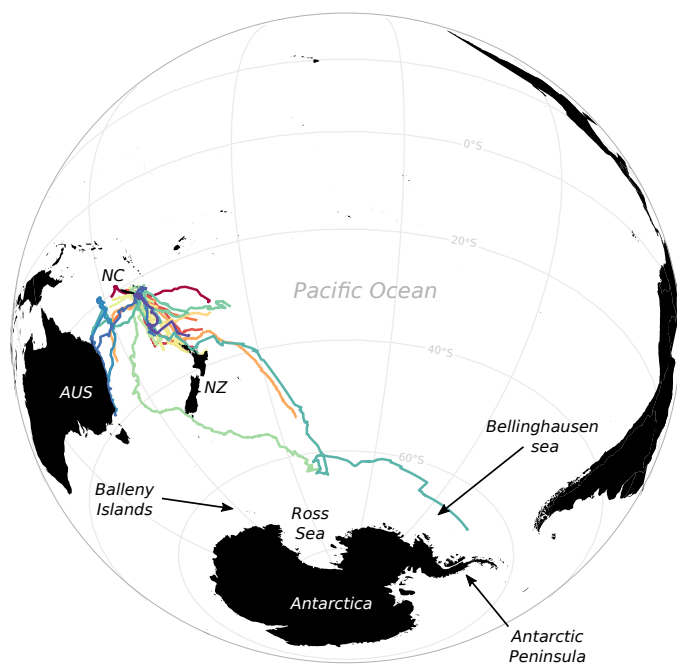


Figure 7.4 South Pacific view of all satellite tags deployed in New Caledonia between 2007 and 2018 ($n = 62$).

Climate change is expected to greatly affect polar marine ecosystems. Changes in prey availability and suitable humpback whale habitat in polar regions will be echoed in the tropical breeding grounds; the impact of such changes cannot be precisely understood without knowledge of humpback whale space use in the Southern Ocean. The identification of feeding destinations is a prerequisite to predicting the impact of environmental changes and habitat degradation throughout the entire humpback whales' life cycle.

7.3 Contributing to humpback whale conservation

The final objective of the present thesis was to apply the acquired knowledge of humpback whale spatial ecology to conservation, from local spatial management of the endangered New Caledonian sub-population, to a global discussion of the impact of climate change on this species. Three main questions were identified:

1. What are the potential anthropogenic impacts on humpback whales in a coastal breeding ground of New Caledonia and is current management action efficient?

The South Lagoon is a major breeding ground for the endangered humpback whale sub-population of New Caledonia. Marine traffic associated with industries and tourism can cause disturbance and increase the risks of collision, particularly in the waters closest to the coast. Females with a calf are particularly at risk given their specific habitat preferences in the South Lagoon. MPAs with various levels of protection already exist in this area, but the ones that restrict human activities are in mismatch with humpback whale preferred habitats.

2. Based on the species-environment relationships identified at multiple spatial scales, can we predict priority conservation areas, in both coastal and offshore waters of New Caledonia?

Shallow waters suitable for humpback whales during the breeding season were identified in the coastal waters under the jurisdiction of the New Caledonian Provinces, and in the remote waters of the Natural Park of the Coral Sea managed by the New Caledonian government. Shallow waters up to 100 m deep (seamounts, banks, lagoons, slopes) constitutes critical habitats over the Lord Howe seamount chain, the Norfolk ridge and the Loyalty ridge. Specific spatial management of these areas is suggested.

3. At an ocean basin scale, what is the potential for adaptation to global warming?

Breeding habitats across Oceania span a large thermal range (22.3°C to 27.8°C on average in August with inter-annual variation up to 2.0°C). After projecting sea surface temperatures in a global warming scenario, many breeding sites were predicted to become unsuitably warm by the end of the 21st century. Based on an apparent plasticity of habitat use patterns, models predicted extensive suitable habitats for relocation, hence supporting a potential for adaptation to climate change in breeding latitudes.

7.3.1 Anthropogenic impacts in the South Lagoon

Anthropogenic impacts concentrate in coastal marine ecosystems where human populations are the largest. The South Lagoon of New Caledonia is no exception to this trend. The importance of a consistent long-term monitoring of whale populations in such context has been demonstrated in Chapter 2. Moreover, Chapter 3 highlighted critical habitat in the sheltered waters closest to the Prony Bay for a social category that is most vulnerable, maternal females with a newborn calf.

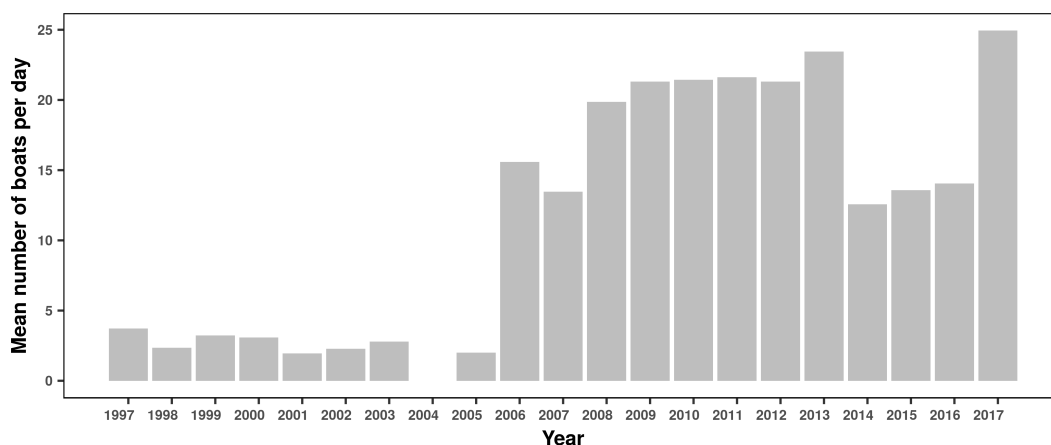


Figure 7.5 Mean number of boats counted per day from the land-based lookout of the South Lagoon (Cape N'Doua). Boats are counted at 9 a.m during every survey day over a predefined grid of the study area.

In the South Lagoon, **marine traffic** has intensified throughout the last two decades (Fig. 7.5). The traffic is mainly composed of large cargo ships and ferries, whale-watching operators, and pleasure boats (Bourgogne *et al.*, 2018). Cargo ships and ferries typically move at speeds exceeding the 14 knots limit above which whale collisions are likely to be fatal (Laist *et al.*, 2001). Using the predicted core areas of use from Chapter 2, I identified the **spatio-temporal window of maximal collision risk** in the South Lagoon. This impact study focused on females with a calf, which are most at risk to be affected by human disturbance and suffer vessel collisions (Lammers *et al.*, 2007; Cartwright *et al.*, 2012). The core area of use for females with a calf was overlaid with the main shipping routes, estimated through AIS (Automatic Identification System, www.marinetraffic.com, Fig. 7.6). The Prony bay and waters nearest to the Cape N'Doua concentrated the highest risks for maternal females, specifically towards the end of the breeding season (first two weeks of September) when females with a calf are most frequently observed (Derville *et al.*, 2017).

Whale-watching has also greatly contributed to the general increase of marine traffic in the South Lagoon since 1995 (Schaffar *et al.*, 2010, 2013). Whale-watching is an increasingly important source of income for Pacific islands with few natural resources outside their large EEZ (Hoyt, 2005; Orams, 2002; O'Connor *et al.*, 2009; Cisneros-Montemayor *et al.*, 2010). In New Caledonia, the number of whale-watching touristic operators has increased from 5 in 1995, to 24 in 2017 (South Province). Correspondingly, the number of privately owned boats cruising in the area has also

increased, resulting in an overall larger number of boats purposefully visiting the South Lagoon to observe humpback whales (Fig. 7.5).

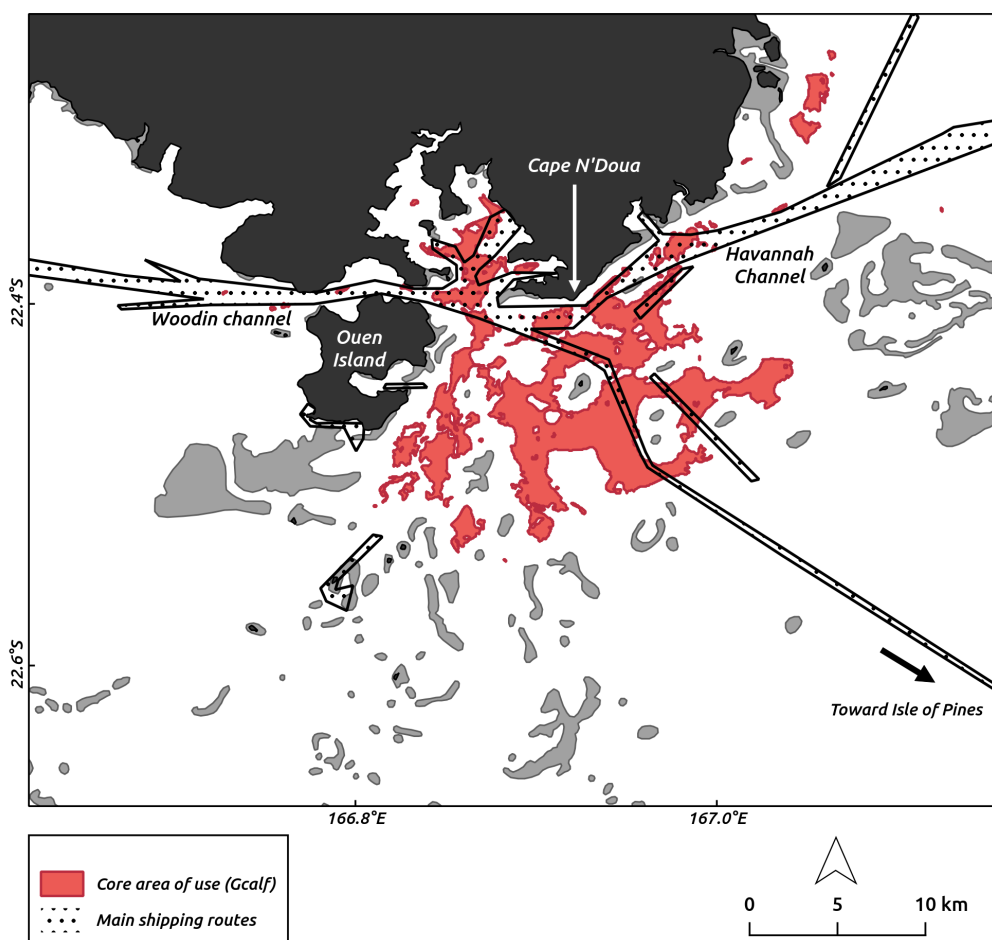


Figure 7.6 Spatial overlap between vessel traffic and potential presence of humpback whale females with a calf. Predicted core area of use for females with a calf (based on [Derville et al., 2017](#)) is shown in red. Main shipping routes identified from AIS data are shown with black dotted polygons.

A **behavioral response** of cetaceans to whale-watching has been demonstrated (e.g., [Corkeron, 1995](#); [Stamation et al., 2010](#); [Schaffar et al., 2013](#); [Avila et al., 2015](#)). Disruption of activity budget and path directionality were the most commonly measured responses to whale-watching vessels (meta-analyses: [Senigaglia et al., 2016](#)). In the New Caledonian South Lagoon, whales tracked from a land-based look-out were shown to increase speed, dive for longer durations and increase path sinuosity as a response to approaching boats ([Schaffar et al., 2013](#)). Impacts of **chronic disturbance at population level** are far more difficult to assess, specially in the case of growing populations such as humpback whales ([Corkeron, 2004](#)). While numeric simulations are an interesting approach to test these latent effects ([McHuron et al., 2018](#)), empirical data recorded on the long term remain a necessity.

In 2008, **whale-watching guidelines** were implemented by the New Caledonia South Province ([Province Sud, 2018](#)). Since then, consistent long-term monitoring has shown that guidelines were

efficient at limiting the observation times and the number of touristic boat operators around whales (Bourgogne *et al.*, 2018). However, given the preference of operators to stay close to the coast, maternal females were identified to be a prime target of whale-watching activity in the South Lagoon (Derville *et al.*, 2017; Bourgogne *et al.*, 2018). Again, because of its specific habitat requirements (as identified in Chapter 3) this vulnerable social category is the one that is under most anthropogenic pressure.

7.3.2 Identification of priority conservation areas in New Caledonia

One of the primary objectives for modeling cetacean habitat is to help produce science-based spatial management (Gregr *et al.*, 2014). Likewise, this thesis identified habitat preferences and provided predicted maps of habitat suitability that can be applied to improve conservation efforts in New Caledonia.

The South Lagoon MPA mismatch

At the **South Lagoon scale** (Chapter 2 & 3) a core area of humpback whale use was identified in the relatively shallow but open waters located outside the Prony bay, south of the Cape N'Doua. This area is not currently included in an MPA with effective restrictions on human activities. In addition, the integral Merlet Reserve (IUCN category Ia), which receives the highest level of protection (no-entry) is very marginally used by humpback whales. Such **mismatch between spatial management and critical habitats** of marine megafauna had already been highlighted for the small population of dugongs found in the lagoons of New Caledonia (Cleguer *et al.*, 2015). The lack of explicit conservation targets at the time of the MPA creation was identified as one the primary reason explaining this mismatch. With an explicit mapping of critical habitats and core areas of use, this thesis provides scientific evidence to improve spatial management of humpback whales in the New Caledonia South Lagoon.

Humpback whale "hotspots" in New Caledonia

At the **New Caledonia EEZ scale** (Chapter 4), the sheltered waters of the South Lagoon, North Lagoon and the Loyalty Islands provided particularly suitable humpback whale habitats. All seamounts and banks of the southern Natural Park of the Coral Sea also formed areas of interest, specifically Capel and Kelso (Lord Howe seamount chain), Antigonina and Torch (Norfolk ridge) and Orne, Durand, Walpole, Ellet (Loyalty ridge). Although part of the Lord Howe seamount chain was in the area of uncertain extrapolation (Fig. 7.7), its use was confirmed by satellite tracking (Chapter 6). Larger shallow areas such as the Fairway-Landsdowne bank and the Chesterfield-Bellona archipelago were predicted to be suitable. In the latter, the banks located in between the Chesterfield and Bellona plateaus appeared particularly suitable (Boussole, Vauban Dumont D'Urville).

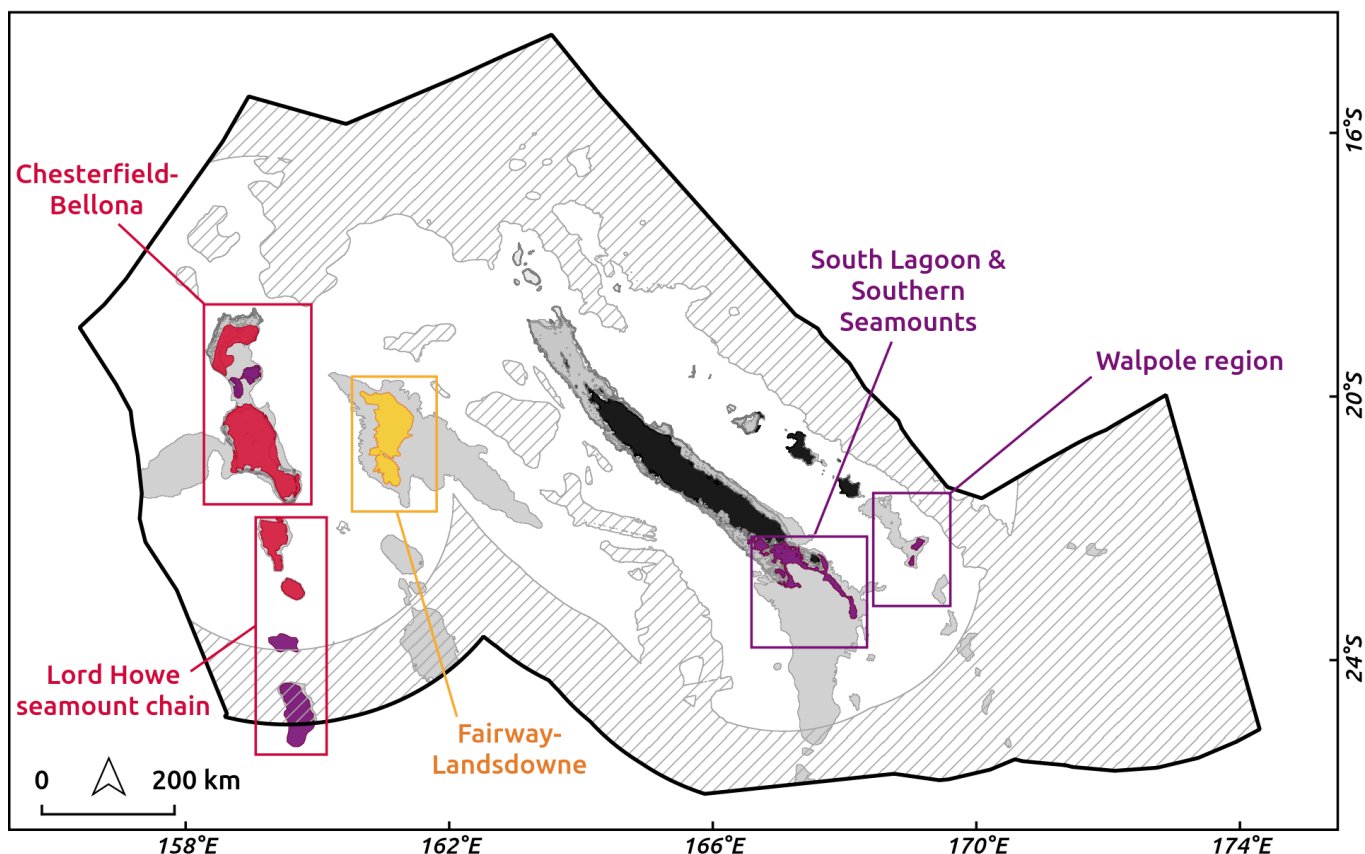


Figure 7.7 Schematic map of critical humpback whale breeding and calving habitats in the New Caledonia EEZ. Areas were ranked with increasing levels of conservation priority from yellow to purple. This ranking was based on several lines of evidence developed along this thesis: predicted maps of habitat suitability, satellite tracking and encounter rates. The 10 % most suitable habitats predicted with generalized additive model based on non-systematic research surveys at sea (Chapter 4) are represented in grey. Predictions cannot be confidently made in dashed areas.

While the New Caledonian lagoons and coral reefs had already been the focus of conservationists and local stakeholders (e.g., UNESCO World Heritage Site), pelagic ecosystems have not been a management priority. In this thesis, we show the importance of seamounts as a critical habitat for humpback whales in New Caledonia. These results are meant to provide a scientific basis to the design of an MPA network within the **Natural Park of the Coral Sea**.

Designation of Important Marine Mammal Areas

Vast MPAs encompassing a diversity of habitats promote ecological interactions between ecosystems (Wilhelm *et al.*, 2014) and favor the protection of wide-ranging species (e.g., White *et al.*, 2017). In this prospect, a combination of coastal and pelagic MPA (Guidetti *et al.*, 2013) is essential to protect wide-ranging species such as humpback whales.

In this thesis, the diversity of critical habitats that they occupy during the breeding season has been demonstrated and applied to help conservation efforts. Several areas of interest

(AoI) for humpback whales were submitted to the '**Important Marine Mammal Areas**' (IMMA, <https://www.marinemammalhabitat.org/imma-eatlas/>) during the regional Pacific Islands workshop in 2017 (Fig. 7.8). IMMAs are defined as 'discrete portions of habitat, important to marine mammal species, that have the potential to be delineated and managed for conservation'. They are promoted by the IUCN Marine Mammal Protected Area Task Force and constitute a novel scientific tool to lead place-based conservation of marine mammals (Corrigan *et al.*, 2014; Di Sciara *et al.*, 2016).

The '**Chesterfield-Bellona Coral Reef Complex and Seamounts**' area was submitted to cover the extent of the Chesterfield-Bellona plateau as well as the seamounts of the Lord Howe seamount chain (Fig. 7.9). This area fulfilled several of the IMMA criteria, namely Criterion A ('Areas containing habitat important for the survival and recovery of threatened and declining species'), Criterion B ('Areas supporting important concentrations of a species or population') and Criterion C ('Areas that are important for a species or population to mate, give birth, and/or care for young until weaning' and 'used for important migration or other movements'). This region was selected as a 'candidate IMMA', pending additional scientific evidence at the time of workshop (which occurred before the 2017 MARACAS surveys in Chesterfield-Bellona).

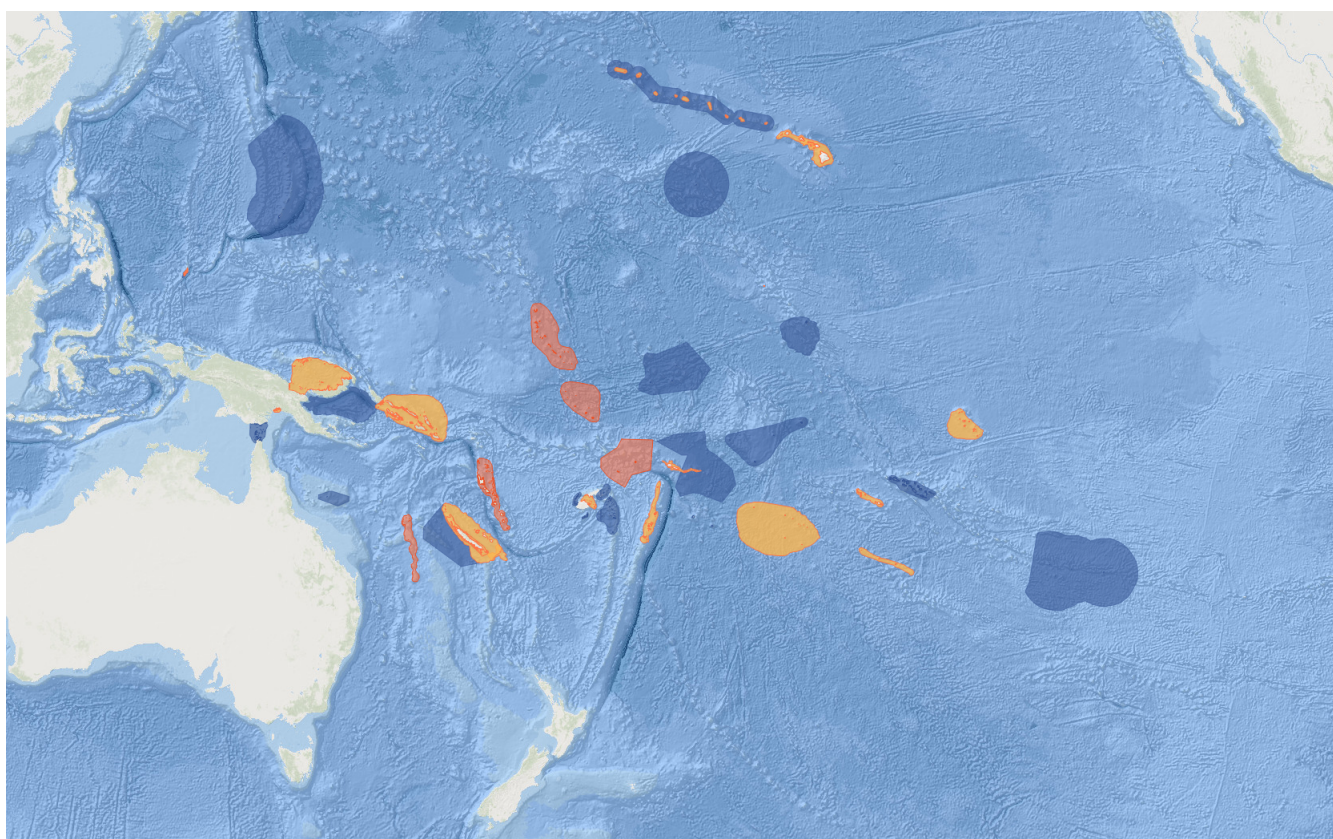


Figure 7.8 Pacific Islands Important Marine Mammal Areas: Pacific Islands IMMA (orange), candidate IMMA (red) and Areas of Interest (blue). Source: <https://www.marinemammalhabitat.org/imma-eatlas/>

The '**New Caledonia Southern Seamounts and Banks**' area was submitted to cover the shallow offshore seabed features located southeast of New Caledonia, specifically Orne bank, Walpole

Island, Ellet bank, Torch bank and Antigonnia seamount (Fig. 7.9). This area fulfilled all the criteria cited above, as well the Criterion D for 'distinctiveness' and 'diversity'. Indeed, the area includes some of the only known purely offshore breeding grounds for humpback whales and is also used by a diversity of marine mammal species (e.g., *Balaenoptera acutorostrata* subsp, *B. omurai*, *Globicephala macrorhynchus*, *Indopacetus pacificus*, *Kogia breviceps*, *K. sima*, *Megaptera novaeangliae*, *Mesoplodon densirostris*, *Physeter macrocephalus*, *Stenella longirostris*, *Tursiops aduncus*, *T. truncatus*, *Ziphius cavirostris*; Garrigue and Poupon, 2013). This area has definitely acquired the IMMA status in 2017.

Finally, the 'New Caledonian Lagoons and Shelf Waters' area was submitted to cover the reef, lagoon, seagrass and mangrove ecosystems surrounding the mainland (Fig. 7.9). This area includes the important South Lagoon humpback whale breeding area. In addition, it is used by a small population of Indo-Pacific bottlenose dolphins and a vulnerable population of dugongs. This area has also definitely acquired the IMMA status in 2017.

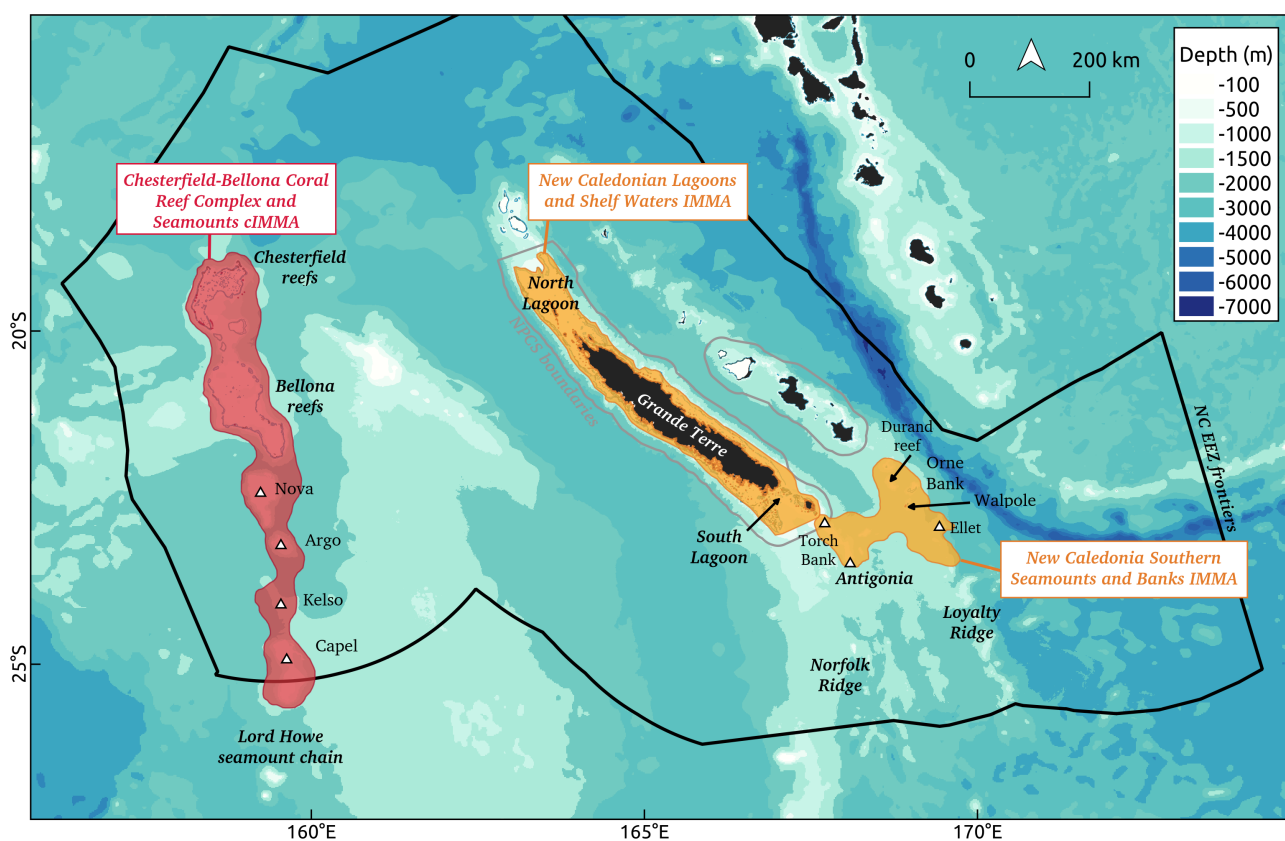


Figure 7.9 Important Marine Mammal Areas proposed for humpback whales in New Caledonia. IMMA as represented in orange, candidate IMMA are represented in red. Polygons were acquired from IUCN-MMPATF (2017). Information about the habitats and species within IMMAs are publicly available on the IMMA e-atlas (e.g., www.marinemammalhabitat.org/portfolio-item/new-caledonia-southern-seamounts/). The frontiers of the New Caledonian EEZ are represented with a black polygon. Grey lines inside the EEZ represent the waters under provincial jurisdiction and not included in the Natural Park of the Coral Sea (NPCS). IMMA created for other species than humpback whales exist in the region but are not represented on this map.

7.3.3 Climate change: the looming threat

The adaption of conservation efforts to environmental change is one of the key research questions for the conservation of cetaceans (Parsons *et al.*, 2015). Indeed, the uncertainty on the nature and magnitude of future responses to climate change precludes the implementation of appropriate anticipatory management (Silber *et al.*, 2017). A long lifespan, low birth rate, and long generation time are common cetacean traits that are likely to hinder rapid evolutionary adaptation to climate change. Yet, some species such as humpback whales have shown a surprising flexibility to environmental fluctuations (Benson *et al.*, 2002; Fleming *et al.*, 2016; Eisenmann *et al.*, 2016). Hence, humpback whales are generally not prioritized with the highest management needs with respect to climatic threats (Silber *et al.*, 2017). On the other hand, their potential for adaptation is exactly the reason why they can be used as 'ocean sentinels' (Bengtson Nash *et al.*, 2018), whose distribution, diet and health could reflect the state of marine habitats, from the poles to the tropics.

Given the high mobility of cetaceans and the fluid and changing environment they live in, static protection is not always efficient for cetaceans. Several studies have highlighted the mismatch between protective policies and habitat occupancy as a function of time (Hartel *et al.*, 2014; Pérez-Jorge *et al.*, 2015). As a result of climate-driven shifts, MPAs that are efficiently protecting species today, might not do so tomorrow (Macleod *et al.*, 2009; Macleod, 2009; Bruno *et al.*, 2018). It is therefore important to consider the dynamics of species distribution, in order to implement effective spatial management plans. Based on the assumption that distribution shifts are one of the most likely response of cetaceans to climate change, we assessed **present and future habitat suitability** for humpback whales in Oceania. Potentially suitable habitats for relocation were identified in the area predicted to encompass the expected thermal range of the species by the end of the 21st century. Increased number of whales could be expected in seamounts and archipelagos located in southern Oceania (e.g., in New Caledonia, Norfolk, the Kermadec Islands, the southern Tonga Islands, the southern Cook Islands, the Australs, the Gambiers and Pitcairn Islands). Monitoring or conservation of humpback whales in these regions can anticipate on future environmental change.

7.3.4 Perspectives

Exploring new potential pelagic breeding grounds

Using extrapolated habitat models and satellite tracking, this thesis defined potentially critical habitats for humpback whales in New Caledonia and in Oceania. Yet, predicted key areas of use require **in situ validation**. The **Lord Howe seamount chain** appears like one of the most promising area for investigation. Indeed, both habitat models and satellite tracking point to the importance of this region for potential breeding activity and population connectivity in the Coral Sea. The collection of individual genetic samples and photographs in this site would allow a greater understanding of migratory routes, population dynamics and cultural exchanges of the Coral Sea humpback whales.

Recognize the value of long-term monitoring

Finally, **long-term monitoring** in New Caledonia provided great insights into the response of humpback whales to environmental fluctuations through time. Such surveillance is necessary to detect the systematic impact of **climate change** on long-lived species and should be maintained in future years. Particularly, Pacific islands located closest to the Equator and currently on the edge of the estimated suitable temperature range for humpback whales should be carefully watched. Breeding grounds such as those located in American Samoa could be “**the canary in the gold mine**” for the rest of the Oceania population. The looming threat of climate change therefore calls for augmented efforts to monitor humpback whale fitness and distribution.

7.4 Concluding remarks

Spatial ecology participates to the conservation of marine megafauna by describing the ecosystemic and behavioural relationships driving species distribution. My research contributed to our understanding of the distribution, habitats and movements of an endangered population of humpback whales in the South Pacific. Future research should be directed at improving the mechanistic understanding of the social and environmental drivers of humpback whale distribution in offshore habitats. The role played by seamounts for breeding activities and migration should be further investigated to build a more comprehensive assessment of humpback whale distribution and connectivity at basin scale.

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