# Distribution et préférences d'habitats des baleines à bosse de l'hémisphère Sud en période de reproduction

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# Thèse de Doctorat
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ÉCOLE DOCTORALE 568 :

Signalisation et Réseaux Intégratifs en Biologie

Spécialité de doctorat: Sciences de la vie et de la santé

Par

**Laurène TRUDELLE**

# Distribution et préférences d'habitats des baleines à bosse de l'hémisphère Sud en période de reproduction

**Thése présentée et soutenue à Paris, le 19 février 2016**

**Composition du Jury :**

| | | |
|---|---|---|
| Mme. Sylvie GRANON | Présidente du jury | Prof. Université Paris-Saclay, France |
| M. Olivier ADAM | Directeur de thèse | Prof. Université Paris-Saclay, France |
| M. Jean-Benoît CHARRASSIN | Co-directeur de thèse | Prof. MNHN, LOCEAN, France |
| M. Vincent RIDOUX | Rapporteur | Prof. Université de La Rochelle, France |
| M. Matthieu LE CORRE | Rapporteur | Prof. Université de La Réunion, France |
| M. Alexandre ZERBINI | Examinateur | Dr. NOAA, USA |

# THESE DE DOCTORAT

Présentée par

**Laurène TRUDELLE**

# Distribution et préférences d’habitats des baleines à bosse de l’hémisphère Sud en période de reproduction

*Aquarelle de Caroline Jacques*

*« Considérant que nous vivons dans un monde si radicalement différent de celui des baleines, que la plupart d'entre nous n'ont jamais l'occasion de les voir et que tout ce qui concerne leur vie demeure un mystère presque total, il est un peu difficile de comprendre pourquoi on s'intéresse à elles. Mais après tout, nous avons surtout besoin de savoir que cet intérêt existe. »*

***« Les baleines ont tendance à s'installer dans le cœur des hommes; parfois elles s'installent en travers et y restent toute la vie. »***

*Pr. Roger Payne, avant-propos du livre de Stanley et al. 1984. Le monde des baleines, guide complet illustré.*

*« Nous pensons que les baleines à bosse sont très intelligentes (ce qu'elles ne sont sans doute pas). Nous les voyons comme de gentils géants (ce qu'elles sont certainement envers nous, mais pas souvent les unes avec les autres). Cependant, elles sont aussi devenues un symbole de notre combat pour sauver la Terre, car si nous ne parvenons pas à sauver les plus grands et les plus majestueux animaux de la planète cela reflète dans quel triste état est notre monde ».*

*Dr. Phil Clapham. Les baleines à bosse, 2001.*

*« Le processus de la recherche est plein de surprises, c'est découvrir des choses auxquelles on ne se serait jamais attendu et essayer de comprendre leur signification. On se retrouve là, à essayer de comprendre ces animaux qui vivent dans un monde différent du nôtre, si majestueux et puissants que pour un chercheur c'est un objet de curiosité et de défi. A tous ceux qui veulent une vie remplie de joie, d'aventures et de découvertes, je suggère de s'intéresser aux mammifères marins et en particulier aux baleines et aux dauphins. Si vous faites ce choix, vous ne le regretterez jamais ! »*

*Pr. Louis Herman, 2015. Humpback whale world congress, Sainte Marie, Madagascar*

# REMERCIEMENTS

Comme l'a dit Roger Payne «Les baleines ont tendance à s'installer dans le cœur des hommes; parfois elles s'installent en travers et y restent toute la vie» : c'est ce qui m'est arrivé je crois. La curiosité et l'envie de comprendre comment vivent ces animaux charismatiques et majestueux m'ont guidée depuis toute petite et m'ont menée jusqu'à cette page de remerciements. Ce long chemin a été ponctué de nombreuses rencontres qui m'ont nourrie, accompagnée, encouragée et ce sont toutes ces personnes que je veux remercier chaleureusement.

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Un GRAND merci à l'association CETAMADA ainsi que tous les éco-volontaires qui la font vivre d'année en année. Une folle équipe et un soutien logistique exceptionnel qui ont rendu possible le projet BAOBAB et bien plus… C'était juste «fantastique» !!! Je souhaite remercier tout particulièrement Anjara, Fifou et Henry avec qui j'ai vécu des moments inoubliables ! Toutes ces heures passées ensemble sur l'eau, à terre, dans les airs, au soleil, sous la pluie, à toute heure de la journée avec toujours le même entrain et la même bonne humeur ! Tous les mois passés sur le terrain est une expérience unique car c'est aussi une jolie aventure humaine (tant de visages me viennent en tête), la découverte d'un pays, Madagascar, avec un de ces petits coins de paradis qu'est l'île Sainte Marie.

Et pendant que nous sommes à Sainte Marie, merci aux baleines à bosse ! Le temps n'existe plus quand c'est la saison des baleines mais elles nous le rendent bien…

Merci également à toutes les personnes avec qui j'ai collaboré pendant cette thèse (dont les personnes de BioGeMME, CeSigma, NMML, WCS, Instituto Aqualie, AAD). Merci Stéphane pour ton aide et tes conseils très utiles notamment en tant que connaisseur de la zone du sud ouest de l'océan Indien. Merci JB pour ta disponibilité, notamment dans les extractions de données (un peu galère…), tes remarques judicieuses, la préparation de soutenance, le partage de ton expérience mais aussi de m'avoir permis de gagner quelques mois afin de finir cette thèse.

Je voudrais adresser des remerciements à Anne-Lise Ughetto et Biotope pour avoir cru en ce projet et avoir fincancé cette thèse dans le cadre d'une bourse Cifre. Merci à Vincent d'avoir fait le lien entre mon travail de recherche et le monde de l'entreprise. J'en profite aussi pour dire merci à Erwan pour sa pédagogie et sa disponibilité durant la période où j'ai été impliquée dans les projets du service R&D.

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Je remercie l'équipe du LOCEAN pour tous les bons moments passés au 5ième puis au 4ième étage ! Un remerciement tout spécial à Dany, pour sa généreuse bienveillance, sa bonne humeur et les nombreux services rendus !

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Karine, avec qui j'ai partagé le désir commun de décrocher une thèse! Une amitié et une aide précieuse tant dans les prises de tête avec les stats, R, la thèse tout court (!) que dans la vie personnelle, merci poulette !

Sara, avec tous ces surnoms que tu m'as donnés…! Tu m'as rendu la vie plus joyeuse et plus légère avec ta bonne humeur et ton coaching personnalisé. Tu m'as soutenue au quotidien à grosses doses de post-it, chocolats et sucreries en tout genre. Pour tout ça…un grand merci.

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Merci à Caroline Jacques pour les aquarelles de début de chapitre, une artiste québecquoise engagée dans la protection de l'environnement.

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Je remercie affectueusement mes amis de longue date qui ont toujours été là, qui entendent parler de cétacés depuis qu'ils me connaissent et savent à quel point c'est important pour moi d'être arrivée jusque là !

Un merci tout spécial à Simon qui a « vécu » cette thèse avec moi ! Patience, compréhension, soutien durant toutes ces années et en particulier les derniers mois de thèse… un challenge que tu as réussi haut la main, check !

Enfin bien évidemment, ceux qui croient en moi depuis le début : mes parents et mon frère. Vous m'avez toujours soutenue les yeux fermés et je ne vous remercierai jamais assez pour cela.

# TABLE DES MATIÈRES

# PUBLICATIONS

Tableau 0. Chapitres asscociés aux publications insérées dans cette thèse.

## Publications présentées dans la thèse

| Chapitre | Titre | Statut |
|---|---|---|
| III | **Trudelle L**, Charrassin JB, Saloma A, Pous S and, Adam O. Temporal and Spatial Patterns of Humpback Whales (Megaptera novaeangliae) in the Sainte Marie Channel, Madagascar, Breeding Ground. | Soumis Plos One |
| IV | **Trudelle L**, Cerchio S, Zerbini AN, Geyer Y, Mayer FX, Jung JL, Hervé, MR, Pous S, Sallée JB, Rosenbaum HC, Adam O, and Charrassin JB. Influence of environmental parameters on movements and habitat utilization of humpback whales (*Megaptera novaeangliae*) in the Madagascar breeding ground. | En preparation<br>MEPS |
| V | **Trudelle L**, Zerbini AN, Double M, Cerchio S, Andrews-Goff V, Andriolo A, Danilewicz A, Geyer Y, Jung JL, Mayer FX, Pous S, Rosenbaum HC, Sallée JB, Adam O, and Charrassin JB. In three ocean basins: comparison of coastal movements and habitat use of humpback whales during the breeding season. | En préparation |

## Autres publications

Cerchio S, **Trudelle L**, Zerbini A, Geyer Y, Mayer FX, Charrassin JB, Jung JL, Adam O, and Rosenbaum HC (*en préparation, MEPS*). Satellite tagging of humpback whales off Madagascar reveals long range movements of individuals in the Southwest Indian Ocean during the breeding season (cf. **annexe A**)

Ropert-Coudert Y, Koubbi P, Hindell P, Phillips R, Charrassin JB, **Trudelle L**, and Raymond B. Biogeographic patterns of birds and mammals. De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz C, et al. (Eds.) (2014) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 364-387.

Labadie G, Tixier, P, **Trudelle L,** Vacquie-Garcia J, Gasco N, and Guinet C: Sperm whales of the Crozet and Kerguelen islands - Photo-identification catalogue 2014. DOI: 10.6084/m9.figshare.1414472.

Cerchio S, **Trudelle L**, Zerbini A, Geyer Y, Mayer FX, Charrassin JB, Jung JL, Adam O, and Rosenbaum HC. Satellite tagging of humpback whales off Madagascar reveals long range movements of individuals in the Southwest Indian Ocean during the breeding season. Paper SC/65a/SH22 presented to the IWC Scientific Committee, Jeju Island, South Korea in June 2013.

**Trudelle L** and Charrassin JB. Le marsouin à lunettes (*In press).* Atlas des mammifères marins de France et d'Outre-Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

**Trudelle L** and Charrassin JB. La baleine franche australe (*In press).* Atlas des mammifères marins de France et d'Outre-Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

**Trudelle L** and Charrassin JB. Le rorqual boréal *(In press)*. Atlas des mammifères marins de France et d'Outre-Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

Charrassin JB and **Trudelle L**. Le petit Rorqual Antarctique (*In press).* Atlas des mammifères marins de France et d'Outre-Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

Charrassin JB and **Trudelle L**. L'hyperoodon austral (*In press).* Atlas des mammifères marins de France et d'Outre-Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

## CONFERENCES ET WORKSHOPS

**Biennial Marine Mammal Conference** – 13.18 décembre 2015 – San Francisco, Californie, USA. **Poster** – Influence of environmental parameters on movements and habitat utilization of humpback whales (Megaptera novaeangliae) in Madagascar.

**Humpback Whale World Congress (HWWC)** – 29 juin au 3 juillet 2015 – Sainte Marie, Madagascar. **Oral** – Influence of environmental parameters on movements and habitat selection of Humpback Whales (Megaptera novaeangliae) in Madagascar.

**Humpback Whale World Congress (HWWC), Student workshop** – 29 juin au 3 juillet 2015 – Sainte Marie, Madagascar. **Oral** – Satellite telemetry for baleen whales.

**Workshop Humpback whale tagging in the Western Indian Ocean: sharing results and increasing collaborative works** – 19.21 novembre 2014 – Ile de La Réunion**. Oral** - Habitat modeling from tagging.

**The 5th Bio-logging Science Symposium** – 22.27 septembre 2014 – Strasbourg, France. **Poster** – Wintering habitat preferences of humpback whales (*Megaptera novaeangliae*) tagged in Madagascar using habitat modelling.

**European Cetacean Society (ECS) Conference** – 5.9 avril 2014 – Liège, Belgique. **Poster** – Temporal and spatial patterns of humpback whales in the Sainte Marie Island, Madagascar, breeding ground.

# PREAMBULE

Après avoir rencontré Olivier Adam en 2007 à l'île Sainte Marie (Madagascar) dans le cadre d'un éco-volontariat de plusieurs semaines sur l'étude et la protection des baleines à bosse, il m'a proposé un stage de Master 1 portant sur l'utilisation de la télémétrie chez les mammifères marins. J'ai par la suite continué à travailler avec lui et à la fin de mon Master 2, nous avons décidé de monter un projet de thèse de doctorat sur les baleines à bosse de Madagascar, sous-population encore peu étudiée. Cette thèse s'est alors inscrite dans un projet pluridisciplinaire plus large intitulé Balises et Acoustiques pour l'Observation des Baleines à Bosse (BAOBAB) financé par la fondation TOTAL. Je tiens donc à préciser ici le contexte scientifique dont j'ai bénéficié au cours de ces trois années notamment lors les campagnes de terrain.

Accueillie au sein du Laboratoire d'Océanographie et du Climat (LOCEAN), j'ai pu collaborer avec des chercheurs experts en océanographie satellitaire, en modélisation de l'océan et en écologie marine. Ce travail a été possible grâce à l'appui logistique et aux jeux de données d'observations opportunistes (whale-watching) de l'association Cétamada. Par ailleurs, nous avons collecté des données de localisations de baleines à bosse par télémétrie satellitaire dans la zone de reproduction de Madagascar dans le cadre du projet BAOBAB et d'une collaboration NeuroPSI/WCS/Cétamada. Grâce à d'autres collaborations internationales, j'ai également pu utiliser des données du même type issues d'autres stocks reproducteurs : les données du stock A (mises à disposition par l'Instituto Aqualie ; PI A. Zerbini) et les données du stock D et E1 (Australian Antartic Division ; PI M. Double). Par conséquent, ce travail a demandé un gros investissement dans les campagnes de terrain mais aussi dans le traitement et la gestion des différentes bases de données. J'ai fait le choix d'en rendre compte dans ce manuscrit en détaillant l'utilisation de la télémétrie satellitaire chez les grandes baleines dans la partie « Site d'étude et méthodes » (Chapitre 3). J'ai participé aux trois saisons de déploiements de balises Argos (2012, 2013 et 2014 ; trois semaines par an) sur les baleines à bosse à Madagascar. Selon les années, j'ai été chargée de la préparation des balises, de la prise de notes de terrain lors des sorties, de photographier les individus observés ou de réaliser les biopsies. En dehors des missions de déploiement de balises, j'ai également été responsable de la prise de biopsies et la gestion des échantillons durant mes missions de terrain à Sainte Marie (en coordination avec l'association Cétamada). J'ai aussi participé à des missions scientifiques se déroulant en parallèle comme le déploiement d'accou-sondes sur des couples mère-baleineau ou l'enregistrement de chants par acoustique passive.

# CHAPITRE I – INTRODUCTION GENERALE

*Aquarelle de Caroline Jacques*

# CHAPITRE I – INTRODUCTION GENERALE

## I. HABITATS ET REPRODUCTION

### A. CONTEXTE THEORIQUE

L'étude des interactions entre les individus et leurs environnements est la définition même de l'écologie (Haeckel 1866). Il existe des facteurs intrinsèques (e.g. taille, âge, sexe, histoire de vie) et extrinsèques (e.g. disponibilité des ressources, prédation, paramètres environnementaux) qui agissent conjointement sur les individus et déterminent leur distribution et leur abondance. Afin de maximiser son succès reproducteur (*ou fitness*), tout organisme vivant s'alimente pour acquérir de l'énergie qu'il va allouer à différentes fonctions de vie : croissance, survie et reproduction (Stearns 1992). De ce fait, de nombreuses études en écologie visent à comprendre quelles stratégies sont adoptées par les organismes pour exploiter les habitats favorables à l'alimentation et la reproduction.

### B. HABITATS FAVORABLES

Un habitat propice à l'alimentation est défini par différents critères tels que la qualité et la disponibilité des ressources. Un habitat favorable à la reproduction est quant à lui défini par la présence de partenaires sexuels, de conditions environnementales particulières (e.g. conditions climatiques et/ou physiographiques) et un risque de prédation réduit. Par ailleurs, pour certaines espèces, les habitats propices à l'alimentation ne sont pas favorables pour la reproduction et inversement ce qui implique une ségrégation spatio-temporelle entre les activités d'alimentation et de reproduction (Fretwell 1972). C'est le cas chez de nombreux animaux (e.g. insectes, poissons, oiseaux, mammifères) dont le cycle de vie est marqué par des périodes de migration. Ainsi, la distance parcourue pendant la migration pourra varier de quelques mètres à des milliers de kilomètres selon les espèces. Certaines espèces de tortues ou d'oiseaux, notamment, parcourent de grandes distances pour rejoindre les zones favorables à leurs besoins et utilisent successivement des habitats très contrastés au cours de leur cycle annuel. Chez les pinnipèdes, la reproduction et la mue ont lieu à terre ou sur la banquise (Barrat 1976, Cornet & Jouventin 1980, Riedman 1990, Weimerskirch et al. 1997, Bonadonna et al. 2000) et les animaux se nourrissent en mer. Chez le phoque gris par exemple, le type de substrat, la topographie ou encore la distance à la plage influencent la distribution des femelles gestantes dans les colonies (Pomeroy et al. 1994, 2000, Twiss et al. 2000). La dégradation de l'habitat aura d'autant plus d'impacts sur les espèces philopatriques (fidélité au site de reproduction).

### C. STRATEGIE DE REPRODUCTION : REPRODUCTEURS SUR CAPITAL

La période de reproduction est une période très coûteuse en énergie (Williams 1966). Les organismes utilisent ainsi différentes stratégies de reproduction pour couvrir la dépense énergétique qui y est associée (i.e. gestation, nourrissage et soins apportés au jeune). Dans le cas d'une séparation spatio-temporelle très prononcée entre les activités d'alimentation et de reproduction, certaines espèces ont adopté une stratégie de reproduction basée sur l'accumulation d'un capital énergétique de réserve, c'est ce l'on appelle la reproduction sur capital (*capital breeding*). Avant la reproduction, les reproducteurs sur capital stockent des ressources sous forme de réserves qui serviront ultérieurement comme support énergétique pour la reproduction. Ils doivent ainsi faire face à une période de jeûne plus ou moins longue pendant la période de reproduction. Cette stratégie est fréquente chez les animaux de grande taille, notamment chez les mammifères marins (Festa-Bianchet et al. 1998, Boyds 2000). Si l'on reprend l'exemple des pinnipèdes, les éléphants de mer et les phoques utilisent les ressources accumulées pendant la période d'alimentation, pour assurer la reproduction et le nourrissage de leurs petits alors que les espèces d'otaries et lions de mer, qui sont de taille plus petite, alternent des voyages en mer pour se nourrir et des périodes à terre pour allaiter (*income breeders*) Chez les cétacés, à la différence de la majorité des odontocètes qui s'alimentent pendant la période de reproduction, les mysticètes sont considérés comme des reproducteurs sur capital (Lockyer 1987, Kasuya 1995).

## II. CYCLE DE VIE DES MYSTICETES

### A. MIGRATION

Chez de nombreuses espèces de mysticètes, on observe une disparité entre les zones de reproduction et les zones d'alimentation. Ainsi, chaque année, celles-ci entreprennent de longues migrations saisonnières (Mackintosh et al. 1929, Corkeron & Connor 1999 , Mate et al. 1999). Bien qu'il existe des variations à l'échelle individuelle et populationnelle dans les schémas migratoires, une ségrégation spatio-temporelle très marquée tend à être observée chez la plupart des espèces parmi lesquelles il existe un exemple caractéristique : la baleine à bosse (Kellogg 1929, Chittleborough 1958, Dawbin 1966, Ross 1974, Whitehead & Moore 1982, Lockyer 1984, Braithwaite et al.2015). Le cycle de vie de ces espèces se caractérise ainsi par deux grandes périodes : la période de reproduction et la période d'alimentation (**Figure 1.1**).

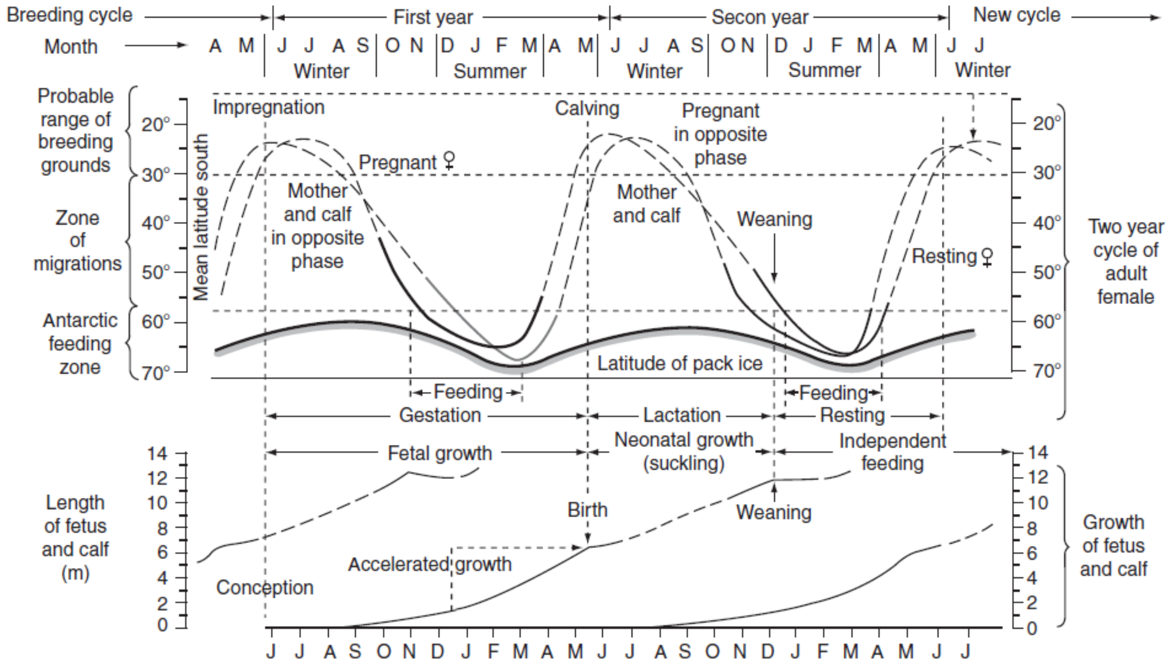

**Figure 1.1**. Modèle de cycle de vie des espèces de mysticètes hautement saisonnières et hautement migratrices dans l'hémisphère Sud (modifié par Bonner 1980, d'après Mackintosh 1965). Elles passent l'automne/hiver à se reproduire et mettre bas dans les basses latitudes puis migrent vers les hautes latiudes (Antarctique) pour s'alimenter durant le printemps/été.

## B. PERIODE D'ALIMENTATION

Les mysticètes se nourrissent principalement de zooplancton et en particulier de krill et de copépodes qu'ils trouvent en grande quantité dans les régions polaires et subpolaires (Nemoto 1959, Bryant et al. 1981, Kawamura 1994, Atkinson et al. 2008). Le zooplancton est un maillon clé dans l'écosystème marin puisqu'il s'alimente de phytoplancton, producteur primaire à la base de la chaine alimentaire, et est lui-même consommé par des organismes des niveaux trophiques supérieurs. Le cycle biologique de nombreuses espèces de zooplancton est associé à la glace de mer sous laquelle se développent les algues de mer dont elles se nourrissent (Atkinson et al. 2004). Par conséquent de grandes concentrations de krill sont observées dans la zone marginale des glaces durant l'été, comme par exemple le krill antarctique (*Euphausia superba*), qui représente la source principale de nourriture des mysticètes dans l'hémisphère Sud (Mackintosh 1965, Kasamatsu et al. 1998, Zerbini, Andriolo, et al. 2006, Cotte & Guinet 2011). Le krill n'étant disponible que durant les mois d'été, la majorité des grandes baleines va se nourrir intensivement pendant 4 à 6 mois de l'année et constituer d'importantes réserves de graisse sur lesquelles elles vivront le reste du temps. Alors que l'océan Austral abrite un écosystème riche en zooplancton, la disponibilité des ressources dans l'hémisphère Nord est plus contrastée. Ainsi, le régime alimentaire des baleines de l'hémisphère Nord se compose souvent de krill mais aussi d'espèces de petits poissons et de calmars. Les mysticètes s'alimentent généralement sur le plateau continental ou dans des zones caractérisées par des structures topographiques favorables à l'accumulation de proies telles que les canyons (Schoenherr 1991, Moore et al. 2000, Croll et al. 2005). La quantité de proies absorbées par jour chez les mysticètes représente 4% de leur poids total soit 4 tonnes par jour pour la baleine bleue (Sergeant 1969, Lockyer 1981, Bannister 2002). Une femelle en gestation devra, notamment, augmenter son poids de 65% afin d'assurer sa survie et l'allaitement de son petit durant l'hiver (Lockyer 1981, Bannister 2002).

## C. PERIODE DE REPRODUCTION

Durant l'hiver, les mysticètes se reproduisent, mettent bas et allaitent leur petit dans les eaux chaudes des basses latitudes (entre 0 et 30° de latitude) ; période durant laquelle, rappelons-le, elles vont cesser de s'alimenter à l'exception d'espèces de baleines franches ou le rorqual tropical (Lockyer 1984, Payne 1995). Après une période de gestation de 10 à 12 mois, les femelles gestantes arrivent en zone de reproduction pour mettre bas et allaiter leur petit. Le lait riche en matières grasses (e.g. ~32-38 % de matière grasse chez les baleines à bosse ; Pedersen, 1952) et en protéines sera l'unique source de nourriture du baleineau durant les 6 à 11 mois suivants sa naissance (Chittleborough 1965). Le processus de sevrage se poursuivra pendant environ 6 mois avant que le baleineau ne se sépare de sa mère vers l'âge d'un an. Durant la période d'allaitement, il grossit de 80 kg/jour et se constitue les réserves adipeuses nécessaires pour survivre dans les eaux froides des zones d'alimentation (Bannister 2002). Bien qu'aucune naissance n'ait encore jamais été observée sous l'eau (Silver et al. 1992, 2002, Ferreira et al. 2014), la naissance d'un baleineau à bosse a été rapportée dans le canal de Sainte Marie, à Madagascar, et des informations sur les premières heures et jours qui suivirent sa naissance collectées par la même occasion (Faria et al. 2013).

Les stratégies de reproduction les mieux connues sont celles des baleines à bosse. C'est en hiver que chez ces dernières, les femelles sont en œstrus et que la production de sperme et l'augmentation de testostérone se produisent chez les mâles (Chittleborough 1958, 1965, Clapham 1996). Des comportements observés chez les mâles uniquement pendant l'hiver ont été associés à une activité de reproduction: activités vocales complexes, chants, compétitions directes entre mâles pour une femelle ou encore l'accompagnement de femelles avec un baleineau (activité d'escorte) (Tyack 1981, Darling et al. 1983, Tyack & Whitehead 1983). Les stratégies de reproduction restent cependant très peu connues chez les autres balaenopteridés (e.g. rorqual commun, rorqual bleue, petit rorqual). Chez les baleines franches et les baleines boréales, la taille des testicules dépasse 900 kg et les comportements agressifs entre mâles sont moins fréquemment observés que chez d'autres espèces ce qui suggère une compétition par le sperme (Brownell & Ralls 1986, O'Hara et al. 2002).

Les aires de reproduction des baleines à bosse et les baleines grises sont actuellement les mieux identifiées (Mackintosh 1965, Nerini 1984, Clapham 1996) tandis que celles des rorquals communs et des baleines bleues, espèces vivant plus au large, sont peu connues, voir totalement inconnues (Mizroch et al. 1984, Laws 1985, Reilly & Thayer 1990).

## III. BIOLOGIE ET ECOLOGIE DE LA BALEINE A BOSSE

### A. TAXONOMIE

La baleine à bosse (*Megaptera novaeangliae,* Borowski, 1781) appartient au sous-ordre des mysticètes (ou cétacés à fanons) qui se diffèrent principalement des odontocètes (cétacés à dents) par le nombre d'évents (deux chez les mysticètes) et la présence de fanons, longues lamelles de kératine servant à filtrer la nourriture. La famille des balaenopteridés, aussi appelés rorquals, recense la majorité des espèces de mysticètes. Les rorquals se distinguent des baleines franches (Balénidés), des baleines pygmées (Néobalénidés) et des baleines grises (Eschrichtiidés) par leurs sillons gulaires qui s'étendent depuis la mâchoire inférieure jusqu'au nombril et qui s'articulent avec le sternum (Beddar 1901, Bannister 2002) (**Figure 1.2**). Megaptera est un des deux genres de la famille des rorquals et ne comprend qu'une seule espèce (Jackson et al. 2014).

## B. CARACTERISTIQUES ET MORPHOLOGIE

La baleine à bosse se distingue nettement des autres espèces de rorquals par la longueur de ses nageoires pectorales qui mesurent un tiers de son corps (~ 4 mètres) (True 1904). De plus, la nageoire dorsale est de très petite taille et possède un renflement à sa base qui lui a valu son nom vernaculaire de « baleine à bosse ». Elle possède une nageoire caudale à bordure dentelée dont la face ventrale possède une coloration et un dessin unique à chaque baleine. Cette dernière est utilisée pour l'identification des individus (Katona et al. 1979). La pigmentation de sa peau est sombre sur la partie dorsale mais varie fortement du noir au blanc sur la partie ventrale (Clapham & Mead, 1999) (**Figure 1.2**). Des protubérances, généralement colonisées par différentes espèces de crustacés, sont présentes sur la mâchoire inférieure et alignées sur trois rangées sur la mâchoire supérieure (Clapham & Mead 1999). A la taille adulte, la baleine à bosse mesure en moyenne entre 14 et 17 m pour environ 40 tonnes. Un dimorphisme sexuel est observé avec des femelles d'un mètre à un mètre cinquante plus grandes que les mâles (Chittleborough 1965). A la naissance, le baleineau mesure entre 4 et 4.5 m et pèse une tonne (Clapham & Mead 1999, Wynne & Schwartz 1999).

Elle possède un répertoire d'émission sonores complexes et variés, le plus souvent produits dans les zones de reproduction (Tyack 1981). Ces signaux sont compris dans une large bande de fréquences (20-40 000 Hz) (Richardson et al. 1995).

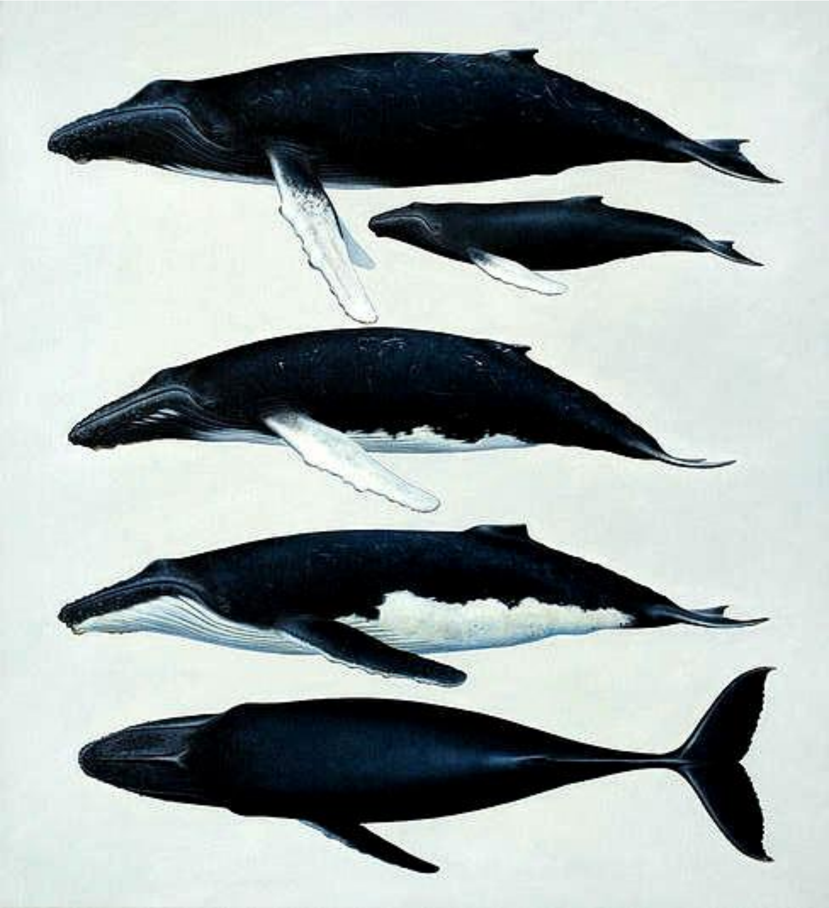

**Figure 1.2.** Morphologie et pigmentation générales de la baleine à bosse (Megaptera novaeangliae) (illustration de C. Brett. Jarrett).

## C. REGIME ALIMENTAIRE ET TECHNIQUES DE CHASSE

Dans l’hémisphère Nord, l’étude des contenus stomacaux a montré une importante variété d’espèces consommées (Clapham et al. 1997) dont principalement des Euphausiacés (krill) (Eupausia spp, Thysanoessa spp, Meganyctipahnes spp) mais aussi des petits poissons pélagiques incluant : le hareng (Clupea spp, Watkins & Schevill 1979, Baker 1985), le maquereau (Scomber spp, Geraci et al. 1989), le capelan (Mallotus spp, Whitehead 1981), la sardine (Sardinops spp, Clapham et al. 1997), l’anchois (Engraulis spp. Rice 1963, Clapham et al. 1997) ou encore le lançon (Amodytes spp. Overholtz & Nicolas 1979, Payne, R. 1986, Weinrich et al. 1997, Friedlaender et al. 2009). Dans l’hémisphère Sud, comme de nombreux mysticètes, les baleines à bosse s’alimentent essentiellement de krill antarctique (*Euphausia superba*) (Nemoto 1959, Mackintosh 1965) localisé en particulier dans la zone marginale des glaces. Par ailleurs, des comportements opportunistes d’alimentation ont été occasionnellement observés dans les basses latitudes en hiver ou lors de la migration vers les zones d'alimentation (Dawbin 1956, Nemoto 1959, Danilewicz et al. 2009, De Sá Alves et al. 2009).

Les baleines à bosse adoptent des stratégies d'alimentation diverses et complexes (e.g. frappe de nageoire caudale, émission de bulles) qui varient selon le type de proies, le moment de la journée (Hain et al. 1982, Friedlaender et al. 2009) mais aussi selon les régions (Etnoyer et al. 2004, Wiley et al. 2011) Ces stratégies peuvent être employées par un individu seul ou en groupe (Johnson & Wolman 1984, Clapham 1993) et inclues des comportements de « surface-feeding » et de « deep-feeding » (Friedlaender et al. 2009). La technique du « filet » ou « rideau » de bulles utilisée en collaboration par plusieurs individus pour piéger un banc de proies est unique aux baleines à bosse (Ingebrigtsen 1929, Jurasz & Jurasz 1979, D'Vincent et al. 1985, Wiley et al. 2011). Il est suggéré que certaines techniques de chasse comme par exemple, la frappe de nageoire caudale sur la surface de l'eau (« lobtailing ») ou certains comportements d'émission de bulles, se transmettent culturellement entre individus (Weinrich et al. 1992, Allen et al. 2013).

### D. STRUCTURE SOCIALE ET COMPORTEMENTS DE REPRODUCTION

La structure sociale des baleines à bosse est caractérisée par l'association temporaire d'individus formant des groupes de deux à plusieurs dizaines (Whitehead & Moore 1982, Clapham 1993). Le couple mère-baleineau est le groupe le plus stable puisqu'ils ne se sépareront que 10 à 12 mois après la naissance du baleineau. On observe ainsi différents types de groupes sociaux dans les zones de reproduction (solitaire, paire, mère-baleineau avec ou sans escorte, groupes compétitifs) qui peuvent être composés d'individus de sexe et de classe d'âge différents (Tyack & Whitehead 1983, Mobley Jr & Herman 1985, Clapham et al. 1992). Le type de groupes sociaux, leur distribution spatiale et temporelle varient selon les zones de reproduction et apportent des indications sur l'utilisation et les préférences d'habitats des baleines à bosse durant la période de reproduction. La présence de groupes reproducteurs et de mâles chanteurs indiquera, par exemple, une zone favorable aux activités de reproduction.

Chez les baleines à bosse, le système reproducteur est de type polygynique où les mâles se reproduisent avec plusieurs femelles pour lesquelles il existe une forte compétition sexuelle (Clapham 1996). Ainsi, en période de reproduction, il est très fréquent d'observer des groupes d'individus, dits 'groupes compétitifs ', associés à une forte activité de sub-surface et des comportements agressifs (Tyack & Whitehead 1983, Whitehead 1983, Clapham et al. 1992). Ces groupes sont composés d'une femelle (individu focal) et de plusieurs mâles (« challengers ») en âge de se reproduire (Clapham 1993, Brown & Corkeron 1995). Le mâle le plus près de la femelle est identifié comme la première escorte (Clapham 1993). Des comportements agressifs observés chez les femelles envers les mâles, en particulier les mâles immatures, laissent penser que les femelles sélectionnent activement leur partenaire (Clapham 1993). Bien que les mâles soient en compétition directe dans les groupes compétitifs, ils utilisent également d'autres stratégies pour accéder aux femelles. Les baleines à bosse mâles émettent des chants lors de la reproduction et moins communément durant la migration et dans les zones d'alimentation (Payne & McVay 1971, Payne & Guinee 1983, Mattila et al. 1987, McSweeney et al. 1989, Clapham & Mattila 1990, Norris et al. 1999, Charif et al. 2001, Clark & Clapham 2004, Clark & Gagnon 2004). En zone de reproduction, les études de comportements associés à ces chants ont montré qu'ils sont utilisés pour attirer les femelles et plus hypothétiquement comme une forme indirecte d'interaction avec les autres mâles compétiteurs (Tyack 1981, Clapham 1996, Darling & Bérubé 2001, Darling et al. 2006). Par ailleurs, les couples mère-baleineau sont très souvent accompagnés d'une escorte. Il a été montré que l'escorte était toujours un individu mâle ce qui suggère deux hypothèses : le mâle espère se reproduire avec la femelle ou bien c'est un comportement protecteur post-accouplement afin d'empêcher la femelle de se reproduire avec d'autres mâles (Clapham 1996).

## E. STATUT DE CONSERVATION ET MENACES

L'espèce est classé comme « préoccupation mineure » par l'IUCN exceptée la population d'Arabie et d'Océanie classées « en danger » depuis 2008 (Reilly et al 2008). Les zones de reproduction des baleines à bosse sont situées dans des habitats côtiers généralement soumis à une forte pression anthropique (e.g. traffic maritime, projets aquacoles, développement de l'écotourisme). Les menaces principales qui pèsent sur les baleines à bosse sont les captures accidentelles dans les engins de pêche (Volgeneau et al 1995, Kiszka et al. 2008, Alava 2012, Zappes et al. 2013), les collisions avec des navires (Laist et al. 2001), la pollution sonore et chimique (Todd et al. 1996, Miller et al 2000, Fossi et al. 2012), la dégradation de l'habitat (Maxwell et al. 2013,) ou encore le dérangement potentiel lors des activités de whale-watching (Schaffar *et al.* 2013, AAMP 2012). Des projets d'exploration et/ou d'exploitation de pétrole et de gaz dans les eaux côtières de zones de reproduction telles que le Brésil, le Gabon, l'Angola, le Mozambique et Madagascar peuvent également avoir un impact direct ou indirect sur l'espèce (Engle et al. 2004, Findlay et al. 2006, Rosenbaum et al 2014). Par ailleurs, la distribution de l'espèce et l'évolution des populations pourront être impacter par des changements à long terme de paramètres physiques (e.g. réchauffement des masses d'eau, modifications de la dynamique de la glace de mer) affectant les proies, notamment le krill antarctique (MacLeod 2009, Fleming et al. 2015).

## IV. DISTRIBUTION ET STRUCTURE DES POPULATIONS DE BALEINES A BOSSE

Les données de captures récoltées durant plusieurs siècles de chasse à la baleine représentent une base solide pour l'étude des grandes baleines et l'évaluation de l'état des populations actuelles. En complément de ces données historiques, les données issues de nouvelles techniques (photo-identification, génétique, acoustique, télémétrie) ont permis, entre autres, de mieux définir les déplacements et de mieux identifier les aires de reproduction et d'alimentation qui leur sont associées (Stone et al. 1990, Clapham et al. 1993, Palsboll et al. 1995a, Palsbøll et al. 1997, Garrigue et al. 2001, Mate et al. 2007a, Dalla Rosa et al. 2008, Robbins et al. 2011). La majorité des espèces de grandes baleines ont été divisées très tôt en entités géographiques qui font références aux différentes populations ou stock[1].

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[1] Définition d'un stock: ensemble d'individus ayant le même processus de reproduction et qui constitue une unité démographique homogène souvent associé à une entité géographique. La notion de stock possède une double signification ; dans un contexte écologique il fait référence à une population et dans un contexte de conservation des ressources vivantes à une unité de gestion (ii) Définition d'un sous-stock: sous unité d'un stock qui se distingue écologiquement, génétiquement (e.g. ADN mitochondrial) ou par le comportement et qui est géographiquement identifiable (cf. p287, IWC, 2014b Annexe I: Report of the Working Group on Stock Definition. J. Cetcean Res. (Supp.) 15,271-288). Dans ce manuscrit, 'stock' et 'population' font référence à la même définition ainsi que 'sous-stock' et 'sous-population'.

# CHAPITRE I – INTRODUCTION GENERALE

## A. POPULATIONS DE L'HEMISPHERE NORD

En Atlantique Nord, on a identifié quatre zones d'alimentation distinctes dont certaines restent encore peu décrites actuellement (Katona & Beard 1990, Stevick et al. 2003) : le golfe du Maine, l'est du Canada (Terre-Neuve, Labrador et golfe du Saint Laurent), l'Ouest du Groenland, l'atlantique Nord-Est (Islande et Norvège). (Palsboll et al. 1995a) ont mis en évidence, grâce à l'analyse de l'ADN mitochondrial, une fidélité au site d'alimentation via la lignée matriarcale. Des études basées sur les catalogues de photo-identification et des analyses génétiques ont montré que la majorité des baleines à bosse passant l'hiver dans les aires précédemment citées migrent dans la Caraïbe pour se reproduire ; depuis Cuba à la côte vénézuélienne et incluant les Bermudes (considéré comme un point d'arrêt pendant la migration, (Stone et al. 1987, Mattila & Clapham 1989, Mattila et al. 1989, Clapham 1993, Robbins & Mattila 2006, Kennedy et al. 2013). Cependant, des analyses génétiques suggèrent qu'une partie de la population de l'Est de l'Atlantique Nord migrerait dans d'autres régions mal connues ou inconnues comme l'archipel du Cap Vert (Palsboll et al. 1995a, Larsen et al. 1996). On observe sporadiquement des individus en Méditerranée (Frantzis et al. 2004), dans le golfe du Mexique (Waring et al. 2011) ou près des côtes irlandaises (Berrow 2001).

Dans le Pacifique Nord, la répartition des aires d'alimentation s'étale du Nord de la Californie au Kamchatka, en passant par l'Alaska, la Colombie Britannique, les îles aléoutiennes et la mer de Béring (Calambokidis et al. 2001, 2008, Kennedy et al. 2014). On dénombre quatre aires de reproduction dont la plus intensément étudiée : les îles Hawaii. Dans le Nord-Est Pacifique, la côte mexicaine (Baja California, golfe de Californie) accueille une grande concentration de baleines à bosse (Jorge Urbán & Anelio Aguayo 1987, Gendron 1993, Calambokidis et al. 2000, Calambokidis & Barlow 2004) et des populations sont présentes aussi sur les côtes d'Amérique centrale (Panama). Dans le Nord-Est Pacifique, les baleines à bosse passent l'hiver dans les îles Bonin, les Philippines et les îles Ryukyu (Acebes et al. 2007, Silberg et al. 2013).

Dans le nord de l'océan Indien, une population résidente de baleines à bosse (stock X) est présente dans la mer d'Arabie (Reeves et al. 1991, Mikhalev 1997, Minton et al. 2011) On observe des individus du golfe d'Aden au Sri LanKa. Une étude génétique récente a confirmé que cette population est isolée des autres populations de baleines à bosse (Pomilla et al 2014)

### B. POPULATIONS DE L'HEMISPHERE SUD

A partir de la fin du XIX siècle, la réduction des populations côtières de grandes baleines et les nouvelles technologies (canon lance-harpon, navire-usine) amenèrent à une extension de la chasse industrielle dans l'Océan Austral et les régions antarctiques. Ainsi, la diminution accrue des populations entraina la création de la Commission Baleinière Internationale (CBI) en 1946, qui avait pour objectif de réglementer les quotas de captures et les méthodes de chasse des grands cétacés. Ce ne sera que bien plus tard que la CBI sera en charge de la gestion des stocks et de l'estimation des taux de récupération des populations de grandes baleines depuis l'interdiction de la chasse commerciale. Initialement, les limites géographiques des stocks de grandes baleines de l'hémisphère Sud ont été définies à partir des régions où un grand nombre de captures avaient été faites durant les campagnes saisonnières de chasse à la baleine (Harmer 1928, Mackintosh 1942).

La délimitation des stocks de baleines à bosse, proposée par la CBI, s'appuie sur les aires de reproduction des basses latitudes nommées de A à G (**Tableau 1.1, Figure 1.3**, Kellogg 1929, Rayner 1940, Mackintosh 1942, IWC 1998a). L'apport constant de connaissances sur les routes migratoires et les mouvements des individus n'ont cessé de faire évoluer les limites initialement reconnues pour certains stocks. Ainsi, la majorité des aires de reproduction à l'exception des stocks A et D ont été divisées en sous-régions ou sous-stocks[1] (**Figure 1.3**).

Défini dans le cadre de la gestion de la chasse à la baleine, on dénombre sept zones géographiques associées à des aires d'alimentation dans l'océan Austral, nommées de I à VI et qui se répartissent tout autour du continent antarctique (**Figure 1.3**) (Mackintosh 1942, Omura 1973, Donovan 1991, IWC 1998a). Les plus fortes concentrations de baleines à bosse ont été observées dans la région ouest de la Péninsule Antarctique (Kasamatsu et al. 1996).

Les recaptures d'individus obtenues à partir de différentes méthodes (« Discovery tags[2] », photo-identification, génétique) suggèrent des associations, parfois encore hypothétiques, entre les aires de reproduction et les aires d'alimentation (**Tableau 1.1**).

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[2] Le terme *Discovery tag* se réfère aux marques (tubes en métal enfoncés dans le lard de l'animal associé à un numéro de série) utilisées lors des campagnes de « marquage-recapture » réalisées pendant la chasse intensive (Brown 1977).

**Tableau 1.1.** Résumé de la structure des stocks et sous-stocks reproducteurs et des aires d'alimentation associées des baleines à bosse de l'hémisphère Sud (IWC 1998a 2005, Jackson et al. 2015). Les points d'interrogation représentent des liens hypothétiques.

| Stock reproducteur | Aire géographique | Sous-stock reproducteurs | Aire d'alimentation supposée |
|---|---|---|---|
| A | Atlantique sud-ouest (Brésil) | | II (incluant Géorgie du Sud, îles Sandwich) |
| B | Atlantique sud-est | B1 : Gabon/Angola | II, III, région d'upwelling du Benguela, Namibie |
| | | B2 : zone de reproduction inconnue | côte ouest de l'Afrique du Sud, région d'upwelling du Benguela, Namibie |
| C | Océan Indien occidental | C1S : Côte Est de l'Afrique du Sud à l'île de Mozambique (15°S)<br>C2N : nord de l'île de Mozambique au Tanzanie/Kenya | II, III |
| | | C2: Mayotte, archipel des Comores et les îles du canal du Mozambique | II, III |
| | | C3 : Madagascar | II, III |
| | | C4 : Iles Mascareignes (La Réunion, île Maurice, Rodrigues) | II, III |
| D | Océan Indien oriental (est de l'Australie) | | III ?, IV et V ? |
| E | Pacifique sud-ouest/ | E1 : Est de l'Australie | IV ? et V |

| Stock reproducteur | Aire géographique | Sous-stock reproducteurs | Aire d’alimentation supposée |
|---|---|---|---|
| | Océanie | E2 : Nouvelle Calédonie | V |
| | | E3 : Tonga | V |
| F | Océanie | F1 : les îles Cook | VI ? |
| | | F2 : Polynésie française | VI ? |
| G | Pacifique sud-est<br>(Colombie, Equateur) | Sous populations ? Superposition avec les zones de reproduction de l’hémisphère Nord (Panama, Costa Rica) | I, sud-est de l’Amérique du sud, sud des îles Shetland, détroit de Magellan (connexion avec Panama/Costa Rica), péninsule antarctique (connexion avec Costa Rica. Equateur/ Colombie) |

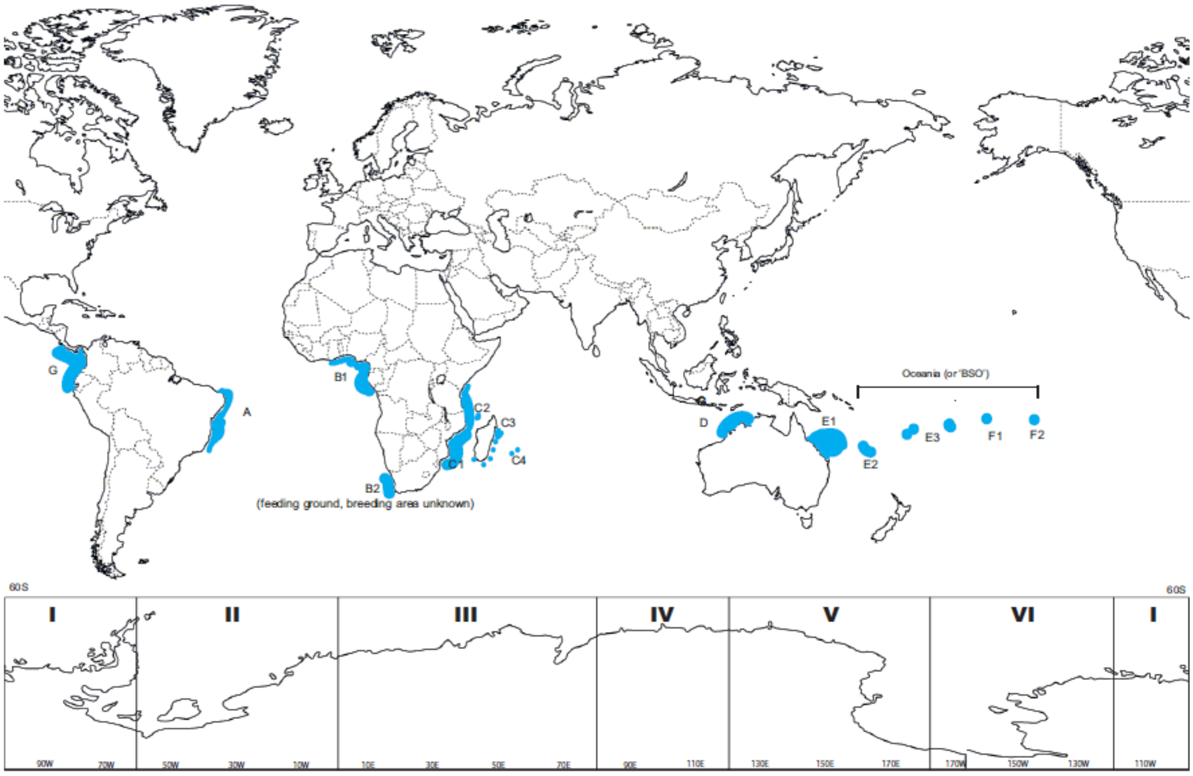

**Figure 1.3.** Carte des stocks et sous-stocks de reproduction (A-G) des baleines à bosse et des aires d'alimentation (I- IV) de l'hémisphère Sud (Jackson et al. 2015).

## C. STOCK REPRODUCTEUR DU SUD-OUEST DE L'OCEAN INDIEN (STOCK C)

### 1. ROUTES ET SCHEMAS MIGRATOIRES

Bien qu'encore mal décrites, trois routes migratoires ont été proposées sur la base de données de capture, d'observations visuelles et d'enregistrements acoustiques (Best et al. 1998) : a) un corridor le long de la côte est de l'Afrique du Sud depuis Knysna (33°S) pour rejoindre les aires de reproduction plus au nord (cf. sous-stock C1N) (Olsen Ø 1914, Best 1993, Findlay et al. 1994) b) un corridor le long de la dorsale océanique au Sud de Madagascar (40°S), passant par les Walters Shoals pour atteindre les eaux malgaches (cf. sous-stock C3) c) un corridor central représenté par le canal de Mozambique pour gagner les îles du nord de ce même canal (cf. sous-stock C2). En revanche, aucune route migratoire à destination des îles Mascareignes n'a été encore identifiée.

Durant la chasse intensive, les premières campagnes de « marquage-recapture » des grandes baleines ont permis d'obtenir les premières informations sur les routes migratoires et les zones d'alimentation associées aux aires de reproduction (Harmer 1928, Dawbin 1956, 1966, Chittleborough 1965). Grâce à ces recaptures, une première connexion a été établie entre Madagascar et l'océan Austral (Rayner 1940). Au total, huit marques ont été déployées sur des baleines à bosse depuis les stations baleinières du sud-ouest de l'océan Indien et 249 dans l'océan Austral (aire III). Deux individus marqués en zone d'alimentation (10°E – 50°E) furent recapturés au sud de Madagascar (Paton & Clapham 2006). En complément de ces données historiques, les données plus contemporaines ont confirmé que les baleines à bosse du sud-ouest de l'océan Indien s'alimentaient dans le secteur III (IWC 1998a, Rosenbaum & Mate 2006). Plusieurs observations de baleines à bosse, principalement des paires mère-baleineau, ont été également reportées dans la région des Walters Shoals (sud de Madagascar) entre novembre et décembre mais le manque d'informations, notamment sur le type de comportements, ne permet pas de savoir si des baleines s'alimentent dans cette région ou bien si cette dernière constitue uniquement un point d'arrêt situé sur un corridor migratoire (Best et al. 1998).

## 2. DISTRIBUTION ET ABONDANCE

La CBI a désigné la population de baleines à bosse du sud-ouest de l'océan Indien comme le stock reproducteur ou population C dont l'aire de distribution se dessine de la côte est de l'Afrique du Sud aux côtes malgaches (IWC 1998a). Ce stock se divise en trois selon trois sous-régions (**Figure 1.3**) : C1 (côte est de l'Afrique du Sud au Mozambique) (Olsen Ø 1914, Best 1993, Findlay et al. 1994), C2 (Canal du Mozambique jusqu'à l'Archipel des Comores) (Best et al. 1998, Kiszka et al. 2007, Hermans & Pistorius 2008) et C3 (eaux côtières de Madagascar) (Bermond 1950, Angot 1951, Best et al. 1995, Rosenbaum et al. 1997, 2009, Rosenbaum 2003, Best & Brandão 2009, Cerchio et al. 2009). A ces trois sous-régions a été ajoutée une 4$^{\text{ème}}$ qui comprend l'île de La Réunion et l'île Maurice (IWC 2011a, 2011b, Dulau-Drouot et al. 2012). Les baleines à bosse y sont largement présentes durant les périodes de reproduction et de mise bas.

### *A) SOUS-POPULATION C1*

Le sous-stock de la côte sud-est de l'Afrique (C1) est lui-même défini par deux régions (IWC 2006, **Figure 1.4**). La région C1S, de la côte est de l'Afrique du Sud à l'île du Mozambique, qui est considérée comme un corridor de migration (Findlay et al. 1994, Findlay & Best 1996). Les captures et les observations indiquent une présence saisonnière de baleines à bosse, en juillet et septembre, le long de la côte de KwaZulu-Natal (~ 300 km au sud de Cap Vidal, Afrique du Sud) (Olsen Ø 1914, Harmer 1928, 1931, Bannister & Gambell 1965). La région C1N s'étend de l'île du Mozambique à la côte kenyane (Wamukoya et al. 1996, Berggren et al. 2001, Findlay 2011, Amir et al. 2012). Une forte concentration des baleines a été observée le long des côtes du Mozambique en août/septembre et en particulier dans les régions plus au sud comprises entre 33 et 35°S et 24 et 27°S (Findlay et al. 1994, 2011). La sous-population C1 est estimée à 8 045 (6 756-9 656) individus avec un taux d'accroissement de 1.1% sur la période 2010-2015 (Jackson et al. 2015).

### *B) SOUS POPULATION C2*

Les campagnes d'observations menées dans les eaux côtières des Comores et de Mayotte indiquent une concentration de baleines à bosse dans les régions d'Anjuan, Mohéli, Grand Comore mais aussi au nord du lagon de Mayotte (banc de l'Iris) et aux abords des bancs du Geyser et de la Zélée (localisés entre Mayotte et Madagascar) (Kiszka et al. 2007, Ersts et al. 2011). Elles sont généralement observées entre juillet et novembre bien que plus tardives dans la région des Comores. Aux Seychelles, les baleines à bosse sont observées à la même période, près de l'Atoll d'Aldabra avec quelques observations également reportées plus au nord, aux abords du plateau de l'île principale de Mahé (Avolio et al. 2002, Hermans & Pistorius 2008). Les trajets acquis par suivi satellitaire indiquent que plusieurs individus ont séjourné plusieurs jours dans les eaux côtières de Mohéli et de Mayotte après le déploiement des balises (Fossette et al. 2014). Cependant, en raison du manque de données concernant les individus fréquentant cette région, ce sous-stock reste peu décrit (Ersts et al. 2011). Par conséquent, aucune estimation d'abondance n'est disponible jusqu'à ce jour. Il a été supposé par l'appui de recaptures photographiques et génétiques ainsi que de données acquises par télémétrie satellitaire, qu'une partie de la population C2 contribue à l’estimation d’abondance de la côte est de Madagascar (C3) (Ersts et al. 2011, Cerchio et al. 2013, Fossette et al. 2014).

### *C) SOUS POPULATION C3*

Historiquement, les données de captures ont révélé que Madagascar était fréquenté par un grand nombre de baleines à bosse (Townsend 1935, Mackintosh 1942, Wray & Martin 1983, Best et al. 1996). Deux campagnes de chasse à la baleine ont été menées à Madagascar. La première de 1937 à 1939 et la seconde de 1949 à 1950 où un total de 2 975 et 1240 baleines à bosse ont été tuées, respectivement (Best et al. 1996). Les baleines sont largement distribuées autour de l’île avec de plus fortes concentrations entre juin et octobre dans les régions du nord-est (incluant la baie d’Antongil et l’île Sainte Marie), du sud (Fort Dauphin) et du sud-ouest (de Toliara à Nosy Be) (Braleys 1849, Starbuck 1878, Bermond 1950, Best et al. 1996, Rosenbaum et al. 1997, Razafindrakoto et al. 2001, Ersts & Rosenbaum 2003, Cerchio et al. 2009). Ce sont aussi les régions les mieux documentées, en particulier la baie d’Antongil (Rosenbaum et al. 1997, Ersts & Rosenbaum 2003, Cerchio et al. 2009). Le temps de résidence en baie d’Antongil est semble court et le taux de recapture relativement faible ce qui suggère l’existence d’une grande population où les individus se déplacent continuellement à travers la région (Cerchio et al. 2009). Un taux de rencontre comparable a été reporté pour la région sud de la côte ouest, près de Tuléar (Cerchio et al. 2013). En revanche, les données récoltées dans la région de Nosy Be (côte nord-est de Madagascar) indiquent de plus faibles concentrations de baleines à bosse avec des pics plus tardifs dans la saison bien qu’aucune estimation n’ait été proposée (Cerchio et al. 2013). Bien que des recaptures individuelles aient été reportées entre la côte est et la côte ouest de Madagascar, le lien entre ces régions reste inconnu à ce jour (i.e. s’agit-il de la même population ?, IWC 2011b). L’estimation d’abondance de la population de Madagascar est de 7 972 (6 409-10 228) individus et le taux d’augmentation des effectifs a été estimé à 0.7% sur la période 2010-2015 (Jackson et al. 2015).

### *D) SOUS POPULATION C4*

Dans les îles Mascareignes, l'observation des baleines à bosse est plus récente. Des études conduites à La Réunion depuis 2004 indiquent une présence entre juin et début novembre (Dulau-Drouot et al. 2008, 2012). Une tendance à l'augmentation du nombre d'individus depuis 2008 ainsi que l'observation de mêmes individus tout au long de la saison suggère que l'espèce recolonise de nouveaux sites de reproduction, ce qui serait possiblement dû à une augmentation de la population dans la région (Dulau-Drouot et al. 2012, Jackson et al. 2015). Des recaptures individuelles et des données acquises par télémétrie satellitaire ont également confirmé l'existence de mouvements intra-saisonniers dans la région (Dulau-Drout et al. *in prep*). Des observations ont aussi été reportées dans les eaux côtières de Tromelin, (~ 500 km au nord de La Réunion ; Dulau-Drouot et al. 2012). Par ailleurs, la présence de baleines dans les eaux de Maurice et de Rodrigues tend à être moins importante qu'à La Réunion (Corbett 1994, Cerchio et al. 2013). Aucune estimation d'abondance n'est disponible pour le moment pour ce sous-stock, estimé dans le sous-stock C3 (Jackson et al. 2015).

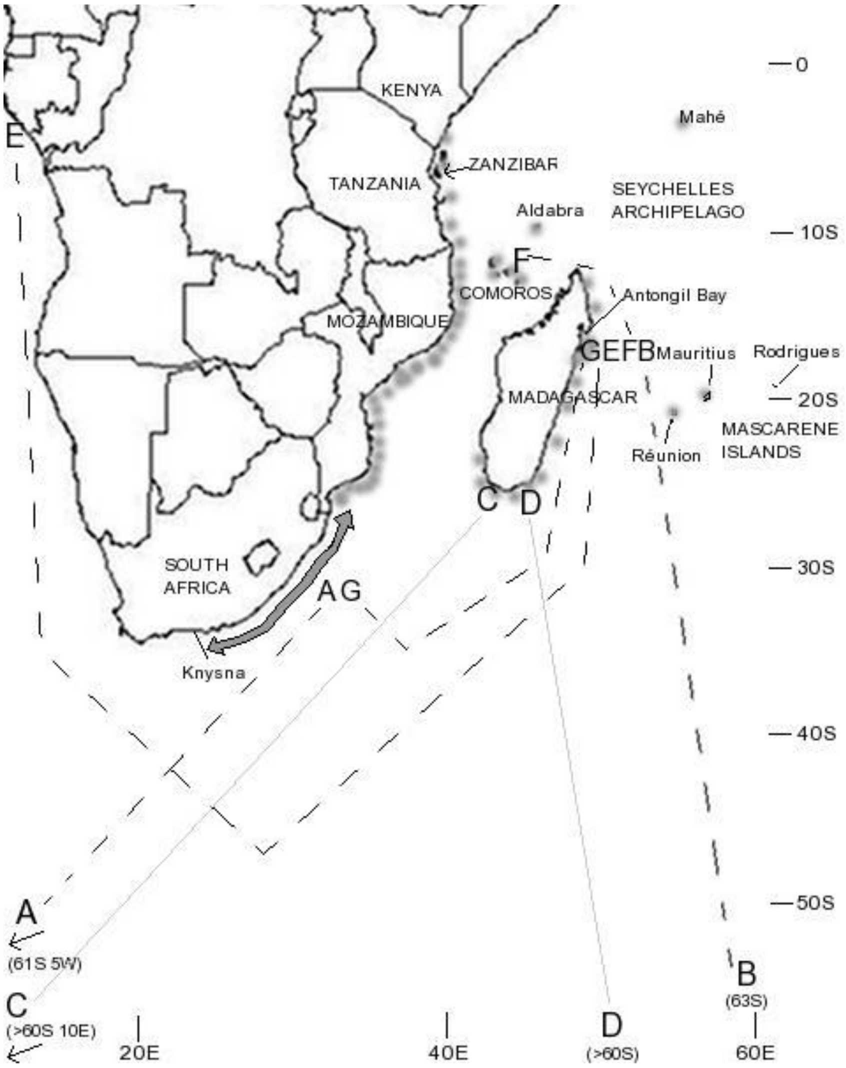

**Figure 1.4.** Zone de reproduction et corridors de migration du stock C. Les flèches grises indiquent les corridors de migrations. La zone grisée représente la zone principale d'hivernage. La double flèche grise représente un corridor de migration saisonnier. Les lignes grises (pleines et en pointillés) indiquent des recaptures génétiques (A et B), les recaptures faites à partir des « Discovery tags » (C et D) entre des zones de reproduction et des zones d'alimentation (Rayner 1940, IWC 1998a, Paton & Clapham 2006, Rosenbaum & Mate 2006). Les lignes pointillées associées aux lettres E et F indiquent des recaptures génétiques entre des sites de reproduction (Pomilla & Rosenbaum 2005, Ersts et al. 2006) alors que la lettre G est associée à des recaptures génétiques et des recaptures par photo-identification entre une zone de reproduction et un corridor migratoire (Pomilla et al. 2006, Cerchio et al. 2008) (d'après Fleming & Jackson 2011).

## 3. STRUCTURE DE LA POPULATION

La chasse à la baleine dans le sud-ouest de l'océan Indien débuta en 1908 et s'intensifia rapidement pour atteindre 19 000 baleines tuées en 1963. Une diminution importante des captures eut lieu aux alentours de 1915 dans la région du Mozambique alors qu'à Madagascar le nombre de captures resta relativement élevé jusqu'en 1950 ; premier indice de l'existence de structure de populations dans la région (Findlay 2001). La dynamique, les échanges et le chevauchement entre les sous-populations de baleines à bosse du stock C sont complexes et encore mal compris (Pomilla 2005, Pomilla & Rosenbaum 2005, Ersts et al. 2006, 2011, Cerchio et al. 2008). Différentes études indiquent notamment d'importants échanges entre les sous-populations du nord du canal du Mozambique (C2) et de Madagascar (C3) (Ersts et al. 2006, 2011, Rosenbaum et al. 2009, Fossette et al. 2014, Cerchio et al. *in prep* ; cf. **annexe A**). On observe aussi une faible fidélité au site de reproduction entre les années (Ersts et al. 2006, Cerchio et al. 2008, Cerchio et al. 2009), ce qui appuie l'hypothèse que les individus ont une très grande mobilité et que les individus se déplacent continuellement durant la saison au sein d'une région et entre les régions. Dans ce contexte de grande variabilité de déplacements et de proximité géographique des sous-régions, la délimitation de ces dernières est remise en cause aujourd'hui.

## D. AUTRES SITES DE REPRODUCTION DE L'ETUDE

### 1. POPULATION DU BRESIL (A)

De manière générale, la structure du stock A semble assez simple ; un seul stock reproducteur connecté à une seule aire d'alimentation (**Figure 1.5**) (IWC 2011b). La population du Brésil s'alimente à plusieurs centaines de kilomètres au large de la Géorgie du Sud et au sud des Iles Sandwichs correspondant à l'aire d'alimentation II (Stevick et al. 2006, Zerbini, Andriolo, et al. 2006, Zerbini et al. 2011). Aucune recapture (photographique ou génétique) n'a été faite entre cette population et les zones d'alimentation de la Péninsule Antarctique et de l'île Bouvet (Dalla Rosa et al. 2004, Engel et al. 2008). Des analyses de l'ADN mitochondrial révèlent des différences significatives entre la population du Brésil et celle de la Péninsule Antarctique (Engel et al. 2008, Rosenbaum et al. 2009). La majorité des baleines quittent la côte brésilienne au nord de 23°S par un étroit corridor de migration situé au large pour rejoindre les zones d'alimentation (Zerbini, Andriolo, et al. 2006, Zerbini et al. 2011).

Entre juin et décembre, les baleines à bosse sont distribuées le long de la côte de Cabo Frio (~23 °S) à Natal (~5°S) (Furtado-Neto et al. 1998, Martins et al. 2001, Zerbini et al.

2004, Andriolo et al. 2006). La plus forte densité d'individus (80% de la population) est cependant reportée dans la région du banc d'Abrolhos (15-18°S) (Andriolo et al. 2006, 2010). Bien que des observations aient également été reportées dans des archipels plus au large (e.g. Trinidad et Martim Vaz), le taux de fréquentation reste inconnu (Lodi 1994). De récentes estimations d'abondance ont montré que la population du Brésil était en augmentation (6.1%) depuis l'arrêt de la chasse commerciale (Freitas et al. 2004, Andriolo et al. 2006, Jackson et al. 2015) ce qui expliquerait la recolonisation de certaines régions. Néanmoins, les déplacements entre ces régions sont encore mal connus (Zerbini, Ward, et al. 2006, Ward et al. 2011). Zerbini et al. (2004) indiquent que plus de 90% des baleines observées sont présentes dans des eaux de moins de 300 m de profondeur.

L'absence de différenciation génétique entre le banc d'Abrolhos et la région nord de Praia do Forte (12°S) suggère l'existence d'une seule population (Cypriano-Souza et al. 2010). A l'inverse, des différences génétiques existent entre le stock A et les stocks B, C et G (Pomilla et al. 2006).

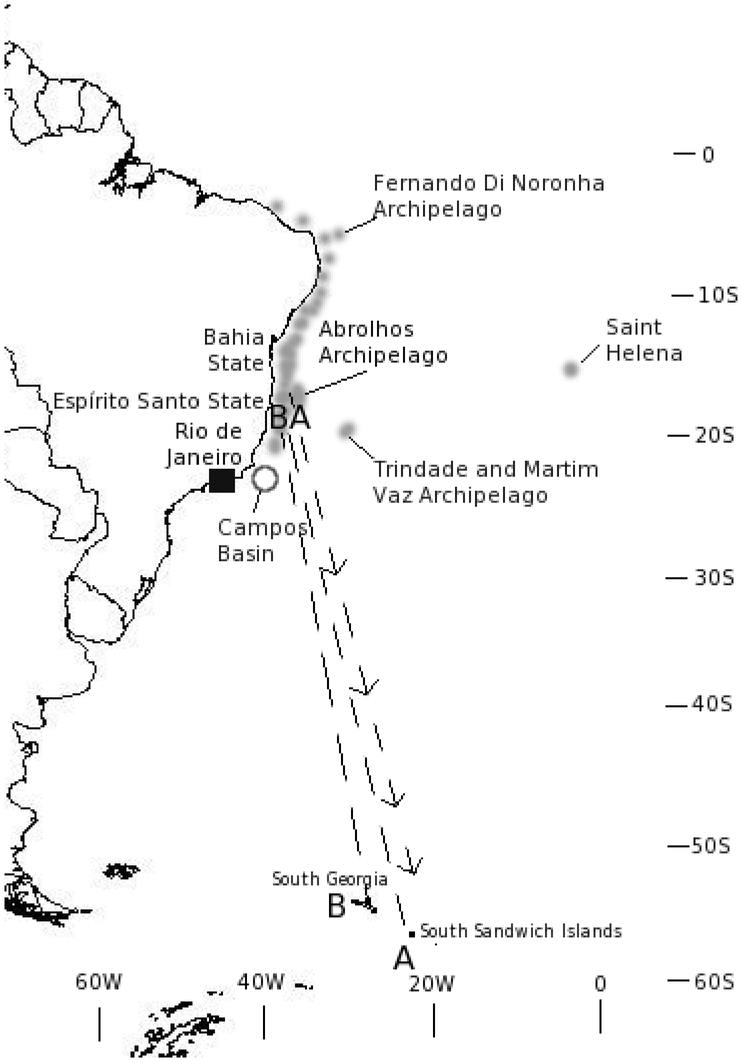

**Figure 1.5.** Zone de reproduction et corridors de migration du stock A. Les flèches grises indiquent les corridors de migrations. La zone grisée représente la zone principale d'hivernage. Les flèches en pointillés indiquent des déplacements issus de suivi satellites vers les zones d'alimentation de l'est la Géorgie du Sud et les îles sandwich du sud (Zerbini, Andriolo, et al. 2006). Les lettres A et B indiquent des recaptures par photo-identification entre le banc d'Albrolhos et les îles sandwich du Sud (Engel & Martin 2009), et une entre le banc d'Abrolhos et la Géorgie du sud (d'après Flemming & Jackson. 2011).

## 2. POPULATION DE L'AUSTRALIE DE L'OUEST (D)

Les échanges documentés à l'aide des « Discovery tags » et des méthodes de recaptures plus contemporaines indiquent un lien entre le stock D et l'aire d'alimentation IV (Rayner 1940, Chittleborough 1965) (**Figure 1.6**). Depuis les aires d'alimentation de l'océan Austral, les baleines migrent le long de la côte ouest australienne entre 15 et 35°S alors que la zone principale d'hivernage est localisée dans la région de Kimberley (15-18°S) (Jenner et al. 2001, 2006). Lors des migrations vers le nord, qui ont lieu de juin à juillet, une partie de la population rejoint la côte ouest australienne par la région d'Albany (34°S) pour remonter ensuite le long de la côte ouest (**Figure 1.6**). On observe différentes routes migratoires vers le sud avec des départs vers le large depuis le sud de la région de Kimberley, depuis l'archipel des Dampier ou bien le bassin de Perth (Jenner et al. 2001) (**Figure 1.6**). Dans les sites localisés le long du corridor migratoire, plusieurs pics d'abondance sont observés au cours de la saison ce qui  s'expliquerait par l'existence d'une ségrégation temporelle des individus selon la classe d'âge et le statut reproducteur (Chittleborough 1965, Dawbin 1997). Les immatures et les femelles en fin d'allaitement arriveraient et repartiraient les premiers, suivis des mâles et des femelles reproducteurs et enfin des femelles gestantes.

Une forte concentration de groupes avec baleineaux sont observés dans le golfe d'Exmouth et la baie des requins fin juillet et mi-septembre suggérant des zones de repos le long de la route migratoire dans les deux sens (Dawbin 1956, 1997, Chittleborough 1965, Bannister 1994, Jenner et al. 2001, Double et al. 2011). Des suivis par télémétrie satellitaire ont cependant révélé que de nombreux individus terminaient leur migration vers les zones de reproduction à plusieurs centaines de kilomètres au sud de la région de Kimberley avant d'entamer leur migration retour. Bien que cette dernière soit identifiée comme la zone principale d'hivernage, les schémas et les comportements de déplacements observés remettent en cause la délimitation de ces zones. Plusieurs études indiquent que les baleines à bosse sont présentes entre juillet et octobre dans la région de Kimberley avec de plus forte concentration près de Camden Sound et des monts sous-marins proches de la côte ('Frost and Tasmanian Shoals') (Jenner et al. 2001).

Les analyses génétiques révèlent des différences significatives avec les populations situées à l'ouest de l'Australie alors qu'aucune comparaison n'a été faite avec la population de la côte Est australienne. Aussi, des différences génétiques ont été notées entre le stock E1 et la population du Sud-Ouest de l'océan Indien (stock C) (Rosenbaum et al. 2006, 2009).

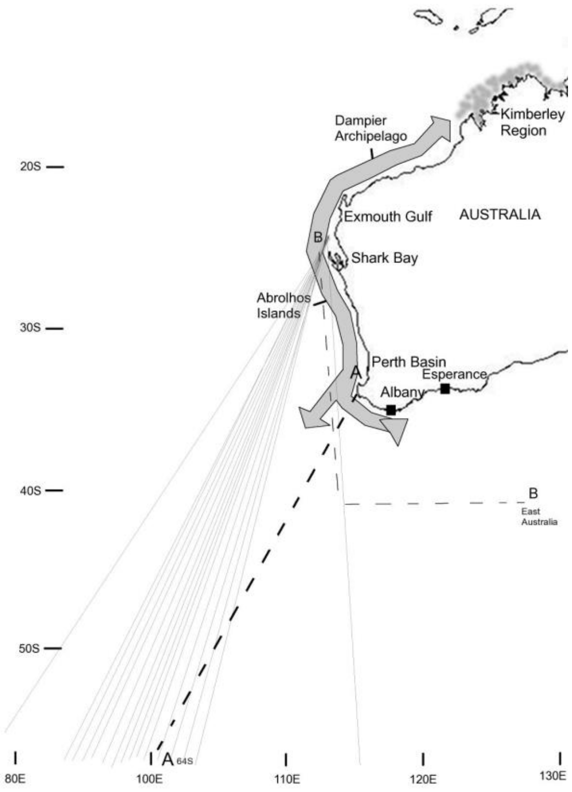

**Figure 1.6**. Zones de reproduction et corridors de migration du stock D. Les flèches grises indiquent les corridors de migrations. La zone grisée représente la zone principale d'hivernage. Les lignes fines grises sont les recaptures faites à partir des « Discovery tags » entre les zones de reproduction et les zones d'alimentation (Rayner 1940, Chittleborough 1965, Paton & Clapham 2006) et la ligne en pointillé associée à la lettre B celle entre les zones de reproduction Ouest et Est australiennes (Chittleborough 1965). La ligne en pointillé associée à la lettre A est une recapture par photo-identification (Gill 1995) (d'après Fleming & Jackson 2011).

### 3. POPULATION DE L'AUSTRALIE DE L'EST (E1)

Les individus qui fréquentent les eaux de la côte Est australienne s'alimentent principalement dans l'aire d'alimentation V (130°-180°) bien que certains exploitent probablement l'aire IV (Chittleborough 1965, Gales et al. 2009). Lors de leurs migrations, les baleines empruntent trois corridors : côte Est de l'Australie, les îles Norfolk (non indiquées sur la carte), le détroit de Cook en Nouvelle Zélande et peut-être aussi les îles Cook (Stamation et al. 2007, IWC 2011b, **Figure 1.7**). Des données issues de la télémétrie satellitaire ont montré qu'une baleine avait également emprunté le détroit de Bass par l'Ouest puis était redescendue par la côte ouest tasmanienne (Gales et al. 2009).

Entre mai et octobre, une forte concentration de baleines à bosse est observée près de la grande barrière de corail (GBC, 16-21°S) (Chittleborough 1965, Paterson & Paterson

1984, Simmons & Marsh 1986) (**Figure 1.7**). Le pic d'abondance a lieu entre juillet et août (Smith et al. 2012). Elles sont présentes également jusque dans la région de l'île de Murray (10°S). Plus tard dans la saison (d'août à octobre), sur la route du retour, les baleines visitent la baie d'Hervey plus au sud (~25°S) (Dawbin 1966, Paterson 1991, DEH 2005). Un fort pourcentage de recaptures individuelles y a été reporté (77%), indiquant que c'est aussi une zone importante d'hivernage et probablement de repos (Forestell et al. 2003).

De récents travaux ont montré que le stock E se divisait en plusieurs sous-stocks : la côte Est australienne et le récif de Chesterfield (E1), la Nouvelle-Calédonie (E2) et Tonga (E3) (Garrigue et al. 2007, Olavarría et al. 2007). Les analyses génétiques indiquent des échanges plus importants avec les populations de l'Océanie qu'avec celles de l'Ouest de l'Australie (Olavarría et al. 2007) et ces résultats sont appuyés par l'analyse des chants (Helweg et al. 1998) (**Figure 1.7**).

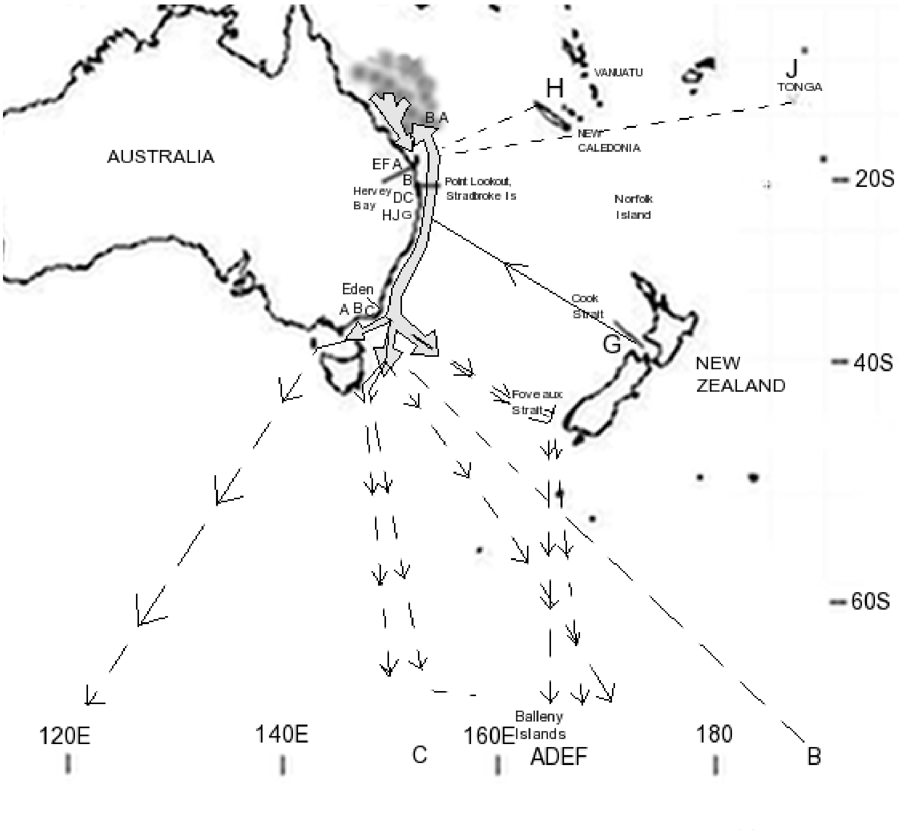

**Figure 1.7**. Zone de reproduction et corridors migratoires du stock E1. Les flèches grises indiquent les corridors de migrations. La zone grisée représente la zone principale d'hivernage. Les lignes pointillées reflètent de manière approximative les trajets individuels acquis par télémétrie satellitaire (Gales et al. 2009). Les lettres (A-J) indiquent des recaptures (intra-saisonnières ou interannuelles) par photo-identification entre la zone de reproduction et les zones d'alimentation ou entre les différentes zones de reproduction du Pacifique Ouest (Garrigue et al. 2007, 2010, Rock et al. 2006, Franklin et al. 2007, 2008, 2011) (d'après de Fleming & Jackson 2011).

## E. UTILISATION DE L'HABITAT DES BALEINES A BOSSE EN PERIODE DE REPRODUCTION

Chez de nombreux mammifères marins, il existe une dissociation spatiale entre les sites de reproduction et d'alimentation. Comme nous l'avons vu précédemment, il est clairement admis que les baleines à bosse ne s'alimentent pas en période de reproduction ou seulement de manière occasionnelle. Par conséquent, leur distribution spatiale pendant la reproduction ne sera pas influencée par la distribution des ressources alimentaires ni par leurs stratégies d'alimentation. Néanmoins, des facteurs écologiques intrinsèques et extrinsèques peuvent agir conjointement pour influencer les schémas de distribution et l'utilisation de l'habitat des baleines à bosse en période de reproduction.

## F. SCHEMAS GENERAUX D'UTILISATION DE L'HABITAT

### 1. A GRANDE ECHELLE

### *A) LA TEMPERATURE DE SURFACE*

Il a été montré qu'à l'échelle des bassins océaniques, la température de surface détermine la distribution hivernale des baleines à bosse. La température de surface de l'ensemble des aires de reproduction est ainsi comprise entre 21.1 et 28.3°C (Rasmussen et al. 2007) à l'exception de l'île de Bonin au Japon et du nord du Pérou (Guidino et al. 2014). Cependant, les différentes populations occupent en hiver des zones bien plus restreintes que celles définies par cette gamme de température (**Figure 1.8**). Ceci suggère que d'autres paramètres environnementaux peuvent influencer la distribution des baleines à bosse en période de reproduction.

### *B) LA DISTANCE A LA COTE*

De manière générale, les baleines à bosse sont côtières pendant la période de reproduction. Elles sont présentes sur le plateau continental, le long des récifs et autour des îles, régions caractérisées le plus souvent de fonds marins meubles (e.g. sable, vase). Lors de déplacements localisés ou de migrations, les suivis individuels par télémétrie satellitaire indiquent qu'elles peuvent se déplacer près des côtes (< 50 km) (e.g. Double et al. 2011, Kennedy et al. 2013). Dans les régions de Shark Bay et d'Exmouth, sur la côte Ouest australienne, les données de captures et d'observations (en mer et aériennes) ont montré que les baleines se trouvaient à moins de 30 km de la côte (Bannister & Hedley 2001). En Polynésie française, la majorité des baleines sont présentes à quelques centaines de mètres de la côte et à moins de 10 km (Gannier 2000, Poole 2006). Bien que dans des régions identifiées comme des corridors de migration, on les trouve parfois plus au large (Jenner et al. 2001, 2006), dans les zones où le plateau continental est très peu étendu, les baleines semblent être généralement observées plus près de la côte (Noad et al. 2008).

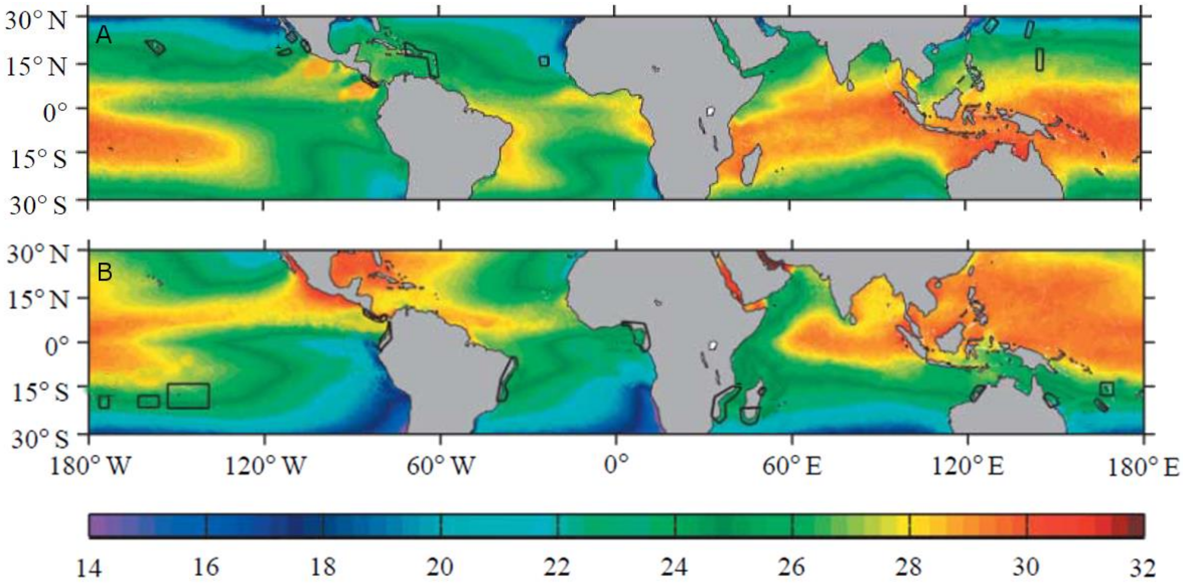

**Figure 1.8.** Aires de distribution des populations de baleines à bosse (identifiées par des polygones) de l'hémisphère Nord (**A**) et de l'hémisphère Sud (**B**) en hiver couplées à la température de surface (février et août) (Rasmussen et al. 2007 modifié).

### *C) LA PROFONDEUR ET LA PENTE*

La largeur du plateau est d'autant plus importante que les paramètres environnementaux caractérisant l'habitat critique utilisé par les baleines en hiver comprennent notamment la bathymétrie ou la pente (Oviedo & Solís 2008). En effet, elles sont observées principalement dans des eaux inférieures à 200 m de profondeur et des zones peu pentues (e.g. Brésil, Zerbini et al. 2004 ; Comores ; Kiszka et al. 2010 ; Costa Rica, Oviedo & Solís 2008 ; Gabon, Strindberg et al. 2011 ; Hawaii, Craig & Herman 2000 ; ouest de l'Australie, Jenner et al. 2001 ; Puerto Rico, Mignucci-Giannoni 1998). Une étude a été réalisée dans la région de la grande barrière de Corail (Est de l'Australie), afin de prédire l'habitat préférentiel des baleines à bosse dans cette zone. Cette étude a montré une affinité pour des profondeurs comprises entre 30 et 58 m (Smith et al. 2012). Cependant, dans de nombreuses régions, la distribution spatiale diffère entre les types de groupes observés.

### 2. A PETITE ECHELLE

A plus petite échelle, la structure sociale (solitaire, paire, paire mère-baleineau, mère-baleineau escorte, groupes compétitifs constitués d'au moins 3 individus adultes) et le statut reproducteur (pour les femelles) semblent guider l'utilisation d'habitats préférentiels des individus (Smultea 1994, Craig & Herman 2000, Ersts & Rosenbaum 2003).

Les couples mère-baleineau montrent de manière générale une préférence pour les eaux peu profondes de quelques dizaines de mètres (<50 m) et des zones très proches de la côte (Abernethy et al. 1992, Craig & Herman 2000, Félix & Haase 2001, Ersts & Rosenbaum 2003, Forestell et al. 2003, Martinez et al. 2015). Dans le royaume de Tonga, 50% des observations de couple mère-baleineau ont été faites dans des eaux inférieures à 36 m de profondeur (Abernethy et al. 1992). Bien qu'encore discutées aujourd'hui, différentes hypothèses sont avancées : les femelles se tiendraient près des côtes probablement pour éviter i) le harcèlement des mâles en rut ou les blessures qu'ils pourraient infliger aux baleineaux, ii) les conditions de turbulence qui prévalent dans les eaux profondes du large ou encore iii) la présence de prédateurs potentiels (Jefferson et al. 1991, Smultea 1994, Corkeron & Connor 1999, Ersts & Rosenbaum 2003, Ford & Reeves 2008). Cependant, la prédation par les orques et/ou les requins ne jouera pas de rôle dans la sélection d'habitats dans notre étude à Madagscar. En effet, les observations d'orques n'ont été reportées que sur la côte nord-ouest de Madagascar, région non étudiée dans cette thèse tandis que les requins ont été victime de la surpêche. La distribution des femelles et les habitats préférentiels pourraient aussi varier en fonction de la période du cycle de reproduction (Craig & Herman 2000). A Hawaii, les femelles avec un baleineau, identifiées par photo-identification, sont observées significativement plus souvent dans les eaux de l'île Maui que près d’Hawaii (‘Big island’) les années où elles sont en présence d’un baleineau (Craig & Herman 2000). Ceci est aussi appuyé par une plus grande proportion de baleineaux observée à Maui (Craig & Herman 2000). Par ailleurs, le courant est un autre paramètre environnemental qui pourrait influencer la présence de couples mère-baleineau qui préféreraient les eaux plus calmes et protégées mais cela a encore été peu étudié (Félix & Botero-Acosta 2011)

A l’inverse les mâles chanteurs ou les groupes de plusieurs adultes sont observés dans des zones plus au large (Frankel et al. 1995, Martins et al. 2001). Au Costa Rica par exemple, les mâles adultes ou chanteurs sont présents dans un habitat favorable à une propagation bidimensionnelle des sons (eaux peu profondes, fonds plats) alors que des études menées dans d’autres localités (îles Hawaii, îles Britanniques, mer des Caraïbes) ont montré leur présence plus au large dans des eaux profondes, aux conditions de propagation différentes (Frankel et al. 1995, Charif et al. 2001, Swartz et al. 2003, Oviedo & Solís 2008). Le chant des mâles peut avoir pour fonction d’attirer une femelle ou d’être un moyen de se mesurer aux autres mâles (Rosenbaum & Collins 2006). D’après Frankel et al. (1995), les vocalises servent à assurer l'espacement entre les chanteurs. Par ailleurs, les groupes d’adultes auront peut-être tendance à préférer les zones plus profondes pour faciliter les comportements reproducteurs (Smultea 1994). Plusieurs études suggèrent que les déplacements et la répartion des mâles seraient déterminés par la distribution des femelles disposées à se reproduire plutôt que par la disponibilité d’habitat favorables au chant (Tyack & Whitehead 1983, Baker & Herman 1984, Frankel et al. 1995, Weinrich 1995, Smith et al. 2008).

A Madagascar, la baie d’Antongil est la zone la plus intensément étudiée (Rosenbaum et al. 1997, Razafindrakoto et al. 2001, Ersts & Rosenbaum 2003, Cerchio et al. 2009). Tous les différents types de groupes sociaux y ont été observés, indiquant que cette localité est utilisée comme zone de reproduction et de mise bas. Les couples mère-baleineau sont présents à de plus faibles profondeurs (< 20 m) comparés aux autres groupes. Les groupes reproducteurs sont observés plus au large que les groupes accompagnés de baleineaux y compris ceux en présence d’une escorte. Il a été aussi observé des changements d’habitats (i.e. profondeur et distance à la côte) selon la période de la journée qui semblent être associés au type de comportements (Ersts & Rosenbaum 2003).

La variabilité des zones que les baleines à bosse sélectionnent et en particulier les différences entre les femelles et les mâles sont encore mal compris. Bien que des observations de baleines à bosse soient reportées tout autour de Madagascar (Cerchio et al. 2009), très peu de zones ont été documentées à ce jour. De plus les déplacements au cours de la saison de reproduction restent peu définis.

## V. OBJECTIFS ET ORGANISATION DE LA THESE

Comme nous l'avons vu dans cette introduction, la séparation entre les périodes de reproduction et d'alimentation se traduit ainsi par de fortes discontinuités géographiques et l'utilisation d'habitats fortement contrastés. L'identification des sites de reproduction et le degré de fidélité des individus à leur région natale vont déterminer l'existence de populations et sous populations. Néanmoins, certains des sites de reproduction où des concentrations de baleines à bosse sont observées restent encore peu documentés comme la région de Sainte Marie à Madagascar.

Durant la période de reproduction, les baleines vont vivre uniquement sur leurs réserves. Par conséquent, leur distribution spatio-temporelle ne sera pas inféodée à l'abondance et la distribution des ressources. Cependant, les conditions environnementales et la structure sociale tendent, à différentes échelles, à influencer la distribution et l'utilisation des habitats des baleines à bosse en période de reproduction.

Par ailleurs, la fidélité des baleines à bosse à leur zone de reproduction est une caractéristique importante à prendre en compte dans la gestion et la protection de ces zones. Identifier les habitats utilisés par ces cétacés et les paramètres qui peuvent influencer leur distribution est essentiel pour mieux protéger ces zones clés. La détérioration ou la disparition de ces habitats pourraient, à long terme, impacter leur succès reproducteur.

En résumé, outre l'acquisition de données fondamentales sur l'écologie des populations des baleines à bosse et en particulier du groupe C, qui intéressent notamment la CBI dans le cadre de l'étude approfondie des baleines à bosse de l'hémisphère Sud, mon travail de thèse aura des implications pour la conservation des lieux de reproduction. Les baleines à bosse à Madagascar comme dans d'autres régions, attirent chaque année de nombreux touristes et c'est pourquoi il est important de mieux connaître leurs habitats de reproduction et de mise bas ainsi que leurs déplacements. Les informations issues de notre étude contribueront ainsi à la gestion des habitats de cette espèce.

Ainsi, les questions associées à la problématique sont les suivantes:

1. **Quelle est la distribution spatiale et temporelle des groupes sociaux de baleines à bosse dans le canal de Sainte Marie ?**
2. **Quelle est la distribution des baleines à bosse de Madagascar (C3) en fonction du sexe et du statut reproducteur ?**
3. **Quel est le rôle des paramètres environnementaux dans l'utilisation de l'habitat des mâles et des femelles pendant la reproduction à Madagascar ? Peut-on mettre en évidence un schéma général de l'utilisation de l'habitat par les baleines à bosse pendant la reproduction, en s'appuyant sur une comparaison entre les déplacements de baleines de plusieurs régions de l'hémisphère Sud ?**

Cette thèse s'appuie sur trois articles scientifiques (soumis ou en préparation). Inclus sous forme de chapitres distincts, ils présentent et discutent les éléments de réponses obtenus durant ce travail de thèse. Dans le chapitre 3, l'étude repose sur des données acquises par observations visuelles opportunistes (5 ans) collectées à petite échelle spatiale. Elle vise à estimer le taux de rencontre et décrire la distribution spatio-temporelle des groupes sociaux dans le canal de Sainte Marie (Madagascar).

Les deux études suivantes se basent sur des données acquises par télémétrie satellitaire durant la période reproduction. Les suivis de déplacements individuels permettent de caractériser les habitats exploités par les baleines à bosse en hiver. L'objectif de la deuxième étude (chapitre 4) est de mettre en évidence les paramètres environnementaux qui influencent l'utilisation d'habitat des baleines à bosse en fonction du sexe afin d'identifier les habitats préférentiels des baleines à bosse à Madagascar.

La troisième étude (chapitre 5), qui comprend une analyse de suivis télémétriques des populations du Brésil et des côtes Est et Ouest de l'Australie, vise à comparer les déplacements côtiers et l'utilisation d'habitat en fonction du sexe dans différentes zones de reproduction de l'hémisphère Sud.

Une discussion générale (chapitre 4) synthétise les principaux résultats de cette thèse et aborde les perspectives ouvertes par ce travail.

# CHAPITRE II – SITES DE L’ETUDE ET METHODES

*Aquarelle de Caroline Jacques*

# CHAPITRE II – SITE D'ETUDE ET METHODES

## I. SITE D'ETUDE

### A. TOPOGRAPHIE ET HYDROLOGIE DE MADAGASCAR

Il existe une forte asymétrie de la topographie entre l'Est et l'Ouest de Madagascar. La côte Ouest se caractérise par un plateau continental étendu avec une largeur maximale d'environ 60 km (~ 16°S) et une pente faible. Le plateau se réduit cependant au sud-ouest où une barrière de corail située au bord du plateau continental s'étend sur 30 km (d'Androka à Marombe) (Pripp et al. 2014). A l'inverse, le plateau continental de la côte Est est peu étendu (~ 25 km) et relativement raide (**Figure. 2.1**). Il s'élargit pour former une plate-forme régulière de faible profondeur dans la région de Sainte Marie et de la baie d'Antongil (~ 18°S ; ~50 km) (Katz & Premoli 1979, Ersts & Rosenbaum 2003). A l'Est, les récifs coralliens les plus développés se situent au nord-est : le long de la péninsule de Masoala, à Foule Pointe et au sud de l'île Sainte Marie. La côte sud de Madagascar est également marquée par une extension du plateau continental (max : 50 km) qui contribue à une circulation océanique atypique dans cette zone (i.e. tourbillons, upwellings). Cette plate-forme côtière est associée à l'existence d'une crête sous-marine qui s'étend sur plus de 1000 km (entre 27 et 34°S) au sud de Madagascar où est localisé le mont sous-marin des Walters Shoals. La pointe nord se distingue par la région du Nord-Est (Nosy-Be et la péninsule de Nosy Iranja) composée d'îlots et de hauts fonds océaniques. Une importante diversité de cétacés y a été recensée dont une population résidente de baleines d'Omura, nouvelle espèce de rorqual décrite récemment (Wada et al. 2003, Cerchio et al. 2015).

Madagascar est situé en amont de l'écosystème marin du courant d'Agulhas et au milieu du courant de surface appelé Courant Equatorial Sud (CES) (**Figure 2.1**). Celui-ci se sépare en deux branches sur la côte Est (~ 17°S) dont une circule vers le nord et l'autre vers le Sud composant alors le Courant Est de Madagascar (CEM). La branche sud, associée à des vitesses fortes (~0.5-0.9 m/s), se déplace le long de la côte pour rejoindre une zone tourbillonnaire dans la région du Cape Sainte Marie. Le courant nord remonte pour dépasser la pointe nord de Madagascar et passer au large des Comores. Une partie va rejoindre la circulation du nord du canal du Mozambique. A l'inverse, bien que la circulation de la côte

Est soit marquée par de nombreuses structures tourbillonnaires bien documentées, la circulation côtière générale reste peu décrite.

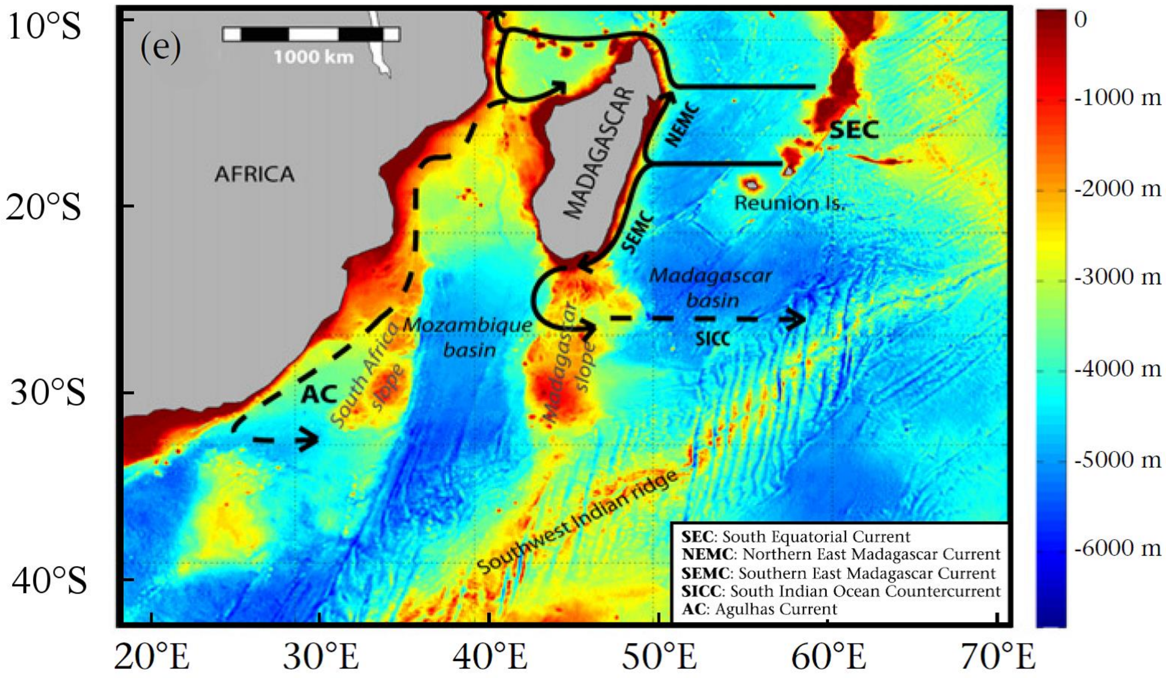

**Figure 2.1.** Circulation océanique de surface et topographie générale de la région du sud-ouest de l'océan Indien. Les principaux fronts sont indiqués : Courant équatorial sud, les branches est et ouest du courant Est de Madagascar, le contre-courant du sud-ouest de l'océan Indien et le courant d'Agulhas (d'après Pinet et al. 2012).

## B. CAS PARTICULIER DU CANAL DE SAINTE MARIE

Le canal Sainte Marie (16°50'S, 49°55'E) est situé au nord-est de Madagascar, entre l'île Sainte Marie et la côte du continent malgache (**Figure 2.2**). Cette région est située à 150 km de la baie d'Antongil, autre région d'étude des baleines à bosse (Rosenbaum et al. 1997, Razafindrakoto et al. 2001, Ersts & Rosenbaum 2003). Le canal mesure 60 km de long et 30 km de large. C'est dans la partie centrale du canal que l'on trouve les profondeurs maximales atteignant 60 m et qu'il se rétrécit pour ne laisser qu'un passage de 7 km entre le continent et l'île Sainte Marie (**Figure 2.2**). Cette dernière est séparée d'un cordon corallien par un lagon de très faible profondeur (~10 m) et qui s'étend au sud de l'île. De plus, elle est située dans la région de la côte est où les courants sont plus faibles.

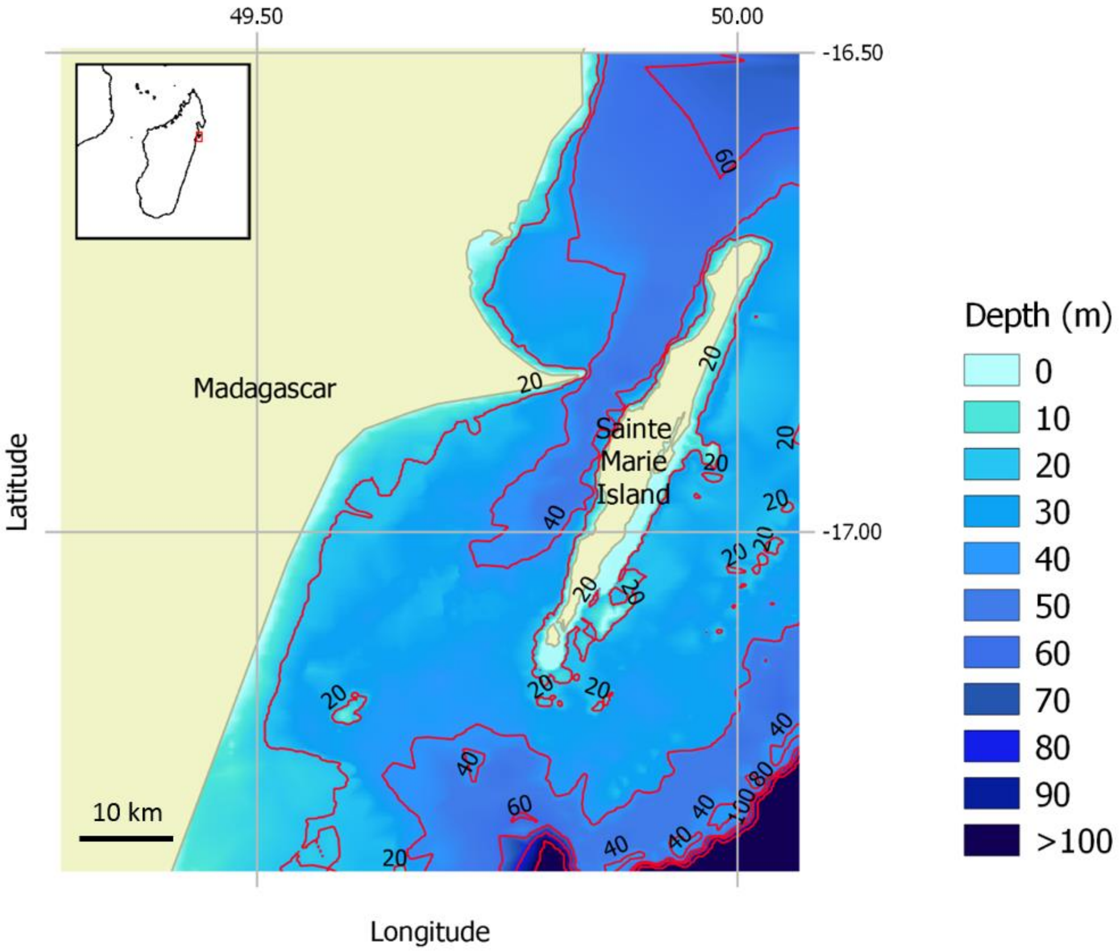

**Figure 2.2.** Carte du canal de Sainte Marie, Madagascar.

La proximité des baleines à bosse présentes dans le canal a aussi favorisé le développement touristique de l'observation des baleines (whale-watching) dès le début des années 90 (Hoyt 1992). Sainte Marie est d'ailleurs la première destination touristique malgache pour l'observation des baleines à bosse en milieu naturel (O' Connor S et al. 2009). De nombreuses données d'observation et de photo-ID ont été collectées à partir des bateaux touristiques, mais n'ont pas encore été analysées (Vely 2009). Une première estimation du taux de recapture a néanmoins révélé une faible fidélité au site (R=0.012, Reynes et al. unpublished data) ce qui renforce l'hypothèse de l'existence d'une population de grande taille (Cerchio et al. 2008, 2009, Dulau-Drouot et al. 2011). La naissance d'un baleineau à bosse a également été reportée dans les eaux de Sainte Marie, indiquant un habitat favorable à la mise bas (Faria et al. 2013). Cependant, à ce jour, aucune étude détaillée de l’abondance et de la distribution de la population reproductrice occupant ce site n’a été réalisée. Par ailleurs, les caractéristiques topographiques, bathymétriques et océanographiques uniques de cette région en font un site particulièrement intéressant pour tester de manière approfondie les hypothèses généralement admises sur l’utilisation de l’habitat par les baleines à bosse en période de reproduction.

## II. UTILISATION DE LA TELEMETRIE SATELLITAIRE ARGOS POUR ETUDIER LES MYSTICETES

Ces dernières décennies, le développement d’un système de localisation et de collecte de données par satellite a permis d’acquérir des informations pertinentes et souvent méconnues sur les déplacements et les comportements des animaux sauvages dans leur milieu naturel. Ceci est d’autant plus vrai pour des animaux inféodés au milieu marin tel que les poissons ou les cétacés. Très tôt, des biologistes se sont intéressés aux déplacements saisonniers des grandes baleines qui étaient présentes en grand nombre dans différentes zones géographiques à certaines périodes de l’année. Ainsi, pour améliorer les connaissances sur les différentes populations et les migrations saisonnières, des baleines ont été marquées de « Discovery tags » à l’époque de la chasse à la baleine (Brown 1971). Cette méthode dite de « marquage-recapture » a permis d’obtenir les premières informations sur les aires de distribution des grandes baleines notamment des baleines à bosse, des baleines franches et des baleines bleues (Scammon 1874, Brown 1977, 1978). Par la suite, d’autres approches de capture-recapture (photographique, génétique) seront utilisées, notamment pour caractériser la structure et la dynamique des populations (e.g. paramètres de croissance ou démographiques, échanges entre population). Cependant, les techniques telles que la photo-identification ou encore l’acoustique passive nous renseignent sur la présence ponctuelle d’un individu ou d’une espèce dans un lieu donné et non sur les déplacements et les comportements individuels. C’est à partir des années 1990 que le développement des techniques de télémétrie (radio, acoustique, satellite) et l’accès aux données environnementales ont ouvert de nouvelles pistes d’exploration et d’analyse (Hussey et al. 2015). Le suivi par télémétrie va permettre d’acquérir des informations (i.e.

déplacements, comportements) sur de nombreuses espèces mais aussi de collecter des informations sur leur environnement (e.g. température, profondeur, fluorescence). En effet, l'ajout de différents capteurs va permettre de collecter des données océanographiques dans des régions difficiles d'accès comme les régions polaires en utilisant les animaux comme instruments de mesure (e.g. les éléphants de mer). Chez les oiseaux marins ou les pinnipèdes, différents appareils enregistreurs tels que les capteurs de température œsophagienne (Ancel et al. 1997) ou stomacale (Wilson et al. 1992), des accéléromètres (Suzuki et al. 2009, Viviant et al. 2010) ou des caméras vidéo (Davis et al. 1992, 2004, Heaslip & Hooker 2008) vont aussi être utilisés pour approfondir l'étude des comportements.

## A. SUIVI SATELLITAIRE ET PRINCIPE DU SYSTEME ARGOS

Les premiers appareils électroniques déployés sur les baleines sont équipés uniquement d'émetteurs radio (VHF) (Watkins & Schevill 1975, Watkins et al. 1978). La zone de réception étant limitée à quelques kilomètres, le suivi individuel nécessite un effort logistique trop coûteux pour le suivi d'espèces pélagiques, se déplaçant sur de grandes distances. Ainsi, par la suite, les balises sont équipées d'émetteur Argos ou PTT (Platform Transmitter Terminal-Argos) qui permettent de transmettre la position de l'animal via le système satellite Argos. La première balise satellite à être déployée sur une baleine sera réalisée par Mate (1989 a, b) sur une baleine à bosse.

Le système Argos créé en 1978 par le CNES (Centre National d'études spatiales) et la NOAA (National Oceanic and Atmospheric Administration) permet de localiser n'importe quel animal équipé d'un émetteur compatible sur la planète. Les émetteurs envoient des signaux radioélectriques courts (360 ms à une fréquence 400 MHz) à intervalle de temps programmé (entre 90 et 200 s). Ces signaux ou messages, contenant le numéro d'identification de l'émetteur sont captés par les six satellites situés en orbite polaire. Le système Argos est basé sur l'effet Doppler-Fizeau qui consiste à calculer une position géographique par le décalage entre la fréquence du signal émis par la balise et la fréquence reçue pas le satellite (Argos 1990). Cette méthode permet d'obtenir des localisations en quasi temps réel et de bonne précision sans avoir à récupérer l'appareil (Argos 1990). La qualité des localisations est fonction de l'estimation de l'erreur calculée et du nombre de messages reçus par le satellite. Il existe des classes de localisation exprimant une estimation de l'erreur qui varie de quelques centaines de mètres à quelques kilomètres (classe 3 : < 250m ; classe 2 ; 250 < < 500 ; classe 1500 < < 1500 ; 0 < 1500 et A, B, Z : absence d'estimation).

## B. BALISES ET SYSTEMES D'ATTACHES

De manière générale chez les cétacés, il existe plusieurs contraintes à prendre en compte dans le choix du type de balises et du système d'attache utilisé. Ces contraintes sont liées à la fois au mode de vie de l'animal (marin), à sa morphologie (forme du corps, type de peau, présence de nageoire dorsale développée) et à son comportement (vitesse, plongée, respiration, saut, frottement entre individus). Le système d'attache est l'élément clé dans le maintien d'une balise sur un animal et en particulier chez les espèces vivant dans l'eau où la résistance à l'écoulement de l'eau y est très important (Read & Westgate 1997). Contrairement aux pinnipèdes, un système de collage serait inadapté car les cétacés ont une peau nue, fragile et une perte de squames importante (Hooker & Baird 2001). Les cétacés sont inféodés au milieu marin et passent relativement peu de temps en surface. Par conséquent, la transmission de messages aux satellites, qui nécessite l'antenne hors de l'eau, sera faible ou absente. La position de la balise sur le corps aura alors son importance pour optimiser le temps d'exposition de l'antenne à l'air afin que celle-ci puisse émettre. Pour certaines espèces, les balises devront aussi supporter des conditions environnementales particulières (e.g. pression).

Chez les grandes baleines, les premières balises (radio ou satellite) sont des cylindres de 13 cm de diamètre placées à quelques mètres derrière l'évent par un système d'hameçons implantés en sous-cutané (**Figure 2.3**). Trop lourdes et trop grosses, la forme est alors modifiée et la taille réduite afin de diminuer les frottements et améliorer la durée d'émission (Mate et al. 2007a). Ce sera vers la fin des années 1990 que la création d'une nouvelle forme permet une implantation de la balise dans le lard de la baleine, ne laissant sortir hors du corps qu'une antenne de 10 cm. Différents modèles basés sur la même forme, de Type 1 (ONR 2009), sont aujourd'hui principalement utilisés chez les grandes baleines et constitués d'un tube cylindrique de 2 cm de diamètre entre 15 et 30 cm de long, d'un système d’attache composé d’une à deux séries de barbillons repliables et d’une pointe triangulaire (Gales et al. 2009, Robbins et al. 2013, Kennedy et al. 2014) (**Figure 2.4**). Les balises (piles au Lithium) sont équipées d’un capteur de conductivité qui détecte quand l’animal est hors de l’eau et déclenche l’émission de signaux (cette technologie prolonge significativement la durée de vie de la batterie). La forme de la balise permet une pénétration de 30 cm de profondeur entre la couche de graisse et le muscle (fascia). Une bague située sur la partie distale contrôle la profondeur de pénétration et assure le maintien de l’antenne à l’extérieur de la baleine (**Figure 2.4**). Bien que l’implantation musculaire présente des avantages, l’implantation dans la couche de graisse reste moins invasive et majoritairement pratiquée (Mate et al. 2007). Ainsi, le système d’ancrage à barbillons a pour but d’optimiser le maintien de la balise en place.

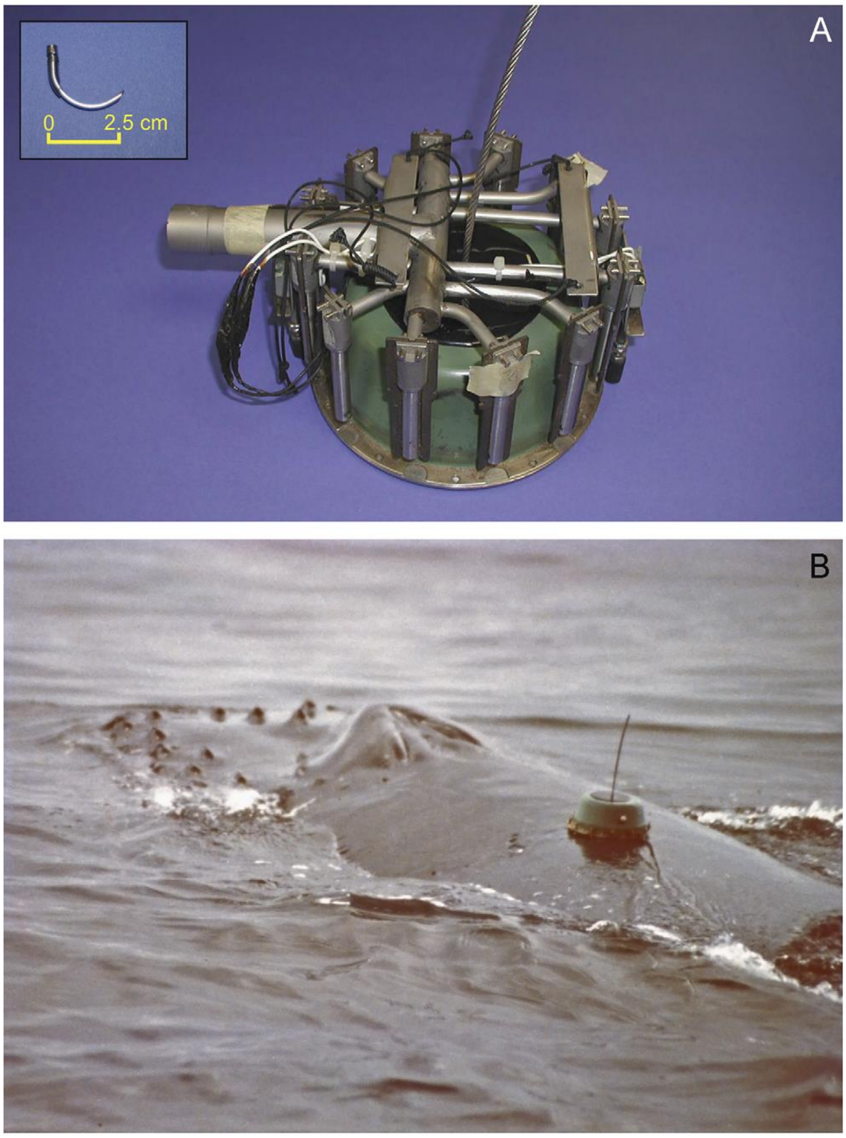

**Figure 2.3**. (A) Balise Argos composée de 12 cylindres chacun constitué d’un système d’ancrage sous-cutané en acier inoxydable. (B) Baleine à bosse équipée en 1987 de ce type de balises (d’après Mate et al. 2007).

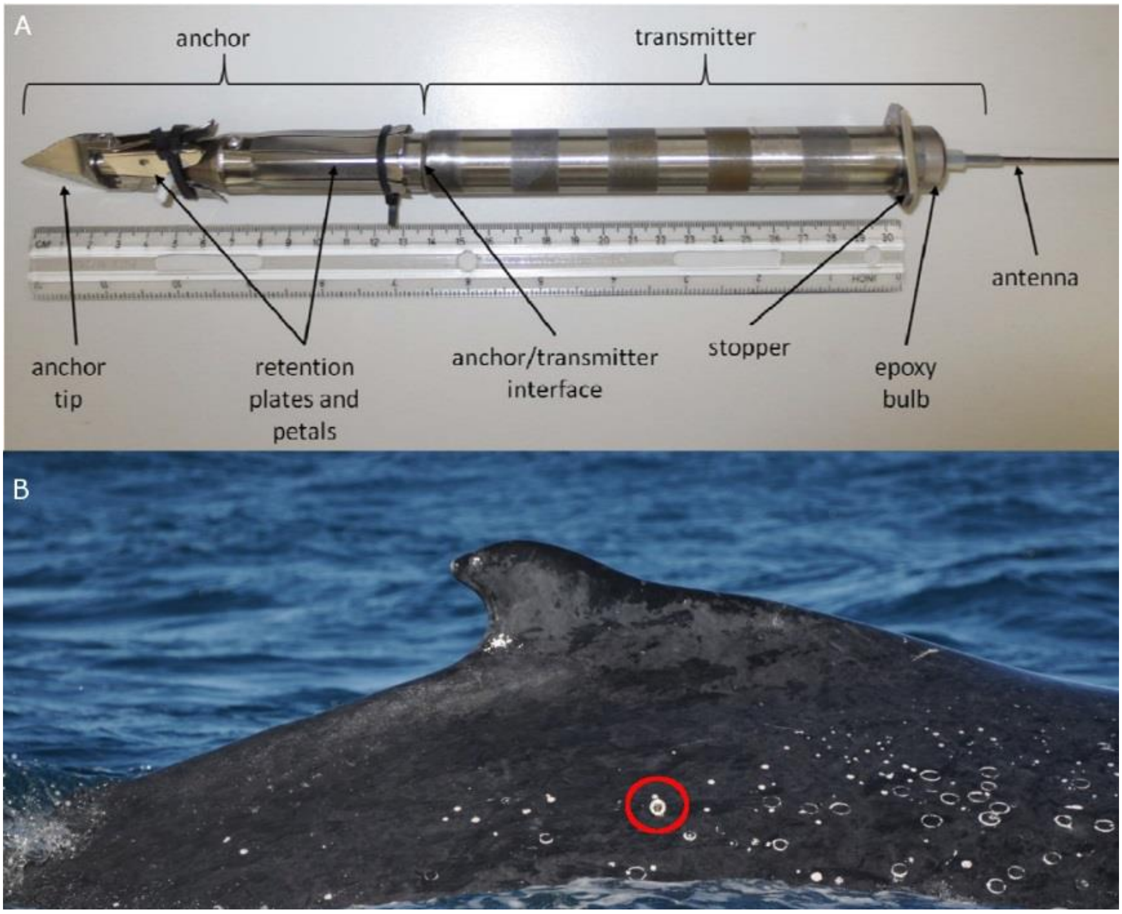

**Figure 2.4.** Exemple de balise Argos implantée chez différentes espèces de cétacés (d'après Robbins et al. 2013). (B) Baleine à bosse équipée par une balise Argos en 2014.

## C. METHODES DE POSE ET DEPLOIEMENT

### 1. IMPLANTATION

La capture d'une baleine est impossible ce qui nécessite d'employer des techniques de déploiement à distance. Les balises peuvent être déployées à l'aide d'une perche en fibre de verre de plusieurs mètres de long, d'une arbalète ou encore d'un fusil à air-comprimé (Heide-Jorgensen et al. 2001, Heide-Jørgensen et al. 2003, Zerbini, Ward, et al. 2006, Dalla Rosa et al. 2008, Gales et al. 2009). Pour ce dernier, la balise est insérée dans « un guide » (tube flottant) lui-même emboité dans le canon du fusil pour permettre une meilleure précision du tir. Le fusil à air-comprimé est plus facile à transporter (moyen de locomotion, passage des douanes) et plus maniable que l'arbalète et sa puissance de projection est réglable (Mate et al. 2007).

### 2. DEPLOIEMENT

La pose de balise nécessite de s'approcher des individus à une distance de 3 à 5 mètres afin de placer avec précision la balise. Pour la baleine à bosse, c'est une zone située sur le flanc gauche ou droite en dessous de la dorsale (**Figure 2.4**). Le comportement de l'individu ciblé est observé afin de préciser sa trajectoire. On utilise le plus souvent de bateaux motorisés de taille moyenne (5-7 m) et maniables tels que des zodiacs © afin de faciliter l'approche. Une plate-forme est généralement installée à l'avant du bateau sur laquelle le « tagueur » (personne chargée de déployer la balise) est positionnée. Placé ainsi en hauteur, ce dispositif compense l'inconvénient principal de ces embarcations basses sur l'eau. Il apporte également une meilleure visibilité au « tagueur » (i.e. visibilité de l'animal par transparence sous l'eau) et une approche moins difficile, en particulier pour les espèces sensibles à l'approche des bateaux (e.g. cachalots) (Mate et al. 2007). La luminosité et l'état de la mer sont aussi des éléments déterminants lors du déploiement de balises.

Un prélèvement génétique (biopsie) à l'aide d'une arbalète est généralement réalisé simultanément (ou lors d'une seconde approche) au déploiement de la balise par une seconde personne. Ceci permettra de déterminer le sexe de l'individu (Jayasankar et al. 2008). Equipée d'un système de prélèvement de tissu, l'utilisation de la perche permet une biopsie simultanée. Des photographies de la nageoire dorsale et caudale (quand c'est possible) sont également prises pour photo-identifier les individus équipés.

## D. LIMITE DE LA METHODE

La principale limite de l'utilisation de la méthode sur les cétacés et en particulier les grandes baleines réside dans la durée d'émission des balises. Celle-ci est très variable, allant de quelques heures à plusieurs mois (Mate et al. 2007). Chez les baleines à bosse, les durées d'émission sont souvent plus courtes que chez d'autres espèces de grandes baleines avec une moyenne d'émission de 20 jours. Néanmoins, dans certaines études, certains émetteurs ont transmis plusieurs mois (e.g. 156 jours, 205 jours) permettant notamment d'obtenir des trajets complets de migration (Zerbini et al. 2006, Gales et al. 2009). Des améliorations dans le développement des balises, l'évolution technique du système d'ancrage et les méthodes de déploiement ont permis d'augmenter la longévité des balises avec un meilleur maintien de la balise sur l'animal (Mate et al. 2007). Cependant, la transmission est souvent interrompue avant la fin de vie théorique des piles et l'animal est rarement revu durant la période d'émission. Par conséquent, en l'absence d'observation visuelle, la cause de l'arrêt du signal reste généralement inconnue. La raison peut être technique comme par exemple un disfonctionnement du matériel électronique ou une casse pendant/ou faisant suite au déploiement ou dû à certains comportements de la baleine (e.g. frottements). Cela peut-être également dû à un rejet naturel de la balise au bout de quelques semaines, considérée comme un corps étranger (Mate et al. 2011, Robbins et al. 2013). Une approche a été proposée pour quantifier ce phénomène de rejet et comprendre les facteurs responsables dans le but d'améliorer le système d'attache. Elle consiste à ajouter un capteur de lumière sur les balises pour estimer la vitesse de rejet et le moment où celle-ci se détache (Kennedy et al. 2013). Par ailleurs, les contraintes de forme et de taille ne permettent pas d'ajouter de capteurs sur les balises de type 1.

## E. IMPACT DE LA METHODE

Le déploiement de balises sur des animaux est une méthode invasive et il est donc nécessaire d'investiguer les impacts physiologiques et comportementaux que peuvent engendrer l'utilisation de cette méthode (Weller 2008, Walker et al. 2012, Moore et al. 2013). Chez les grandes baleines, peu d'études ont été conduites sur les effets de l'utilisation de cette méthode et la majorité sont basées sur des balises qui ne sont plus utilisées ou ont été largement modifiées (Kraus et al. 2000, Best & Mate 2007, Mate et al. 2007a, Weller 2008, ONR 2009, Mizroch et al. 2011, Baker et al. 2012, Walker et al. 2012). Ainsi, une étude de suivi a été réalisée sur des baleines à bosse dans le Golfe du Maine (population intensément étudiée) équipées de balises de Type 1. Cette étude indique que l'ensemble des baleines équipées en 2011 (19 individus) ont été revues l'année suivante (Robbins et al. 2013). Dans de nombreuses études, on a reporté que la durée et la nature des comportements post-déploiements étaient très variables d'un individu à un autre (Walker et al. 2012, Robbins et al. 2013, Kennedy et al. 2014). Cependant aucun trouble n'a été observé chez ces mêmes individus lors de leur observation les jours suivants. Des lésions et des gonflements au niveau de la zone d’implantation de la balise peuvent être observés durant une période relativement longue (pendant plus d’un an pour un individu (Robbins et al. 2013). Ces blessures pourraient être dues à la casse de la balise ou à une mauvaise implantation (i.e. balise mal implantée, zone d’implantation mal choisie). Le suivi des effets et des impacts de l’implantation de balises devrait contribuer à la fois à améliorer la forme des balises, leur temps de fixation et à minimiser l’impact sur les animaux. Bien que peu de données existent sur l’impact physiologique des balises implantées sur des baleines à bosse, les informations obtenues sur quelques individus indiquent que les réactions physiologiques sont variables selon les individus et qu’il ne semble pas y avoir d’effets à long terme sur le taux de reproduction des femelles équipées (Robbins et al. 2015). L’étude de ces impacts sur les animaux est essentielle pour la compréhension et la conservation de l’espèce mais permet également de faire avancer la technologie de cette méthode.

# CHAPITRE III – DISTRIBUTION SPATIO-TEMPORELLE DES BALEINES A BOSSE DANS LE CANAL DE SAINTE MARIE

*Aquarelle de Caroline Jacques*

# CHAPITRE III – DISTRIBUTION SPATIO-TEMPORELLE DES BALEINES A BOSSE DANS LE CANAL DE SAINTE MARIE

## RESUME

- Dans ce chapitre, l'objectif est d'étudier la fréquentation et la distribution spatio-temporelle des types de groupes sociaux des baleines à bosse au cours de la saison de reproduction dans une zone géographiquement restreinte mais pour laquelle on possède un suivi temporel (saisonnier et interannuel) conséquent. Notre étude est la première réalisée dans le canal de Sainte Marie, zone de forte fréquentation des baleines à bosse en période de reproduction et de mise bas. Le canal de Sainte Marie est large de 30 km en moyenne et est caractérisé par de faibles profondeurs (< 60km) et un rétrécissement de 7 km.
- Des données d'observations visuelles opportunistes (date, point GPS, type de groupes) ont été collectées lors de chaque saison de reproduction entre 2009 et 2013 (exploitation de la base de données de l'association Cétamada). Un total de 4680 observations ont été collectées durant 1254 sorties en mer entre juin et septembre avec un pic saisonnier en juillet et août.
- Nous montrons qu'il existe une ségrégation temporelle d'un mois entre la présence de groupes sans baleineaux dominant la première partie de saison et les groupes avec baleineaux domainant la seconde. Des différences interannuelles ont été observées entre les taux de rencontre pour l'ensemble des groupes et les groupes avec baleineau avec de plus fortes valeurs en 2009, 2011 et 2013 (2.1, 2.3, and 2.3 observation/heure). En revanche celui des groupes sans baleineaux reste relativement stable au cours des années. La bathymétrie influence la distribution des groupes avec une probabilité de trouver des couples mère-baleineau dans les eaux les moins prodondes (0-20m). Le nombre d'escortes accompagnant les couples mère-baleineau augmentent avec la distance à la côte. Notre étude s'étend sur une échelle spatiale restreinte et un environnement peu contrasté, néanmoins les facteurs environnmentaux influent sur la distribution des groupes sociaux en période de reproduction. Bien que la distribution spatiale des baleines à bosse dans le canal de Sainte Marie suive des schémas déjà observés dans d'autres zones de reproduction, la stucture particulière de la zone (canal avec une partie central

réduite) et ses faibles profondeurs expliquent propablement la forte concentration de baleines à bosse dans le canal de Sainte Marie.

# CHAPITRE III – DISTRIBUTION SPATIO-TEMPORELLE DES BALEINES A BOSSE DANS LE CANAL DE SAINTE MARIE

## Temporal and Spatial Patterns of Humpback Whales (*Megaptera novaeangliae*) in the Sainte Marie Channel, Madagascar, breeding ground

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# CHAPITRE III – DISTRIBUTION SPATIO-TEMPORELLE DES BALEINES A BOSSE DANS LE CANAL DE SAINTE MARIE

## I. ABSTRACT

The Sainte Marie Channel (eastern coast of Madagascar), an important breeding area where the first observation of humpback whale birth was documented, has never been investigated for the phenology and habitat use of humpback whales. The channel is an extensive shallow area less than 60 m deep and is characterized by a narrow coastal passageway (7 km). We used opportunistic sightings data collected from whale-watching boats to examine temporal and spatial patterns and the encounter rate of different social groups of humpback whales during the breeding season. A total of 4680 sightings were collected during 1254 whale-watching trips conducted between June and September from 2009 to 2013. The encounter rate peaked in July and August and most of animals had left the area by the end of September. During the study period, groups without calves dominated the first 30 days of the breeding season, followed by an increase in groups with calves. Inter-annual differences were observed in encounter rates with significantly higher global encounter rates in 2009, 2011 and 2013 (2.1, 2.3, and 2.3 sightings/hour respectively) and similarly for the mean encounter rates for groups with calves. In contrast, the encounter rate of groups without calves was similar over the study period. Water depth influenced the distribution of social groups with mother-calf pairs more frequently found in relatively shallow water (0-20 m). The number of escorts with mother-calf pairs increased with increasing distances to shore. Although our study area exhibits poorly contrasting physiographical features due to its restricted spatial scale, we observed an influence of environmental factors on the distribution of social groups in the Sainte Marie Channel.

# CHAPITRE III – DISTRIBUTION SPATIO-TEMPORELLE DES BALEINES A BOSSE DANS LE CANAL DE SAINTE MARIE

## II. INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a highly migratory baleen whale with a strong spatial and temporal separation of behaviors during the species annual cycle (Dawbin 1966). Humpback whales spend summers feeding in productive high-latitude waters and winters migrating to low latitudes to mate and give birth (Chittleborough 1965, Dawbin 1966, Clapham 1996). The purpose of this migration is still not clear, though previous studies have suggested that whales migrate to warm and coastal tropical waters in the winter for one or more reasons: ice cover in polar waters may restrict prey access; to avoid calf thermal stress and/or predators; to gain energetic advantages (by spending time in warm waters); and/or because migration is a vestigial behavior from the geologic past when breeding grounds were in close proximity to feeding grounds (Evans 1957, Corkeron & Connor 1999).

Whaling studies reported that migration of humpback whales to breeding grounds is characterized by successive departure of sexual and maturational classes. Lactating females accompanied with weaning yearlings have been shown to be the first to arrive at the breeding grounds; followed by immature individuals, mature males, and finally, late pregnant females (Chittleborough 1965, Dawbin 1966, Nishiwaki, 1966, Dawbin, 1997). Classes that are the first to arrive in the breeding grounds are also the first to return south (note that pregnant females become mothers with newborn). This temporal segregation of migration probably determine the changes in the social group composition (singletons, pairs, mother-calf pairs, mother-calf-escort, competitive groups) in the locales over the breeding season. In addition to whaling-derived information, changes in the proportion of social groups have been directly observed in several breeding localities (Garrigue et al. 2001, Martins et al. 2001, Morete et al. 2007, Franklin et al. 2011, Dulau-Drouot et al. 2012). However, few studies have yet assessed the inter-annual variability of the relative abundance of social groups at a given breeding site (Smultea 1994, Craig & Herman 2000).

At the basin scale, the distribution of humpback whale breeding grounds is thought to be determined by a preferential sea surface temperature (SST) range between 21.1 and 28°C (Rasmussen et al. 2007). However, the wintering distribution of humpback whale populations appears confined to smaller areas than those defined by the potential thermal preferences described by Rasmussen et al (2007) (Rasmussen et al. 2007). At a smaller scale, environmental parameters seem to interact with social organization and reproductive status that influence patterns in humpback whale distribution (Félix & Haase 1997, Martins et al. 2001, Ersts & Rosenbaum 2003, Sanders et al. 2005, Oviedo & Solís 2008, Betancourt et al. 2012). Breeding humpback whales are generally found in warm and relatively shallow waters of islands or reefs. More specifically, mother-calf pairs tend to be associated with very shallow waters (Félix & Haase 1997, Craig & Herman 2000, Félix & Botero-Acosta 2011) suggesting a preference for calm waters. However, the reasons for this are still being debated, and may also vary according to the breeding areas (Smultea, M.A. 1994, Craig & Herman 2000, Ersts & Rosenbaum 2003).

The population of humpback whales breeding in the southwest Indian Ocean is termed breeding stock C by the International Whaling Commission (IWC), with whale aggregations occurring in four main sub-regions (Best et al. 1998, IWC 1998a). These sub-regions encompass the coasts off southeast Africa, including Tanzania (the sub-region C1); (Findlay et al. 2011), the central Mozambique Channel islands (the sub-region C2); (Best et al. 1998, Kiszka et al. 2007, Hermans & Pistorius 2008) and Madagascar (the sub-region C3); (Angot 1951, Best et al. 1996, Rosenbaum et al. 1997). A fourth sub-region (C4), comprising of the Mascarenes Islands, has been recently proposed (IWC 2011a, Dulau-Drouot et al. 2012). Within the Madagascar sub-region C3 during winter, humpback whales have been observed off the east coast of Antongil Bay, Fort Dauphin and the western coast from Tulear to Nosy Be (Best et al. 1998, Cerchio et al. 2008, Best & Brandão 2009, Cerchio et al. 2009). To date, while sightings have been recorded in the different areas of Madagascar, there have been limited observation efforts and/or little published information. Consequently, the temporal and spatial patterns of humpback whales still remain unknown within these areas. Humpback whales frequently occur in the waters around Sainte Marie Island, a small island located on the northeast coast of Madagascar. The Sainte Marie Channel is a 30 km wide passageway with a shallow bathymetry (≤ 60 m), and is characterized by a distinctive funnel-shaped physiography. Compared with other regional breeding grounds, this locality was identified of significant importance in terms of the numbers of births, breeding-related activities and the annual high number of identified individuals. The photo-identification data set has shown that between 2012 and 2014 (292 sampling days), 1000 humpback whale individuals were photo-identified in the

Sainte Marie Channel (Reynes et al. unpublished data). In comparison, 572 individuals were identified during 2000-2006 (214 sampling days) in the East Africa breeding ground (Cerchio et al. 2008). The fluke catalogues of Antongil Bay and Réunion Island included 1021 individuals (2000-2006, 217 sampling days) and 320 individuals (2001-2010, 500 sampling days), respectively (Cerchio, S et al. 2009, Dulau-Drouot et al. 2011). The time interval between the first and second observation of an individual in the Sainte Marie Channel ranged between 1 and 33 days. Of the individuals photo-identified in the channel in winter, 4 females were accompanied by a calf, suggesting that individuals stayed within the area to give birth locally. In addition, whales (including mothers with calves) equipped with satellite tags in 2013 off Anakao (southeast of Madagascar) an in Réunion Island, were shown to visit the Sainte Marie Channel during the breeding season (Cerchio et al. in prep, Dulot-Drouot et al. in prep), suggesting that Sainte Marie is a preferred breeding ground for humpback whales around Madagascar. Sainte Marie is also the main whale-watching spot in Madagascar with more than 14 000 tourists participating in 2008 (O’ Connor S et al. 2009). However, while, the first observation of a humpback whale birth was recorded in its coastal waters (Faria et al. 2013) no study has yet reported on the occurrence patterns of humpback whales in Sainte Marie.

Here we analyzed a large, five-year data set of opportunistic encounter records, in order to provide the first information on the relative abundance, social composition and distribution of humpback whales in the Sainte Marie Channel during the breeding season over multiple years. Moreover, we investigated the main environmental features that likely influence the spatial distribution of breeding humpback whale social groups in the Sainte Marie Channel.

## III. MATERIALS AND METHODS

All collected sightings data reported in this manuscript were undertaken with approval from the Ministry of Fisheries and Halieutic Resources of Madagascar using permit 43/14-MRHP/SG/DGRHP.

The study area, approximately 4500 km² in size, is located in the northeast sector off Madagascar, and encompasses the Sainte Marie Channel, which lies between Sainte Marie Island

(16°50’S, 49°55’E) and the east coast of mainland Madagascar (**Figure 3.1**). The Sainte Marie Island is separated from Madagascar by a 60-km-long, 30-km-wide channel characterized by a narrow coastal passageway 7 km wide in the middle of the channel and by shallow waters (maximum depth of ~ 60 m). The Sainte Marie Island itself is 60 km long and 7 km wide, and is separated from the smaller ‘Ile aux Nattes’ Island (10 km², **Figure 3.1**). Both islands are surrounded by a barrier reef which encloses a narrow lagoon of shallow waters (≤ 10 m). In the Sainte Marie Channel (49°50’E - 50°10’E, 16°60’S -17°55’S), the surface temperature during the breeding season (June-October) ranged from 24.7 to 25.7°C between 2009 and 2013 and was calculated of data collection using the NASA AQUA MODIS satellite data (http://disc.sci.gsfc.nasa.gov/giovanni). The South Equatorial Current (SEC) flows westward between 6°S and 15°S in the Indian Ocean and splits up off the east coast of Madagascar into a northward branch and a southward branch termed the East Madagascar Current (EM). The EMC is particularly strong (i.e. ~ 0.5 m/s) and narrow along the east coast of Madagascar in comparison to the northward branch, while ocean currents in the Sainte Marie region are much slower (i.e. ~ 0.2 m/s) than along of the rest of the EMC. The study was conducted in southern part of the channel, outside of the lagoon, where most of the whale-watching activity takes place.

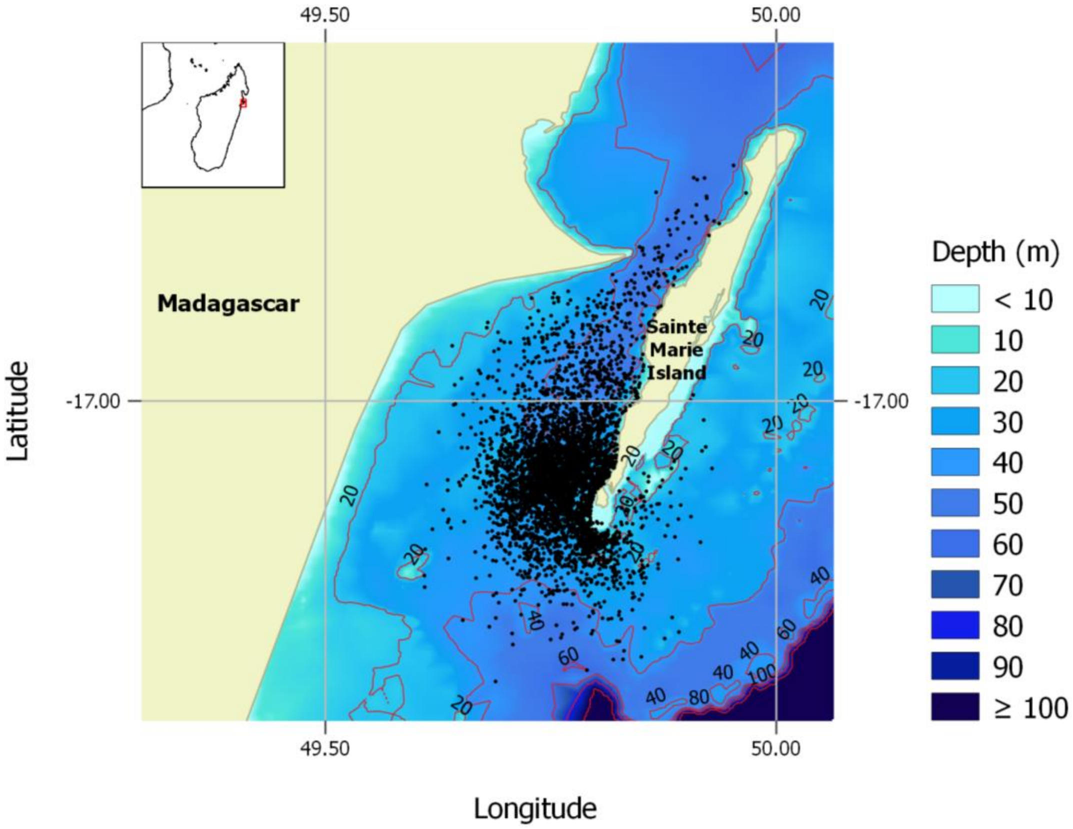


**Figure 3.1.** Distribution of humpback whales sightings in the Sainte Marie Channel (Madagascar), June to September, 2009 to 2013.

## A. DATA COLLECTION

Encounter data were collected opportunistically from whale-watching boats during the humpback whale breeding season (between June and September) over five years (2009-2013). The small motorized boats used for whale-watching measured between 6 and 10 m long with capacities ranging from 8 to 20 passengers. General weather conditions and tourist affluence constrained the daily number of whale-watching trips. Moreover, the boat route, direction and distance were not planned in advance but were chosen according to the daily weather conditions, whale occurrence, distribution of other whale-watching trips, and continuously updated information on the presence of whales. The boats spent three to four hours at sea per trip, with two trips a day during the peak of the whale-watching season (July and August).

As members of the Non-Governmental Organization (NGO) Cetamada, the whale-watching operators provided space aboard the whale-watching boats for a trained volunteer to collect the data. Volunteers spent a minimum of three weeks in the field, and were trained during a 10-day period to learn the protocol for collecting and storing the data. The persons searching for whales included the volunteer of the NGO, the pilot of the boat, as well as assistance from the majority of tourists. The data were collected and stored in the Cetamada humpback whale database (http://www.cetanet.org/), and they included the trip schedule (departure and return, date and time), weather conditions, whale encounter location, group composition, and the individual or group behavior. The procedure for whale approaches followed the whale-watching guidelines edited by Cetamada (e.g. closing distance, encounter duration, boat position in relation to the orientation of the whale), while whale-watching guidelines were written based on Malagasy ministerial decree (see http://cetamada.com/ecotourism/code-de-bonne-conduite). All groups were approached, observed and recorded as an encounter. The duplications of encounters (when several boats were watching the same group of whales at the same time) were deleted from the database so that only a single record was retained in the dataset. The social groups were classified as singleton (S), pair (P), mother-calf pair (MC), mother-calf-escort (MCE), mother-calf and more than one escort (MCES) and, competitive group (CG) (for definitions see **Table 3.1**).

**Table 3.1.** Definition of different social groups of humpback whales observed in breeding grounds.

| **Group** | **Definition** |
|---|---|
| Singleton | Lone individual of unknown sex and age class (Clapham et al. 1992). |
| Pair | Association of two individuals of unknown sex and age class. It can be two males, two females, one female and one male or an adult with a subadult (Clapham et al. 1992). |
| Mother-calf pair | A female with a calf. |
| Mother-calf-escort | A female with a calf accompanied of one escort. Escort is assumed to be a male awaiting the opportunity to mate with the lactating female when she comes into post-partum oestrus (Tyack & Whitehead 1983, Clapham et al. 1992). |
| Mother-calf and more than one escort | Competitive group involving a mother-calf pair (Tyack & Whitehead 1983, Clapham et al. 1992). |
| Competitive group | Group without calf and often with clear structure. It consists of a mature female "nuclear animal" that appeared to be passive and males which are usually involved in aggressive behaviors for access to the female. Principal escort maintains position next to nuclear animal and a variable number of challengers compete for his position (Tyack & Whitehead 1982, Baker & Herman 1984, Clapham et al. 1992). |

## B. DATA ANALYSIS

The encounter rate (ER) was calculated for each whale-watching trip by dividing the number of whale groups encountered by the searching effort (defined as the time spent transiting between observations, excluding the time spent observing whales). The mean encounter rate during the breeding season was calculated on a fortnightly, monthly, and annual basis, and was considered as a proxy of relative abundance (Martins et al. 2001, Rasmussen et al. 2011, Dulau-Drouot et al. 2012). Regular boat GPS positions were not available for the present study, meaning that the study lacked spatial coverage of each boat.

However, based on the time and position of sightings, we computed the sum of time spent within a range of distance to shore classes (defined below), and considered it as a proxy of the spatial coverage of boats at sea.

A polygon enclosing the total area of whale encounters was used to give an approximation of the study area and compare the depth distributions of whale encounters with the bathymetry of the total study area. We used the kernel method provided by the R package "adehabitat" (Calenge 2011) to plot the monthly density distributions of whale encounters (June-September). The bathymetric data was based on the SHOM (Service Hydrologique et Océanographique de la Marine, France) map of the Sainte Marie Channel (map number 6313, edition 1980, scale 1/49900). This map was used to build a grid of 200 x 200 m cells by a krigging neighborhood method using Quantum GIS (version 2.0.1), and the bathymetric depth was extracted for each encounter location. In addition, the distance to the nearest coastal feature was calculated for each encounter position using ArcGIS. To analyze the distribution of whale groups in relation to bathymetry we defined six bathymetry depth classes: ≤10 m, 11-20 m, 21-30 m, 31-40 m, 41-50 m, and > 50 m. The same method was applied to the distribution of whale groups in relation to their distance from shore with the following distance classes: 5 km, 6-10 km, 11-15 km, 16-20 km, and > 20 km.

### C. STATISTICAL ANALYSIS

All statistical analyses were conducted using the R software (R, version 3.1.2). Significant differences between the searching efforts were estimate by the Chi square test ($p < 0.05$), while significant differences between the mean sightings rates were analyzed by the Kruskal-Wallis test ($p < 0.05$). A generalized linear model (GLM) was fitted to examine the relationship between our binary response variable ("absence" vs "presence" of calf) and the explanatory variables including environmental variables (bathymetry, distance from shore) and temporal variables (year and month). Missing and outlier values were removed from the dataset prior to analyses. Non-collinearity was verified between continuous variables using Pearson correlation (coef <= 0.5) and the variance inflection factor (VIF) (Zuur et al. 2010). All explanatory variables were standardized (centered and scaled) to facilitate model convergence and enable comparison of their respective contribution (using their corresponding slope coefficients). Model selection was performed using likelihood ratio tests starting from a full model with terms retained only if they improved the fit ($p < 0.05$, Zuur et al. 2010). The results were then evaluated such that the most parsimonious model was also the model with the lowest Akaike’s Information Criteria (AIC). Finally, the GLM was validated by examining the residuals distribution (i.e. normal distribution) and checking for any potential trend between residuals and each explanatory variable (i.e. verification of homogeneity) (Zuur et al. 2009, Herve 2014). One-way ANOVAs ($p < 0.05$) were used to investigate the effect of bathymetry and distance to shore on social groups (S, P, MC, MCE, MCES, and CG). Least square means (LSMeans, $p < 0.05$) were used to compare differences of bathymetry and distance to shore between social groups. Correlational analysis was conducted using Spearman rank correlation ($p < 0.05$).

# IV. RESULTS

## A. DATA COLLECTION AND SEARCHING EFFORT

A total of 4680 humpback whale encounters were recorded by 24 different whale-watching boats in the Sainte Marie Channel during 2433 hours of navigation (**Table 3.2**). The searching effort of all boats varied significantly between years (Chi square test, $p <0.001$) ranging from 354 hours on-effort in 2009 to 619 hours in 2013. There were no significant differences in searching effort between 2010 and 2012 and between 2011 and 2013. The number of trips, the searching effort and encounter rate peaked in July and August for all years included in the study. The mean ER varied significantly between years (Kruskal-Wallis test, $p <0.001$) with a minimum of 1.64 sighting $hr^{-1}$ in 2012 and a maximum of 2.3 in 2011 and 2013, with most encounters occurring between July and August (**Table 3.2**). Sighting conditions were considered good if wind speed did not exceed Beaufort sea-state of 3 or less, and was observed for 4 247 of sightings included in the study (91%). Encounters were concentrated off the southwest coast of Sainte Marie Island in a polygon covering approximately 1700 $km^2$ (**Figure 3.1**). The whales moved progressively towards the south of

Saint Marie Channel as the breeding season advanced, an area characterized by a wider continental shelf and extensive shallow waters (**Figure 3.2**).

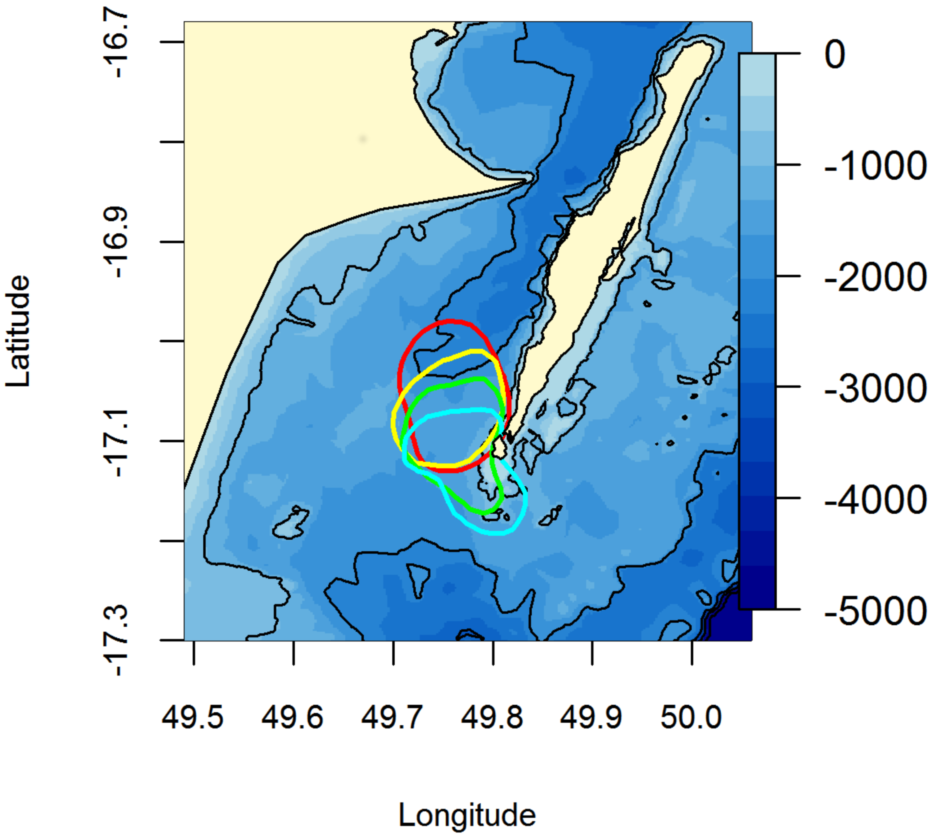


**Figure 3.2.** Contours showing the kernel home range (90%) for humpback whale encounters in June (red), July (yellow), August (green) and September (blue) for all years (2009 – 2013).

**Table 3.2.** Searching effort and number of encounters from whale-watching boats during the 2009-2013 breeding seasons, in the Sainte Marie Channel, Madagascar. Annual total searching efforts and encounter rates not showing the same superscript were significantly different (p-value < 0.05).

| Year | Months | Mean searching effort by boat (hours) | Searching effort (hours) | Number of sightings by month | Mean encounter rate (sightings/hour) |
|---|---|---|---|---|---|
| **2009** | June | - | - | - | - |
| | July | 28 (SE=11) | 83.0 | 182 | 2.46 (SE=0.2) |
| | August | 26 (SE=12) | 159.0 | 360 | 2.27 (SE=0.1) |
| | September | 37 (SE=16) | 112.0 | 172 | 1.62 (SE=0.1) |
| | **Total** | **-** | **354** | **714** | **2.1 (SE=0.1)$^{a}$** |
| **2010** | June | 8 (SE=3) | 16.0 | 13 | 1.24 (SE=0.4) |
| | July | 16 (SE=6) | 179.0 | 374 | 2.27 (SE=0.2) |
| | August | 19 (SE=7) | 173.0 | 284 | 1.8 (SE=0.2) |
| | September | 16 (SE=8) | 63.0 | 70 | 1.19 (SE=0.1) |
| | **Total** | **0** | **431$^{a}$** | **741** | **1.9 (SE=0.1)$^{b}$** |
| **2011** | June | 9 (SE=4) | 18.0 | 18 | 1.29 (SE=0.4) |
| | July | 22 (SE=5) | 218.0 | 446 | 2.22 (SE=0.1) |
| | August | 28 (SE=7) | 255.0 | 588 | 2.6 (SE=0.2) |
| | September | 39 (SE=3) | 79.0 | 126 | 1.72 (SE=0.2) |
| | **Total** | **-** | **570$^{b}$** | **1178** | **2.3 (SE=0.1)$^{a}$** |
| | June | 7(SE=2) | 21.0 | 28 | 1.29 (SE=0.2) |

| | | | | | |
|---|---|---|---|---|---|
| **2012** | July | 31 (SE=10) | 184.0 | 319 | 1.89 (SE=0.2) |
| | August | 31 (SE=9) | 186.0 | 319 | 1.66 (SE=0.1) |
| | September | 23 (SE=10) | 68.0 | 67 | 1.03 (SE=0.1) |
| | **Total** | **-** | **459$_{a}$** | **733** | **1.6 (SE=0.09)$^{b}$** |
| **2013** | June | 5 (SE=2) | 20.0 | 28 | 1.78 (SE=0.4) |
| | July | 22 (SE=6) | 174.0 | 459 | 2.74 (SE=0.1) |
| | August | 33 (SE=8) | 261.0 | 561 | 2.25 (SE=0.1) |
| | September | 27 (SE=8) | 164.0 | 266 | 1.8 (SE=0.1) |
| | **Total** | **-** | **619$^{b}$** | **1314** | **2.3 (SE=0.08)$^{a}$** |
| **TOTAL** | | | **2433** | **4680** | |

The index of spatial coverage of boat trips (% of time spent by class of distance from shore) was concentrated within 10 km of the shore for all years and over the breeding season (**Figures S3.1 and S3.2**). The spatial coverage of boat trips during the breeding season remained fairly constant for each distance class, though for the ≤ 5 km, and 6-10 km classes were higher (25-30%) than the more distant classes (0-15%) (**Figure S3.1**). In 2012, the time spent within 5 km of shore was lowest (27%), and highest between 11 and 15 km (24%) (**Figure S3.2**). The time spent in less than 11km (adding the ≤ 5 km and 6-10 km classes) of shore was not significantly different between years (Chi square test, P=0.7).

## B. GROUP COMPOSITION

The group size was recorded for 4587 of the 4680 groups, with a mean value of 2.53 ± 1.4 (range = 1-19 individuals). Pairs made up the bulk of encounters (42%) while more than 80% of groups contained three or fewer individuals. Among the 4680 encounters, we found 1 121 competitive groups (24%), 1 074 pair groups (23%), 868 mother-calf pairs (18%), 834 of singletons (18%), 660 mother-calf-escort groups (14%) and, 123 were mother with calf associated with two escorts or more (3%).

## C. TEMPORAL DISTRIBUTION OF GROUP OCCURRENCE

The temporal encounter distribution of groups with calves and groups without calves across the season is shown in **Figure 3.3**. The mean ER of groups without calves peaked in early July (2.48 ± 0.13), and then decreased steadily throughout the season. By contrast, the mean ER of groups containing calves increased sharply from mid-July and peaked in early September (1.21 ± 0.08).

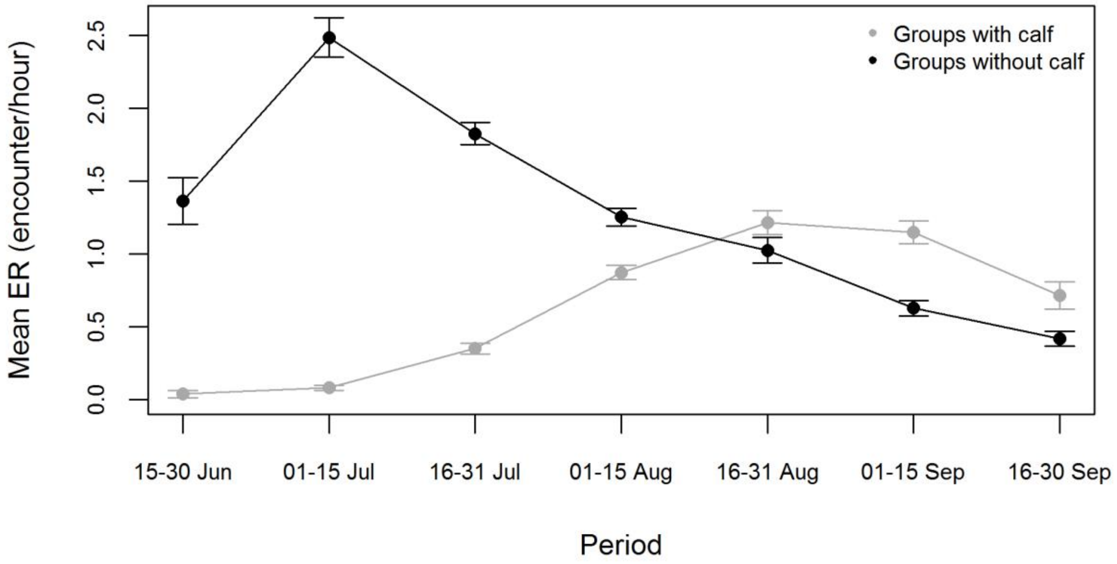


**Figure 3.3.** Mean encounter rate (ER) for all groups, groups without calves, and groups with calves by fortnight period from 15 June to 15 October (2009-2013).

For all years, the mean ER of groups without calves was consistently higher than for groups with calf. However, the mean ER of groups with calves and groups without calves varied significantly among years (Kruskal-Wallis test $p < 0.001$ and $p < 0.001$, respectively, **Tables S3.3 and S3.4, Figure 3.4**). There were no significant differences in ER between 2009, 2011 and 2013 and between 2010 and 2012. In contrast groups without only calves varied significantly between 2011 and 2012 (**Tables S3.3 and S3.4, Figure 3.4**).

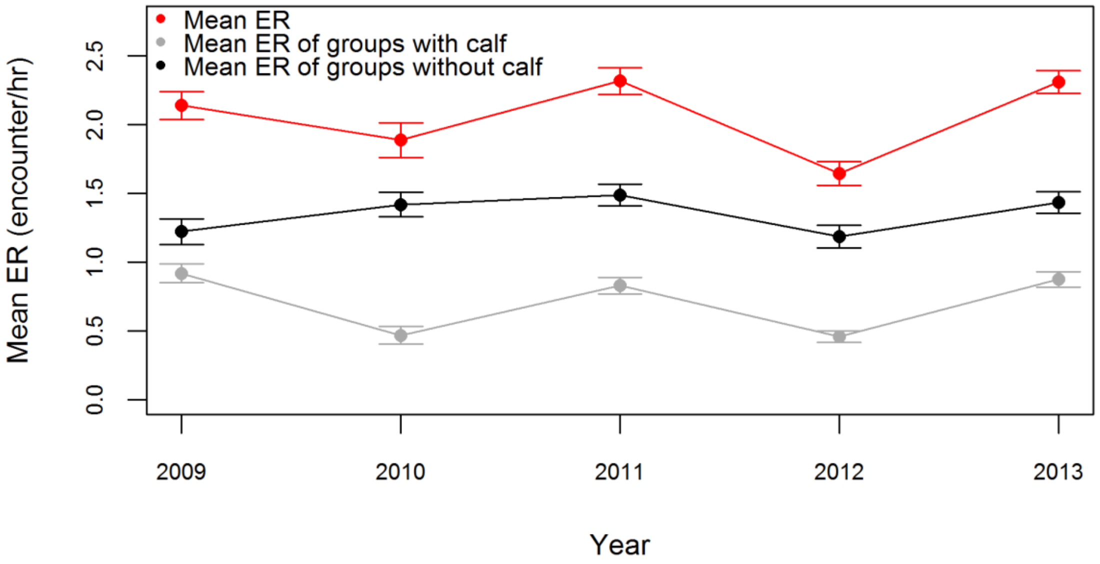


**Figure 3.4.** Mean encounter rate (ER) for all groups, groups without calves, and groups with calves by year.

## D. SPATIAL DISTRIBUTION OF GROUP OCCURRENCE

The mean water depth of the whale encounter area was 30 m ± 0.11 (with a maximum of 55 m), while 38 % of the whale encounter area lied in waters 21-30 m deep (**Figures 3.1 and 3.5**). No collinearity was found between environnemental parameters included in the model. The most parsimonious model describing the probability of observing a group with a calf included physical (sea floor depth, distance from shore) and temporal (year and month) variables (**Table 3.3**). Specifically, the probability of observing groups with calves increased significantly with decreasing sea floor depth. In 2011, 2012 and 2013, the probability of observing groups with calves were not significantly different to 2009, while in 2010 a significantly lower number of groups with calves were observed. There was a significantly higher probability of observing a group with a calf in August and September than in June and July. However, distance from shore had no significant effect on the occurrence of groups with calves. Groups with calves were found in higher proportion (39%) in the 20-30 m depth range, whereas groups without calves were more often associated with sea-bottom depths between 31 and 40 m (44%). Groups with calves were also found in higher proportions (27%) within shallow waters (0-20m) than groups without caves (6%), while these bathymetric depths only occupy 12% of the whale encounter area (Fig 3.5). In contrast, groups without calves were more frequent (57%) than those with calves (34%) over deeper bottom depths (> 30 m).

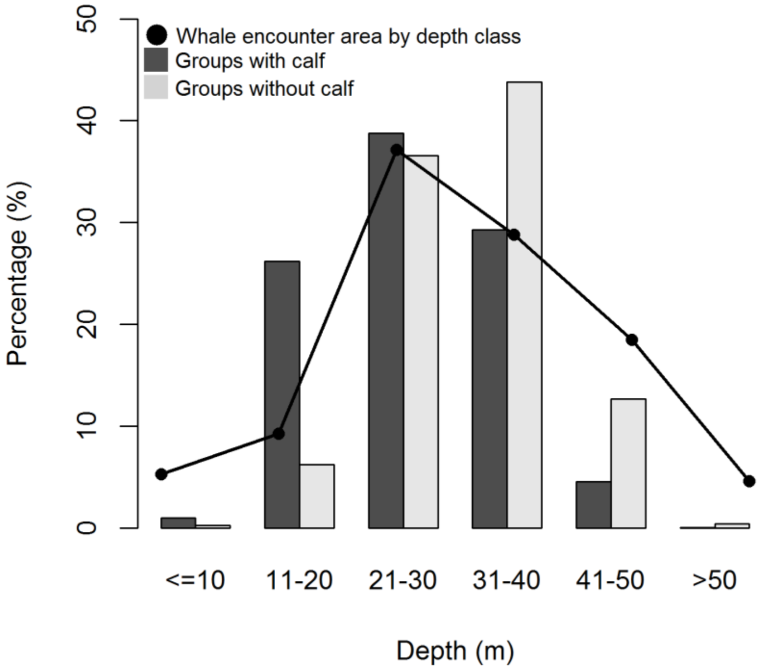


**Figure 3.5**. Proportion (%) of groups with calves and groups without calves according to sea-bottom depth intervals (m), and proportion (%) of the whale sighting area according to sea-bottom depth intervals (m).

**Table 3.3.** Results for the most parsimonious model relating presence of a calf in a group to its environment. Term coefficients, SE and p-values are presented. Significant terms ($p < 0.05$) are denoted by bold characters.

| **Distribution binomial** | **Occurrence of group with calf** | | |
|---|---|---|---|
| n observations: 4678 | | | |
| Explanatory variables | Coefficient | Std. Error | p-value |
| Intercept | 3.17 | 0.60 | <0.001 |
| **Sea floor depth** | **-0.53** | **0.04** | **<0.001** |
| Distance from shore | 0.28 | 0.51 | 0.58745 |
| **as factor (year) 2010** | **-0.36** | **0.13** | **0.00578** |
| as.factor (year) 2011 | 0.01 | 0.11 | 0.91851 |
| as.factor (year) 2012 | -0.21 | 0.13 | 0.09868 |
| as.factor (year) 2013 | 0.10 | 0.11 | 0.34547 |
| as.factor (month) 7 | 1.15 | 0.60 | 0.05372 |
| **as.factor (month) 8** | **3.05** | **0.59** | **<0.001** |
| **as.factor (month) 9** | **3.63** | **0.60** | **<0.001** |
| Distance from shore: as.factor (month) 7 | -0.62 | 0.52 | 0.23252 |
| Distance from shore: as.factor (month) 8 | -0.43 | 0.51 | 0.23252 |
| Distance from shore: as.factor (month) 9 | -0.34 | 0.52 | 0.50881 |

While the probability of observing groups with calves were not significantly influenced by distance from shore in our model, the mean distances to shore of the social group types were significantly different ($F_{5,4674} = 40.876$; $p < 0.001$). LSMEANs test (**Table S3.4**) indicated significant differences in distances to shore between mother-calf pairs with all others groups except mother-calf-escort groups. Mother-calf-escort groups also differed significantly with groups without calves with respect to distance to shore. However, distances to shore of mother-calf with more than one escort were similar to those of other groups (singles, pairs, and, mother-calf-escort groups) except competitive groups and mother-calf pairs. The relationship between distance from shore and the number of escorts in a group (0, 2, 3, > 3) was positively significant (Spearman ran rank correlation, Rs = 0.1, N=1651, p < 0.001).

# V. DISCUSSION

This is the first study on humpback whales in the Sainte Marie Channel off Madagascar, an area characterized by a distinctive funnel-shaped physiography, where a high number of humpback whales occur during the breeding season. Our data highlighted clear and consistent differences in relative abundance (inferred by encounter rates), and structure of groups across the seasons. The first phase of the breeding season was dominated by groups without calves followed 30 days later by a period when groups with calves were mostly observed. Moreover, we observed clear inter-annual variability in the proportion of whales with calves. At fine spatial scale, the distribution pattern of social groups was influenced by sea floor depth with mother-calf pair groups clearly showing a preference for shallow waters, and mother-calf pairs was found significantly closer to the coast than other groups.

## A. USING WHALE-WATCHING DATA TO ASSESS PATTERNS OF WHALE OCCURRENCE

Using whale-watching boats as opportunistic platforms for the collection of encounters implies several potential sources of bias (Oviedo & Solís 2008, Félix & Botero-Acosta 2011). Whale-watching boats tend to select the closest whale concentrations, meaning that encounters were collected primarily near the coast, which potentially constituted the main confounding factor. In addition, even though most duplicates were removed from the database, the same individual could be sighted several times on the same day or over subsequent days. However, given that the strategy of whale-watching boats was always to find the closest groups of whale, and that the same protocol of data collection was consistently applied during the study, it is most likely that these biases were systematic and similar over years. The large number of encounters made every year also probably provides our dataset with sufficient statistical power to reliably capture spatio-temporal trends in spite of the aforementioned potential confounders.

We expect the distribution of boat observations do not give bias to whale sighting distribution because whale-watching boats are instead expected to be influenced by whale distributions. The time spent at different distances from shore was not uniformly distributed within the study area, but the distribution pattern of boat observations was similar across seasons. Furthermore, the time spent at different distances from shore was broadly similar from year to year, except for 2012 when the boats tended to be located further offshore than the previous years, which was presumably the whale-watching boats' response to the lower encounter rate observed that year. These results suggest that observed changes in encounter rates and the temporal succession of groups (according to boat observations) were reflecting a biological signal and were not a sampling artefact. It is therefore likely that our dataset could be used to detect temporal and spatial trends in areas surveyed by commercial whale-watching boats. Finally, as the season progressed we showed a general southward displacement of sightings, which reinforces our assumption that the boats accurately reflect true whale distribution patterns, including specific social group distributions in the Sainte Marie Channel.

### B. TEMPORAL PATTERNS OF BREEDING HUMPBACK WHALE SOCIAL GROUPS

We showed that the annual peak of encounters in Sainte Marie was between July and August; a period similar to that observed in most Southern hemisphere breeding grounds (Garrigue et al. 2001, Zerbini et al. 2004, Weir 2007). For example, whale numbers off Réunion Island (also located in the southern Indian Ocean) peak between July and September (Dulau-Drouot et al. 2012). However, Findlay (2009) reported that in Southern Madagascar, peak whale encounters occur between August and September. In Antongil Bay located 150 km North of Sainte Marie Island – the highest whale concentrations are observed between July and early September (Cerchio et al. 2008).

Our whale sighting data also showed that the frequency in the group composition changed over the breeding season. Such consistent patterns therefore suggest that Sainte Marie Island is a suitable area for important life-history traits such as mating, calving, and nursing for humpback whales. We show a clear seasonal pattern in the proportion and structure of groups which probably corresponds to  the temporal segregation of different sex and maturational classes observed during migration in whaling catch data (Chittleborough 1965, Nishiwaki. 1966, Dawbin 1997). For instance, our observations revealed that the first part of the breeding season was characterized by a high proportion of whales without calves (i.e., singletons, pairs, competitive groups), followed by a second period dominated by groups with calves including newborn calves. We should consider that pregnant females arriving in the first period of the season could have been classified in group without calf, then in group with calf after having given birth suggesting a potential bias in the temporal segregation pattern. However, pregnant females are known to prolong their stay in Antarctic waters and to be the last class to migrate towards breeding grounds (Craig et al. 2003). Based on whaling data for Madagascar, Dawbin (1966) (Dawbin 1997) noted that there was a 16-day lag in arrival time of pregnant females compared with the groups of mixed females (unspecified late-lactating females and resting females). In Hawaii a long time-series of photo-identification data indicate that the first identification of females with calves was on average 24.5 ± 20.3 (n=40) days later than in years when the same individuals were without calves (Craig et al. 2003). An early departure from the breeding ground of newly pregnant females such as described by Dawbin (1966) may have also contributed to the observed decrease in the relative abundance of groups without calves in the second period of the season. Overall, our results are consistent with the temporal segregation of breeding females migrating to and from breeding grounds described in the whaling-based and photo-ID-based studies. Based on our whale-watching data, recorded at a small spatial scale, we showed a clear bimodal seasonal pattern in group structure in the Sainte Marie Channel over multiple years.

## C. INTER-ANNUAL CHANGES IN RELATIVE ABUNDANCE OF BREEDING HUMPBACK WHALE SOCIAL GROUPS

We found that the encounter rates of groups with calves varied significantly from year to year while the encounter rates of groups without calves remained fairly constant. High encounter rates of groups with calves coincided with high global encounter rates in 2011 and 2013. The lowest global encounter rates were found in 2010 and 2012 as well as the lowest encounter rates of groups with calves. Studies in Hawaii have also shown significant inter-annual variations in the number of whales with calves (Mobley et al. 1999, Craig & Herman 2000). In the context of increasing humpback whale populations in the southwest Indian Ocean (International Whaling Commission. 2011a, Kiszka et al. 2007, Dulau-Drouot et al. 2012), our results showed inter-annual changes in relative abundance at the local scale (as given by encounter rates), which could be partly driven by the observed variability of mothers with calves occurrence. Factors explaining such variability could include individual changes of breeding areas between seasons. These inter-annual variations could also be due to broader scale changes in prey distribution and availability which could in turn influence the timing and range of humpback whale migration, breeding timing, and reproductive success (Fiedler 2002, Nicol 2006, Moore 2014, Braithwaite et al. 2015). To date, our time series is still too short for examining how varying physical and biological conditions may influence the relative abundance of humpback whales in breeding grounds of Madagascar. However, we expect that an additional years of whale-sighting records in this region will provide sufficient data for envisaging these types of analyses.

## D. SPATIAL PATTERNS OF HUMPBACK WHALE BREEDING GROUPS IN THE SAINTE MARIE CHANNEL

The extensive continental shelf and shallow coastal waters of the Sainte Marie Channel are consistent with environmental features of preferred breeding and calving areas of humpback whales at local scale (Whitehead & Moore 1982, Ersts & Rosenbaum 2003, Felix & Haase 2005). Although the Sainte Marie Channel is characterized by shallow waters with a weak bathymetric gradient, water depth significantly influenced the distribution of the humpback whale social groups migrating to the area during the breeding season. We showed that whales were more likely to be located closer to shore and further south towards the shallow waters of the south-western end of Saint Marie Island as the season progressed. The proportion of observed groups with calves (mainly mother-calf pairs) also increased at the same time, and the mother-calf pairs were found to be the group closest to shore. Interestingly, escorted-maternal female groups were found at mid-distance from shore, and groups without calves were observed further offshore in deeper waters. First, mothers can take advantage of the Sainte Marie Island coast as a physical barrier to prevent interactions with unwanted males. We show that the distance from shore of group with calves is positively influenced by the number of escorts in the groups with calves in line with the idea that the spatial distribution of maternal females is in part driven by males avoidance (Craig et al. 2014). Spatial segregation is known to be a male avoidance strategy used by female with a calf in several large whale species, including southern right whales (Félix & Botero-Acosta 2011, Craig et al. 2014). Second, it should be noted that ocean currents are much slower in the Sainte Marie region than further offshore, and this could offer to mothers and calves an area to shelter from strong currents. As suggested for other regions, females with calves in Sainte Marie Channel may favor shallow waters and short distances from shore to avoid male harassment, to protect young calves from accidental injury, and to provide offspring with calm sea conditions (Mattila et al. 1989, Ersts & Rosenbaum 2003, Craig et al. 2014). Third, other groups without calves are likely found further offshore because water depth is an ecological constraint for the 3D movements of males which display competitive and attractive behaviors in the water column (Smultea, 1994, Clapham 1996). Competitive groups are made up of two or more males (the maximum group size was 19 in Sainte Marie Channel), which could explain why larger groups were found farther offshore than smaller groups (Smultea 1994, Ersts & Rosenbaum 2003). The Sainte Marie Channel’s particular physiography, including the narrowness and the shallow waters of the corridor, probably explain the relatively high density of humpback whales occurring there during the breeding season.

## VI. CONCLUSIONS

In conclusion, we have used a unique, five-year long time series of whale-watching data to provide the first evidence of spatial and temporal patterns of humpback whales in the Sainte Marie Channel breeding ground. We showed that the Saint Marie Channel hosts competitive groups and groups with new born calves during winter with a seasonal peak between July and August. Our five-year time series demonstrates the clear temporal patterns of the different social groups; specifically, groups without calves consistently preceding groups with calves by 30 days upon arrival at the breeding grounds each year of our study. This pattern is consistent with the temporal segregation according to age, sex and breeding status during the migration previously found in whaling data. Moreover, despite increasing global population trends we revealed inter-annual variability in the relative abundance of mothers with calves. Finally, while Sainte Marie Channel is characterized by a restricted depth range, we confirm that interaction between social condition and habitat use influences humpback whale distribution, with groups with calves most frequently found in shallow waters. Future studies combining our on-going time series of sightings with photo-ID data will provide more information on the spatial and temporal patterns in Madagascar humpback whales.

## VII. ACKNOWLEDGMENTS

We wish to thank NGO Cetamada for sharing its data set and its logistical support in the field. Most of the field work was conducted with help of many Cetamada volunteers aboard whale-watching boats and the whale-watching operators. We are grateful to Jean-Baptiste Laurent and Mickaël Mézino for ArcGis ouput data and Maxime Hervé for his statistical advice. Claire Garrigue and Phil Clapham provided insightful comments on an earlier draft of the manuscript. We also thank Caroline von Stein and Malcom O'Toole for editorial help.

# VIII. APPENDIX

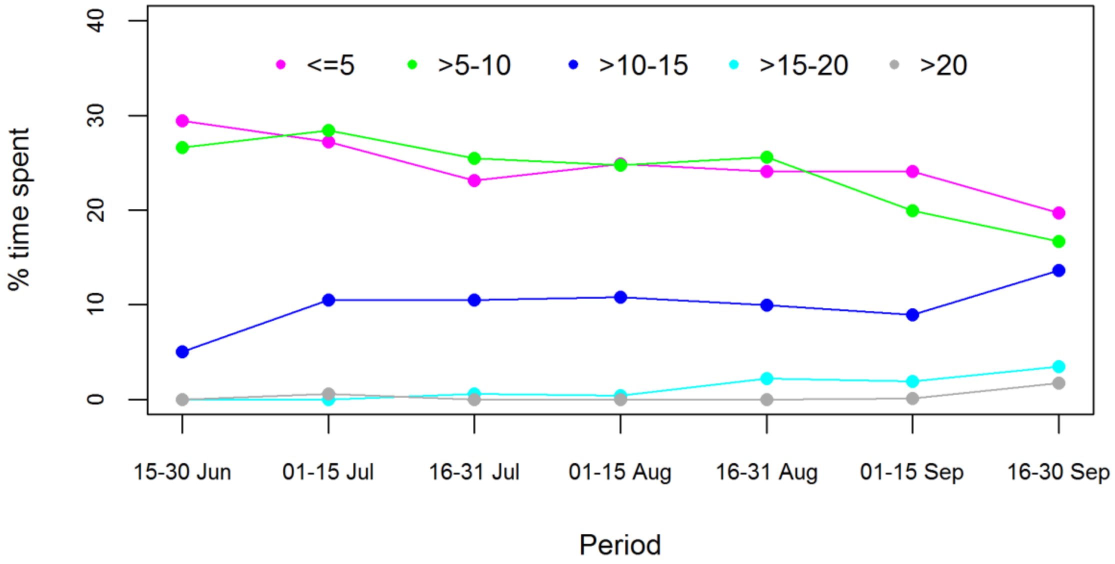


**Figure S3.1.** The spatial coverage of boat trip (% of time spent by class of distance from shore) by fortnight period from 15 June to 15 October (2009-2013).

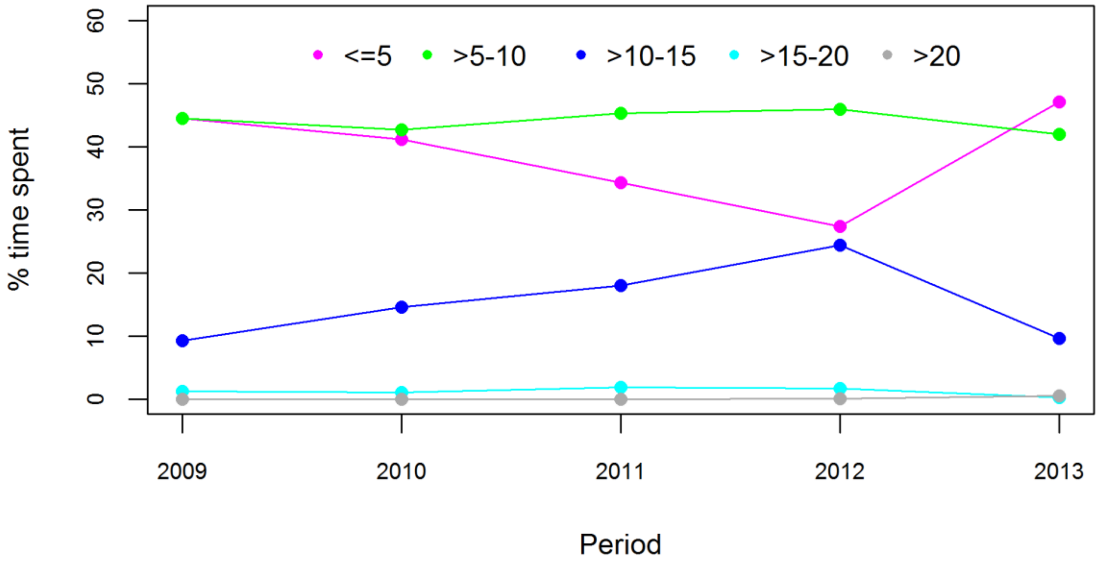


**Figure S3.2.** The spatial coverage of boat trip (% of time spent by class of distance from shore) by years.

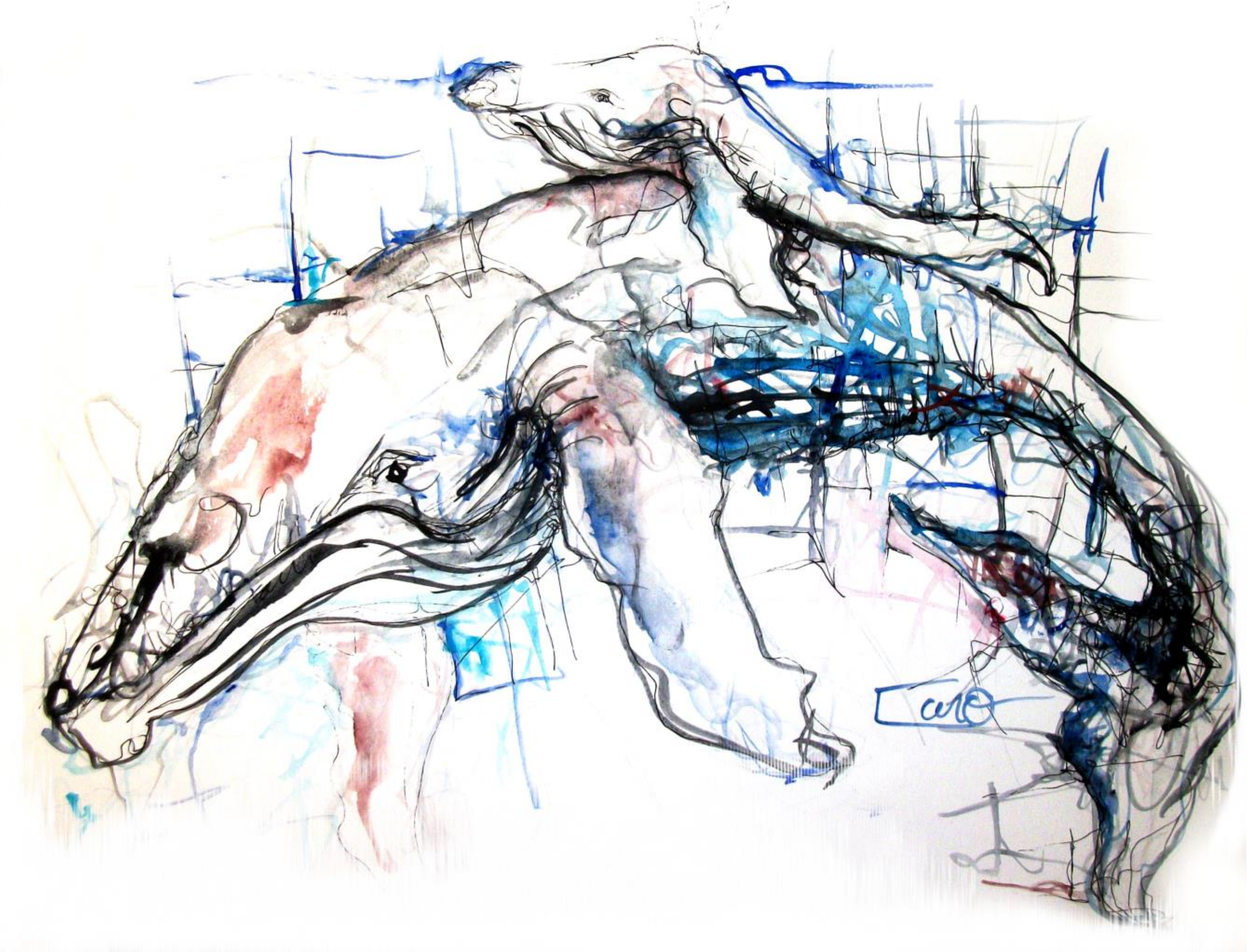
**Table S3.3.** LSMEANs test for the sea-bottom depth according to social group types (Singleton, Pair, Competitive Group, Mother-Calf pair, Mother-Calf-Escort, Mother-Calf with more than one escort). Depth (m) of humpback whale group categories, SE: Standard Error, * significant difference (p < 0.05) between social group categories.

| **Social Groups** | **Singleton** | **Pair** | **CG** | **MC** | **MCE** | **MCES** |
|---|---|---|---|---|---|---|
| **Depth (m)** | 31.9 ± 0.2 | 32.1 ± 0.2 | 32.1 ± 0.2 | 26.4 ± 0.2 | 27.1 ± 0.3 | 27.7 ± 0.6 |
| Singleton | | 0.99 | 0.98 | 0.00* | 0.00 * | 0.00* |
| Pair | | | 1.0000 | 0.00 * | 0.00* | 0.00* |
| AG | | | | 0.00 * | 0.00* | 0.00* |
| MC | | | | | 0.49 | 0.47 |
| MCE | | | | | | 0.96 |

**Table S3.4.** LSMEANs test for the distance from the shore according to social group types (Singleton, Pair, Competitive Group, Mother-Calf pair, Mother-Calf-Escort, Mother-Calf with more than one escort). Distance from shore (km) of humpback whale group categories, SE: Standard Error, * significant difference (p < 0.05) between social group categories.

| **Social Groups** | **Singleton** | **Pair** | **CG** | **MC** | **MCE** | **MCES** |
|---|---|---|---|---|---|---|
| **Distance from shore (km)** | 6.3 ± 0.1 | 6.7 ± 0.1 | 7.2 ± 0.1 | 5.4 ± 0.1 | 5.7 ± 0.1 | 6.3 ± 0.3 |
| **Singleton** | | 0.1 | 0.00* | 0.00* | 0.00 * | 1 |
| **Pair** | | | 0.00 * | 0.00* | 0.00* | 0.75 |
| **CG** | | | | 0.00* | 0.00* | 0.05* |
| **MC** | | | | | 0.23 | 0.02* |
| **MCE** | | | | | | 0.34 |

# CHAPITRE IV – DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR.



*Aquarelle de Caroline Jacques*

# CHAPITRE IV - DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR

## RESUME

- L’objectif de ce chapitre est d’étudier l’influence des paramètres environnementaux sur l’utilisation de l’habitat en fonction du sexe et du statut reproducteur des baleines à bosse de Madagascar par l’analyse du suivi individuel de leurs déplacements en mer en période de reproduction.

- Vingt-cinq baleines ont été équipées de balises Argos entre juillet et août dans le canal Sainte Marie (Nord-Est de Madagascar) en 2012 et 2014 et à Anakao (Sud-Est de Madagascar) en 2013 afin d’étudier l’influence des paramètres environnementaux sur les déplacements des baleines à bosse, ces derniers caractérisés par deux index: un indice de comportement (b-mode) et une vitesse propre de nage. Après avoir utilisé un modèle espace - état pour filtrer les données et estimer l’indice de comportement (b-mode) pour chaque position, des variables physiographiques (bathymétrie, pente, distance à la côte) et océanographiques (mesurées par satellite : température, courant géostrophique de surface, chlorophylle a) ont été extraites sous chaque position.

- Nos résultats ont montré que lors des déplacements côtiers, les femelles passaient 69% de leur temps sur le plateau (bathymétrie <200m) contre 45% pour les mâles. Les femelles ont réalisé davantage de déplacements localisés dans des eaux plus profondes et plus loin de la côte que ce qui a été précédemment noté dans les études basées sur des observations visuelles. En revanche, bien que les mâles nagent plus lentement dans les zones de faibles profondeurs, ils semblent être moins sélectifs que les femelles dans leurs préférences d’habitat, et être probablement essentiellement influencés par des facteurs sociaux. Lors des déplacements en zone océanique, différents types d’habitats ont été identifiés tels que le mont sous-marin des Walters Shoals, situé au sud de Madagascar, qui pourrait être une zone d’alimentation opportuniste. Lors de ces déplacements en zone océanique, les individus diminuent leur vitesse de nage dans des zones de faibles profondeurs et des zones de faibles courants. La vitesse observée résulte

principalement de la nage active des baleines. Néanmoins, au départ de Madagascar, les individus partant vers le nord et vers le sud, zones caractérisées pas de forts courants, tendent à suivre la direction du courant. Bien qu’en période de migration, elles ajustent probablement continuellement leurs angles de nage par rapport au courant en fonction de leur destination, il semble qu’en période de reproduction, elles aient tendance à se déplacer dans la même direction du courant quand celui-ci est fort.

# CHAPITRE IV - DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR

## Influence of environmental parameters on movements and habitat utilization of humpback whales (*Megaptera novaeangliae*) in the Madagascar breeding ground.

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# CHAPITRE IV - DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR

## I. ABSTRACT

Globally, humpback whales migrate to coastal areas of low latitudes to breed and mate during winter. Assessing patterns of breeding-site movements and key habitat features is a prerequisite for the conservation management of such a philopatric species. In this study, we investigated the links between humpback whale movements and habitat use by assessing the influence of a range of environmental variables on behavioral metrics and general movement patterns off Madagascar. Movement data were obtained from twenty-five satellite tags deployed in the northeast and southwest coast of Madagascar, in July and August of 2012-2014. For each recorded position, we collated estimates of environmental variables (bathymetry, distance from shore, bathymetric slope, sea surface temperature, current speed, chlorophyll a concentration), and computed two behavioral metrics (likelihood of exhibiting localized movements, and active swimming speed, i.e. the satellite-observed swimming speed from which the effect of ocean currents was subtracted). The influence of environmental parameters on whale behavior was quantified with linear mixed-effects models. Females and males spent 69% and 45% of their time, respectively over the continental shelf (waters shallower than 200 m). On the shelf, females showed localized behavior in deep water and at large distances from shore suggesting that their breeding habitat extends beyond the shallow coastal waters. Males' active swimming speed decreased in shallow waters, but we found no influence of environmental parameters on their likelihood to exhibit localized movements, which was probably dominated by social factors instead. In oceanic habitats, both males and females showed localized behaviors in shallow waters and high chlorophyll a concentrations. The active swimming speed accounts for a large proportion observed direction of tagged. However whales tended to be closer to the current direction when the current intensity was high.

# CHAPITRE IV - DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR

## II. INTRODUCTION

Most baleen whales are highly mobile, and their distribution and abundance are influenced by the marine environment at different spatial and temporal scales (Acevedo-Gutiérrez 2009). The spatially broad range of migratory species, such as the humpback whale (*Megaptera novaeangliae)* requires animals to explore a variety of habitats (e.g. feeding versus breeding grounds in the case of migratory baleen whales). Distribution and habitat preferences over the annual cycle are partially dependent on environmental parameters, including oceanographic and climatological characteristics (Borcard et al. 1992). While the most frequently invoked factor to explain movement and habitat patterns in animals is resource availability (Stevick, et al. 2002), other factors such as predation risk or social interaction with conspecifics can affect both temporal distribution and habitat selection (Acevedo-Gutiérrez 2009). Habitat heterogeneity, biological requirements, and social behavior of a given species interact to influence patterns of distribution and habitat use.

The migratory cycle of humpback whales alternates seasonally between a summer feeding period in productive high latitudes and a winter breeding period in low latitudes (Dawbin, W.H. 1966, Clapham 2000). Since the biological productivity is often low in wintering areas, humpback whale winter activities generally do not focus on feeding (Clapham 1996). The aggregation of humpback whales in localized breeding areas is a consequence of their mating system which involves intrasexual competition among males for females (Clapham & Zerbini 2015). Furthermore, the widespread distribution of females is assumed to result from the absence of predation and prey (Clapham, 1996). In this context, social organization, breeding status or environmental variables seem to shape the selection of habitat (Ersts & Rosenbaum 2003, Craig & Herman 2000).

Studies on different humpback whale breeding areas around the world show that animals occur in high densities in a variety of habitats, including continental coasts, coastal and oceanic islands, reef systems, or over shoals (e.g. Mattila et al. 1989, Félix & Haase 1997, Craig & Herman 2000, Ersts & Rosenbaum 2003, Garrigue et al. 2010, 2015). Humpback whales are frequently found in warm (21.1 to 28 °C), shallow (15 to 60 m depth), nearshore or shelf waters (Dawbin 1966, Herman & Antinoja 1977, Herman 1979, Mobley et al. 1999, Rasmussen et al. 2007). In particular, it is believed that females with calves tend to prefer shallow waters in protected areas (20 m depth or less) (Craig & Herman 2000, Félix & Haase 2001, Félix & Botero-Acosta 2011). Although humpback whales are considered primarily coastal during the breeding period, they also occur over deep waters during winter (Zerbini et al. 2006, Kennedy et al. 2013) where movement patterns and habitat use are poorly known. To date, only one study has investigated the movements of individual humpback whales on a breeding ground and established direct links with environmental parameters (Smith et al. 2012, Eastern Australia).

The range of the southwestern Indian Ocean humpback whale population, referred to as Breeding Stock C by the International Whaling Commission (IWC), extends from southeastern Africa to the Mascarenes Islands (Best et al. 1998, IWC 1998a). Within this region, Madagascar Island, defined as the sub-region C3, is an important breeding ground for humpback whales (Bermond 1950, Angot 1951, Best et al. 1995, Rosenbaum et al. 1997, 2009, Rosenbaum 2003, Best & Brandão 2009, Cerchio et al. 2009). The population abundance of humpback whales around Madagascar in 2015 was estimated at 8,854 (95% CI of 6,906-16,106) whales (Cerchio et al 2009, Jackson et al. 2015). Humpback whales are widely distributed around Madagascar but higher concentrations are reported in certain areas including the north-east (Ile Sainte Marie, Antongil bay), and the southern region from Toliara to Fort Dauphin (Braleys 1849, Starbuck 1878, Bermond 1950, Best et al. 1996, Rosenbaum et al. 1997, Razafindrakoto et al. 2001, Ersts & Rosenbaum 2003, Cerchio et al. 2009).

While the western coast of Madagascar is characterized by a wide continental shelf and an extensive barrier reef (90 km at its widest, ~ 16°S; Pripp et al. 2014), the east coast features a narrow continental shelf of 25-50 km width and an abrupt break in the slope below 1000 m (Katz & Premoli 1979). The northeastern coast is where the continental shelf is the widest, with Antongil Bay and Ile Sainte Marie characterized by extensive shallow waters (Ersts & Rosenbaum 2003). The southern tip of Madagascar is also characterized by a wide continental shelf extending 50 km from land and is referred to as the Madagascar Plateau (Goslin et al. 1980). Sightings of humpback whales have been recorded further south than the southern tip of Madagascar around the seamount of Walters Shoals located 645 km south of Madagascar and as shallow as 18 m depth (Collette & Parin 1991, Best et al. 1998).

The strongest geostrophic currents (0.2 - 1 m.s) are observed on the east coast of Madagascar, up to the south of Ile Sainte Marie and Antongil Bay region (**Figure S4.1,** reconstructed from the dataset of SWIO12 climatological model, see *extraction of environment parameters*). The South Equatorial Current (SEC) that flows westward at around 20°S, splits into two branches as it approaches the eastern Madagascar coast: one branch flows northward to the northern tip of Madagascar; and the other flows southward along Madagascar, referred to as the East Madagascar Current, EMC (Lutjeharms & Machu 2000, De Ruijter et al. 2004) (**Figure S4.1**). The ocean circulation of the west coast is poorly known, and is defined by slower currents and a strong mesoscale structures (i.e. eddies) southwest of Madagascar (Lutjeharms 2006, Braby 2014). Whether and how these contrasting oceanographic characteristics affect humpback whale habitat utilization around Madagascar during the breeding period has not been investigated to this point (**Figure S4.1**).

The biology of humpback whales is one of the best known among large whales, but our knowledge of habitat utilization and movement patterns during the breeding season remains limited and probably biased due to a lack of data in regions that are logistically challenging to sample, such as, offshore areas (Clapham 2000, Kennedy et al. 2013). Recent technological improvements in cetacean satellite telemetry have increased information on seasonal distribution ranges, movements into remote areas, as well as migration route and stock structure (Mate et al. 2007, Zerbini et al. 2006, 2011, Gales et al. 2009, Kennedy et al. 2013). It is also now possible to relate the individual whale’s horizontal movements to their physical environment at appropriate spatial and temporal scales, and to better understand how environmental parameters influence whale’s distribution.

In this study we used data from Argos satellite tags attached to humpback whales off Ile Sainte Marie (northeast Madagascar) and Anakao (southwest Madagascar) during three breeding seasons to investigate movement patterns and habitat utilization of humpback whales in relation to sex and reproductive status. We then investigated how key environmental variables along the whale tracks influenced humpback whale movements.

## III. MATERIAL AND METHODS

### A. TAG DEPLOYMENT

Twenty-five humpback whales were equipped with Wildlife Computer SPOT 5 satellite transmitters during the breeding season over the years 2012-2014 (**Table 4.1**; hereafter we will refer to individual whale using their alphabetical ID as shown in that table). Whales were tagged in two distinct regions of Madagascar: Ile Sainte Marie (16°50’S, 49°55’E) in 2012 and 2014, and off Anakao (23°40’S, 43°39’E) in 2013. The sex of each tagged individual was inferred in the field based upon their role in the group of whales, when possible and except for one whale was subsequently confirmed through genetic analysis from biopsy samples (Jayasankar et al. 2008). Whale locations were obtained through the Argos data collection system (Argos 1990). Further details about tag anchoring, deployment and whale selection can be found in Cerchio et al. (2013, in review). In 2012, we used both an 8 m long carbon fiber pole, and modified pneumatic tag deliverer (ARTS) to deploy tags on whales, and in subsequent years we only used the ARTS (Zerbini et al. 2006, 2011, Kennedy et al. 2013). Tags deployed in 2012, were duty cycled to transmit 6h on, 6h off for the first three months after deployment, and then every other day until the end of transmission. In 2013, tags were duty cycled to a 9h on, 3h off to increase data collection. In 2014, tags were duty cycled to transmit 2h on 5h off during the day, and 2h on 4h off during the night.

### B. DATA PROCESSING

All locations classified invalid by Argos (Argos location class “Z”) and all locations on land were removed from the dataset. We retained Argos locations classes 3, 2, 1, 0, A and B (see http://www.argos-system.org/manual/3-location/34_location_classes.htm) and assumed as invalid any location implying a travel rate greater than 12 km/h (e.g. Garrigue et al. 2010) as indicated by R package Trip (R Development Core Team 2006). Bayesian Switching State Space Model (SSSM) was used to model estimated positions and associated error based upon the raw Argos locations (Jonsen et al. 2005, 2006) to provide the best estimate of each whale's path. A 12h time step was used to minimize the number of positions estimated when the tags were not transmitting. The model was fitted using WinBUGS v1.4. Two Markov Chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 50 000 simulations. The first 20 000 samples were discarded as a "burn-in" and the remaining samples were thinned, retaining every 30th sample to reduce autocorrelation. The 1000 retained iterations for each chain, giving a total of 2000 independent samples, were used to compute the posterior distribution of the parameters of interest, including behavioral mode (bmode) The behavioral mode parameter measures the likelihood of exhibiting localized movements based on the mean turning angle ($\theta$), and the autocorrelation in speed and direction ($\gamma$) into the first difference random walk model within the SSSM (Jonsen et al. 2005) (**annex B**). A behavioral mode less than 1.25 was considered as an indication of a transiting behavior (Jonsen et al. 2007). Details on estimation procedure are presented in Jonsen et al. (2005, 2006). The probability that an individual change fron the current mode to another one is estimated with $\alpha$ parameter (**annex B**).

To avoid introduction of unrepresentative estimated locations or behavioral state values, all tracks shorter than 8 days were excluded from analysis (whales E, H, N, P, X; **Table 4.1**). For tracks showing long transmission gaps (e.g. 16 days and 12 days for whales A and D, respectively; **Table 4.1**), tracks were split into two segments that were analyzed separately. The first segment of whale A and the second segment of whale D being less than 8 days, were excluded from subsequent analyses.

### C. DATA ORGANIZATION

The whale position data were split into two categories: coastal and oceanic according to whale position relative to the continental shelf (**Figure 4.1**). Whale movements were defined as coastal when located over the continental shelf or around the shelf break. The large majority (78%) of coastal locations were found over the continental shelf (< 200 m water depth). Whale movements were defined as oceanic when animals were leaving the Madagascar continental shelf toward deep ocean waters.

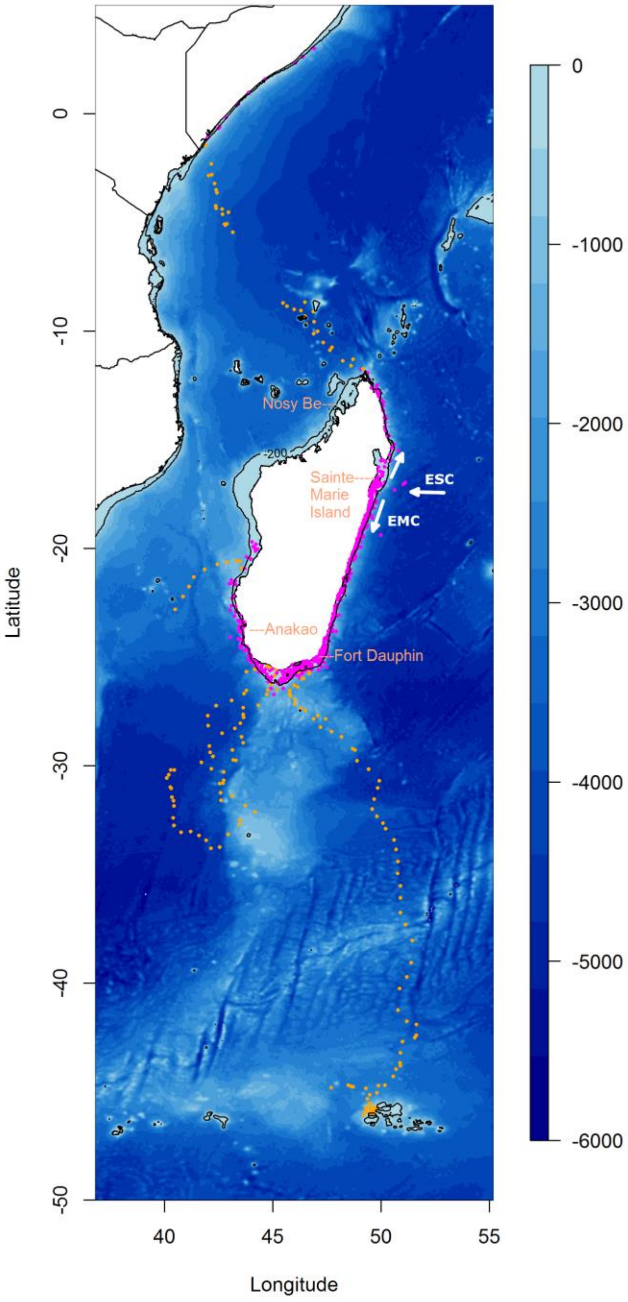

**Figure 4.1.** Whale locations associated with the type of movements (purple = coastal, orange= oceanic). Arrows illustrate the East Madagascar Current (EMC) and the southern branch of the EMC, known as the South East Current (SEC).

# CHAPITRE IV - DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE MADAGASCAR

## 1. ENVIRONMENTAL PARAMETERS

The environmental variables investigated included 1) Sea surface temperature (SST), since at the basin scale, the distribution of humpback whale breeding grounds is defined by a relatively narrow sea surface temperature range; 2) sea-bed depth and 3) distance from shore, because humpback whales are frequently seen in shallow waters and reef areas during breeding season, suggesting that these variables could be important drivers of their distribution; 5) ocean current speed and direction, since they are likely to influence the whale's heading and active swimming speed; and 6) the surface chlorophyll a concentration used as a proxy for the marine ecosystem productivity, in order to investigate if whales could feed during the breeding period.

## 2. MOVEMENT DATASETS

From the 19 whales that displayed coastal movements, 11 were females and 8 were males. Whale movements were analyzed using linear mixed-effects models (LMMs, see below for details of analysis) considering the logit of behavioral mode values and whale active swimming speed values as response variables, and SST, bathymetry, distance from shore, slope, and current speed as explanatory variables.

Seven whales displayed oceanic movements including six females and one male. These oceanic movements were analyzed using LMMs considering the logit of behavioral mode values, whale active swimming speed, and whale deviation from the current (H-C angle) values as response variables, and SST, bathymetry, slope, current speed, and the surface chlorophyll a concentration as covariates.

## D. BEHAVIORAL METRICS

Two metrics were used to characterize the whale movements: 1) the behavioral-mode from SSSM outputs described earlier (*see data processing*), and 2) the whale active swimming speed. The observed whale speed vector (T) was estimated by computing the distances, in the x and y directions, between the two consecutive locations and then dividing by the time elapsed. It was systematically computed as:

$$T(t) = [X(t + \Delta t) - X(t)] / \Delta t, \qquad (1)$$

Where [X(t), X(t + Δt)] are the two successive positions over a time interval, t. The observed whale speed vector (T) can also be written as the sum of the whale's active swimming vector (A), and the current vector (C) (e.g. Gaspar et al. 2006):

$$T (t) = A (t) + C (t). \quad (2)$$

In other words, the mean active swimming speed (A) computed over the time interval [t, t + Δt] can be expressed as the difference between T (t) and the averaged current speed during the same time interval (namely [C(t) + C(t+Δt)]/2; e.g. Galli et al., 2012). To simplify notation, A(t) will be noted A, T(t) will be noted T, and [C(t) + C(t+Δ1)]/2 will be noted C, so (Eq. 2) is written:

$$A = T - C. \quad (3)$$

The resulting tracks from the SSSM are made of positions estimated with a fixed sampling period Δt = 12h. To extract environmental variables between two successive positions, whale tracks were re-sampled at a higher temporal resolution (every 6h) by linear interpolation (using R package adehabitat, function redisltraj; Calenge 2011). Then, the computed whale active swimming speeds were assigned to each interpolated location and environmental variables were extracted for these locations. The latter positions were used in the modeling analysis to link the active swimming speed metric and environmental variables.

## E. EXTRACTION OF ENVIRONMENT VARIABLES

Three static variables (bathymetry, bathymetric slope, and distance from shore) and three dynamic variables (daily surface chlorophyll-a concentration (CHL); SST; and surface currents) were estimated at each whale time and position. The GEBCO bathymetry Grid-database (30s per cell, http://www.gebco.net/) was used to compute bathymetry depth, bathymetry slope and distance from shore. Bathymetric slope (hereafter “slope”) was derived using the R package raster (function *terrain*; Hijmans & Van Etten 2014). The whale distance from shore was calculated as the distance between each location and the nearest coastline defined by a positive bathymetry.

CHL was estimated from the merged daily GlobColour product at a 4 km (0.1°) spatial resolution (http://www.globcolour.info/). We computed a spatial and temporal average around each estimated (or interpolated) whale position. The spatial means were calculated in 0.25° bins (~27 $km^2$), and the time mean within the 15-day period prior to the whale location. The temporal average was set 15 days prior to whale location as an attempt to consider the time of development of intermediate trophic levels in planktonic communities. These spatial and temporal means allowed us to fill gaps in satellite data availability due to cloud coverage, as well as to remove any potential local noise. We averaged over 0.25° bins rather than over 0.1° bins did because this not qualitatively change our results, and using the 0.1° removed some locations from the analysis.

SST was extracted from a daily sea surface temperature dataset produced and distributed by JPL (http://ourocean.jpl.nasa.gov/SST/, G1SST product) at a 1 km spatial resolution. For consistency with the surface chlorophyll analysis we used a mean value within a 0.25° bin around each whale location.

For the open-ocean dataset, daily geostrophic currents were computed from the daily merged and gridded satellite altimetry product produced by Aviso (http://www.aviso.altimetry.fr/) with a spatial resolution of 0.25° (latitude, longitude).

Because altimetry-derived ocean velocity are noisier closer to a coast, surface currents for the coastal dataset was not availble from Aviso products. Instead, we used a climatological estimate of a geostrophic current from a regional ocean model configuration. The model configuration is based on the NEMO ocean general circulation modelling system (Madec 2008) and is a subset from the global 1/12° resolution (i.e. cell size ~9 km) configuration described by Deshayes et al. (2013) covering the southwestern Indian Ocean sub-domain (31°E - 66.25°E; 3°S - 29°S). This model successfully reproduces the major currents (mean and variability) as well as water masses properties. For the purpose of this study, only winter (June to October) surface currents are considered and used to calculate temporal mean and standard deviation over years 1995-2009 which constitute the climatology from which current data were extracted underneath the whale tracks.

### F. STATISTICAL ANALYSIS

All statistical analysis were performed using R Program version 3.1.2 (R Core Team 2014). We fitted a series of LMMs using the R software package nlme (function lme; Pinheiro et al. 2007) following the steps described in Zuur et al. (2009) to examine the relationship between three response variables (behavioral mode, active swimming speed, angle between whale's heading and surface current) and the explanatory environmental variables. Behavioral state is the proportional likelihood of exhibiting localized movements, ranging between 1 (transit) and 2 (localized). As a consequence, behavioral mode values were logit transformed before the analysis (O'Toole et al. 2015). An autocorrelation term (corAR1) was added to account for the lack of temporal independence within telemetry data for each whale (Zuur et al. 2009). The individual whale was included as a random term. Both predicted location associated with missing environmental values and outliers (values that were ecologically unreasonable to include) were removed from analysis. Non collinearity was verified between continuous variables using Pearson correlation (coef <=0.5) and the variance inflection factor (VIF) (Zuur et al. 2009) and one of each highly correlated pair were removed. Explanatory variables were standardized (centered and scaled) to facilitate model convergence and enable comparison of their contribution (using their corresponding slope coefficients). Model selection was performed using likelihood ratio tests starting from a full model with terms retained only if they improved the fit ($p < 0.05$, Zuur et al. 2010). The results were then evaluated such that the most parsimonious model was also the model with the lowest Akaike's Information Criteria (AIC). The resulting optimal model was then fitted using restricted maximum likelihood (REML). The normality and homogeneity of residuals were checked graphically (Zuur et al. 2010, Hervé 2014).

### G. OCEANIC MOVEMENTS: SURFACE CURRENT AND TRAJECTORY

We calculated the angles between T and C vectors (T-C angles) as an estimate of how whale movements in the open ocean were related to surface current direction. Angles close to 0° indicate that observed whale movements were following current direction, whereas angles close to 180° indicate movements oriented against the surface current. Similarly, we calculated angles between A and C vectors (A-C angles) as a mean to estimate how whales orient their swimming direction with respect to the current. We assessed the respective contribution of currents (C) and whale's active swimming (A) on whale observed movements (T) by projecting respectively the C-vector onto the T-vector (PCT) and A-vector on the T-vector (PAT) (see Galli et al. (2012) and **supplement S4.1**).

## IV. RESULTS

### A. GENERAL TRACKING INFORMATION

Whales were selected for tagging based on sex, reproductive classe and behavioral subclass (Cerchio et al. 2013, *in prep*). Whales were tracked for an average duration of 24.2 days (range 2-58 days) yielding 5631 locations raw Argos location. Five tracks shorter than 8 days were discarded from our analysis, providing us with twenty trips, or 1039 estimated locations after application of SSSM (11 females, 8 males, and one unknown sex; **Table 4.1, Figures 4.2, S4.2.1 and S4.2.2**).

Whales traveled along the east, southwest, and southern coasts of Madagascar with a high inter-individual variability in swimming direction (**Figures 4.2, S4.2.1 and S4.2.2**). The distances travelled during the tag transmission period (calculated from estimated SSM positions) ranged from 488 to 4575 km, with an average (+/- SE) travelling speed of 31 ± 1 km per day (**Table 4.1**). While most tagged individuals stayed relatively close to the Madagascar coast, one displayed a southward migration and reached as far as the Crozet Islands (~2000 km south of Madagascar coast; whale V) and another one (whale I) visited the Walters shoals seamount before coming back to south of Madagascar (**Figure 4.2**).

**Table. 4.1.** Summary of the tracking dataset of humpback whales equipped at Sainte Marie channel (SM) and Anakao (AO) and main characteristics of breeding movements based on switching State space model (SSSM) positions estimated every 12h. Group types include Singleton; S, Pair; P, Competitive Group; CG, Non Competitive Group; NCG, Mother-Calf pair; MC, Mother-Calf-Escort; MCE, Mother-Calf with more than one escort; MCES. Whale's tracks are defined by coastal (C) or/and oceanic (O) movements. Mean are expressed ± se. Stars indicate that mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| Whale id | Tag location | Sex | Group type | Tag date | Tag longevity (days) | Number of locations data points | Number of estimated locations after application of SSSM | Type of movements | Travelled distance per day (km) | B-mode average | Observed speed (m/s) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A | SM | M | S | 24-July-2012 | 32 | 123 | | | | - | - |
| | | | | | 3 | - | | - | | - | - |
| | | | | | 13 | - | 27 | C, O | 47 ± 6.88 | 1.26 | 1.02 ± 0.12 |
| B | SM | M | CG | 30-July-2012 | 31 | 231 | 62 | C | 22 ± 2.4 | 1.88 | 0.46 ± 0.03 |
| C | SM | M | P | 30-July-2012 | 20 | 169 | 41 | C | 29 ± 2.97 | 1.63 | 0.62 ± 0.09 |
| D | SM | F | MC | 31-July-2012 | 25 | 58 | | | | - | - |
| | | | | | 8 | - | 17 | C | 34 ± 8.6 | 1.44 | 0.72 ± 0.17 |
| | | | | | 4 | - | | - | | - | - |
| E | SM | M | MCE | 01-August-2012 | 5 | 21 | | - | | - | - |

| **Whale id** | **Tag location** | **Sex** | **Group type** | **Tag date** | **Tag longevity (days)** | **Number of locations data points** | **Number of estimated locations after application of SSSM** | **Type of movements** | **Travelled distance per day (km)** | **B-mode average** | **Observed speed (m/s)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F | SM | M | P | 31-July-2012 | 10 | 71 | 20 | C | 31 ± 4.4 | 1.79 | 0.65 ± 0.09 |
| G | SM | F | MC | 31-July-2012 | 13 | 102 | 27 | C, O | 38 ± 3.6 | 1.05 | 0.85 ± 0.09 |
| H | SM | M | CG | 01-August-2012 | 3 | 21 |  | - |  | - | - |
| I | SM | F | CG | 01-August-2012 | 58 | 368 | 116 | C, P | 44 ± 2.8 | 1.19 | 1 ± 0.06 |
| J | SM | F | MC | 01-August-2012 | 30 | 222 | 61 | C | 29 ± 3.2 | 1.32 | 0.6 ± 0.06 |
| K | SM | M | CG | 03-August-2012 | 15 | 104 | 30 | C | 28 ± 4.9 | 1.65 | 0.6 ± 0.12 |
| L | SM | F | CG | 03-August-2012 | 23 | 196 | 46 | C, O | 43 ± 4.8 | 1.05 | 0.9 ± 0.09 |
| M | AK | X | NCG | 16-July-2013 | 15 | 206 | 31 | C, O | 37 ± 3.6 | 1.25 | 0.86 ± 0.09 |
| N | AK | F | P | 17-July-2013 | 21 | 8 |  | - |  | - | - |
| O | AK | F | P | 17-July-2013 | 42 | 473 | 85 | C | 37.± 3.1 | 1.17 | 0.8 ± 0.06 |
| P | AK | F | P | 17-July-2013 | 2 | 13 |  | - |  | - | - |

| **Whale id** | **Tag location** | **Sex** | **Group type** | **Tag date** | **Tag longevity (days)** | **Number of locations data points** | **Number of estimated locations after application of SSSM** | **Type of movements** | **Travelled distance per day (km)** | **B-mode average** | **Observed speed (m/s)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Q | AK | M | P | 17-July-2013 | 34 | 480 | 68 | C, O | 30 ± 2.6 | 1.24 | 0.71 ± 0.73 |
| R | AK | M | CG | 21-July-2013 | 23 | 307 | 45 | C | 30 ± 2.5 | 1.57 | 0.7 ± 0.06 |
| S | AK | M | CG | 21-July-2013 | 8 | 85 | 10 | C | 54 ± 9.3 | 1.39 | 0.96 ± 0.12 |
| T | AK | F | MBE | 23-July-2013 | 23 | 269 | 36 | C | 44 ±5.7 | 1.03 | 0.83 ± 0.06 |
| U | AK | F | CG | 25-July-2013 | 17 | 129 | 34 | C | 28 ± 3.9 | 1.31 | 0.6 ± 0.06 |
| V | AK | F | NCG | 27-July-2013 | 56 | 786 | 105 | C, O | 32 ±1.9 | 1.24 | 0.74 ± 0.06 |
| W | AK | F | MC | 28-July-2013 | 52 | 807 | 104 | C | 22 ± 1.8 | 1.17 | 0.48 ± 0.03 |
| X | SM | M | MCES | 21-August-2014 | 4 | 15 |  | - |  | - | - |
| Y | SM | F | MC | 23-August-2014 | 37 | 367 | 74 | C | 23 ± 2.06 | 1.36 | 0.52 ± 0.06 |
|  |  |  |  |  |  |  |  | **C** |  | **1.34 ± 0.01*** | **0.8 ± 0.02*** |
|  |  |  |  |  |  |  |  | **O** |  | **1.14 ± 0.01*** | **1.12 ± 0.05*** |
|  |  |  |  |  |  |  |  | **O (whale V not included)** |  | **1.17 ± 0.02*** | **1.21± 0.08*** |

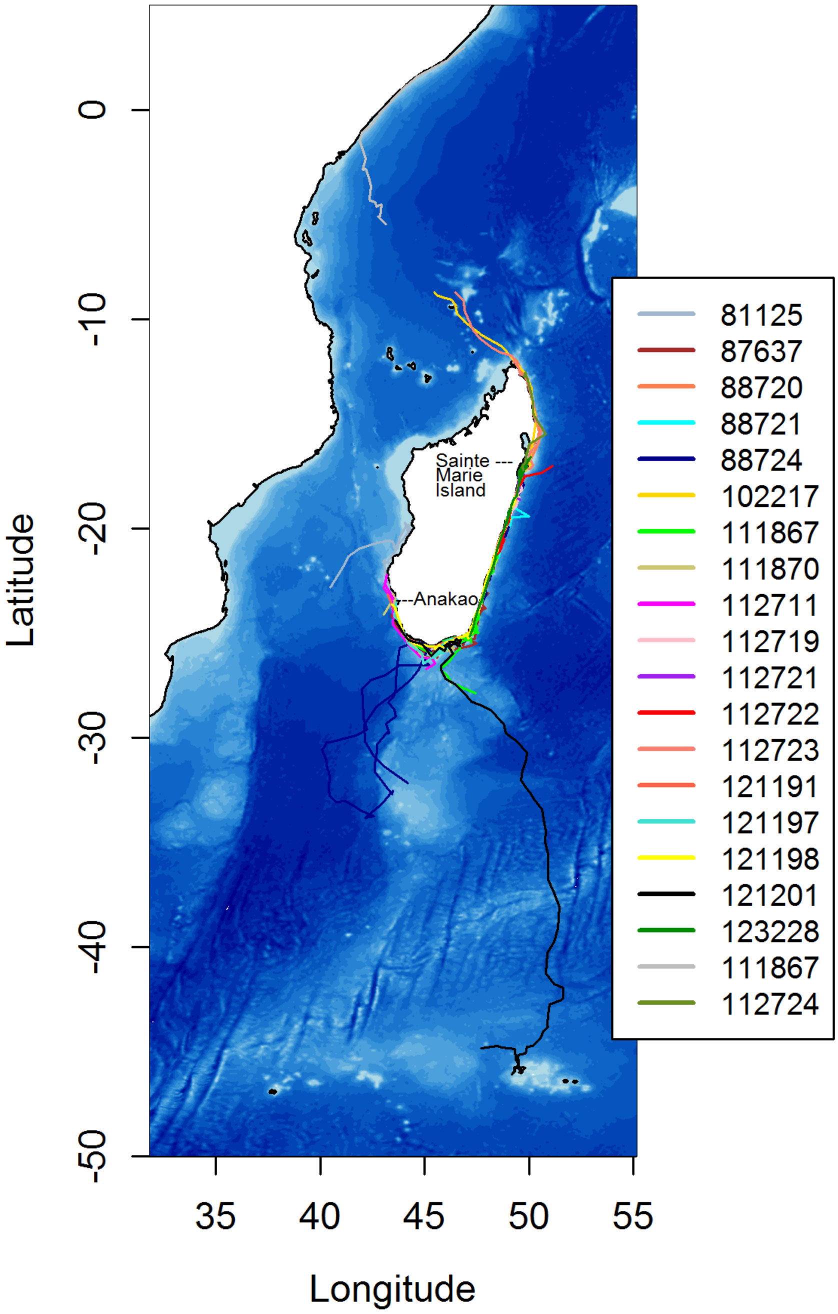

**Figure 4.2.** Trajectories of all tracked humpback whales in the Madagascar breeding ground. Trips shorter than 8 days are not represented.

All humpback whales in our study spent time in the coastal waters of Madagascar, with the vast majority of received locations (78%) classified as coastal (**Figure 4.1**). Among those, twelve whales (B, C, F, J, K, O, R, S, T, U, W, and Y) remained exclusively over the continental shelf of Madagascar for the duration of tag transmission (**Figures S4.2.1 and S4.2.2**). Seven whales (A, G, I, L, M, Q, and V) stayed within coastal waters of Madagascar before heading toward the deep waters (**Figures S4.2.1 and S4.2.2**). The mean tag transmission was slightly longer (Wilcoxon test, $p < 0.001$) for tracks containing an oceanic part (33 ± 7 days) than for tracks that were only coastal (26 ± 3 days). Most animals that undertook oceanic movements were female (five), with one male, and one was of unknown sex. Whales spent more time per unit area in coastal waters (4 ± 0.12 h per 0.1° X 0.1°bins) than in oceanic waters (2 ± 0.07 h per 0.1° X 0.1°bins).

In coastal habitat, even though whales exhibited a wide variety of long distance movements over the Madagascar shelf, no whales tagged in Sainte Marie or in Anakao visited the northwestern coast of Madagascar (**Figure 4.1**). Whale trajectories were mostly to the east and south coast of Madagascar, with six individuals performing round trips along the coast (whales C, J, L, Q, O, and W, **Figures S4.2.1 and S4.2.2**). Whales tagged in Sainte Marie generally travelled along the central east coast, with five whales (A, D, G, J, L) heading northwards and two whales (B and Y) heading southward. Out of the five whales heading northward, one (whale J; **Figure S4.2.2**) reached the northern tip of Madagascar, before turning back southward, and one started a southward trip until the central coast, before turning back northward (whale L; **Figure S4.2.1**). Whales tagged in Anakao travelled mostly along the southwest and south coasts of Madagascar. Three whales (R, S, and U) lingered on the southern plateau, and five whales (I, O, Q, T, and W) visited the east coast. Overall, all whales equipped in Anakao steered southward except whale M which moved northward. Whale movements and sub-stock exchange are presented in more detail in Cerchio et al. (in prep).

## B. COASTAL MOVEMENTS

### 1. GENERAL CHARACTERISTICS OF MOVEMENTS AND HABITAT IN COASTAL AREAS ACCORDING TO SEX AND REPRODUCTIVE STATUS

Overall, both females and males used shallow waters and remained on the continental shelf (**Table S4.1**). Females spent a significantly higher portion of their time over the shelf (≤ 200 m water depth) than males (69 ± 5 %, and 45 ± 10% respectively, permutation t-test, *p*=0.034). However, there was no significant difference in the mean distance from shore between females (15.1 ± 2.8 km) and males (20.58 ± 3.9 km) (permutation t-test, *p*=0.28) (**Table S4.1, Figure S4.3**). Similarly, there was no significant difference in the mean distance from shore (12.1 ± 3 km and 19 ± 4 km respectively, permutation t-test, *p*=0.2) or mean water depth between females with calves and females without calves (187 ± 58 m and 233 ± 66 m respectively, permutation t-test, *p*=0.5). Mean SST in the area used by whales ranged between 21 and 26°C (24 ± 0.04°C). The mean current speed in the same area was 0.29 ± 0.01 m/s.

Transiting behavior was found in higher proportion in females (58%) than males (38%) (**Figures S4.4.1, S4.4.2, S4.5.1, S4.5.2, S4.6**). Likewise, in coastal habitat, the mean behavioral mode of females was significantly lower than the mean behavioral mode of males (1.25 ± 0.12 and 1.52 ± 0.39 respectively; permutation t-test, p=0.016), suggesting that males performed more localized movements in coastal areas than females. There was no significant difference between the behavioral mode of females with a calf (1.30; 6 individuals), and females without a calf (1.1; 5 individuals) (permutation t-test, p=0.26). The females' observed rate of travel was not significantly lower than males' (0.85 ± 0.11 m/s, 0.88 ± 0.11 m/s respectively; permutation t-test, p=0.8). Additionally, the observed rate of travel of females with a calf (0.82 ± 0.08 m/s) was not significantly different from females without a calf (0.89 ± 0.13 m/s) (permutation t-test, p=0.69).

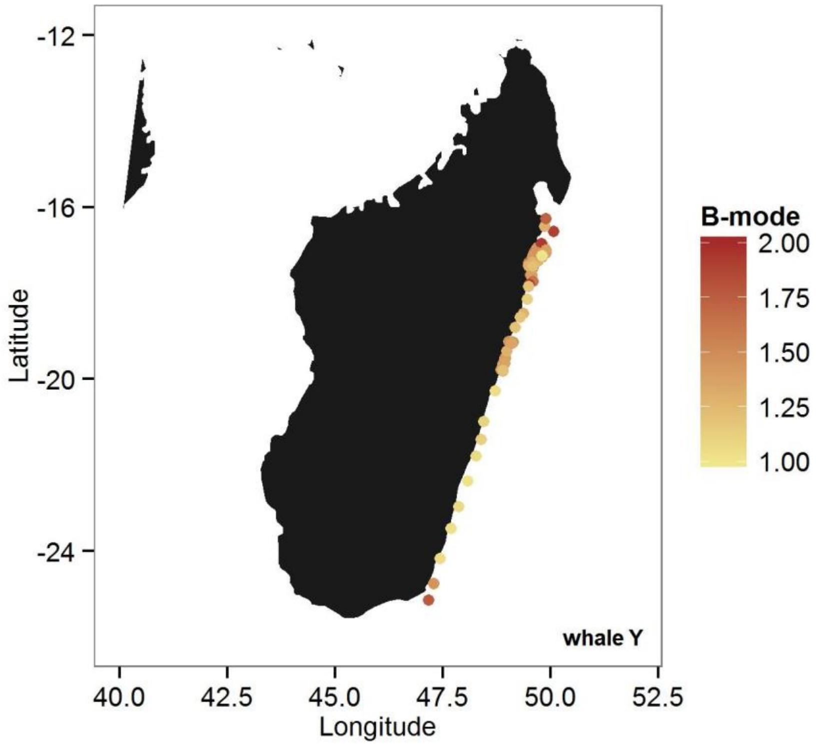

**Figure 4.3.** Whale Y track showing an example of the B-mode values for each location. It ranges from 1, meaning low probability of localized movement to 2 meaning high probability of localized movement**.**

## 2. INFLUENCE OF ENVIRONMENTAL CONDITIONS ON BOTH FEMALES AND MALES BEHAVIORAL MODE AND SWIMMING SPEED.

The influence of environmental variables on the behavioral mode of females was most parsimoniously described by a model including water depth and distance to shore (**Table 4.2**). Residuals are normally distributed and homogeneous (**annex C**). Namely, the probability of performing localized movements was positively correlated to depth and to distance from shore. In contrast, the most parsimonious model describing the behavioral mode of males included all environmental variables except distance from shore (collinear with the depth, **annex D**) but none was associated significantly with movement patterns (**Table 4.2**).

The active swimming speed of females was most parsimoniously described by a model including only the speed of the surface current (**Table 4.3, annex E**): female active swimming speed increased with decreasing current speed. For males, the most parsimonious model indicated swimming speed was positively correlated with water depth and negatively correlated with current intensity. The most parsimonious model describing the behavioral mode of males included all environmental variables except distance from shore (collinear with the depth, **annex F**)

**Table 4.2.** Summary of regression coefficients from the most parsimonious models (LMMs) relating B-mode (logit) to environmental parameters for the females and males during coastal movements. Coefficients are presented ± SE with their p-value associated. Significant parameters are highlighted in bold characters. Parameters included in the full model but not retained in the model selection are indicated by a slash mark.

| | **Coastal Model - Females** | | **Coastal Model - Males** | |
|---|---|---|---|---|
| | **B-mode** | | **B-mode** | |
| | n=380, 11 whales | | n=213, 7 whales | |
| Random effects: ~1\| Whale ID | | | | |
| | (Intercept) | Residual | (Intercept) | Residual |
| StdDev | 0.91 | 1.17 | 0.85 | 0.94 |
| Explanatory variables | Coef ± SE | p-value | Coef ± SE | p-value |
| Intercept | -1.39 ± 0.3 | 0.0 | 0.42 ± 0.34 | 0.21 |
| Sea surface temperature | / | / | 0.17 ± 0.15 | 0.1 |
| Bathymetry | **0.19± 0.07** | **< 0.01** | 0.08 ± 0.06 | 0.18 |
| Distance from shore | **0.19 ± 0.09** | **0.04** | | |
| Slope | | | - 0.07 ± 0.06 | 0.27 |
| Current speed | / | / | -0.003 ± 0.09 | 0.9 |

**Table 4.3.** Summary of regression coefficients from the most parsimonious models (LMMs) relating whale swimming speed to environmental parameters for the females and males during coastal movements. Coefficients are presented ± SE with their p-value associated. Significant parameters are highlighted in bold characters. Parameters included in the full model but not retained in the model selection are indicated by a slash mark.

| | **Coastal Model - Females** | | **Coastal Model - Males** | |
|---|---|---|---|---|
| | **Swimming speed** | | **Swimming speed** | |
| | n=317, 11 whales | | n=160, 7 whales | |
| Random effects: ~1\| Whale ID | | | | |
| | (Intercept) | Residual | (Intercept) | Residual |
| StdDev | 0.07 | 0.48 | 0.06 | 0.45 |
| Explanatory variables | Coef ± SE | p-value | Coef ± SE | p-value |

| | **Coastal Model - Females** | | **Coastal Model - Males** | |
|---|---|---|---|---|
| | **Swimming speed** | | **Swimming speed** | |
| | n=317, 11 whales | | n=160, 7 whales | |
| Intercept | 0.6 ± 0.05 | 0 | 0.6 ± 0.04 | 0 |
| Sea surface temperature | / | / | / | / |
| Bathymetry | / | / | **0.09 ± 0.04** | **< 0.01** |
| Slope | | | / | / |
| Distance from shore | / | / | | |
| Current speed | **-0.15 ± 0.04** | **<0.001** | **-0.16 ± 0.04** | **< 0.001** |

## C. OCEANIC MOVEMENTS

### 1. GENERAL CHARACTERISTICS OF MOVEMENTS IN OCEANIC AREAS

During offshore movements, humpback whales traveled over deep waters (mean depth 2944 ± 105 m), and encountered an average current speed of 0.3 ± 0.02 m/s (**Table S4.2**). The CHL along their tracks ranged between 0.08 mg. m$^{-3}$ and 1.4 mg. m$^{-3}$ (mean of 0.3 ± 0.02 mg. m$^{-3}$) (**Figure 4.4**). The mean SST values ranged from 2 to 26 °C (mean of 18 ± 0.6°C). The highest mean CHL concentration (0.5 ± 0.04 mg.m$^{-3}$, max: 1.4 mg. m$^{-3}$) and the lowest mean SST (10.8 ± 0.9 °C, min: 2 °C) were encountered by whale V, where it arrived at the Polar Frontal Zone (~45°S) in late September (**Figures.S4.2.2, 4.4**).

The behavioral mode associated with oceanic movements of whales ranged from 1 to 1.9 (1.14 ± 0.01). Transiting behavior (behavioral mode less than 1.25) was found during 79% of the oceanic movements (**Figures. S4.4 and S4.5**). Observed speed was significantly higher in deep waters (migration track not included) than in coastal waters (1.15 ± 0.08 m/s and 0.86 ± 0.08 m/s respectively; permutation t-test, p=0.03).

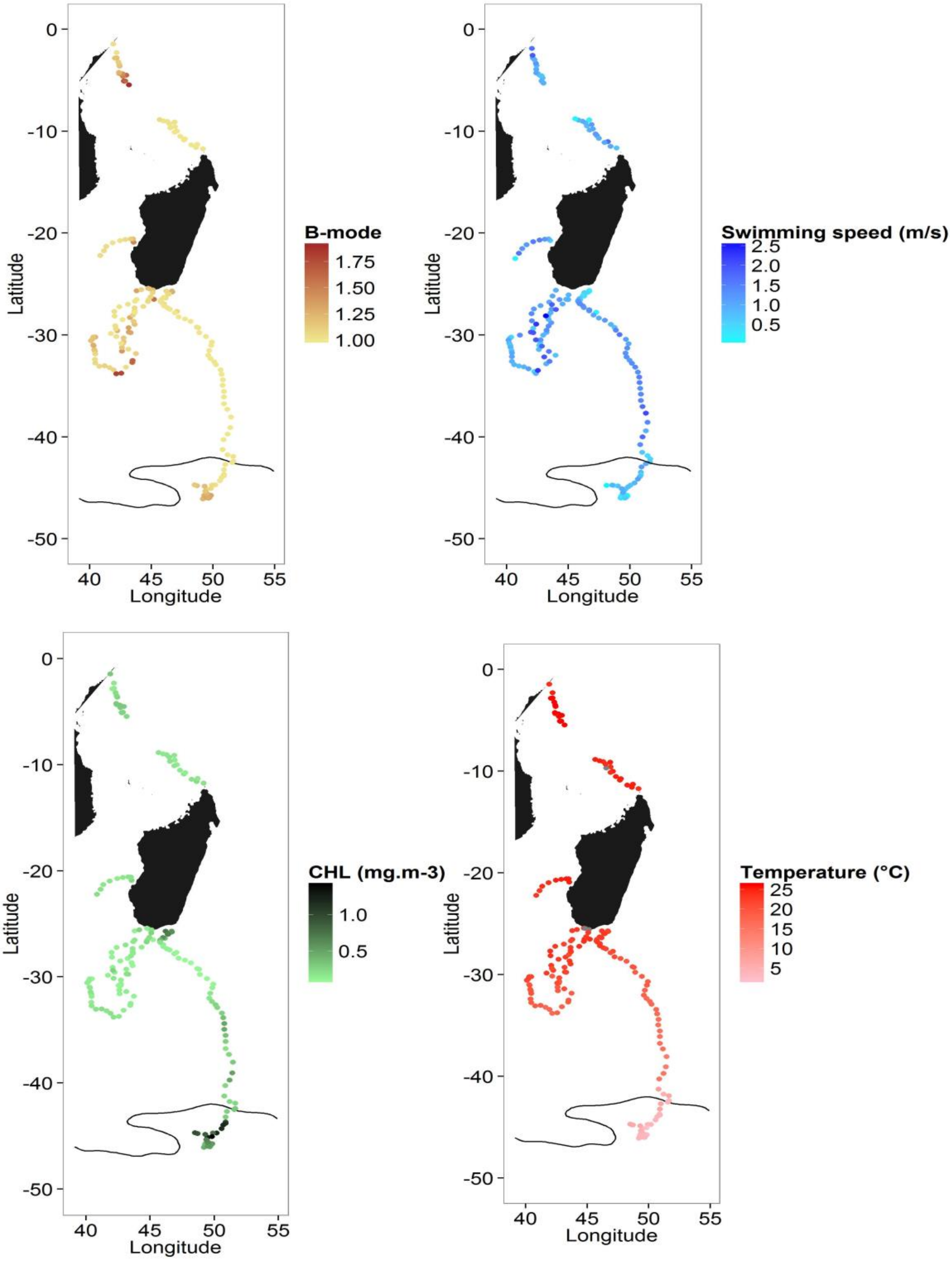

**Figure 4.4.** Locations for whale oceanic movements. Values of the B-mode (top left), the active swimming speed (top right), the CHL (bottom left), and the current speed (bottom right) are expressed for each location. Polar Frontal Zone from Roquet et al. (2013) is represented by the black line.

## 2. INFLUENCE OF ENVIRONMENTAL CONDITIONS ON BEHAVIORAL MODE AND SWIMMING SPEED

The behavioral mode of open ocean movements was most parsimoniously described by a model including only two environmental variables: current speed and water depth; no significant influence of slope or CHL concentration was detected (**Table 4.4**). Residuals are normally distributed and homogeneous (**annex G**). The probability of exhibiting localized movements was negatively related to both deeper waters and higher current speed.

Active swimming speed was most parsimoniously described by a model including only water depth and CHL concentration (**Table 4.5**). Residuals are normally distributed and homogeneous (**annex H**). Whales swam faster in deeper waters and in areas with lower CHL concentration (**Figure. 4.4**). No significant effect of slope and current speed was detected.

It is interesting to note that for all oceanic movements, the mean active swimming speed was always found to be 2-5 fold greater than the mean surface current speed they encountered.

**Table 4.4.** Summary of regression coefficients from the most parsimonious models (LMM) relating B-mode (logit) to environmental parameters for the seven whales which travelled in oceanic areas. Coefficients are presented ± SE with their p-value associated. Significant parameters are highlighted in bold characters.

| | **Oceanic Model** | |
|---|---|---|
| | **B-mode** | |
| | n=172, 7 whales | |
| Random effects: ~1\| Whale ID | | |
| | (Intercept) | Residual |
| StdDev | 0.97 | 0.99 |
| **Explanatory variables** | **Coef ± SE** | **p-value** |
| Intercept | -1.99 ± 0.42 | 0.00 |
| Sea surface temperature | | |
| Bathymetry | **-0.35 ± 0.11** | **< 0.01** |
| Slope | / | / |
| Current speed | **-0.19 ± 0.1** | **<0.05** |
| Chlorophyll concentration | / | / |

**Table 4.5.** Summary of regression coefficients from the most parsimonious models (LMMs) relating whale swimming speed to environmental parameters for the seven whales which travelled in oceanic areas. Coefficients are presented ±.SE with their p-value associated. Significant parameters are highlighted in bold characters.

| | **Oceanic Model** | |
|---|---|---|
| | **Swimming speed** | |
| | n=172, 7 whales | |
| Random effects: ~1\| Whale ID | | |
| | (Intercept) | Residual |
| StdDev | $3.8.10^{-5}$ | 0.55 |
| **Explanatory variables** | **Coef ± SE** | **p-value** |
| Intercept | 1.05 ± 0.05 | 0.000 |
| Sea surface temperature | | |
| Bathymetry | **0.17 ± 0.06** | **< 0.01** |
| Slope | / | / |
| Current speed | / | / |
| Chlorophyll concentration | **-0.12 ± 0.05** | **< 0.01** |

### 3. OCEAN CURRENTS INFLUENCE ON ANIMAL DIRECTION IN OCEANIC HABITAT

The mean magnitude of C, the surface current, along oceanic whale tracks ranged from 0.16 to over 0.51 m/s, while the mean magnitude of A ranged from 0.87 to over 1.27 m/s and was larger than C for all whales (**Figure 4.5**). Only whale M, which moved offshore toward the Mozambique Channel showed an A higher (1.27 m/s) than T (0.97 m/s). In addition, in all pelagic whale movements, the PATs (the projection of the active swimming vector onto the observed direction vector) were higher than the PCT (the projection of the current vector onto the observed direction vector (**Figure 4.6**). This demonstrates that the whales actively swam regardless of current speed

As shown in **Figure 4.7**, even though A-C angle and current speed were negatively correlated (Pearson's r= - 0.27, $p < 0.001$; df = 173) the whale active swimming speed did not depend on current speed, and plateaued at around 1m/s for current speeds increasing from 0.2 to 1 m/s. (**Figure 4.7**). As further shown in **Figure 4.8**, when whales moved away from

Madagascar to north or south, the A-C angle was low and then varied according to each individual whale's path (**Figure. 4.8, Figures S4.7.1 and 4.7.2**). Whales were oriented in the same direction as prevailing currents when current were strong in the oceanic sectors (**Figure 4.8**). We note however that no environmental parameter was retained in the deviation model with A-C angle and current speed.

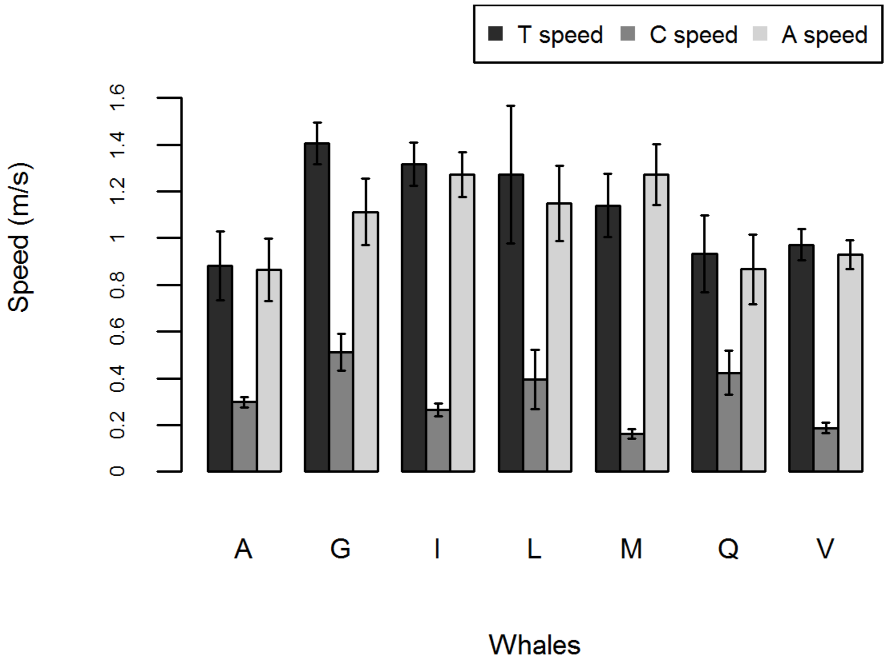

**Figure 4.5.** Mean speed ± se of the observed whale speed (T), the current (C) and whale's active swimming speed (A) vectors for the each individual whale during oceanic movement. The value of C speed shows the mean intensities of the currents along each whale trajectory while A provide a measure of each whale's active swimming effort.

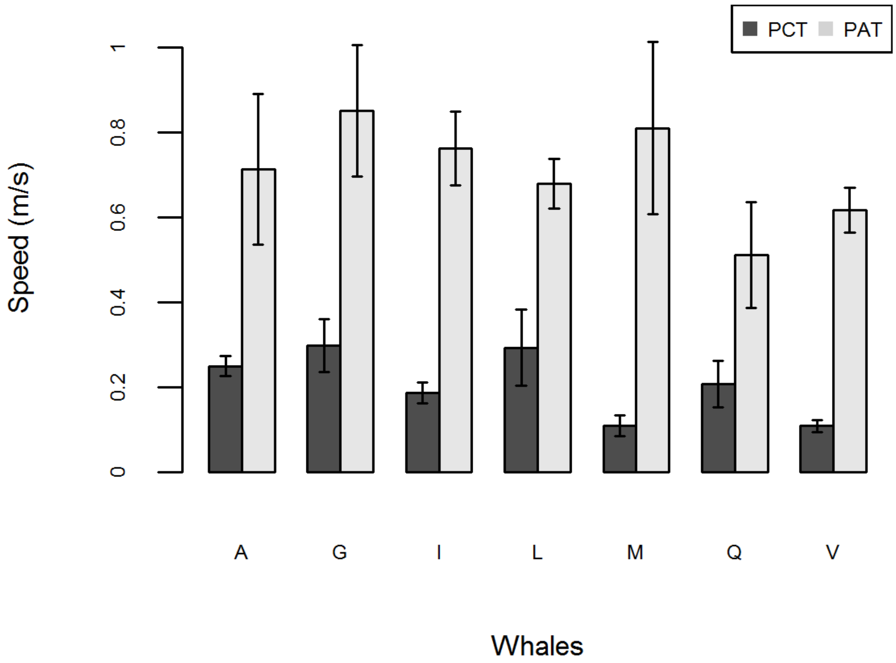

**Figure 4.6.** Mean ± se projections of the C vector on T vector (PCT) and A vector on T vector (PAT) for the each whale.

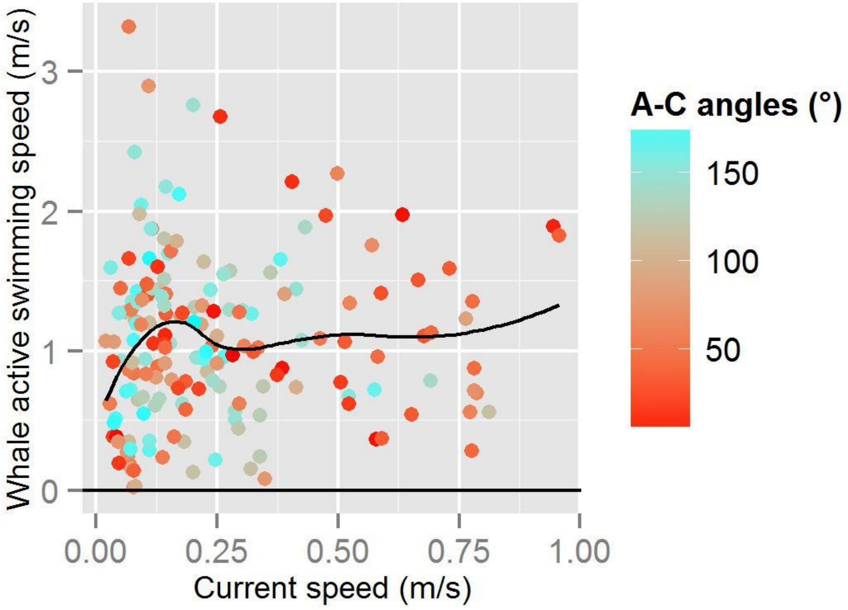

**Figure 4.7.** Whale active swimming speed (A) by current speed (C). Color scale show angles between A and C vectors (A-C angles).

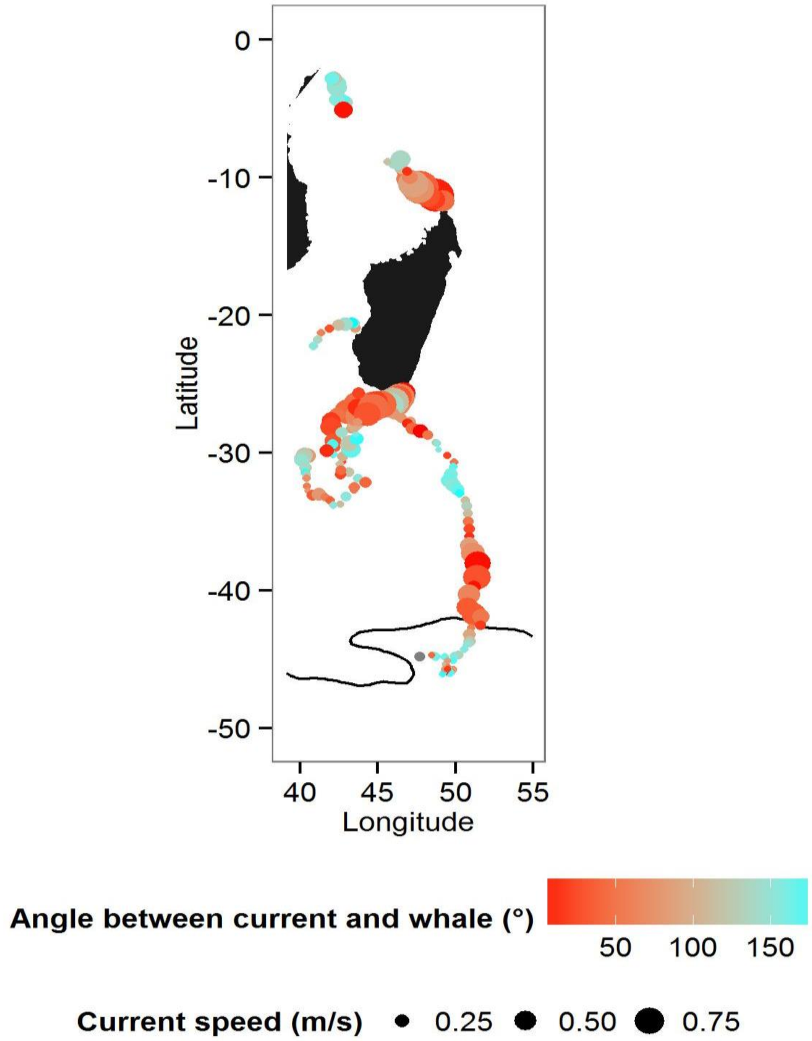

**Figure 4.8.** Current speed for each whale oceanic location. Color scale show angles between A and C vectors (A-C angles).

# V. DISCUSSION

## A. GENERAL PATTERNS OF COASTAL AND OCEANIC MOVEMENTS

In this study, humpback whales preferentially used the continental shelf over open ocean waters. In addition, they spent, on average, more time per unit area when performing coastal movements than during oceanic movements. This concurs with the lower observed whale speed and more localized behavior (i.e. lower behavior mode) found in coastal waters. Altogether, these results suggest that the shelf is a key habitat on which whales were engaged in intense local breeding-related activities (e.g. searching, pairing, mating, and resting; Jenner et al. 2001). Whales reduced their swimming speed, and increased the time spent in a given area, while interacting with conspecifics on the shelf. Both females and males increased their active swimming speed with decreased current speed, suggesting that in coastal habitats when whales were engaged in mate-searching movements, current speed did not influence their movement patterns (Chapman et al. 2011). In contrast, in oceanic habitats the currents influenced whale behavioral mode and could impact the whale headings. Our models did not show any influence of SST on humpback whale movement patterns, perhaps as a result of the low variations in SST within the Madagascar coastal region, and/or because SST does not impact the way whales use their habitat once they reach the breeding grounds.

## B. COASTAL MOVEMENTS OF FEMALES AND MALES IN RELATION TO HABITAT CHARACTERISTICS

While all whales spent more time visiting coastal than oceanic areas, females performed more transiting than localized movements during their time in the coastal environment, as indicated by their mean behavioral mode. Although no significant differences were found in behaviors and habitat use between females with calves and females without calves, females with calves tended to performed more localized movements and occurred in nearer-shore areas than females without calves. The most important environmental parameters affecting the movement patterns of females were the sea floor depth and distance from shore. All females exhibited more localized movements at greater distances from shore and in deeper waters, suggesting that they used the offshore habitat more intensively than expected. Because of the difficulty of identifying females in the field in the absence of a calf, little information exists on non-parous females' movements and potential influence of habitat features. Non-parous females (migrating to the breeding grounds solely to mate) can be found in competitive groups or pairs that are mostly observed in deeper waters, farther from shore (Frankel et al. 1995, Martins et al. 2001, Félix & Botero-Acosta 2011). This is consistent with our results, suggesting that non-parous females preferentially use areas favorable for reproductive behaviors. Previous studies show that mother-calf pairs have a preference for shallow coastal waters and areas close to shore (Smultea 1994, Craig & Herman 2000, Martins et al. 2001, Zerbini et al. 2004, Félix & Botero-Acosta 2011). Although many previous research studies including boat-based and shore-based studies of humpback whales spent little time in offshore areas, others studies sampled both inshore and offshore areas in a relatively comparable way and found mother-calf pairs preferentially in coastal waters (e.g. Jenner et al. 2001, Zerbini et al. 2004, Andriolo et al. 2006, Findlay K P et al. 2011). Females with calves may change movement patterns and habitat use across the season as the calf matures by moving more extensively in offshore areas and deeper waters on the shelf. It could be expected that females introduce breeding locations to their newborns or prepare them for migration, although this has never been demonstrated (Darling 2001, Félix & Botero-Acosta 2011). Our tracking data revealed that females, including mothers with calves, use offshore areas on the shelf, suggesting that females likely exploit a more extended range of reproductive habitat than previously thought. While habitat preferences of groups with calves have been well studied in nearshore areas, non-parous female's habitat is still poorly known.

Our models did not reveal any significant effect of environmental parameters on the type of movements (localized or transiting) performed by males. However, male active swimming speed was positively influenced by depth indicating that animals slowed down in shallow waters. The absence of influence of key environmental parameters on the behavioral mode suggests that males were not very selective in their breeding habitat, possibly in order to increase the number of interaction opportunities with receptive females. The mating system of humpbacks whales includes alternative mating strategies adopted by males (e.g. engaging direct competition with other males, singing, or escorting) to successfully attract reproductive females and to maintain a consistent competitive mating superiority during the breeding season (Clapham, 1996, Cerchio et al. 2005). Male songs are known to play a role in the humpback whale mating system (Payne & McVay 1971, Clapham, 1996), suggesting that acoustic conditions could influence the occurrence and habitat utilization of singing males (Frankel et al. 1995, Bass & Clark 2003). However, several studies found that male movement patterns may be mostly driven by mating prospects, and by the temporal distribution of receptive females, rather than by favorable singing habitats (Frankel et al. 1995, Tyack & Whitehead 1983, Baker & Herman 1984, Weinrich 1995, Smith et al. 2008).

## C. OCEANIC MOVEMENTS IN RELATION TO HABITAT CHARACTERISTICS

Overall, in oceanic habitat, whales displayed highly directional movements in deep waters but also performed more erratic movements in oceanic shallow habitats such as Walters Shoals seamount or the Crozet Plateau during migration.

### 1. DIRECTIONAL MOVEMENTS

The tracks of tagged whales revealed that whales used oceanic habitats during the breeding season and performed highly directional and consistent movements both in deep open waters and in areas with strong currents. Non-migrating animals traveled faster in oceanic than in coastal habitats with an average observed speed of 1.21 ± 0.08 m/s. This value is slightly lower than the speed found in whales migrating southward from Moheli and Mayotte (Fossette et al. 2014) but, is comparable to swimming speeds of humpback whales migrating between the breeding to the feeding grounds in the South Atlantic (Brazil; Zerbini et al. 2011), the North Atlantic (Caribbean Sea; Kennedy et al. 2013), and the North Pacific Ocean (Hawai'i; Mate et al. 1998, Mexico; Lagerquist et al. 2008). This the first time that humpback whale swimming speed between breeding sites was investigated. Our findings suggest that during offshore movements between breeding sites, humpback whales generally swam at rate of travel similar to mean travelling speeds of migrating whales. However, humpback whales exhibited meandering and slower movements in response to shallow sea floor depth, elevated chlorophyll concentration and low current speed observed on Walters Shoals Seamount and on Crozet Island Plateau.

## 2. MOVEMENT ON WALTERS SHOALS

One individual (whale I) displayed slower, more erratic movement patterns over the offshore Walters Shoals seamount suggesting that this area constitutes either a previously undescribed breeding habitat or a potential winter feeding habitat. Humpback whales have been previously observed in the Walters Shoals seamount in September, the same period as whale I (M. Le Corre. pers. comm, 28/22/2014). Furthermore, occurrence of humpback whales over shallow seamounts during the breeding period has been documented elsewhere in the southwestern Indian Ocean (La Perouse seamount off Réunion Island, Dulau-Drouot et al. in prep), and in the Pacific Ocean (Antigonia seamounts, Garrigue et al. 2010), suggesting that seamounts likely represent important habitats for humpback whales during both the breeding and migratory periods (Garrigue et al., 2015). The aforementioned seamounts are located closer to the primary documented breeding habitat than the Walters Shoals seamount, suggesting that they are likely extensions of the breeding habitat. Since this movement pattern was unexpected and performed by a female tagged as a nuclear animal in a competitive group, Cerchio et al. (*in prep*) also proposed that the female may have become pregnant and started her migration to higher latitudes, but returned back to the Madagascar coast after the pregnancy had presumably failed. However, it is also possible that whale undertook a short trip to feed on Walters Shoals seamount. While the chlorophyll concentration was relatively low during the time that the whale was on the area, the Walters Shoals are located downstream to productive regions: south of Madagascar and the subtropical South Indian Ocean countercurrent (Penven et al. 2006, Sielder et al. 2006, Lutjeharms 2007). Interestingly, a number of humpback whales have also been sighted on the Walters Shoals seamount in summer (November and December), a time of increased productivity in the area (Colette & Parin, 1991, Best et al. 1998, Shotton 2006). The shallow waters of seamount habitats are favorable for humpback whale breeding activities, yet the abrupt topographies and the occurrence of localized physical processes (e.g. tides, eddies, and upwelling) surrounding seamounts are known to favor prey aggregation attracting marine mammals (Kaschner 2008, Porteiro & Sutton 2008, Morato et al. 2010) such as humpback whales (Tynan et al. 2005, Mate et al. 2007). Consistently, the Walters Shoals area is also known to be a seabird foraging hot spot (Le Corre et al. 2012, Pinet et al. 2012). Further investigation and larger sample sizes are needed to fully understand the presence of humpback whales in that region at that time of the year.

### 3. MIGRATION

Our results indicate that whales engaged in oceanic movements decreased their swimming speed in response to high chlorophyll concentrations. One individual (whale V) migrated south and spent six days in productive waters in the west part of the Crozet plateau before the tag stopped transmitting. This suggests that this individual may have stopped to feed in this area where a phytoplankton bloom is present all year long (Venables et al. 2007) and supports zooplanktonic populations such as copepods (Fielding et al. 2007). A recent study reporting a humpback whale migration from Mayotte toward northwest of the Crozet plateau also suggested that humpback whales could forage in that area either before migrating to Antarctic feeding grounds or could remain within the plateau area during summer (Fossette et al. 2014). According to whaling and sighting data, Crozet Island is not known as area used by humpback whales on migration corridors (IWC 2011b, Ropert-Coudert et al. 2014). However, our individual movement data confirm the idea that humpback whales may do a stopover on the Crozet plateau to feed en route to high latitude foraging areas.

## D. MOVEMENT DIRECTION

We investigated for the influence of currents on the whale active swimming speed and direction of travel during the offshore sections of tagged whale tracks. We note that, to our knowledge, this is the first time current influence on whale movements has been investigated using current values extracted under the whale positions. Humpback whales exhibited highly directional travelling movements over deep waters. The active swimming speed accounts for a large proportion of the whale observed speed, which is consistent with our model showing that animals did not change their active swimming speed in response to the current speed. In contrast, observed direction of tagged whales tended to be closer to the current direction when the current intensity was high. We found that whales tended to follow the currents when they moved away from Madagascar. Then, depending to their headings, they may adjust their movement direction to the local current conditions. Few studies have investigated the influence of ocean currents on swimming speed and direction of large migratory species, and previous work has mostly concerned leatherback turtle (*Dermochelys coriacea*, Luschi et al. 2003, Gaspar et al. 2006, Lambardi et al. 2008, Fossette et al. 2010, Galli et al. 2012). A tracking study of humpback whales migrating from the Brazilian breeding grounds to the South-Atlantic feeding grounds has suggested that whales would tended to keep a constant heading regardless of current direction, but their analyses were based on regional mean currents (Horton et al. 2011). Chapman et al. (2011) discussed the same results from a theoretical point of view, and suggested that whales could use a compensation strategy that involves an animal altering its heading into the flow to achieve a track coincident with its desired direction, regardless of current direction. However, these authors also noted that animals could not persistently compensate for currents over very long journeys, and might adjust their strategy to the local environmental context. In this study, we found that whales did not compensate for current direction in the strongest current area suggesting that they tended to adjust their swimming strategy to local environment. During migration, whales probably perform a current compensation strategy, as previously described for south Atlantic humpback whales. In our study we showed that in non-migratory offshore movements (e.g. between breeding sites), humpback whales could alter their headings to local environmental conditions such as in the presence of strong currents.

## VI. CONCLUSION

Our satellite tracking-based study described movement patterns and habitat utilization of humpback whales on the Madagascar breeding grounds. During the winter breeding season, humpback whale habitat was not restricted to coastal waters, but also included offshore habitat. Whales from Madagascar used offshore habitats and moved to other coastal areas in the Indian Ocean (e.g. east coast of Africa). Humpback whale movement patterns were significantly related to bathymetric features, in both coastal and oceanic habitats. In the former, females spent most of their time on the shelf where they performed localized movements while at a distance from inshore areas. Our study showed that females (with or without calf) use a wider range of breeding habitats than nearshore waters only. Unfortunately, our sample size was too small to investigate in detail the influence of environmental parameters on movements according to female sub-classes. We also found that whales performed offshore movements during breeding season and that their observed swim speeds were represented in large part by their active swimming speeds. While only seven whales performed offshore movements, we found that humpback whales do not constantly employ a compensation strategy but can alter their direction based on local currents. This study highlights the need to increase the sample size of tagged whales and extend the duration of the tag anchoring system to better identify different strategies of females (with or without calf) within breeding seasons and to better assess the different winter movements.

## VII. ACKNOWLEDGMENTS

Many individuals made this work possible. This study represents a collaborative effort between the Wildlife Conservation Society (WCS), Cetamada, Centre de neurosciences Paris-Saclay (NeuroPSI) and NOAA National Marine Mammal Lab (NMML). Maria Faria and Henry

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# VIII. APPENDIX

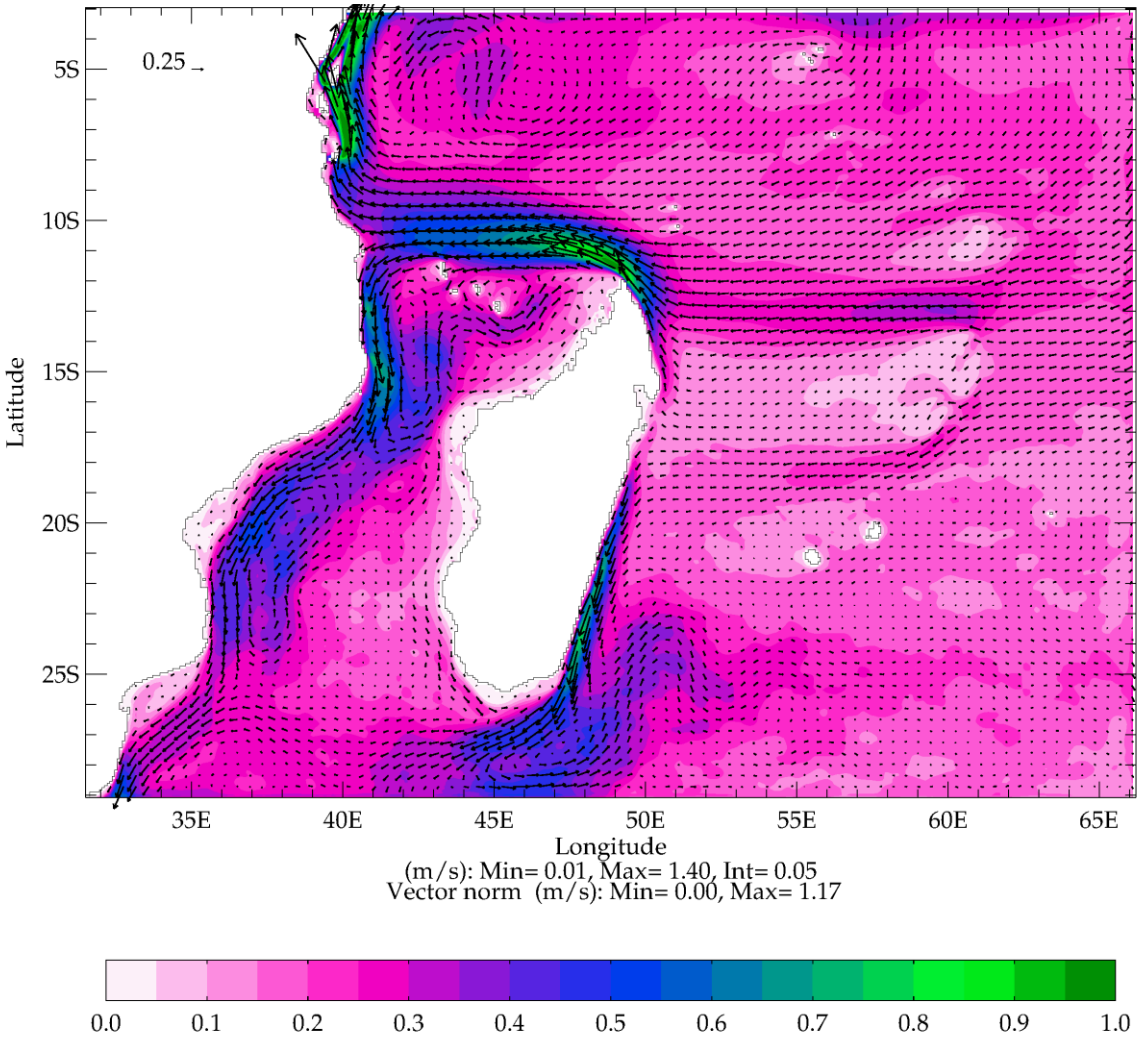


**Figure S4.1**. Mean surface current (m/s) in the Southwest Indian Ocean during the winter 1995-2009 according to the SWIO12 climatological model. Southward branch of the South equatorial current represents the East Madagascar Current (EMC).

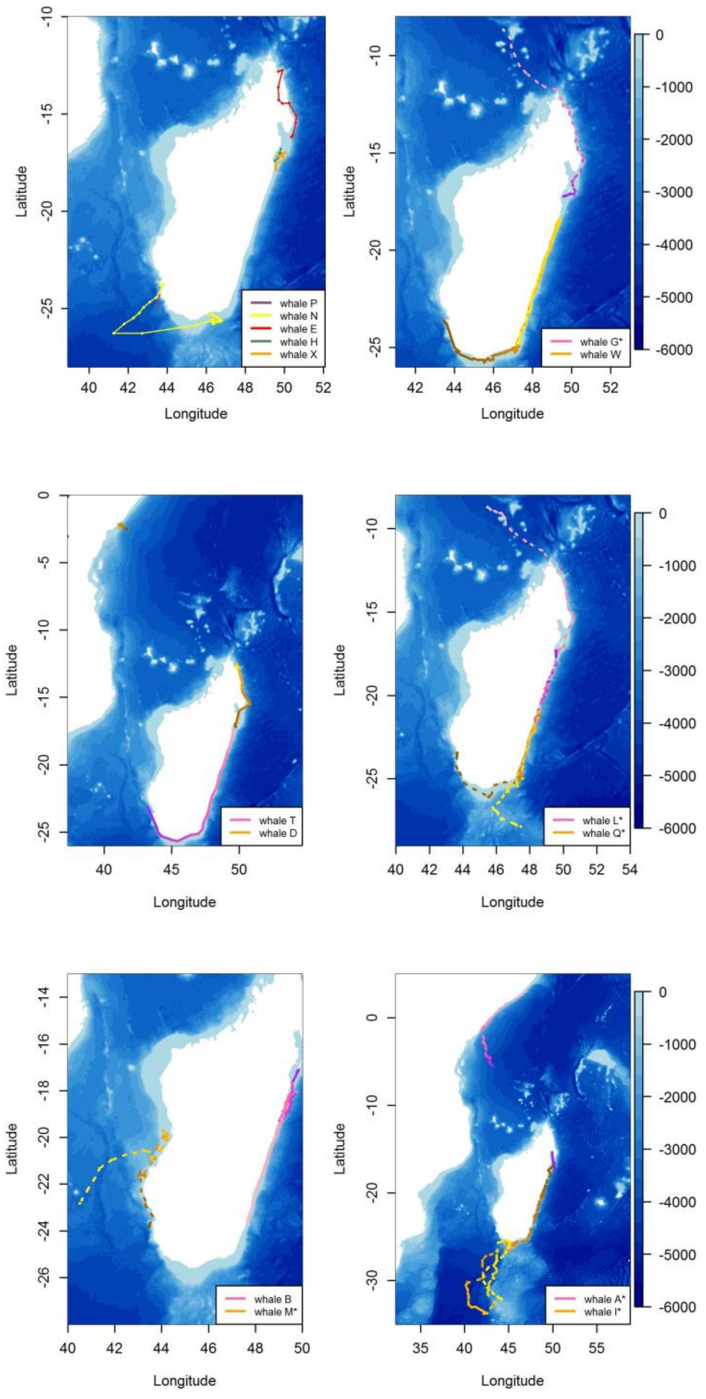


**Figure S4.2.1.** Movements of each humpback whale tracked in this study (2012-2014) after application of SSSM to filtered Argos locations to estimate improved locations. The top left map shows the whale tracks removed from analyses. Note that two whale tracks are shown on each figure. The colour scale indicates the bathymetric depth (m). The temporal progression is represented with continuous colour gradients (the first initial location after tagging is represented in purple or brown and the final location is represented in pink or yellow). Stars and dotted lines indicate tracks with an oceanic part.

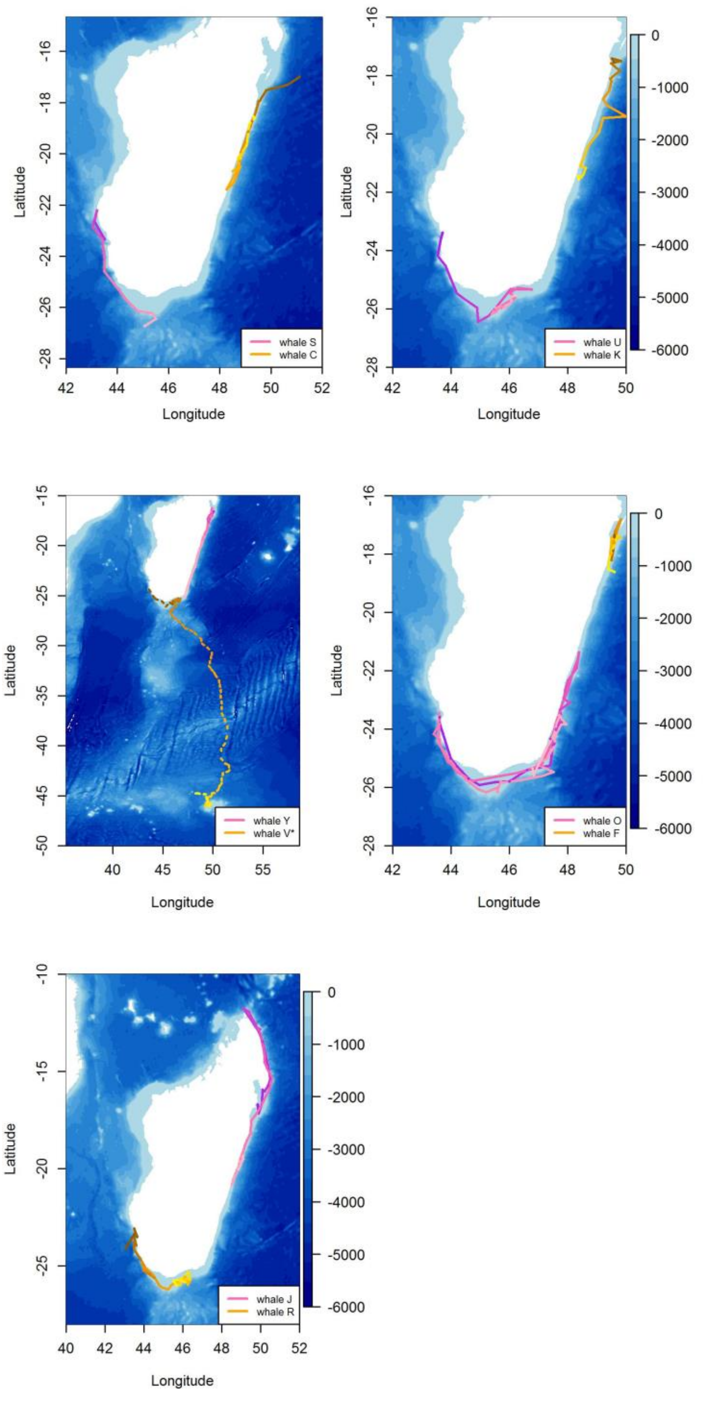


**Figure S4.2.2.** Movements of each humpback whale tracked in this study (2012-2014) after application of SSSM to filtered Argos locations to estimate improved locations. Note that two whale tracks are shown on each figure. The color scale indicates the bathymetric depth (m). The temporal progression is represented with continuous color gradients (the first initial location after tagging is represented in purple or brown and the final location is represented in pink or yellow). Stars and dotted lines indicate tracks with an oceanic part.

**Table S4.1.** Summary of environmental variables for each whale coastal track. Values are presented as mean ± se. Individuals include females (F) alone or with calves and males (M). Distance from shore is the average of distances between closest positive bathymetric value and each whale position. Stars indicate that mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| Whale id | Sex | Group type | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m.s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| A2 | M | S | 285 ± 105 | 2 ± 0.7 | 11.9 ± 2.5 | - | 25 ± 0.2 |
| B | M | CG | 178 ± 44 | 2 ± 0.4 | 10 ± 0.8 | 0.37 ± 0.01 | 24 ± 0.1 |
| C | M | P | 630 ± 222 | 3 ± 0.6 | 19 ± 5 | 0.4 ± 0.03 | 24 ± 0.1 |
| D1 | F (with calf) | MC | 450 ± 220 | 2 ± 0.5 | 10 ± 2 | 0.1 ± 0.02 | 24 ± 0.2 |
| F | M | P | 139 ± 110 | 0 ± 0.2 | 13 ± 2 | 0.22 ± 0.02 | 25 ± 0.1 |
| G | F (with calf) | MC | 213 ± 106 | 2 ± 1.1 | 12 ± 2 | 0.15 ± 0.02 | 25 ± 0.2 |
| I | F | CG | 212 ± 65 | 1 ± 0.3 | 19 ± 2 | 0.35 ± 0.03 | 24 ± 0.1 |
| J | F (with calf) | MC | 163 ± 48 | 1 ± 0.3 | 7 ± 1 | 0.25 ± 0.02 | 24 ± 0.1 |
| K | M | CG | 667 ± 208 | 3 ± 0.6 | 18 ± 4 | 0.39 ± 0.04 | 25 ± 0.1 |
| L | F | CG | 222 ± 60 | 2 ± 0.6 | 11 ± 1 | 0.37 ± 0.03 | 25 ± 0.1 |
| O | F | P | 469 ±89 | 3 ± 0.3 | 22 ± 2 | 0.37 ± 0.02 | 23 ± 0.1 |
| Q | M | P | 249 ± 68 | 2 ± 0.4 | 18 ± 2 | 0.45 ± 0.03 | 23 ± 0.1 |
| R | M | CG | 542 ± 110 | 3 ± 0.7 | 32 ± 3.1 | 0.17 ± 0.009 | 23 ± 0.1 |
| S | M | CG | 1262 ± 233 | 4 ± 1 | 43 ± 10 | 0.21 ± 0.03 | 23 ± 0.2 |
| T | F (with calf) | MBE | 129 ± 63 | 1 ± 2.5 | 7 ± 1 | 0.24 ± 0.03 | 24 ± 0.2 |
| U | F | CG | 200 ± 53 | 2 ± 0.6 | 35 ± 4 | 0.17 ± 0.02 | 22 ± 0.1 |
| V | F | NCG | 135 ± 38 | 1 ± 0.2 | 27 ± 2 | 0.13 ± 0.02 | 23 ± 0.1 |
| W | F (with calf) | MC | 60 ± 9 | 1 ± 0.1 | 8 ± 1 | 0.27 ± 0.01 | 23 ± 0.1 |
| Y | F (with calf) | MC | 34 ± 4 | 0 ± 0 | 7 ± 0.5 | 0.1 ± 0.02 | 25 ± 0.1 |

| Whale id | Sex | Group type | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m.s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| **Total** | | | **273 ± 21*** | **1.8 ± 0.1*** | **16 ± 0.6*** | **0.29 ± 0.007*** | **24 ± 0.04*** |
| **Females** | | | **191 ± 20*** | **1.4 ± 0.1*** | **14 ± 0.6*** | **0.27 ± 0.008*** | **24 ± 0.05*** |
| **Males** | | | **418 ± 48*** | **2.4 ± 0.2*** | **19 ± 1.3*** | **0.34 ± 0.01*** | **24 ± 0.07*** |

**Table S4.2.** Summary of environmental variables for each whale oceanic movements. Values are presented as mean ± se.

| Whale id | Sex | Group type | Bathymetry (m) | Slope (°) | Current speed (m.s) | Chlorophyll a concentration (mg.m$^{-3}$) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| A2 | F | CG | 3356 ± 199 | 0.7 ± 0.6 | 0.3 ± 0.02 | 0.3 ± 0.01 | 25.8 ± 0 .1 |
| G | F (with calf) | MC | 3637 ± 275 | 3.3 ± 1.5 | 0.5 ± 0.1 | 0.2 ± 0.01 | 24.8 ± 0.1 |
| I | F | CG | 3539 ± 194 | 1.4 ± 0.5 | 0.3 ± 0.03 | 0.2 ± 0.005 | 21.2 ± 0.3 |
| L | F | CG | 3183 ± 503 | 6.6 ± 3.7 | 0.4 ± 0.1 | 0.2 ± 0.005 | 24.5 ± 0.2 |
| M | - | NCG | 2261 ± 286 | 1.3 ± 0.3 | 0.2 ± 0.03 | 0.2 ± 0.008 | 24.2 ± 0.3 |
| Q | M | P | 1783 ± 139 | 2.3 ± 0.5 | 0.4 ± 0.09 | 0.3 ± 0.07 | 22.5 ± 0.7 |
| V | F | NCG | 2493 ± 165 | 1.9 ± 0.2 | 0.2 ± 0.02 | 0.5 ± 0.04 | 10.8 ± 0.9 |
| **Total** | | | **2944 ± 105** | **2 ± 0.22** | **0.3 ± 0.01** | **0.3 ± 0.02** | **18 ± 0.6** |

Supplement S4.1.

Projection of C on T vector (PCT) was calculated as C x cos (Ac-At) where C is the current speed, Ac is the direction of the C vector and At is the direction of the T vector. The projection of H vector on T one (PHT) is calculated in the same way with the appropriate changes.

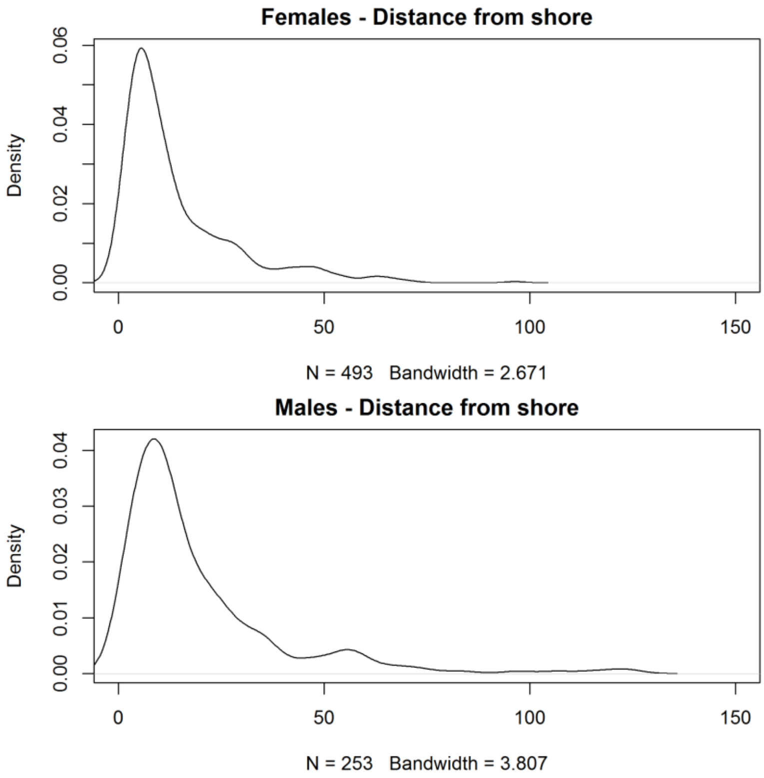


**Figure S4.3.** Density distributions of the distance from shore for females and males during coastal movements.

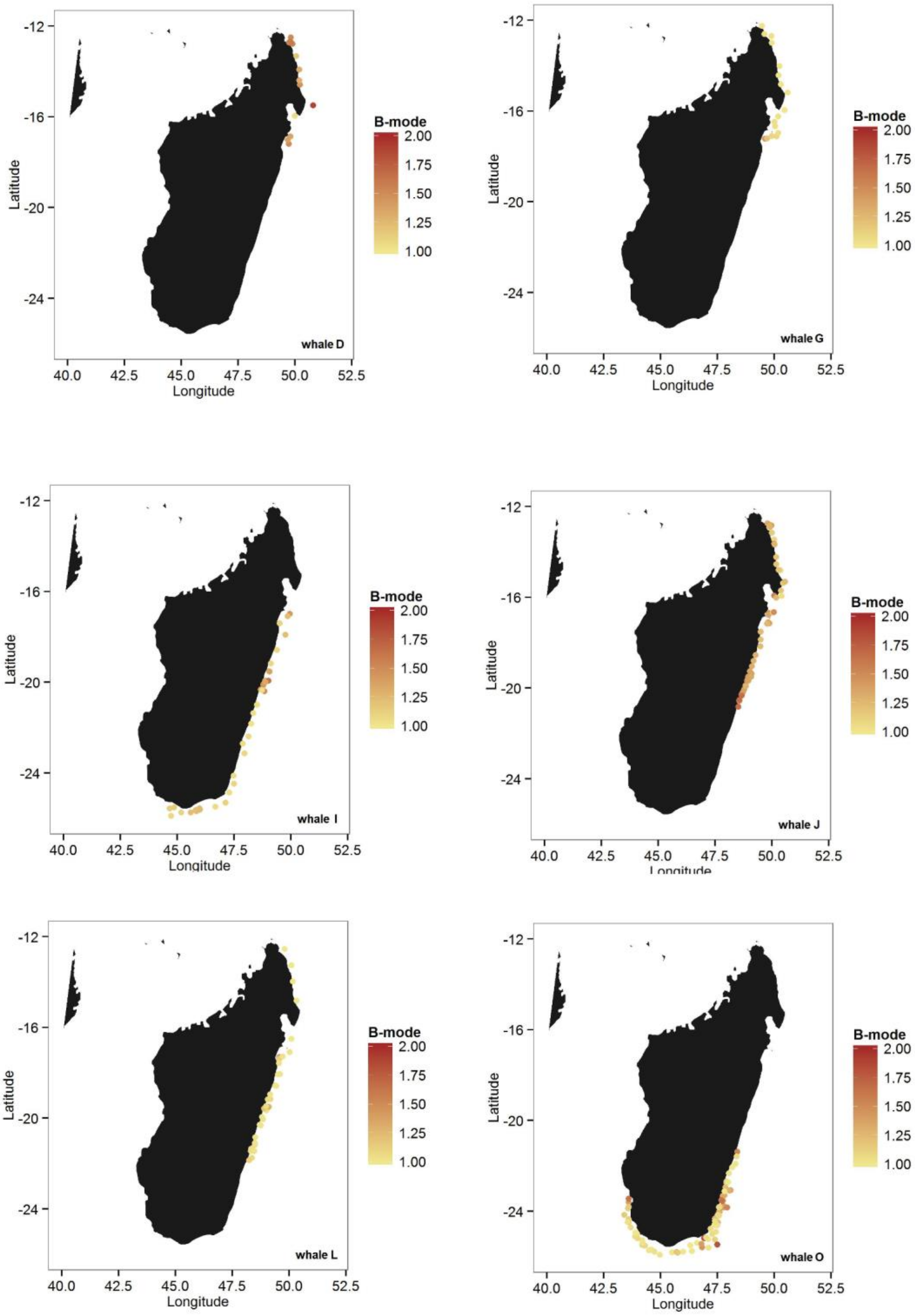


**Figure S4.4.1.** Maps of female coastal movements showing B-mode values for each estimated location. It ranges from 1, meaning low probability of localized movement and 2 meaning high probability of localized movement. In alphabetical order: whale D, whale G, whale I, whale J, whale L, and whale O.

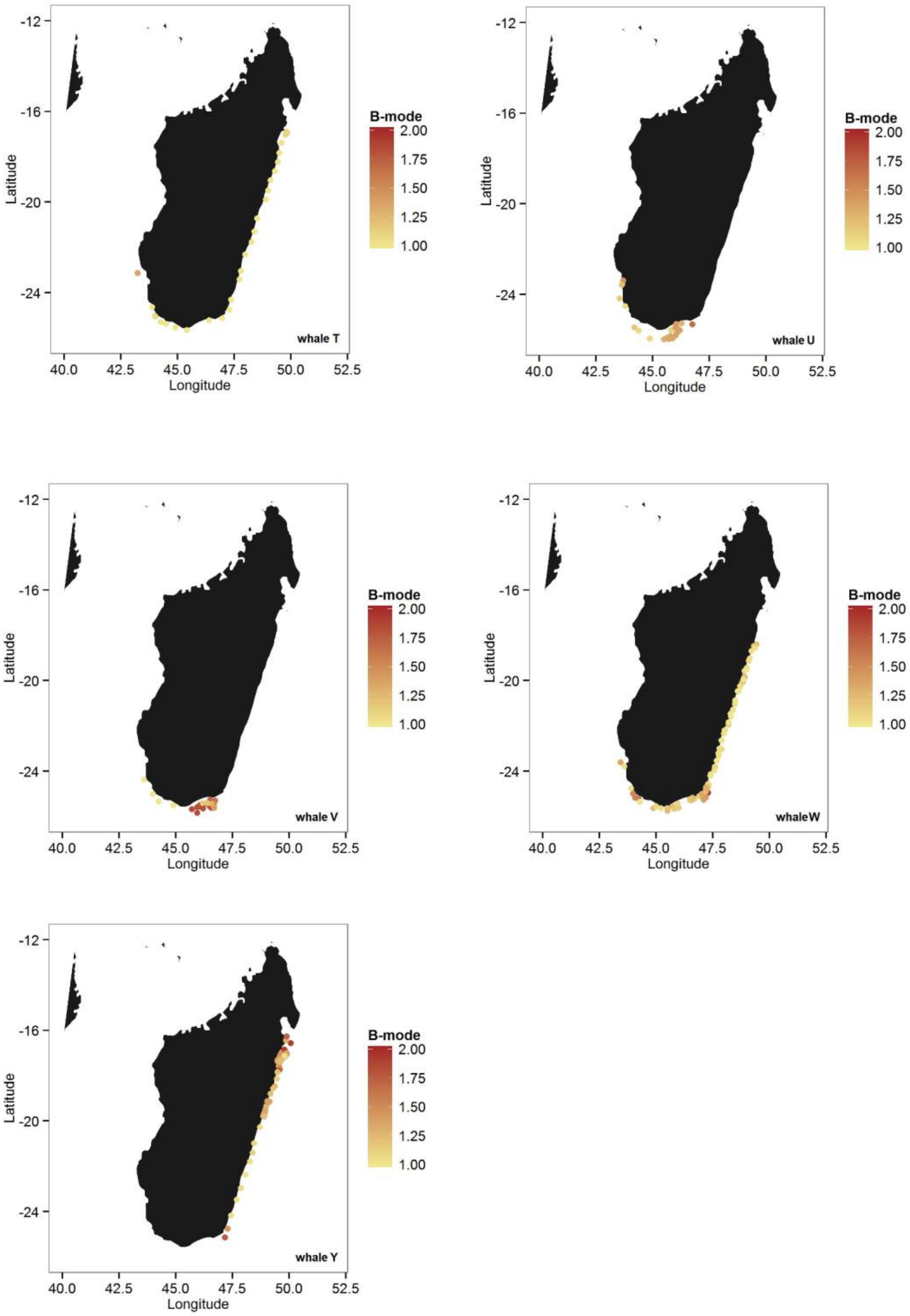


**Figure S4.4.2.** Maps of female coastal movements showing B-mode values for each estimated location. It ranges from 1, meaning low probability of localized movement and 2 meaning high probability of localized movement. In alphabetical order: whale T, whale U, whale V, whale W, and whale Y.

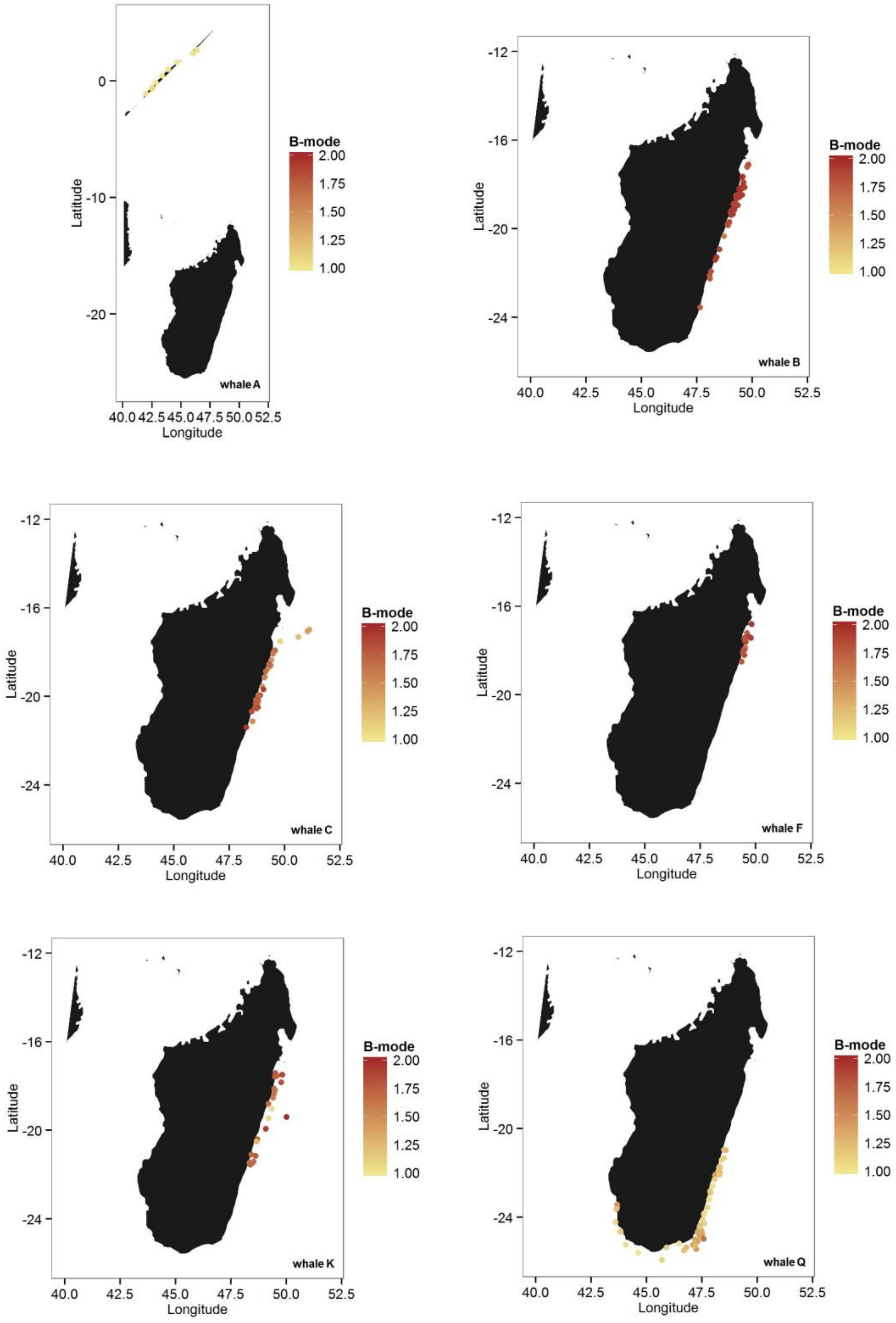


**Figure S4.5.1.** Male coastal movements showing B-mode values for each estimated location. It ranges from 1, meaning low probability of localized movement and 2 meaning high probability of localized movement. In alphabetical order: whale A, whale B, whale C, whale F, whale K, and whale Q.

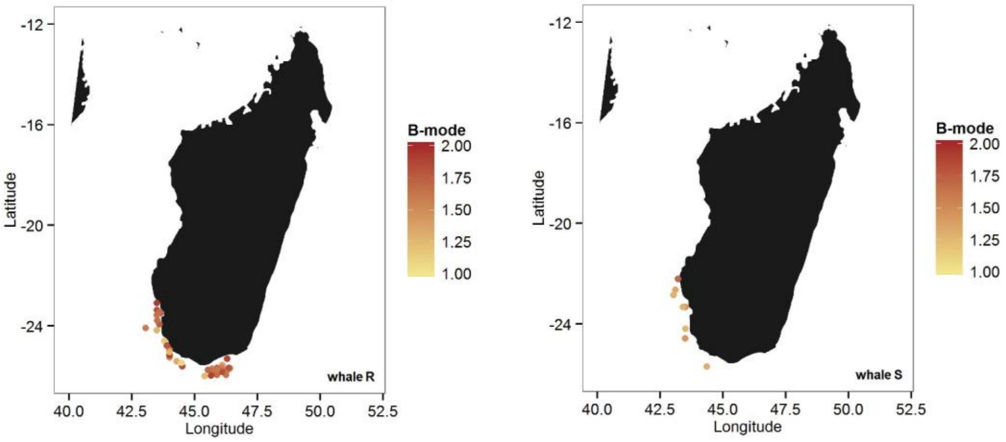


**Figure S4.5.2.** Male coastal movements showing B-mode values for each estimated location. It ranges from 1, meaning low probability of localized movement and 2 meaning high probability of localized movement. In alphabetical order: whale R, and whale S.

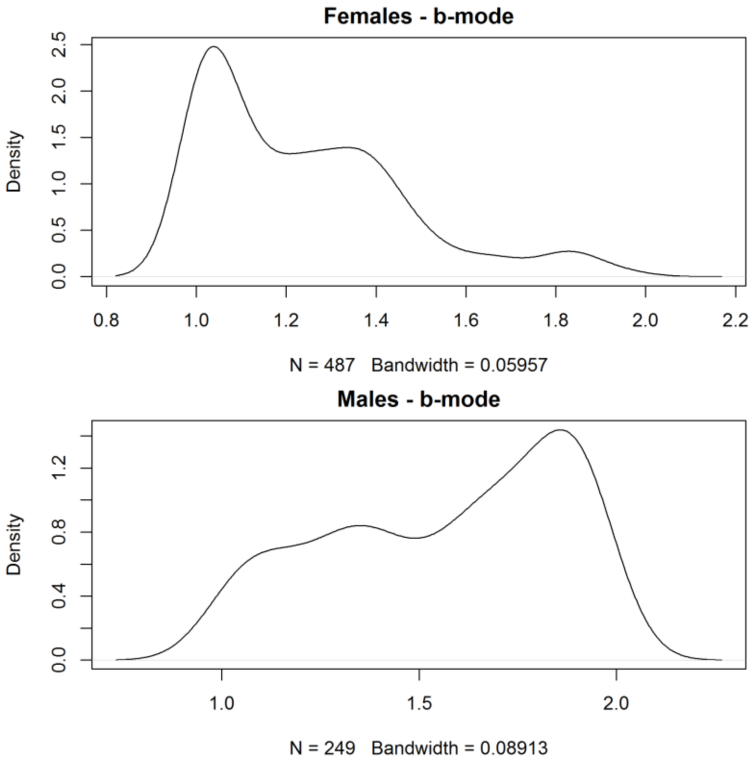


**Figure S4.6**. Density distributions of B-mode values for females and males during coastal movements.

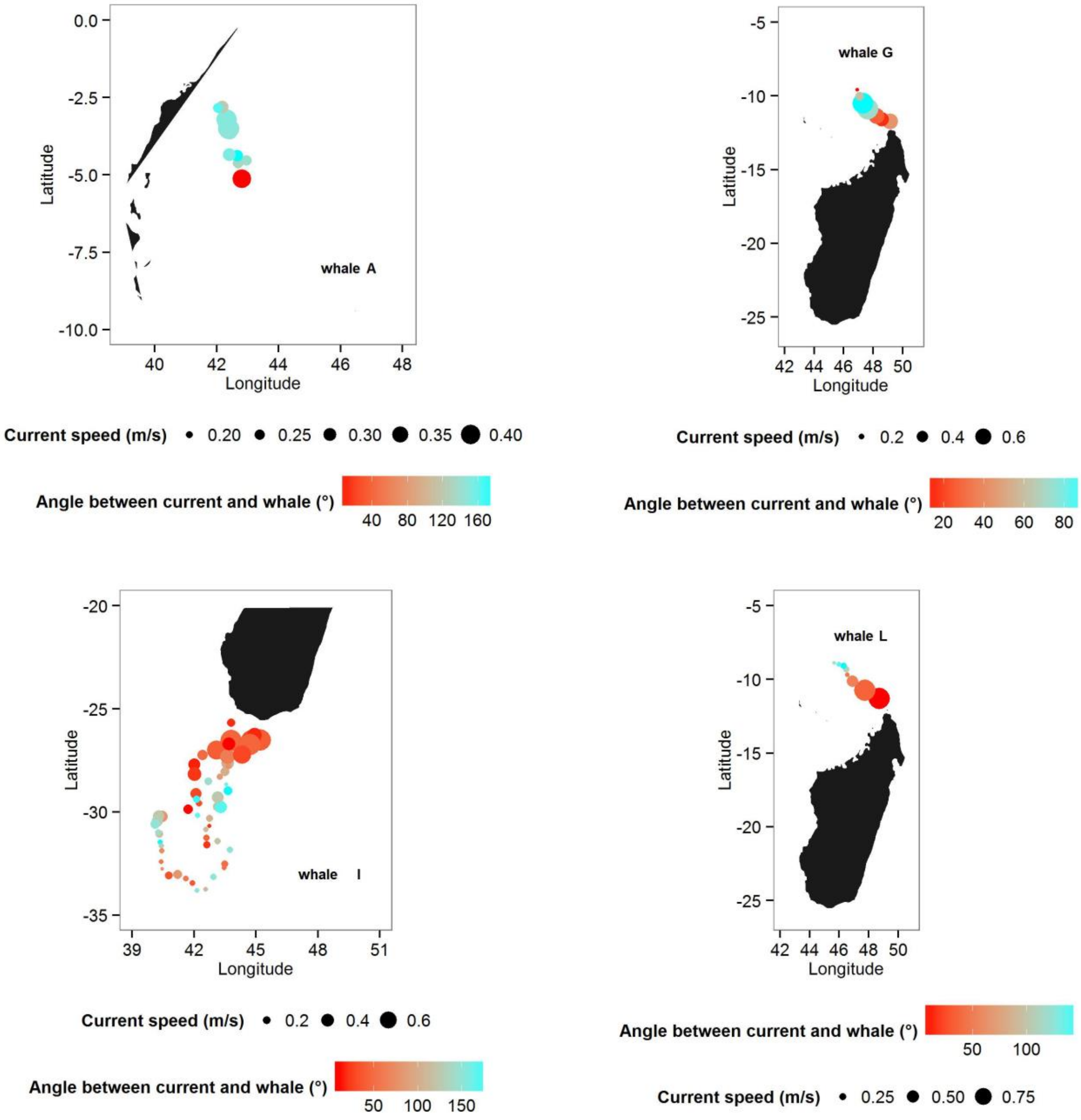


**Figure S4.7.1**. Current speed for each whale oceanic location. Color scale show angles between A and C vectors (A-C angles). Whales are in alphabetical order.

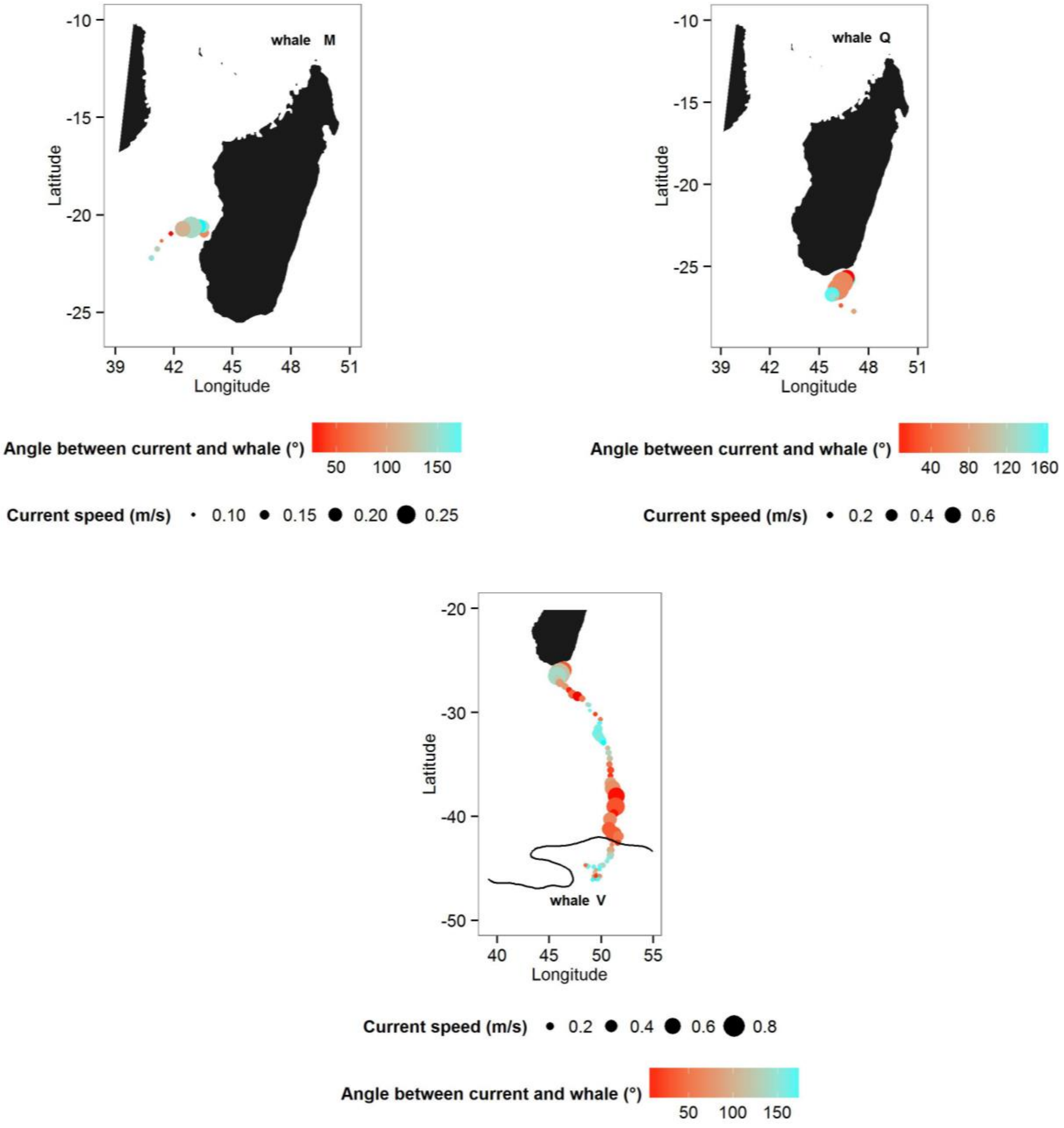
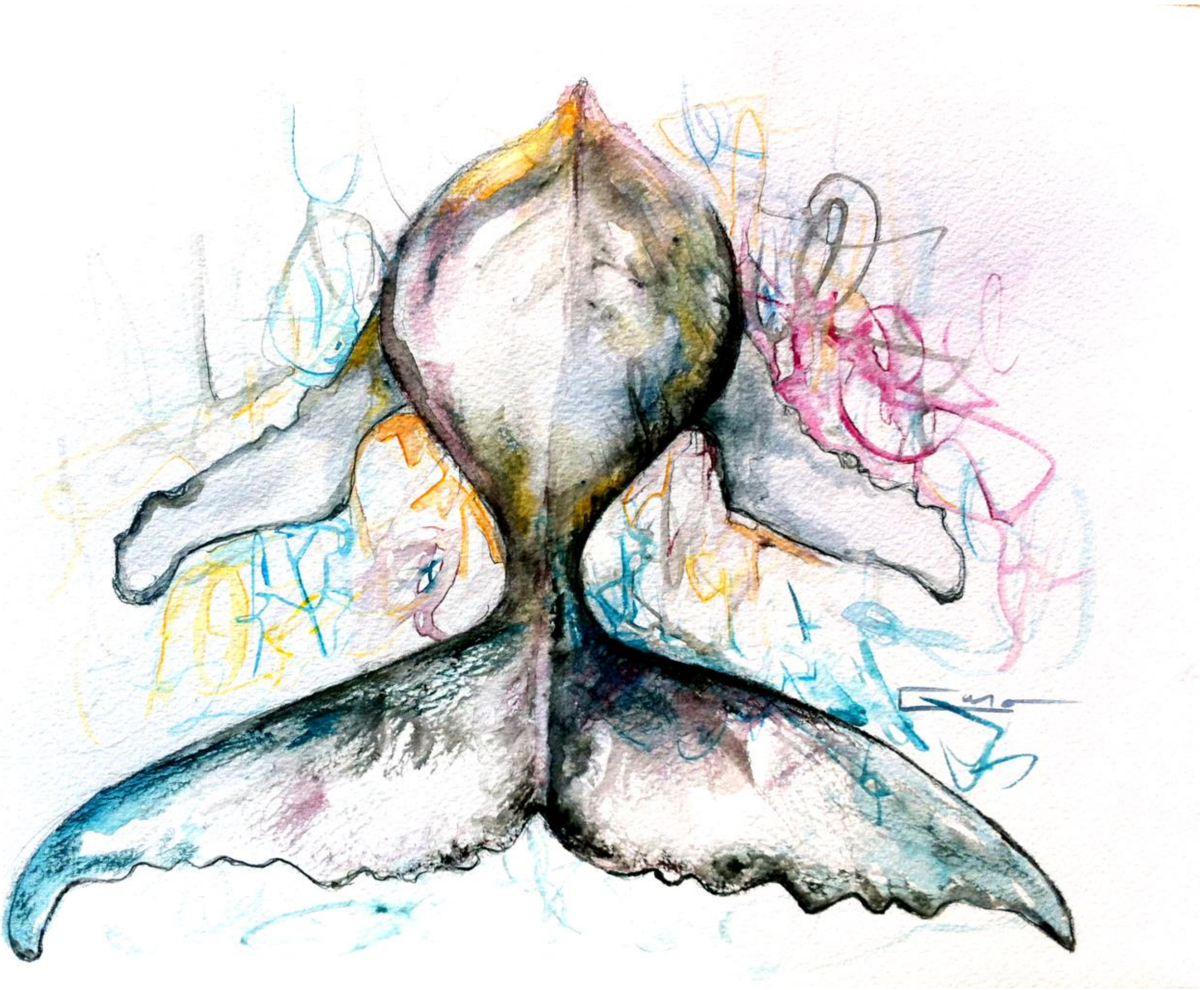


**Figure S4.7.2**. Current speed for each whale oceanic location. Color scale show angles between A and C vectors (A-C angles).

# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L'HEMISPHERE SUD



*Aquarelle de Caroline Jacques*

# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L'HEMISPHERE SUD

## RESUME

- Ce chapitre vise à comparer le lien entre les déplacements des baleines à bosse et les paramètres environnementaux à différentes périodes de la saison de reproduction (début, « pic » et fin de saison, correspondant respectivement à la phase migratoire d'arrivée vers la zone de reproduction, à la période passée sur la zone de reproduction, et au début de la migration de retour) en fonction du sexe et du statut reproducteur et ceci à partir de suivis individuels issus de différentes zones de reproduction de l'hémisphère Sud (Brésil, Madagascar, Australie de l'Ouest et Australie de l'Est).
- Les trajectoires sont issues de baleines équipées de balises Argos dans quatre populations différentes : le Sud-Ouest de l'Atlantique (Stock A, 82 individus), Madagascar (Stock C3, 20 individus), l'Ouest de l'Australie (stock D, 20 individus) divisées en deux types de déplacements, migration vers le nord et migration vers le sud (n=13 et n=13) et l'Est de l'Australie (stock E1, 13 individus). Les méthodes utilisées sont similaires à celles du chapitre 4.
- Nos résultats révèlent que la distribution spatiale et le type d'habitats utilisés par les baleines à bosse varient en fonction de la période de la saison (i.e. du stade de la migration), entre les sites et en fonction du sexe. Lors de la migration vers le nord (en début de saison), les mâles de la côte Est et Ouest de l'Australie nagent directement vers le Sud de la Grande Barrière de Corail et de la région de Kimberley où ils concentrent leurs déplacements par la suite. En revanche sur la côte ouest, les femelles transitent par différentes zones situées entre le golfe d'Exmouth et la région de Kimberley, zones probablement associées à des zones de repos. Lors de la migration vers le nord les femelles empruntent deux principaux corridors ; les femelles sans baleineau tendent à emprunter des corridors plus au large (~50 km de la côte) alors que les femelles avec baleineau longent la côte ce qui suggère des différences dans les déplacements et le choix d'habitats en fonction du statut reproducteur. Lors de la migration vers le sud les mâles utilisent un corridor migratoire plus au large, au-delà-de 200 mètres de

profondeur, tandis que les femelles accompagnées d'un baleineau vont nager le long de la côte indicant une préférence pour les eaux côtières de faible profondeur. Cette variabilité dans le type de déplacements chez les mâles et les femelles est observée chez les individus équipés à Madagascar en milieu de saison. Comme dans cette dernière région, bien que les mâles soient présents dans des eaux plus profondes, les femelles exploitent une gamme d'habitats plus large que ce qui était attendu. En fin de saison, les baleines équipées le long de la côte du Brésil présentent des schémas de distribution similaires à ceux observés dans les régions de la Grande Barrière de Corail et de Kimberley, indiquant une concentration des individus mâles et femelles dans la région principale de reproduction du banc d'Albrolhos. La côte brésiliene n'a pas été identifiée comme un corridor de migration ce qui expliquerait que les déplacements des individus soient plus localisés et probablement associés à des activités de reproduction et d'allaitement. Les couples de femelle-baleineau sélectionnant des habitats plus proches de la côte et de plus faibles profondeurs que les femelles sans baleineau suggèrent également une influence du statut reproducteur dans les préférences d'habitats des femelles.

# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L’HEMISPHERE SUD

## In three ocean basins: comparison of coastal movements and habitat use of humpback whales during the breeding season.

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# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L'HEMISPHERE SUD

## I. ABSTRACT

Although much is known about the humpback whale (*Megaptera novaeangliae*), studies on movement patterns between sexes are central to understand the differences in mating strategies. Our aim was to compare the humpback whales' coastal movement patterns in a range of breeding habitats and to investigate interactions between their movements at sea and environmental conditions according to sex and breeding status. Movement data were obtained after humpback whales were satellite tagged in four breeding grounds of the Southern Hemisphere, in three ocean basins: the Southwestern Atlantic Ocean (breeding stock (BS A, n=81), the Southwestern Indian Ocean (BS C, n=20), the Southeastern Indian Ocean (BS D) shared between northern and southern movements (n=13 and n=13), and the Southwestern Pacific (BS E1, n=11). .We extracted key environmental variables along the whale tracks and computed two behavioral metrics (B-mode, i.e. likelihood of exhibiting localized movements, and active swimming speed). We used linear mixed effect models (LMM) to quantify the influence of environmental parameters on humpback whales' movements. Overall, the movement patterns are mainly influenced by bathymetry, with whales using predominantly the extensive shallow waters areas and most often areas shallower than 50 m. Our results reflect variations in the spatial range of movements and in habitat selection by humpback whales according to the breeding sites and sex. In Brazilian and East Australian coasts, where shallow areas are relatively restricted, both females and males mostly concentrated their movements in the Abrolhos Bank and the Grand Barrier Reef, respectively, previously defined as important breeding grounds. In contrast, in the western Australian breeding ground, humpback whales performed a combination of transiting movements and localized movements between and within breeding locations likely associated with migration and regional breeding behaviors. Similarly, humpback whales performed both extensive and localized movements along the east coast of Madagascar. No significant differences in active swimming speed and B-mode were observed between males and females among sites and within sites except for Madagascar. While males used deeper waters and more offshore areas than females, the latter used a wider habitat than generally expected, as found in a previous study on the

Madagascar population. In Brazil, females with calves performed more localized movements and were found closer to shore than females without calves suggesting that the habitat selection by females could depend on the reproductive status. According to the migratory stage, whales tend to perform different movements and change of habitat according to sex and breeding status.

## II. INTRODUCTION

Understanding spatial and temporal movement patterns of wide-ranging species is essential for clarifying their population structure, understanding the foraging ecology or for conservation management of these species. Of key importance for the comprehension of these patterns is to quantify how ecological and environmental factors affect the distribution of animals, which requires knowledge on dispersal movements of individuals (Clobert et al. 2001). Because the migratory large whales strictly compartmentalize breeding and feeding at different times and separate locations over their annual cycle, and therefore use radically different habitat to fulfill their ecological requirements, they are good species candidates to to study how environmental parameters influences the spatial and temporal patterns of large migratory vertebrates. Historically, knowledge on coarse-scale seasonal movements of whales and migratory routes has been gained from whaling data including the deployment and recovery of discovery tags between the 1930s-1960s (e.g. Rayner 1940, Mackintosh 1942, Chittleborough 1958, Brown 1971). Modern data from photo-identification (Gill 1995, Franklin et al. 2007, Garrigue et al. 2007, Cerchio et al. 2008), genetic sampling (Calambokidis et al. 1996, Palsbøll et al. 1995, 1997, Patenaude et al. 2007, Rosenbaum et al. 2009) and satellite telemetry (Mate et al. 1998, 1999, Zerbini et al. 2006, Gales et al. 2009) have provided a wealth of information on these movement patterns and have contributed in a better identification of boundaries delineating important habitats. Investigating the relationships between the whale movements and the associated environmental features is crucial to understand the patterns of habitat use, and crucial for and effective management of critical habitats and the conservation of whales.

# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L'HEMISPHERE SUD

Humpback whales (*Megaptera novaeangliae*, Borowski, 1781) globally are seasonal breeders and travel thousands kilometers yearly between high latitude summer feeding grounds and low latitudes winter breeding grounds (Dawbin 1966, Clapham & Mead 1999). In the Southern Hemisphere, they migrate from feeding grounds around the Antarctic and congregate around coastal tropical or subtropical regions on both eastern and western coasts of Africa, South America, and Australia, and in several south-Pacific islands. Currently, seven breeding stocks, labelled breeding stocks A to G, have been recognized by the IWC (IWC 1998a, SH 2007). Based upon current knowledge, types of movements (e.g. movements within a final breeding destination, migration movement) and distribution (e.g. aggregation in local areas or wide distribution along the coast) of humpback whales greatly differ between the different southern hemisphere breeding stocks, and also among the different sub-stocks.

Between June and December, humpback whales are observed in the wintering ground off Brazil (breeding stock A) between 5°S and 25°S but most of the population is concentrated in Albrolhos bank (Siciliano 1995, Martins et al. 2001, Zerbini et al. 2004, Andriolo et al. 2010). Abrolhos Bank is the most important east Atlantic calving/nursing area with a high proportion of mother and calves (Siciliano 1997, Martins et al. 2001, Andriolo et al. 2010). In Abrolhos Bank, humpback whales tend to be found off islands and reef systems (Andriolo et al. 2006). While on the Brazilian coast, humpback whales congregate commonly in the main area of Albrolhos bank, in others breeding grounds humpback whales perform more complex temporal and geographical movements.

The western Australian stock, referred to as breeding stock D, is present in a vast area including both migration routes and breeding areas. Humpback whales are found along the Australian west coast (15-35°S) between June and October, with resting/nursery areas located in Shark Bay and Exmouth Gulf, and with a major reproductive/calving area found in the Kimberley region (Bannister 1994, Jenner et al. 2001, Double et al. 2010, 2011). Off Northwestern Australia, humpback whales occupy a wide longitudinal range, and use an offshore corridor when migrating southward (Double et al. 2011). In the Kimberley region, humpback whales aggregate in the Frost and Tasmanian Shoals and Camden Sound (Jenner et al. 2001, Double et al. 2011). The large latitudinal range of humpback whale and the observed variety of movements complicate comprehensive understanding of the breeding habitat use in this region.

Similar patterns have been identified off the east coast of Australia (breeding stock E1). Each winter (between May and October), humpback whales migrate along the east coast from 10°S to 37°S with the major breeding aggregation located in the Great Barrier Reef (16-21°S, GBR) (Simmons & Marsh 1986, Chaloupka & Osmond 1999). Smith et al. (2012) used a habitat modelling approach to link the whales' distribution and environmental parameters and identified two key areas of high habitat suitability in the GBR: the southern part of the lagoon and offshore areas off the Capricorn and Bunker islands groups. As observed in the western coast of Australia, a coastal site, Hervey Bay, was identified as a major resting/nursery area along the southern migratory path (Chaloupka & Osmond 1999, Martinez et al. 2015).

At the basin scale, the breeding grounds are defined by a preferential sea surface temperature range of 21.1°C et 28.3°C (Rasmussen et al. 2007). At local scale, environmental features as well as social organization and reproductive status influence the habitat preferences of humpback whales (Craig & Herman 2000, Ersts & Rosenbaum 2003, Félix & Botero-Acosta 2011). Breeding humpback whales are generally concentrated close to continental shelf areas, oceanic islands and reefs. Mother and calves are frequently found in very shallow, sheltered or coastal waters in comparison to other reproductive groups (Mattila et al. 1989, Smultea 1994, Martins et al. 2001) with the exception of the Au'au Channel in Hawaii (Cartwright et al. 2012). While mothers and calves maintain a preference for shallow waters, they could alter their habitat use according to local pressure such as human disturbance (Cartwright et al. 2012). Predominance of maternal females (i.e. female with a calf) in shallow waters can be driven by the mitigation of predation risk, energy conservation, or male avoidance (Smultea 1994, Craig et al. 2002, 2014, Ersts & Rosenbaum 2003, Elwen & Best 2004). In contrast, receptive females (i.e. female that migrate only to become fertilized) are mostly found in large reproductive groups (i.e. competitive group) or pairs but their patterns of habitat use is still poorly known (Pomilla et al. 2006, Cypriano-Souza et al. 2010, Herman et al. 2011). Similarly, habitat use and influence of environmental parameters on male distribution have been little investigated. Males are observed in all different social groups (i.e. singleton, pairs, mother-calf-escort, competitive groups), while some studies suggest that males select suitable singing habitats such as deep waters (Frankel et al. 1995, Oviedo & Solís 2008). While sex segregation of habitat by humpback whales has been reported, in particular for maternal females, relationships between movement patterns and environmental parameters according to sex are not well understood.

Our study uses a multi-year and large scale set of satellite tag deployments to compare the whale coastal movements and habitat use between males and females in four of the main Southern Hemisphere breeding grounds including the Southwestern Atlantic Ocean (breeding stock A, BSA), the Southwestern Indian Ocean (breeding stock C, BSC), the Southeastern Indian Ocean (breeding stock D, BSD) and the Southwestern Pacific (breeding stock E1, BSE1). In these different breeding grounds whales were tagged at different stages of the migration cycle: early in the beeding season, at the season peak and late in season. In addition, these breeding grounds differ in their main environment characteristics such as topography (width of continental shelf slope), geographical configuration (island, continent) and oceanographic parameters (sea surface temperature, current). In this context, we aimed i) to compare the coastal movements patterns according to sex and breeding regions at the different stages of the breeding season and ii) to investigate the link between movements and environmental parameters according to sex and breeding regions at the different periods of the breeding season. We expect to observe a variety of range of different movement patterns between sex and time of the season. During northward (early part of the season) and southward (late part of the season) migrations, whales could display more directional movements than whales tagged during the peak of the breeding season. Most of the tagged females were mothers with calves, so we expect that females use preferentially shallow and coastal waters whereas males are expected to be found in the same habitats but shouldn't be strongly clearly influenced by environmental features as we previously found in Madagascar.

# III. MATERIAL AND METHODS

## A. TAG DEPLOYMENT

Our study brings together datasets from four distinct humpback whale breeding regions of the Southern Hemisphere (**Figure 5.1**): Southeastern Brazil (BSA), Madagascar (BSC3), Western Australia (breeding stock, BSD), and Eastern Australia (BSE1). In the Brazilian study, tag location changed over time and was conducted between August and November from Conceiçao da Barra (18°30', 39°30'W) in 2003, from Nova Vicosa in 2004-2007, 2012, from a research cruise along the whale range of the population in the breeding ground in 2008 and 2012 and, from Barra Grande in 2009-2011. Details on tag deployment and transmitter configuration can be found in Zerbini et al. (2006, 2011). In Madagascar, tag deployments were conducted between July and August in Sainte Marie Channel (16°50'S, 49°55'E) in 2012 and 2014 and off Anakao (23°40'S, 43°39'E) in 2013. Details on tag deployment and transmitter configuration can be found in Cerchio et al. (*in prep*, cf. **annex A**). In Western Australia, tags were deployed in two distinct regions at different places: North West Cape (Exmouth Gulf, ~ 21°59'S, 114°7'E; Ningaloo reef; ~22°40'S 113°39'E) and Kimberley region (Broome, Pender Bay, Buccaneer, and Camden Sound; ~22.56°S, 113.62°E). Tags were deployed in August 2005 and July 2011 in North West Cape (hereafter named "BSD-WAC") and between July and September of 2008 and 2009 in the Kimberley region (hereafter named "BSD-WAK"). The deployment location in Eastern Australia was in Evans Head (29°07'S, 153°26'E) in June 2009. Tags and methods are described in details by (Gales et al. 2009, 2010).

## B. DATA PROCESSING AND ARGOS LOCATIONS FILTERING

Data processing used in this study are described in chapter 4 of this PhD dissertation, section Material & Methods. The behavioral mode parameter measures the likelihood of exhibiting localized movements based on the mean turning angle, and the autocorrelation in speed and direction into the first difference random walk model within the SSSM (Jonsen et al. 2005). It ranges from 1, meaning low probability of localized movement and 2 meaning high probability of localized movement (Jonsen et al. 2007). Details on estimation procedure are presented in Jonsen et al. (2005, 2006).

Because our study deals with habitat use on the breeding grounds, we only considered the whale position between the coastline and the 500 m isobaths for our analysis. For Western Australian data, based on the literature (Chittleborough 1965, Hedley et al. 2001, Jenner et al. 2001) and the density distribution of positions, we removed positions to the south of Shark Bay where movements have been clearly identified as migration. For the whale 121189.12 (312 days of transmission) that migrated to feeding gound before moving back to Brazilian coast, we analysed separately the two coastal segments of the track (hereafter named 121189-1.12 and 121189-2.12).

### 1. ENVIRONMENTAL VARIABLES

Extraction of environmental variables is described in chapter 4. Because estimating geostrophic currents in coastal areas using satellite altimetry has proven problematic, we chose in the BSC3 study in Madagascar (chapter 4) to use a climatological estimate of a geostrophic current in the coastal area instead of daily estimates from satellite altimeters. However, in the Australian and Brazilian sectors studied here, we do not have access to reliable climatological estimate of geostrophic current in the coastal areas. We therefore used the daily estimates of geostrophic currents from satellite altimeters (Aviso product), but we note that a number of current estimates (~30 %) at whales positions were available in the coastal area. In addition, SST datasets from JPL products (previously used in Madagascar study; see chapter 4) not being available before 2010, we extracted SST from a daily sea surface temperature dataset produced and distributed by NCDC (National Climatic Data Center; https://podaac.jpl.nasa.gov/dataset/NCDC-L4LRblend-GLOB-AVHRR_OI) at 0.25° spatial resolution (Reynolds, et al. 2007).

## 2. STATISTICAL ANALYSIS

The general methods of statistical analysis used in this study are described in chapter 4 of the present dissertation, section Material & Methods. Whale movement were analyzed using LMMs considering the logit of behavioral mode (B-mode) values and the whale active swimming speed values as response variables, and SST, bathymetry, distance from shore, slope, and current speed as covariates. In this study, the response variables were standardized (centered and scaled) by individual prior to analyses to correct for non-Gaussian distribution.

Permutation tests (PERMANOVA, permutation t-test) were used to compare behavior metrics and environmental metrics between i) sites, ii) sex between sites iii) sex within each site and vi) female classes (i.e. with or without calf) within each site when individuals of both classes were tagged. Distribution of position data were investigated qualitatively by calculating kernel density. With only two females, Eastern Australia was not included in the female analysis. Spatial distribution of behavioral states were evaluated by plotting the standardized mean of B-modes on a 0.3° grid: each cell contained a mean of individual means for all positions in that cells.

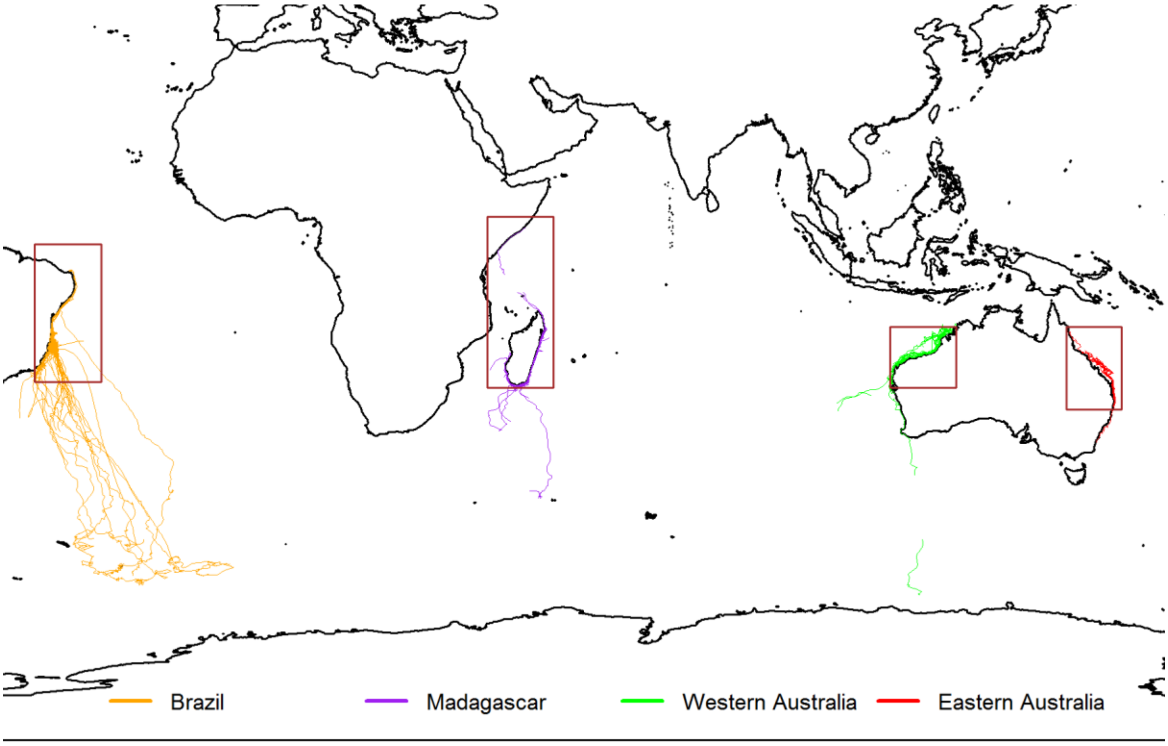

**Figure 5.1**. Trajectories of all satellite tracked humpback whales in four breeding grounds of the Southern Hemisphere: Brazil (BSA), Madagascar (BSC-3), Western Australia (BSD), and Eastern Australia (BSE1). Coastal movements included in the study are localized in the brown squares.

## IV. RESULTS

Our study brings together datasets from four distinct humpback whale breeding regions of the Southern Hemisphere (**Figure 5.1**): Southeastern Brazil (BSA), Madagascar (BSC-3), Western Australia (BSD), and Eastern Australia (stock BSE1). A part of Brazilian tracks were described in Zerbini, et al. (2006, 2011), and Andriolo et al. (2014). However, we briefly describe the general movement patterns of BSA individuals included in the present study. We also examined thoroughly the whale movements from the Eastern and Western Australian breeding grounds which have not yet been described in the literature. The Madagascar tracks have already been comprehensively described in Cerchio et al. (*in prep*, cf. **annex A**) and in chapter 4 of this dissertation. As a consequence, we will refer to results from chapter 4 to compare whale patterns among the different breeding grounds

# CHAPITRE V – ETUDE COMPARATIVE : DEPLACEMENTS ET HABITATS DES BALEINES A BOSSE DE L'HEMISPHERE SUD

## A. BRAZIL BREEDING GROUND

### 1. GENERAL INFORMATION

Ninety one tags were deployed on humpback whales (92 females, 68 males) late in the breeding season (September-November) during 10 breeding seasons between 2003 and 2012 2012. Deployments were conducted at different coastal locations and during a tagging cruise covering an area from Rio de Janeiro (~ 22° 52' S, 22°52'W) to Rio Grande do Norte (5°44', 36°33'W) (Castro et al. 2014). The total tag duration ranged from 3 days (tag #33006.06) to 312 days (tag #121189.12) and 59 out of 68 females were accompanied by calf (**Table S5.1**). The total mean traveled distance was 1458 ± 205 km (range 36 – 20016 km) and the average observed speed was 0.66 ± 0.01 m/s (0.05- 2.17 m/s). Eighty two tracks were decribed and analysed (60 females, 22 males) after having excluded tracks shorter than 8 days and split into different segements.

### 2. MOVEMENT PATTERNS

Because of the high number of tracks along the Brazilian coast, we divided the large BSA dataset into four sub-groups according to the whale movements (i.e. migration movements, movements within Abrolhos Bank, movements towards north or toward south) to get a better visibility of tracks. i) All whales performed convoluted coastal movements in a restricted area between 16°S and 20°S. Some Individuals (n=10) stayed in Abrolhos Bank region and then moved southward along the coast to reach the Cabo Frio region (**Figure 5.2.A**). ii) One third of humpback whales moved away from the coastal breeding areas in a southeastward direction (n=30). Of these, eight individuals migrated to feeding grounds in the South Georgia and South Sandwich Islands regions (10946.05, 21810.03, 24641.05, 24642.03, 87732.12, 87783.09, 111871.12, 121189.12 **Figure 5.2.B**) but migration movements were not described in the present study. A part of the whales stayed in the Abrolhos Bank area before transmission ceased (**Figure 5.2.C**). While most of the tags deployed in different locations north of Conceição da Barra showed southward movements within the Abrolhos Bank, whales 87768.08 and 87770.08 travelled north as far as the region of Rio grande do Norte (n= 22, **Figure 5.2.D**).

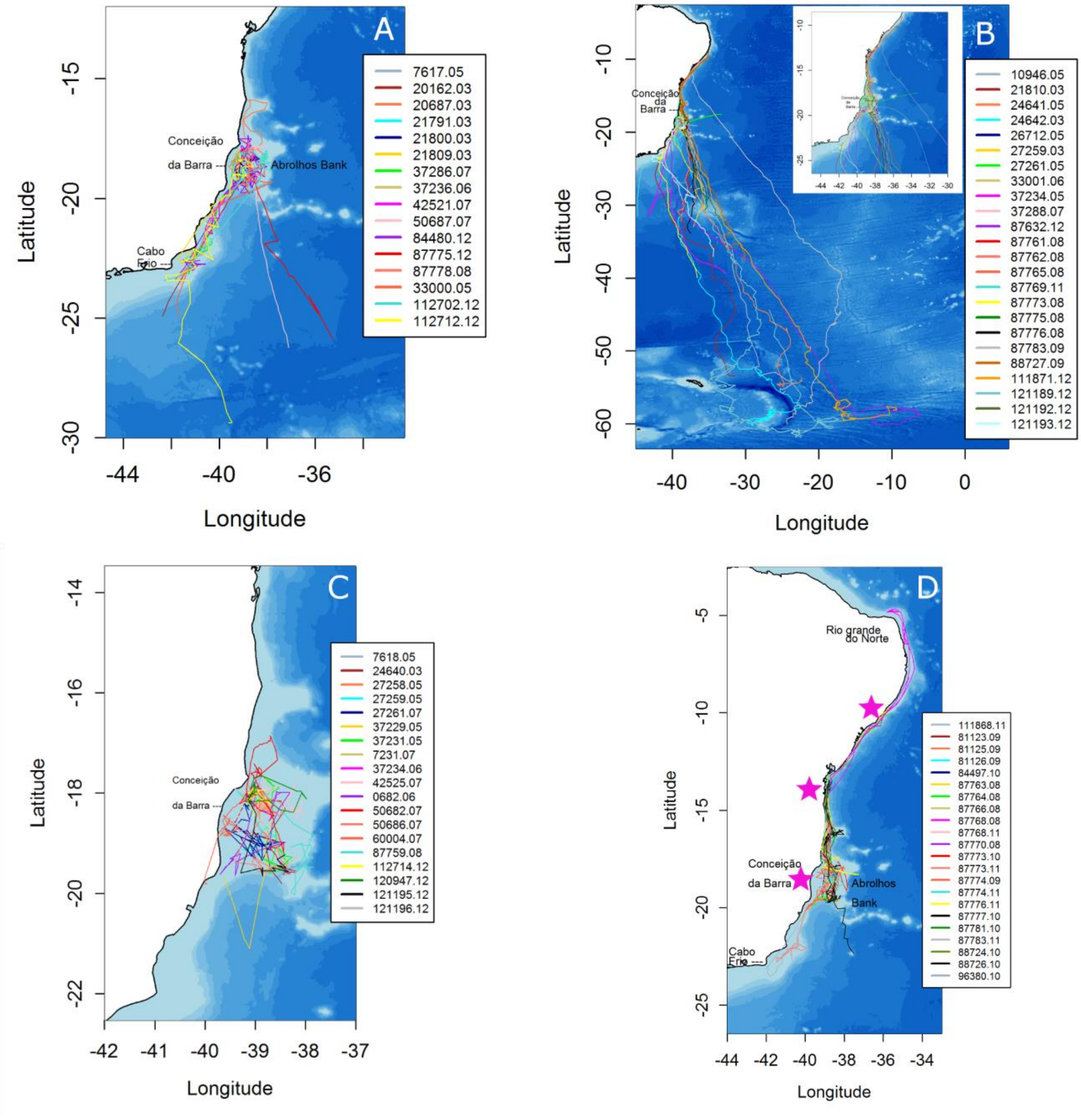

**Figure 5.2.** Trajectories of satellite tracked humpback whales in the Brazil breeding ground (BSA). Trips shorter than 8 days are not represented. Stars indicate the coastal locations of tag deployment. Some Individuals (n=10) stayed in Abrolhos Bank region and then moved southward along the coast to reach the Cabo Frio region (A). Some humpback whales moved away from the coastal breeding areas in a southeastward direction (n=30) (B). Some whales stayed in the Abrolhos Bank area before transmission ceased (C). Most of the tags deployed in different locations north of Conceição da Barra showed southward movements within the Abrolhos Bank, whales 87768.08 and 87770.08 travelled north as far as the region of Rio grande do Norte (D).

## B. WEST AUSTRALIAN BREEDING GROUND

### 1. GENERAL INFORMATION

Twenty-six tags (16 females, 10 males) were deployed during July, August and September over four different years: 2005, 2008, 2009, and 2010 (**Table S5.2**). The tag deployment was undertaken in two distinct regions of Western Australia, the North West Cape (**Figure 5.3**), and the Kimberley region (**Figure 5.4**). Among females, only two individuals (#98107, #98126) were observed without calf in groups of three individuals. Tracking duration ranged from 9 days (#40616) to 108 days (#96382). The total mean traveled distance was 1458 ± 205 km (range 175-5078). The types of movements observed on the west coast of Australia can be categorized into two subclasses: i) Whales tagged in the North West Cape during the peak of the breeding season (July-August) roaming mostly within the tagging region or/and heading northwards (**Figure 5.3**); two routes were used by individuals to travel north, one passing through the Barrow Island region when the second was more coastal (**Figure S5.1**); ii) Whales tagged later in the season (late July/early August, late August/early September) in the Kimberley region displayed movements localized within the region and/or traveled in a southward direction (**Figure 5.4**). Most of the tracks were characterized by both an offshore and a coastal component. Between Broome and Exmouth, most of whales displayed southward movements along the coast (brown arrow, (**Figure 5.4**), while some individuals followed a more offshore route (green arrow, **Figure 5.4)**.

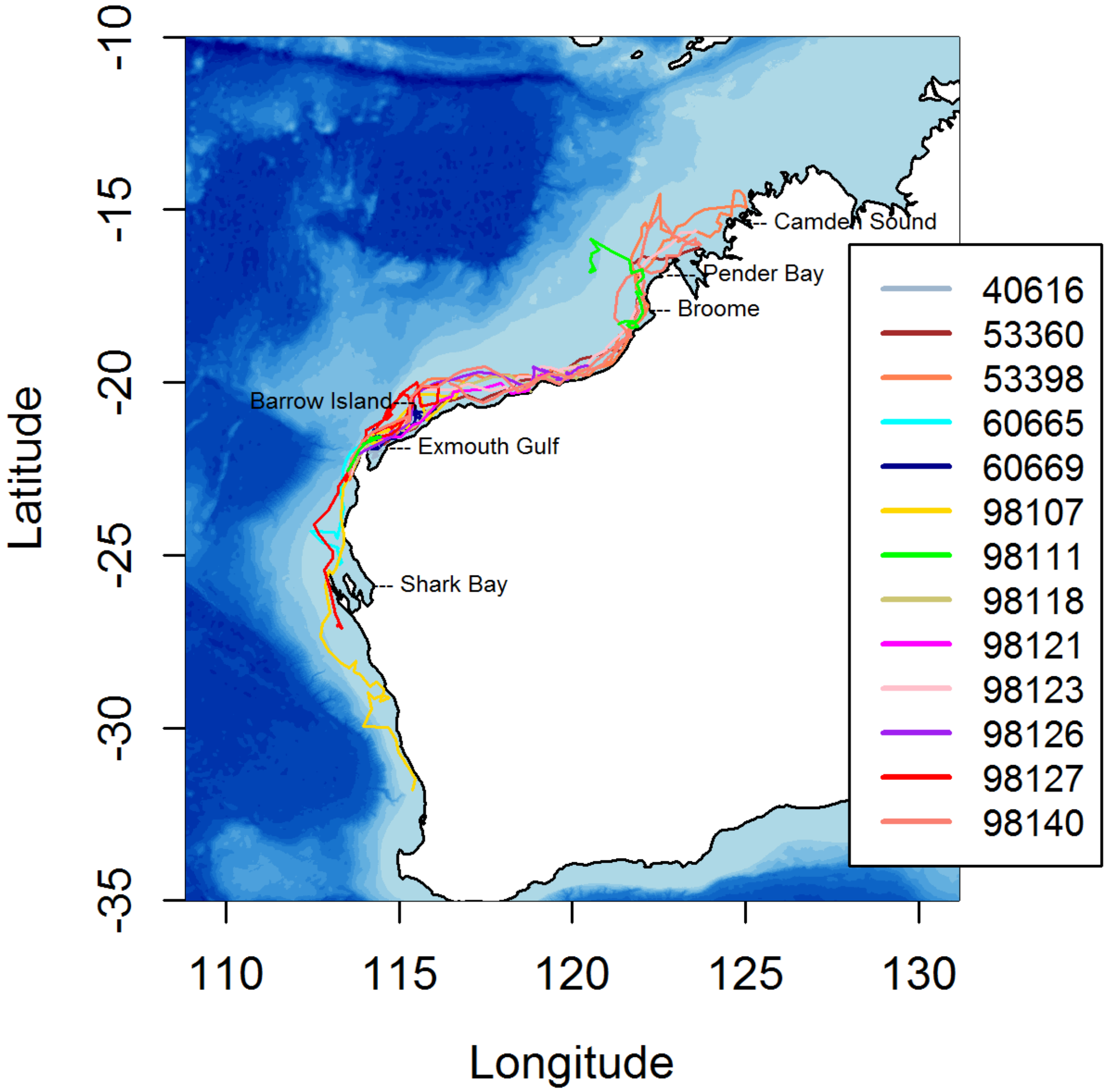

**Figure 5.3.** Trajectories of satellite tracked humpback whales tagged in the North West Cape (Western Australia, BSD-WAC). Trips shorter than 8 days are not shown.

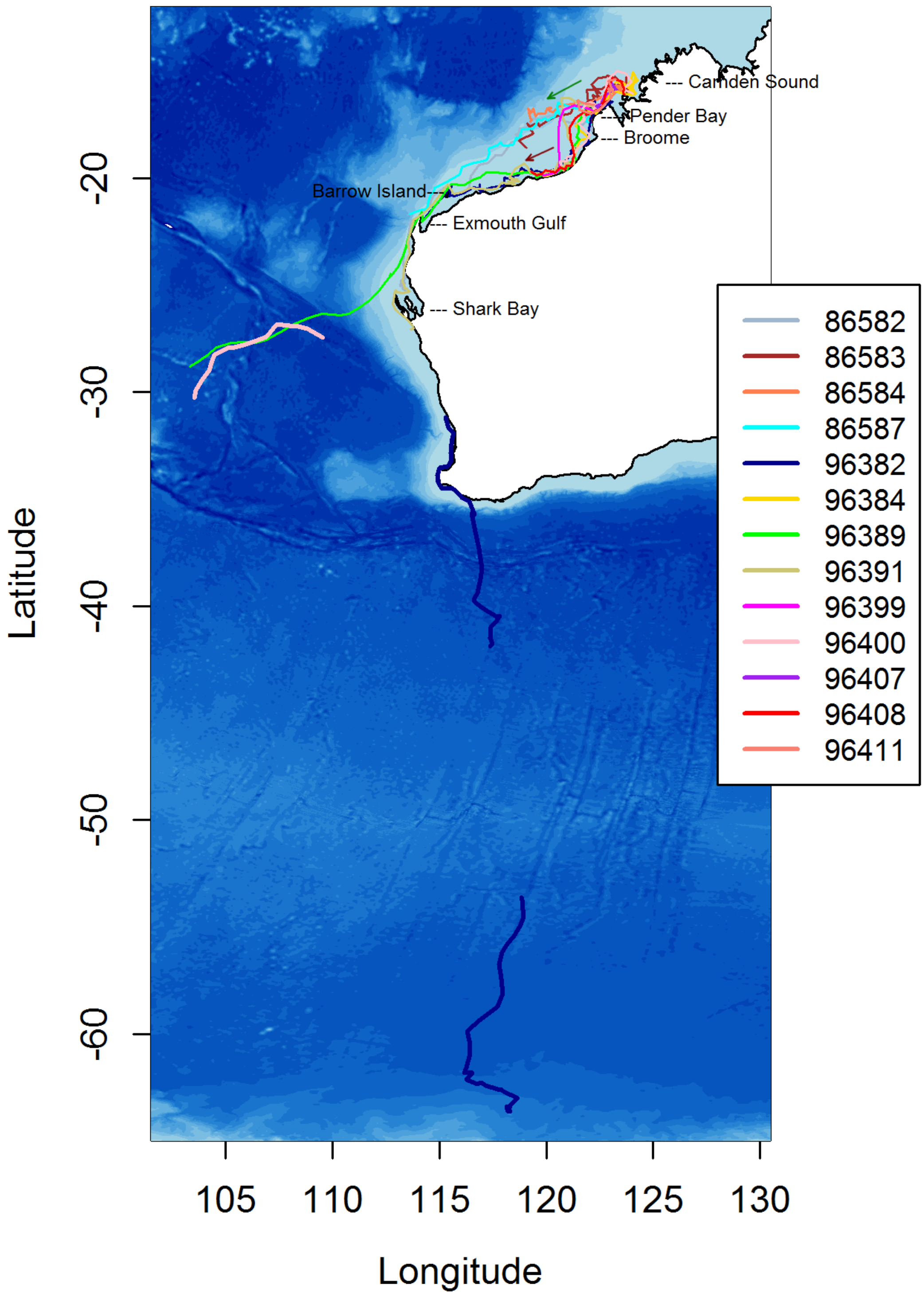

**Figure 5.4.** Trajectories of tracked humpback whales in the Kimberley region (Western Australia, BSD-WAK). Trips shorter than 8 days are not shown. Arrows indicate the two main routes (coastal and offshore) used by whales.

### 2. WHALES TAGGED IN THE NORTHWEST CAPE (NORTHWARD MOVEMENTS)

Two mothers with calves (#40616 and #60669) remained around the Exmouth Gulf for the entire duration of the deployment. Whale 40616 stayed in the Exmouth gulf and whale 60669 traveled along the north coast and ended in the Barrow Island region. Whales 98118 and 98121, two mothers with calves, travelled steadily north for approximatively 700 km (off Port Hedland) before the tag 98121 stopped transmitting, while whale 98118 spent 18 days meandering in the Port Hedland region before transmission ended. While the track of female 98126 was similar to both previous females, she passed through the Barrow Island region before continuing navigating to the Port Headland region. Five whales, one female (with a calf) and four males, reached the Kimberley calving ground. Three males (#53398, #98123, and #98140) displayed similar trajectories, following an offshore route in the west of the Barrow Island. In contrast, a mother with calf (#53360) travelled along the north coast for approximatively 1350 km, over 20 days, and reached Pender Bay (16°74'S, 122°71'W). Whale 53398 moved further north off Camden Sound meandering in the Kimberley region for 15 days, then turned back south and followed a more inshore trajectory after having passed Broome. A male (#98111) travelled north before the tag temporally stopped transmitting for 14 days. The tag resumed transmitting when the whale was approximatively 950 km north of the tagging site, near Broome. It then moved in a northwestward direction in off-shore waters before the tag ceased. It is likely that this individual moved steadily on a direct course during 14 days, a period during which he could have either followed the northern route (off Barrow Island) or the southern route (along the coast). In contrast, male 60665 headed southwards until he reached Shark Bay, travelling more than 400 km. Both female 98107 and male 98127 travelled north, lingering in the area between Exmouth and Karratha for 8 days and 15 days respectively before returning south and reaching Shark bay.

## 3. WHALES TAGGED IN KIMBERLEY (SOUTHWARD MOVEMENTS)

Two mothers with calves (#96407 and #96411) stayed near the tagging area off Pender Bay for the 8 days of tag transmission. A mother with a calf #96384) tagged in Camden Sound moved erratically for 5 days in the tagging area, then started to travel southwards along the coast. Two mothers with calves (#96399 and #96408) navigated southwards with some meanderings off Pender Bay. They displayed offshore movement before moving closer to shore 150 km away from Broome. A mother with calf (#96389) travelled more than 2400 km from Pender Bay (tagging location) for 34 days. This individual passed north of Barrow Island and travelled steadily in a southwestward direction, departing the continent before the tag stopped transmitting in an oceanic area at around 30 °S, 105 E. Whale 96400 (mother with a calf) closely followed the coast in a southward direction from the Broome region, when the tag stopped transmitting for 44 days. It resumed transmission when the whale was approximatively at 400 km away, navigating in a similar southwest direction as whale 96389 before it definitely ceased. Whale 96382, a mother with calf, travelled south to reach an Antarctic feeding ground at around 63°S (Area IV) in 108 days. After reaching the Exmouth gulf, the tag temporally stopped transmitting for 17 days before resuming transmission when the whale was travelling southward along the coast (~115°E, 31°S). A mother with a calf (#96391) lingered in Port Hedland region, passed off Barrow Island and followed the coast beyond Shark Bay when the tag ceased. Two males (#86582 and #86587) tagged in Broome followed similar trajectories, navigating offshore, passing close to Barrow Island, reached Exmouth and transmitted until Shark Bay. In contrast, two males (#86583 and #86584) spent a few days in the Broome region before navigating southward following a more offshore route.

## C. EAST AUSTRALIAN BREEDING GROUND

### 1. GENERAL INFORMATION

Eleven tags were deployed (on 2 females and 9 males), in Eden Head at the end of June 2009 (**Table S5.3**, **Figure 5.5**). No females were accompanied by calves when tags were deployed. The total tag duration ranged from 14 days (whale 88747) to 60 days (88754). The mean traveled distance was 1750 ± 259 km (range 880 – 3889) at a mean observed travel rate of 0.7 ± 0.02 m/s (**Table S5.3**). All whales left the area right after tagging and followed slightly similar routes.

### 2. MOVEMENT PATTERNS

An adult male (whale 88730) travelled steadily from Evans Head to the Great Barrier Reef, before performing meandering movements while moving further north to the Cairns region. It is the northernmost area visited by tagged whales on the east coast; the whale covered more than 2700km in 45 days. Two males (#88736 and #88747) traveled steadily 30km/day for 15 days to reach the Great Barrier Reef. Two males and one female (88734, #88737, and #88742) covered a mean distance of 1500 km in 23 days (range 21-26 days) following a similar trajectory than previous males and stayed within the Great Barrier Reef until the tags ceased. Male 88750 traveled steadily for 8 days then meandered along the Great Barrier Reef while male 88751 lingered off MacKay for 6 days. Whale 88756 moved to the Great Barrier Reef, remained there for 15 days, and then travelled back south (35°S) before the tag stopped transmitting. Whale 88755 covered about 1920 km in 41 days to reach the Great Barrier Reef before turning back southwards. Female 88754 travelled along the coast, spent 16 days within the Great Barrier Reef, and turned back south along the coast, with the tag ceasing within 150 km of the southern tip of the Australian east coast.

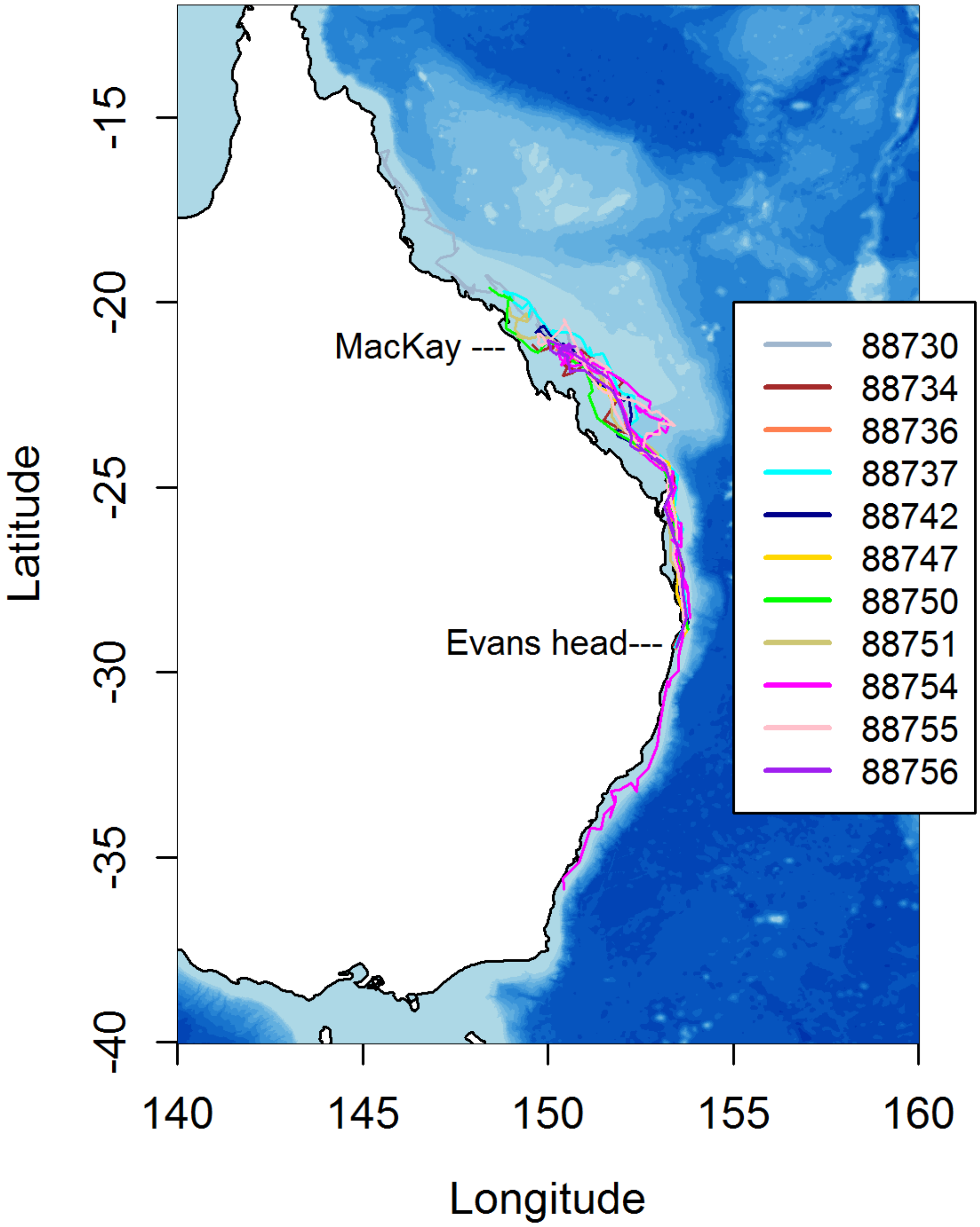

**Figure 5.5.** Trajectories of satellite tracked humpback whales in the Eastern Australia breeding ground (BSE1). Trips shorter than 8 days are not represented.

## D. SPATIAL DISTRIBUTION OF WHALE MOVEMENTS WITHIN BREEDING SITES

The spatial distribution of movements and movement patterns according to sex were similar in two regions (Brazil and Eastern Australia) and differed in two regions (Western Australia and Madagascar). In Brazil and Eastern Australia, movements were aggregated in similar, relatively restricted areas for both sexes (**Figure 5.6A and 5.6B**). In Brazil, these movements were concentrated within Abrolhos Bank. While only two females were tracked in Eastern Australia, their movements were patched within the same area as males within the Great Barrier Reef. In Western Australia, tag deployments were carried out in two regions, and the spatial distribution of movements for both areas are shown separately (**Figure 5.6C and 5.6D**). Females tagged in Exmouth region displayed movements in two patches located near Exmouth Gulf and off Port Hedland, while males used mainly the area off Exmouth Gulf and travelled further north to the Kimberley calving area (**Figure 5.6C**). Females tagged in the Kimberley area were primarily concentrated along the Kimberley coast and secondarily to the south of Broome (**Figure 5.6D**). Movements of males were spread across the Kimberley region, at higher distances from shore than females (**Figure 5.6D and S5.2**). In Madagascar whale movements were spread out with different spatial patterns between females and males (**Figure 5.6E**). Females used the whole eastern coast and the southeast coast while males mostly occupied an area located in the south of Sainte Marie Island (18 to 21°S).

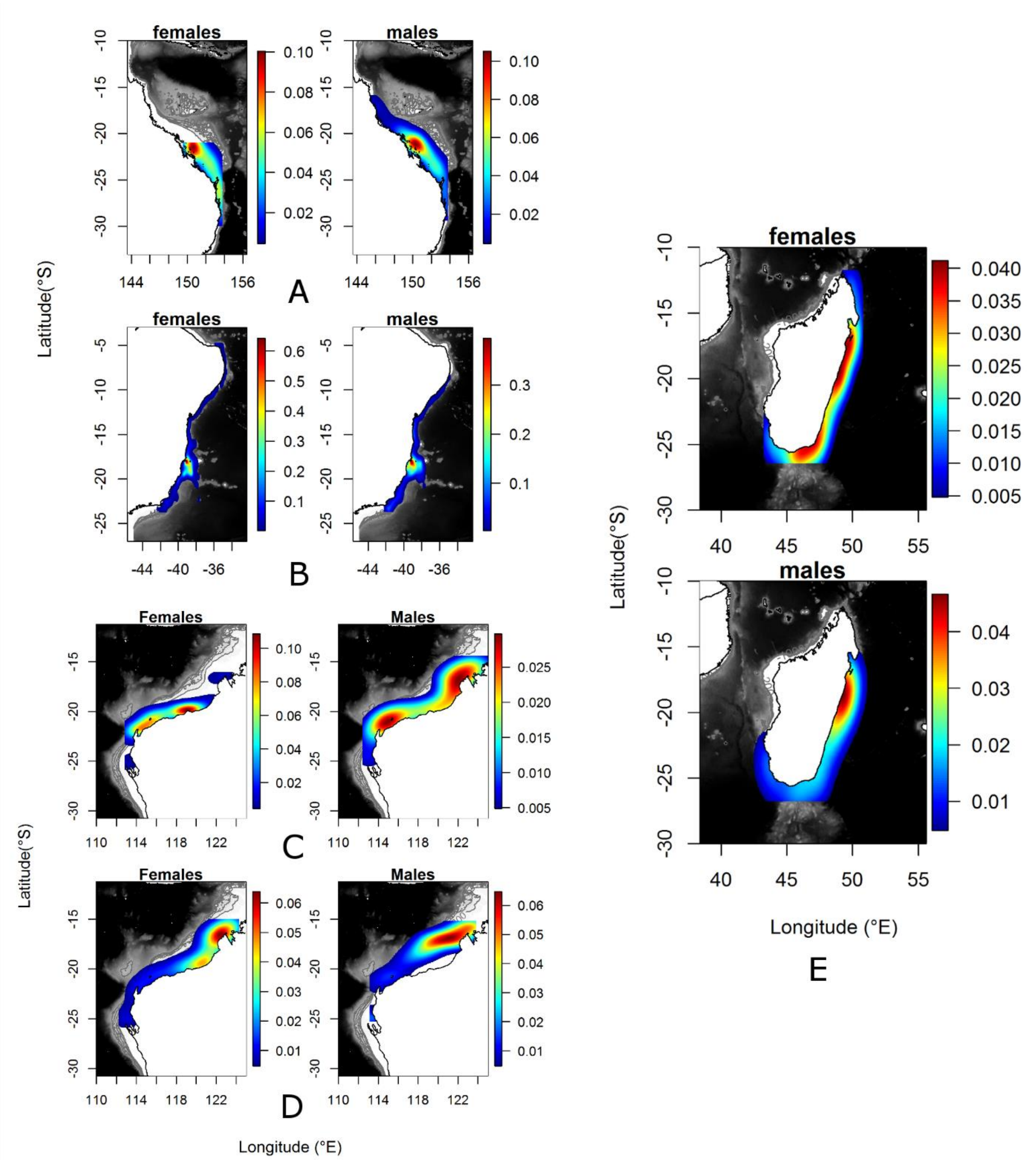

**Figure 5.6.** Kernel density maps of whale estimated locations according to sex from the different breeding areas: Eastern Australia (A), Brazil (B), North West Cape (C) and Kimberley (D), and Madagascar (E).

## E. COMPARISON OF BEHAVIORS AND HABITAT USE ACCORDING TO SEX

In this section we compared quantitatively the behavior of whales in the different breeding grounds (**Table 5.1**).

### 1. BEHAVIORAL MODE

Behavioral modes were significantly different between sites. (PERMANOVA, p < 0.001, **Table 5.1**) except between East Australia (1.40 ± 0.01), and the Kimberley region (1.41 ± 0.01) (all pairwise comparisons, p=0.4). The mean behavioral mode is significantly higher in Brazil (1.5 ± 0.01) than in the other sites. While a significant difference between females and males was found in Madagascar (1.25 ± 0.12 and 1.52 ± 0.39 respectively; permutation t-test, p=0.02), no significant differences between females and males were found in the North West Cape, in the Kimberley region, and in Brazil (Permutation t-tests, p=0.1, p=0.8, and p=0.5, respectively.

In the Eastern Australia and in Brazil, both females and males performed more localized movements in the south of the Great Barrier Reef and in Brazil within the Abrolhos Bank and the Cabo Frio region (**Figures 5.7A and 5.7.B**). When distinguishing between northbound and southbound movements for Western Australia, both females and males tend to display localized movements in distinct locations (**Figures 5.7C and D**). Northbound females performed localized movements in a wider area between Exmouth Gulf and Port Hedland regions) than males (off gulf of Exmouth and off Broome) (**Figure 5.7C**). Males moving towards south showed a highest degree of localized movement in offshore areas (beyond 200m isobaths) (**Figure 5.7D**).

The female behavioral mode was significantly lower in Madagascar than in Brazil (1.2 ± 0.05 and 1.5 ± 0.03 respectively; all pairwise comparisons, p=0.02). While, it is not significantly different, spatial plots of standardized B-mode show that for Brazil and Madagascar females without calves performed more localized movements (higher B-modes) than females with calves (**Figure. S5.3, Table S5.4**). In Madagascar, areas of localized movements appear to be located on the central east and south east coasts (**Figure S5.3**). In Brazil, mothers with calves showed a significant higher B-mode (1.54 ± 0.01, n=6) than females without calves (1.27 ± 0.01, n=54) (Permutation t-test, p=0.02) (**Figure. S5.3**). Females with calves moved also in the region of Cabo Frio that no females without calve visited (**Figure S5.3**).

### 2. OBSERVED SWIMMING SPEED

The mean observed swimming speed of humpback whales from Brazil is significantly lower than for whales from other sites (**Table 5.1**). The mean observed swimming speed is significantly higher in Madagascar than in Eastern Australia (0.8 ± 0.02 m/s and 0.7 ± 0.02 m/s respectively; all pairwise comparisons, p=0.034). No difference was found in the mean observed swimming speed between females and males within each site. The mean observed speed differed between Brazil and Madagascar females (0.5 ± 0.001 m/s and 0.8 ± 0.02 m/s respectively; all pairwise comparisons, p=0.03). However, no difference between sites was found for the males' observed swimming speed. Similarly, no difference was found between observed speed of females with or without calf within each site and among sites (i.e. Brazil, Madagascar, and North West Cape).

**Table 5.1.** Summary of whale behavioral mode and whale observed swimming speed during coastal movements for all individuals, for females and for males in each breeding ground. Mean values were computed on all location values whereas mean values used in statistical tests were computed by individual. B-mode and observed swimming speed not showing the same superscript were significantly different (p-value < 0.05).

| | **B-mode** | | | | **Observed swimming speed (m/s)** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Total of individuals** | **Females** | **Males** | **Females vs males** | **Total of individuals** | **Females** | **Males** | **Females vs males** |
| **Madagascar** | 1.34 ± 0.01 (n=20) $^{a}$ | 1.23 ± 0.01 (n=11) $^{a}$ | 1.57 ± 0.01 (n=8) | **p<0.05** | 0.8 ± 0.02 (n=20) $^{a}$ | 0.8 ± 0.03 (n=11) $^{a}$ | 0.8 ± 0.03 (n=8) | p=0.8 |
| **Brazil** | 1.52 ± 0.01 (n=82) $^{b}$ | 1.53 ± 0.01 (n=60) $^{b}$ | 1.49 ± 0.01 (n=22) | p=0.5 | 0.6 ± 0.001 (n=82) $^{b}$ | 0.5 ± 0.001 (n=60) $^{b}$ | 0.7 ± 0.02 (n=22) | p=0.2 |

| | **B-mode** | | | | **Observed swimming speed (m/s)** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Total of individuals** | **Females** | **Males** | **Females vs males** | **Total of individuals** | **Females** | **Males** | **Females vs males** |
| **Kimberley region** | 1.4 ± 0.01 (n=13) $^{c}$ | 1.4 ± 0.01 (n=9) $^{a,b}$ | 1.4 ± 0.02 (n=4) | p=0.9 | 0.8 ± 0.01 (n=13) $^{a,c}$ | 0.8 ± 0.02 (n=9) $^{a,b}$ | 0.8 ± 0.03 (n=4) | p=0.8 |
| **North West Cape** | 1.3 ± 0.01 (n=13) $^{d}$ | 1.4 ± 0.02 (n=7) $^{a,b}$ | 1.1 ± 0.01 (n=6) | P=0.5 | 0.7 ± 0.02 (n=13) $^{a,c}$ | 0.7 ± 0.03 (n=7) $^{a,b}$ | 0.8 ± 0.03 (n=6) | p=0.6 |
| **Eastern Australia** | 1.4 ± 0.01 (n=11) $^{c}$ | 1.3 ± 0.02 (n=2) $^{a,b}$ | 1.4 ± 0.01 (n=9) | - | 0.7 ± 0.02 (n=11) $^{c}$ | 0.8 ± 0.04 (n=2) $^{a,b}$ | 0.7 ± 0.02 (n=9) | - |
| **Among region** | **p < 0.001** | **p < 0.05** | **p=0.6** | - | **p < 0.001** | **p < 0.05** | **p=0.4** | - |

### 3. HABITAT USE

Overall, whales exhibited movements over bottom depths and at distances from shore which differed significantly between sites (PERMANOVA, $p < 0.001$, PERMANOVA, $p < 0.001$, respectively). Whales used deeper waters in Madagascar (273 ± 21 m) and moved at larger distances from shore in Brazil (46 ± 0.7 km) than in Australian regions (Kimberley, 10.5 ± 1 km; North West Cape, 20 ± 1 km and Eastern Australia, 38.9 ± 3 km) (**Tables S5.5, S5.6, S5.7**) Whales from the North West Cape performed movements in shallow waters (30 ± 2 m) and close to shore (10 ± 0.5 km). In both Kimberley and North West Cape regions, females were found in significantly shallower waters (Permutation t-test, $p<0.01$, and Permutation t-test, $p< 0.05$ respectively) and closer to shore (Permutation t-tests, $p <0.001$, and Permutation t-tests, $p<0.001$ respectively) than males (**Table S5.6**). In Brazil, females with calves (47 ± 3 km) moved closer to shore than females without calves (58 ± 10 km) (Permutation t-tests, $p<0.001$). The mean SST in all areas used by whales was 24 ± 0.01°C (ranged 19-28°C). The mean current speed in all areas used by whales was 0.2 ± 0.004 m/s (range 0-2 m/s).

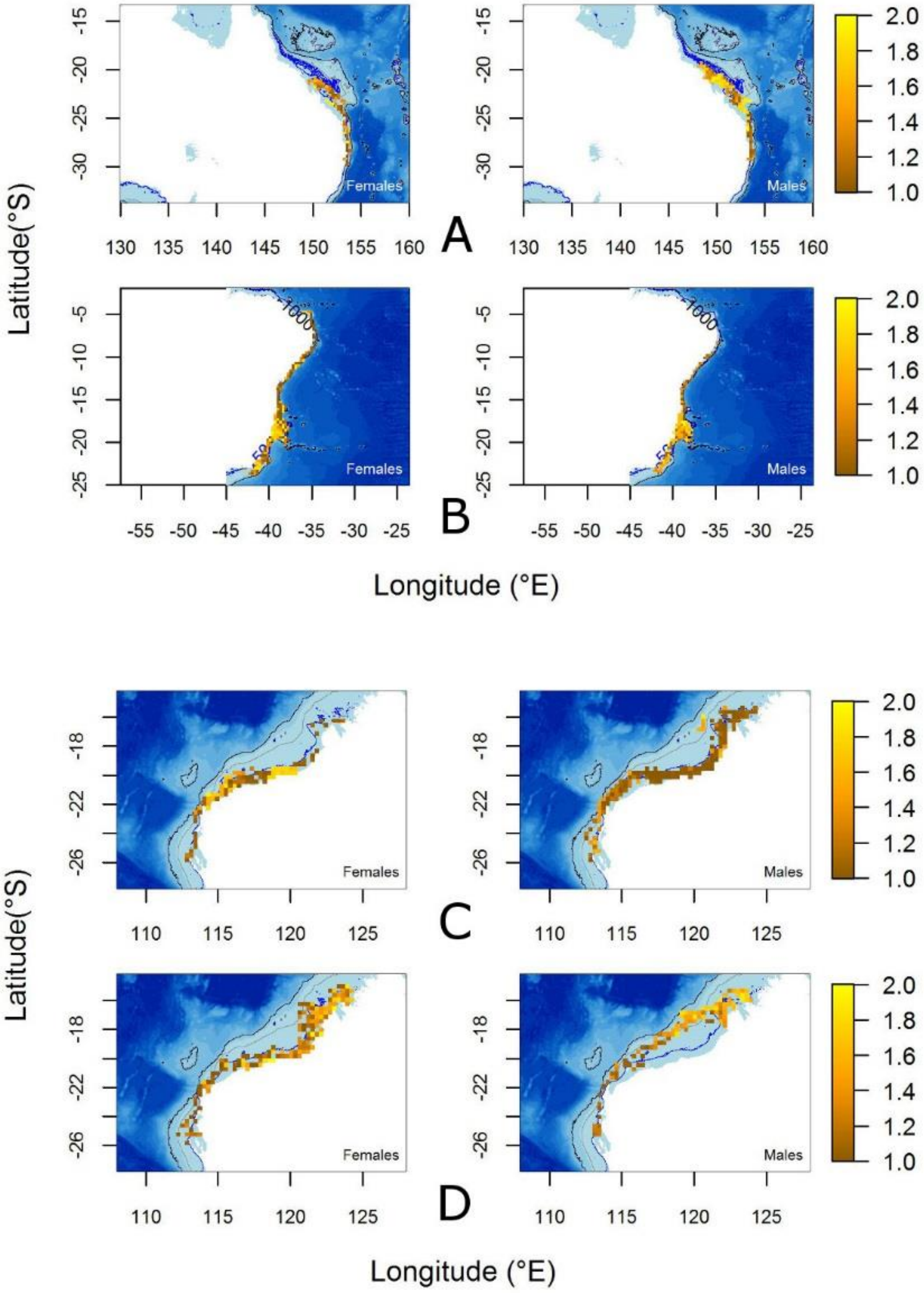

**Figure 5.7.** Averaged B-mode into 0.3x0.3° grid cells for both females' and males' coastal tracks from the different breeding areas: Eastern Australia (A), Brazil (B), North West Cape (C) and Kimberley (D).

## F. INFLUENCE OF ENVIRONMENT PARAMETERS ON COASTAL MOVEMENTS ACCORDING TO SEX

Models were fitted for each location separately in order to better understand humpback whales behavioral response to their local environment. With only two females tagged in East Australia region, no model was fitted for females in that site. The model results for Madagascar data have been presented in Chapter 4 (**Tables 4.2 and 4.3**) of the thesis. Collinearity was tested between variables and for some models, one of each highly correlated pair were removed (**annexes I-V**). For all models, residuals are normally distributed and homogeneous (**annexes I-V**).

### 1. BEHAVIORAL MODE

For females, no environmental variables influenced significantly the probability to perform localized movements in Brazil and the Kimberley region. The probability of performing localized movements in the North West Cape increased significantly with increasing bathymetry but decreased with increasing distance from shore (**Table 5.2**).

For males, the probability to perform localized movements in Brazil increased with distance from shore (**Table 5.2**). For the three Australian breeding sites, the probability to perform localized movements increased significantly with increasing bathymetry. In the Kimberley region, a negative relationship was observed between the behavioral mode and SST as well as with the advance of season. In contrast, in Eastern Australia, the probability of performing localized movements was positively related to SST and the advance of the season.

### 2. ACTIVE SWIMMING SPEED

In Brazil, the active swimming speed of females decreased with increasing current speed, increasing SST, the advance of season, and increasing distance from shore (in order of importance, **Table 5.3**), while an inverse relationship was found for slope. In the Kimberley region (WAK), swimming speed responded significantly to current speed and bathymetry, increasing with decreasing current speed but increasing with increasing bathymetry. In the North West Cape area, the swimming speed also increased with decreasing distance from shore.

The active swimming speed of males increased with decreasing bathymetry and decreasing current speed in Brazil (**Table 5.3**). In the North West Cape, the most parsimonious model included SST and distance from shore: swimming speed decreased with increased SST, but increased with increasing distance from shore. In the Kimberley region, the male swimming speed increased with increasing SST and increased as season advanced, while in Eastern Australia, swimming speed decreased with SST and as season advanced. In this latter region, the swimming speed increased with increasing distance from shore and increasing slope.

**Table 5.2.** Summary of regression coefficients from the most parsimonious models (LMMs) relating B-mode (logit) to environmental parameters for females and males in each breeding site (Brazil, BSA; Madagascar; BSC3, North West Cape; BSD-WAC, Kimberley region; BSD-WAK, Eastern Australia; BSE1). Coefficients are presented ± SE. Significant parameters are highlighted in bold characters. Parameters included in the full model but not retained in the model selection are indicated by a slash mark. Parameter of "Day of year" not considered in the Madagascar model is represented by a black square.

| **B-mode** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Females** | | | | | **Males** | | | | |
| **Breeding sites** | BSA | BSC3 | BSD-WAC | BSD-WAK | BSA | BSC-3 | BSD-WAC | BSD-WAK | BSE1 |
| **Explanatory variables** | | | | | | | | | |
| **Sea surface temperature** | -0.04 ± 0.04 | / | / | 0.12 ± 0.11 | / | 0.42 ± 0.34 | / | **-0.29 ± 0.09*** | **0.2 ± 0.06*** |
| **Bathymetry** | / | **0.19± 0.07*** | **0.26 ± 0.12*** | -0.13 ± 0.08 | / | 0.08 ± 0.06 | **0.18 ± 0.08*** | **0.27 ± 0.08**** | **0.18 ± 0.06**** |
| **Distance from shore** | 0.04 ± 0.03 | **0.19 ± 0.09** | **-0.34 ± 0.1*** | | **0.12 ± 0.06** | | | | / |
| **Slope** | | | | 0.02 ± 0.07 | | - 0.07 ± 0.06 | / | / | / |
| **Current speed** | -0.04 ± 0.03 | / | / | -0.08 ± 0.08 | / | -0.003 ± 0.09 | / | / | / |

| **B-mode** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Females** | | | | | **Males** | | | | |
| **Breeding sites** | BSA | BSC3 | BSD-WAC | BSD-WAK | BSA | BSC-3 | BSD-WAC | BSD-WAK | BSE1 |
| **Explanatory variables** | | | | | | | | | |
| **Day of year** | -0.02 ± 0.04 | ■ | / | | / | ■ | / | **-0.26 ± 0.08**** | **0.5 ± 0.08**** |

**Table 5.3.** Summary of regression coefficients from the most parsimonious models (LMMs) relating whale swimming speed to environmental parameters for females and males in each breeding site (Brazil, BSA; Madagascar; BSC3, North West Cape; BSD-WAC, Kimberley region; BSD-WAK, Eastern Australia; BSE1). Coefficients are presented ± SE. Significant parameters are highlighted in bold characters. Parameter of Day of year not considered in the model of Madagascar is represented by a black square.

| **Active swimming speed** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Females** | | | | | **Males** | | | | |
| **Breeding sites** | BSA | BSC3 | | BSD-WAC | BSD-WAK | BSA | BSC3 | BSD-WAC | BSD-WAK |
| **Explanatory variables** | | | | | | | | | |
| **Sea surface temperature** | **-0.08 ± 0.02**** | / | / | / | / | / | **-0.18 ± 0.09** | **0.3 ± 0.1*** | **-0.22 ± 0.07*** |
| **Bathymetry** | / | / | / | **0.18 ± 0.07**** | **-0.1 ± 0.04** | **0.09 ± 0.04*** | / | / | / |
| **Distance from shore** | **-0.04 ± 0.02** | / | **-0.24 ± 0.11** | | / | | **0.24 ± 0.08*** | | **0.19 ± 0.08**** |
| **Slope** | **0.049 ± 0.02** | | / | / | **0.09 ± 0.04** | / | / | / | **0.09 ± 0.03*** |
| **Current speed** | **-0.27 ± 0.02**** | **-0.13 ± 0.04** | / | **-0.25 ± 0.07**** | **-0.3 ± 0.05**** | **-0.16 ± 0.04**** | / | | |
| **Day of year** | **-0.06 ± 0.02*** | ■ | / | | / | ■ | / | **0.42 ± 0.09**** | **-0.35 ± 0.09**** |

# V. DISCUSSION

Our study describes and compares coastal movement patterns and habitat use of humpback whales according to sex and female breeding status in four major breeding grounds of the Southern Hemisphere. Our results show variations in spatial range of movements and in habitat selection of humpback whales according to breeding sites, sex and stage of the breeding season when tags were deployed: northward migration early in the season, activity during the peak of breeding, and southward migration during the late part of the season. Overall, breeding humpback whales were mainly influenced by bathymetry, using waters within 200 m isobaths and preferentially shallower than 50 meters depth. During the northbound migration along the East Australian coast, all males tagged off Evans Head head in the southern GBR. In Madagascar, whales tagged at the peak of the season performed a larger variety of movements than in others breeding sites suggesting that whales were engaged in either migration movements or movements linked to resting or breeding behaviors. On the west coast of Australia, both northbound and southbound females showed less direct migration paths than males. Northbound and southbound males used deeper waters and moved in direct pathways passing through offshore areas. Females used shallower waters and were found closer to shore than males. However, females without calves tend to travel northward at greater distance from shore (Barrow and Monte Bello islands) than females with calves. Southbound females (including only females with calves) travelled along the shore in contrast to males which moved offshore. On the Brazilian coast, while as whales have been tagged later in the season (September-November) than other regions, we observed lower localized behavior and lower swimming speed. In addition, females with calves performed more localized movements and were found closer to shore than females without calves.

### A. DISTRIBUTION OF WHALE'S MOVEMENTS AMONG SITES AND BETWEEN SEXES DURING THE BREEDING SEASON.

On the east Australian coast, where humpback whales were tagged early in the season (June) and therefore at a more southerly location, all whales including mostly males headed north to concentrate their activity in the GBR, off Mackay region. These results are consistent with males' movement patterns observed in the western Australian breeding ground where humpback whales were tagged during their northbound migration off Ningaloo reef and Exmouth later in the season (July/August). During the northbound migration along the West Australian coast, females used two areas located between

Exmouth Gulf and Port Hedland whereas males also used the Exmouth Gulf area but tended to travel further north and congregated in the Kimberley area, the major reproductive area of BSD (Jenner et al. 2001). On the east coast, Humpback whales are known to congregate in the GBR during the breeding season in particular in the southern GBR (Chittleborough 1965, Simmons & Marsh 1986, Smith et al. 2012). Previous studies have reported that a part of southbound humpback whales travel into the shallow and sheltered waters of Hervey Bay (about 100 km south of the southern end of the GBR, 25°S) later in the season (late June to November) where a high proportion mothers and calves are regularly observed (Chaloupka & Osmond 1999, Paton et al. 2011, Franklin et al. 2011, Martinez et al. 2015). In our study, no whales travelling up the northeastern coast stayed in Hervey Bay. As most of tagged whales were males, it is not clear whether they did not stop in Hervey Bay because they were in the northbound part of their migration, and/or because there exists a sexual difference in habitat use (with for instance males performing more direct movements towards the breeding site than females). However, consistent with Paterson (1991) who found that humpback whales only stopped in that area during their southern migration, we suggest that this also applies to males which probably use a direct route when migrating towards their main breeding site. As suggested for males from Eastern Australia, during their northbound trip along the West Australian coast, males head in a quite direct fashion towards key reproductive areas. While Exmouth gulf on the West Australian coast was identified as a resting area for southbound whales (that may be compared to Hervey Bay on the East Australian coast), northbound whales may also use more intensively that area than previously thought (Jenner et al. 2001). In the Kimberley region, both females and males concentrated movements in an area between Broome and Camden Sound. However, it has been suggested that the Kimberley region is not the unique calving ground for this population since mother-calf pairs have been seen off Noth West Cape (Double et al. 2011). In addition, some whales turned back south before reaching the Kimberley region (whales 98107 and 98127) supporting evidence that whales likely used other suitable local breeding habitats (Double et al. 2011).

In the height of the season (July-August), results from chapter 4 and from this study show that in Madagascar, females performed dispersive and transiting movements along the east coast whereas males exhibited mostly localized movements concentrated on the central east coast. When compared to the patterns of whales from other sites examined in this study, the movements patterns of Madagascar whales appear less clearly defined than for the other sites (with whales heading northwards, westwards, or focusing their movements in limited areas (cf. Chap 4). This may result from the fact that Madagascar east coast could be used either as a breeding area or a migration corridor (IWC, 2011). In addition, Madagascar whales were tagged in the height of the season (July-August) while they were tagged early in the season in eastern Australia and later in the Kimberley and Albrolhos Bank. However, whales tagged in North West Cape at the same period showed clearly direct pathways to the Kimberley region. Therefore, the whales tagged in Madagascar may have been migrating north (late individuals), south (early ones), or were engaged in their breeding activity locally, thereby complicating interpretation of the patterns observed.

Later in the season (August/September), movement patterns during the southbound migration from Western Australia differed between males and females. Males travelled offshore on the continental shelf indicating that they initiate their southward migration using direct routes across deep waters. In contrast, we show that females moved along the coast closer to shore, and concentrated their movements in the region between Port Hedland and Broome before continuing their southward trip. In Brazil, both females and males tagged between September and November concentrated their movements in the region to Abrolhos Bank. In Western Australia, while Double et al. (2011) have previously described the global movement patterns during the southward migration of these whales, we described into more details the whales' movements. All females tagged in the Kimberley region were accompanied by a calf, but we can hypothesize that females without calf use the same direct migration pattern as males to reach the feeding grounds after fertilization. However, additional sampling is needed, in particular on females without calf, to better support that hypothetical migratory pattern in Western Australia. On the Brazilian coast, humpback whales are known to spend the breeding season in a relatively wide range of latitudes in eastern Brazil, from Rio Grande Do Norte (6°S) to Cabo Frio (21°S) regions (Zerbini et al. 2006, 2011). However, boats and aerial survey reported that Abrolhos Bank is the main breeding area where about 80% of the BSA population is concentrated (Siciliano

1997, Martins et al. 2001, Andriolo et al. 2010). In constrast to the whales tagged in the Kimberley region (Western Australia), in Brazil whales moved offshore to migrate towards their feeding grounds without hugging the coast as observed in Australia and in Madagacscar whales (Zerbini et al. 2006, 2011) and were probably only using used coastal habitats to perform localized movements during the breeding season.

Overall, when compiling observed patterns from the four breeding sites at the different tagging times, and combining with published studies (Jenner et al. 2001, Zerbini et al. 2004, 2006, Double et al. 2010, 2011, Andriolo et al. 2010, Smith et al. 2012, Castro et al. 2014), our comparative approach allows us to propose a general movement pattern for males and females humpback whales during the breeding season (**Table 5.4**). Males tagged early in the season during their northward migration head directly to their main breeding site, where they display localized movements during the height of the season. At the end of the season they migrate south again following a most direct path. In contrast, females tagged early in the season migrate along the coastline and may slow down in specific areas. They then perform localized movements during the height of the season, before migrating back south in two ways depending on their breeding status. Females with calf travel following the coastline and use a number of resting sites along their migrating pathway, while females without calf travel in a more direct fashion across the open ocean.

**Table 5.4.** Synthesis of movement patterns and habitat use of humpback whales at three stages of the breeding season according sex and breeding staus.

| **Stage of the breeding season** | **Beginning** | **Peak** | **End** |
|---|---|---|---|
| **Females without calves** | | | |
| Movements | Localized | Transiting and localized | Directional and localized |
| Habitat | Along the coast and offshore continental shelf | The same goes for that stage | The same goes for that stage |
| Biological hypothesis | Better maneuverability in reproduction behaviors (Smultea 1994, Elwen & Best 2004) - Minimize the cost of transport (energy conservation) to supply the energy needed for survival and reproduction activities (Braithwaite et al. 2015) | The same goes for that stage + Expose themselves to a high number of males | The same goes for that stage |
| Examples of tagging region | Western Australia-Exmouth gulf (BSD) | Madagascar (BSC3)/Western Australia-Exmouth gulf (BSD) | Brazil (BSA) |
| **Females with calves** | | | |
| Movements | Directional/Stop-overs | Localized | Localized/Stop-overs |
| Habitat | Along the coast | | |
| Biological hypothesis | Avoidance of males/predators (protection of calf) (Corckeron & Connor 1999, Herman et al. 2011, Craig et al. 2014) - Energy saving to support survival, nursing (Cartwright and Sullivan, 2009, Félix and Botero-Acosta 2011, Braithwaite et al. 2015) | | |
| Examples of tagging region | Western Australia-Exmouth gulf (BSD) | Madagascar (BSC3)/Western Australia-Exmouth gulf (BSD) | Western Australia-Kimberley region (BSD)/Brazil (BSA) |

| **Stage of the breeding season** | **Beginning** | **Peak** | **End** |
|---|---|---|---|
| **Males** | | | |
| Movements | Directional | Transiting and localized | Localized and directional |
| Habitat | Along the coast, deeper waters than females | Along the coast and offshore continental shelf | Offshore continental shelf, deeper waters than females |
| Biological hypothesis | Better maneuverability in reproduction behaviors (Smultea 1994, Elwen & Best 2004) - Minimize the cost of transport (energy conservation) to supply the energy needed for survival and reproduction activities (Baker and Herman 1984, Pack et al. 1998, 2009, Herman et al. 2008, Braithwaite et al. 2015) | The same goes for that stage + Prospection for mates in local areas | The same goes for that stage |
| Examples of tagging region | Eastern Australia (BSE1)/ Western Australia-Exmouth gulf (BSD) | Madagascar (BSC3)/Western Australia-Exmouth gulf/Kimberley region (BSD) | Western Australia-Kimberley region (BSD)/Brazil (BSA) |

## B. FEMALE HABITAT USE

During northward migrations along the Western Australian coast, female movements were mainly influenced by bathymetry and distance from shore. When heading north, females used areas with shallow waters. While northbound females performed localized movements in very shallow waters (< 50m), females without calves tend to be located further from shore in the region of Barrow and Monte Bello islands than females with calves. Although females from North West Cape were found in shallower waters and closer to shore than males, it ispossible that females used areas further from shore when shallow waters extends offshore. Jenner et al. (2001) reported that North of Exmouth Gulf, northbound whales use a migration corridor passing along the coast and another one passing on the west side of the Montebello Island.

For southward migrating females, bathymetry is also a key environmental factor that influences behavior, with swimming speed increasing with increasing bathymetry. However, our results did not reveal a significant influence of environment parameter on the probability to perform localized movements. Females performed localized movements in the Kimberley region whereas transiting movements were observed along the coast in southward movements. In addition, females with calves tended to display dispersive movements inshore and offshore of the Kimberley region. They were found in shallower waters and closer to shore than males. In addition, all females tagged in Kimberley region were accompanied by a calf. These results support that females with calves likely used Kimberley region as calving/resting areas (Jenner et al. 2001, 2006). In contrast to males, females with calves likely migrate south by following the coast in the shallowest waters available. They spend time resting in favorable areas, which could contribute to energy conservation and nursing (Braithwaite et al. 2015, **Table 4.5**). In Brazil, similarly to females from the Kimberley region, our model did not reveal any significant effect of environmental parameters on the type of movements (localized or transiting). However, swimming speed decreased with increasing distance from shore as opposed to Kimberley whales, increasing sea surface temperature (SST) and advance of the season but increased with increasing slope. The areas of Abrolhos bank has been recognized as the main breeding area for this population (Siciliano 1995, Martins et al. 2001, Andriolo et al. 2010). Aerial surveys showed that a high proportion of whales were concentrated offshore, near islands and reef systems of the Abrolhos Bank (Andriolo et al. 2006). The absence of influence of environmental parameters on the behavioral mode could suggest that the whales were engaged in a large variety of movements and types of habitat use. Females tend to move faster when close to the shore line and in areas with steep continental slope. The Brazilian coast being characterized by a narrow continental shelf, the females likely travelled along the coast and stayed preferentially into the shallow waters of the extensive Abrolhos bank, Royal Charlotte Bank (north of Abrolhos Bank, ~16°S), and Cabo Frio region. As observed in Madagascar at the peak of the season, females with calves displayed more localized movements and were found closer to shore than females without calves. It is therefore likely that females with calves used preferentially coastal waters than females without calves during the breeding season (**Table 4.5**). In contrast to males and females with calves, no females without calves visited the Cabo Frio region. The observed differences in movement patterns between the two reproductive classes of females suggest that receptive females performed more transiting movements across the breeding ground than females with calves in order to mate. In addition, with the growth of humpback whale populations in the Southern Ocean, they reoccupy historical areas of distribution (Zerbini et al. 2004). These factors could explain the concentration of movement observed in Cabo Frio regions.

While the factors affecting the preference of females with calves for shallow waters remain debated (Cartwright et al. 2012), females with calves could preferentially use corridors along the coast and spend time in resting areas inshore to decrease predation pressure, reduce exposure to rough sea conditions, conserve energy, and avoid male harassment (Smultea 1994, Corkeron & Connor 1999, Ersts & Rosenbaum 2003, Elwen & Best 2004, Félix & Botero-Acosta 2011, Craig et al. 2014, Braithwaite et al. 2015). Similarly to our finding on Madagascar whales (Chapter 4), females from Brazil and the Kimberley region decreased their swimming speed in presence of strong currents. In addition, Findlay et al. (2011) reported that in Mozambique coastal waters whales were not distributed in faster or slower currents This supports the hypothesis that current speed do not influence whale movements within coastal breeding sites.

## C. MALE HABITAT USE

In eastern Australia, whales were tagged early in the season and performed migration movements northwards to reach the GBR. Males increased localized movements with increasing bathymetry, SST and advance of season. They also increased their swimming speed with increasing distance from shore and slope and decreased their swimming speed with increasing SST and advance of season. This suggests that males performed directional and fast movements to the GBR located further north and slowed down when they reached the breeding site. Based partly on the same dataset, Smith et al. (2012) reported two important breeding areas in the GBR: between Proserpine and Mackey (21°S) and islands off Glastone (23°S). This is consistent with the areas where males performed mostly localized movements. Smith et al. (2012) also demonstrated a preference for very shallow waters (less than 60 m depth) and waters with SST ranging between 21 and 23°C. These habitat preferences are relevant for both females and males from other breedings grounds examined in our study, in particular during the peak of the season. In Western Australia, when migrating northwards, males swam faster when they were away from shore than when they were closer to the shore. Males performed mostly transiting movements on the shelf between Exmouth Gulf and the Kimberley region. This indicates that northbound males most likely migrated in deep waters and offshore areas to reach the warm waters of the northern breeding sites.

When migrating southwards, males from the Kimberley region displayed localized movements both close to the coast and further away from shore with movements tending to be more localized with increasing bathymetry. Their swimming speed also increased with the advance of year. Males performed localized movements in the Kimberley regions off Pender Bay and Camden Sound. Our results suggest that males likely use coastal habitats characterized by shallow waters (< 50 m) as well as offshore habitats and deeper waters (> 200 m) within breeding sites and during migration. It is thought that they performed localized movements closer to shore between Pender Bay and Camdem Sound then moved southwards further offshore. In addition, males moved faster during their southward migration suggesting that with the advance of season males optimize their migration strategy by swimming faster and heading south through deeper waters. In Brazil, males increasing their localized movements with increasing distance from shore. Their swimming speed decreased with increasing current speed and bathymetry. Males also decreased their swimming speed in areas with steep continental slope. In the same way as females, most of localized movements were found in Abrolhos and Royal Charlotte banks and around Cabo Frio. Therefore, it appears that males used habitat characterized by extensive shallow waters where females are also concentrated. The North Brazilian coast being characterized by a relatively narrow shelf except in the regions previously mentioned, it could explain that males were concentrated in these restricted sustainable areas. Our results also reveal that they exploit offshore areas on shelf as it was previously indicated for males tagged in other studied breeding grounds and suggest that they can use that type of habitats in link with social role and reproduction strategies (**Table 5.4**).

## VI. CONCLUSION

This study compare the movements and habitat use of humpback whales at different times in the breeding season and in coastal breeding grounds characterized by different environmental conditions. We showed that humpback whales adopted different movement patterns according to sex and stage of migration. During northward migration, males appear to head most directly to the main breeding area. At the peak of the season, humpback whales concentrated their movements in warm areas characterized by wide continental shelf and extensive shallow waters such as Abrolhos Bank, the central East coast and, south coast of Madagascar or the Kimberley region. Females tend to perform movements in shallower waters than males. Late in the season, males travelled southward in direct paths using offshore waters whereas females tend to move along the coast. We also found indications that female movement patterns and habitat use depend on their reproductive status, although the sample size of class of the females without calves' class was too limited to allow a firm conclusion. Future tagging effort should focus on increasing the sample size in some breeding sites (i.e Madagascar, Western Australia, Eastern Australia), in sex class and in reproductive status to improve our understanding on movement patterns and general habitat features of humpback whales. Tagging should also be conducted done in the height of the breeding season to maximize the regional breeding movements and reduce the bias between types of movements.

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## VIII. APPENDIX

**Table S5.1.** Summary of the tracking dataset of humpback whales equipped in Brazil (from 3 to 312 days of transmission) and main characteristics of breeding movements based on switching State space model (SSSM) positions estimated every 12h. Stars indicate that mean values were computed on all location values.

| Whale Id | Tag location | Sex | Calf | Tagging date | Tag longevity (days) | Travelled distance (km) | Mean observed speed (m/s) | Mean B-mode |
|---|---|---|---|---|---|---|---|---|
| 7617.05 | Abrolhos Bank | F | Y | 11/10/2005 | 17 | 471.94 | 0.33±0.04 | 1.84±0.01 |
| 7618.05 | Abrolhos Bank | F | Y | 11/10/2005 | 15 | 159.35 | 0.13±0.02 | 1.89±0.01 |
| 10946.05 | Abrolhos Bank | F | Y | 19/10/2005 | 77 | 4727.58 | 0.72±0.03 | 1.06±0.01 |
| 20162.03 | Abrolhos Bank | M | N | 19/10/2003 | 15 | 931.48 | 0.72±0.06 | 1.54±0.01 |
| 20687.03 | Abrolhos Bank | F | Y | 27/10/2003 | 23 | 1024.86 | 0.53±0.04 | 1.09±0.01 |
| 21791.03 | Abrolhos Bank | F | Y | 28/10/2003 | 14 | 821.31 | 0.68±0.07 | 1.12±0.02 |
| 21792.03 | Abrolhos Bank | M | N | 27/10/2003 | 5 | 167.86 | 0.39±0.08 | 1.51±0.01 |
| 21800.03 | Abrolhos Bank | F | Y | 28/10/2003 | 31 | 1605.82 | 0.6±0.05 | 1.75±0.02 |
| 21809.03 | Abrolhos Bank | F | Y | 27/10/2003 | 18 | 865.53 | 0.54±0.05 | 1.47±0.03 |
| 21810.03 | Abrolhos Bank | M | N | 18/10/2003 | 78 | 4643.38 | 0.69±0.04 | 1.22±0.01 |
| 24640.03 | Abrolhos Bank | F | N | 19/10/2003 | 9 | 328.71 | 0.45±0.09 | 1.65±0.02 |
| 24641.05 | Abrolhos Bank | F | Y | 19/10/2005 | 113 | 5692.49 | 0.59±0.03 | 1.34±0.02 |
| 24642.03 | Abrolhos Bank | F | Y | 27/10/2003 | 205 | 10324.82 | 0.58±0.02 | 1.6±0.02 |
| 26712.05 | Abrolhos Bank | F | Y | 11/10/2005 | 17 | 947.02 | 0.64±0.09 | 1.51±0.02 |
| 27258.05 | Abrolhos Bank | F | Y | 19/10/2005 | 30 | 906.44 | 0.35±0.04 | 1.94±0.01 |
| 27259.03 | Abrolhos Bank | F | Y | 19/10/2003 | 39 | 2692.59 | 0.81±0.05 | 1.56±0.02 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 27259.05 | Abrolhos Bank | F | Y | 16/10/2005 | 19 | 597.86 | 0.36±0.04 | 1.91±0.01 |
| 27261.03 | Abrolhos Bank | M | N | 19/10/2003 | 7 | 513.25 | 0.85±0.12 | 1.62±0.01 |
| 27261.05 | Abrolhos Bank | F | Y | 12/10/2005 | 47 | 2744.22 | 0.68±0.08 | 1.73±0.01 |
| 27261.07 | Abrolhos Bank | F | Y | 12/09/2007 | 25 | 1086.32 | 0.5±0.08 | 1.95±0.01 |
| 33000.05 | Abrolhos Bank | F | Y | 19/10/2005 | 26 | 1291.18 | 0.59±0.06 | 1.64±0.01 |
| 33000.06 | Abrolhos Bank | F | Y | 12/10/2006 | 3 | 145.81 | 0.56±0.16 | 1.47±0.02 |
| 33001.05 | Abrolhos Bank | F | Y | 19/10/2005 | 7 | 467.92 | 0.77±0.09 | 1.66±0.02 |
| 33001.06 | Abrolhos Bank | F | Y | 25/10/2006 | 16 | 1356.4 | 1.05±0.06 | 1.02±0.01 |
| 37229.05 | Abrolhos Bank | F | Y | 16/10/2005 | 8 | 469.43 | 0.72±0.11 | 1.66±0.01 |
| 37231.05 | Abrolhos Bank | F | Y | 16/10/2005 | 19 | 568.01 | 0.35±0.04 | 1.87±0.01 |
| 37231.07 | Abrolhos Bank | M | N | 12/09/2007 | 14 | 241.84 | 0.2±0.03 | 1.71±0.01 |
| 37234.05 | Abrolhos Bank | F | Y | 16/10/2005 | 33 | 3221.69 | 1.13±0.08 | 1.26±0.01 |
| 37234.06 | Abrolhos Bank | F | Y | 28/10/2006 | 10 | 201.45 | 0.23±0.07 | 1.7±0.01 |
| 37236.06 | Abrolhos Bank | F | Y | 26/10/2006 | 10 | 166.78 | 0.2±0.02 | 1.69±0.01 |
| 37286.07 | Abrolhos Bank | F | Y | 14/09/2007 | 15 | 881.48 | 0.7±0.07 | 1.38±0.03 |
| 37288.06 | Abrolhos Bank | F | Y | 20/10/2006 | 4 | 136.92 | 0.4±0.11 | 1.6±0.01 |
| 37288.07 | Abrolhos Bank | F | Y | 14/09/2007 | 37 | 2149.83 | 0.68±0.05 | 1.31±0.03 |
| 42521.07 | Abrolhos Bank | F | Y | 8/09/2007 | 41 | 1326.44 | 0.37±0.03 | 1.77±0.02 |
| 42525.07 | Abrolhos Bank | F | Y | 16/09/2007 | 16 | 816.54 | 0.62±0.07 | 1.89±0.02 |
| 50682.06 | Abrolhos Bank | F | Y | 25/10/2006 | 17 | 647.67 | 0.45±0.07 | 1.76±0.02 |
| 50682.07 | Abrolhos Bank | F | Y | 15/09/2007 | 46 | 906.77 | 0.23±0.03 | 1.91±0.01 |
| 50686.07 | Abrolhos Bank | F | Y | 15/09/2007 | 16 | 742.1 | 0.55±0.05 | 1.7±0.02 |
| 50687.07 | Abrolhos Bank | F | Y | 16/09/2007 | 26 | 1265.63 | 0.56±0.05 | 1.63±0.01 |
| 60004.07 | Abrolhos Bank | M | N | 16/09/2007 | 44 | 501.97 | 0.21±0.04 | 1.89±0 |
| 60007.07 | Abrolhos Bank | F | Y | 8/09/2007 | 3 | 111.05 | 0.64±0.33 | 1.66±0.05 |
| 81122.09 | Abrolhos Bank | F | N | 27/09/2009 | 5 | 346.2 | 0.89±0.17 | 1.5±0.01 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 81123.09 | Barra Grande region | F | N | 24/09/2009 | 8 | 429.21 | 0.66±0.13 | 1.38±0.02 |
| 81124.09 | Abrolhos Bank | M | N | 25/09/2009 | 4 | 173.08 | 0.63±0.18 | 1.47±0.05 |
| 81125.09 | Barra Grande region | M | N | 24/09/2009 | 8 | 467.48 | 0.72±0.11 | 1.65±0.02 |
| 81126.09 | Barra Grande region | F | Y | 25/09/2009 | 11 | 531.56 | 0.58±0.09 | 1.26±0.05 |
| 84480.12 | Abrolhos Bank | F | Y | 2/11/2012 | 46 | 3023.66 | 0.77±0.04 | 1.71±0.02 |
| 84497.1 | Barra Grande region | F | N | 1/10/2010 | 28 | 1612.55 | 0.68±0.07 | 1.51±0.03 |
| 87631.1 | Abrolhos Bank | F | Y | 5/10/2010 | 7 | 527.49 | 0.87±0.11 | 1.15±0.04 |
| 87632.12 | Abrolhos Bank | F | Y | 26/10/2012 | 170 | 10122.46 | 0.69±0.02 | 1.32±0.02 |
| 87759.08 | Abrolhos Bank | M | N | 27/08/2008 | 12 | 528.65 | 0.51±0.08 | 1.54±0.03 |
| 87761.08 | Abrolhos Bank | M | N | 28/08/2008 | 31 | 2534.75 | 0.96±0.05 | 1.03±0.01 |
| 87762.08 | Abrolhos Bank | M | N | 29/08/2008 | 39 | 2126.86 | 0.64±0.03 | 1.03±0.01 |
| 87763.08 | Alagoas region | F | Y | 30/08/2008 | 55 | 2205.82 | 0.46±0.03 | 1.17±0.01 |
| 87764.08 | Alagoas region | F | Y | 6/09/2008 | 48 | 1883.81 | 0.46±0.03 | 1.56±0.04 |
| 87765.08 | Abrolhos Bank | F | N | 7/09/2008 | 33 | 2338.93 | 0.82±0.05 | 1.14±0.03 |
| 87766.08 | Alagoas region | M | N | 8/09/2008 | 21 | 1508.69 | 0.85±0.06 | 1.1±0.02 |
| 87767.08 | Abrolhos Bank | F | Y | 7/09/2008 | 6 | 1093.28 | 2.17±0.71 | 1.25±0.08 |
| 87768.08 | Alagoas region | F | Y | 12/09/2008 | 54 | 3357.16 | 0.73±0.04 | 1.21±0.03 |
| 87768.11 | Barra Grande region | F | Y | 22/10/2011 | 31 | 1355.13 | 0.51±0.04 | 1.47±0.03 |
| 87769.11 | Abrolhos Bank | F | Y | 1/10/2011 | 30 | 2245.51 | 0.86±0.06 | 1.38±0.03 |
| 87770.08 | Barra Grande region | M | N | 12/09/2008 | 10 | 771.31 | 0.94±0.07 | 1.3±0.02 |
| 87773.08 | Abrolhos Bank | F | Y | 12/09/2008 | 42 | 2752.66 | 0.78±0.04 | 1.02±0 |
| 87773.1 | Barra Grande region | M | N | 18/09/2010 | 13 | 800.54 | 0.74±0.11 | 1.44±0.04 |
| 87773.11 | Abrolhos Bank | F | Y | 29/09/2011 | 36 | 1810.18 | 0.59±0.04 | 1.16±0.02 |
| 87774.09 | Barra Grande region | F | Y | 15/09/2009 | 50 | 3185.83 | 0.74±0.03 | 1.27±0.02 |
| 87774.11 | Barra Grande region | M | N | 30/09/2011 | 28 | 1051.14 | 0.45±0.04 | 1.69±0.01 |
| 87775.08 | Abrolhos Bank | F | N | 16/09/2008 | 36 | 2028.46 | 0.66±0.05 | 1.05±0.01 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 87775.12 | Abrolhos Bank | F | Y | 28/10/2012 | 13 | 1132.5 | 1.08±0.19 | 1.77±0.01 |
| 87776.08 | Abrolhos Bank | F | N | 16/09/2008 | 28 | 1829.69 | 0.77±0.05 | 1.1±0.01 |
| 87776.11 | Barra Grande region | F | Y | 29/09/2011 | 23 | 972.05 | 0.5±0.07 | 1.68±0.01 |
| 87777.08 | Abrolhos Bank | F | Y | 16/09/2008 | 5 | 295.53 | 0.76±0.15 | 1.51±0.03 |
| 87777.1 | Barra Grande region | F | Y | 5/10/2010 | 23 | 1210.19 | 0.63±0.06 | 1.64±0.04 |
| 87778.08 | Abrolhos Bank | M | N | 17/09/2008 | 35 | 1772.84 | 0.59±0.04 | 1.32±0.02 |
| 87781.1 | Barra Grande region | F | Y | 1/10/2010 | 11 | 815.37 | 0.85±0.08 | 1.26±0.05 |
| 87783.09 | Abrolhos Bank | F | Y | 18/09/2009 | 139 | 8059.61 | 0.68±0.03 | 1.4±0.02 |
| 87783.11 | Barra Grande region | F | Y | 10/10/2011 | 20 | 917.56 | 0.53±0.06 | 1.52±0.05 |
| 88724.1 | Barra Grande region | F | Y | 1/10/2010 | 9 | 501.58 | 0.68±0.09 | 1.37±0.03 |
| 88726.1 | Barra Grande region | F | Y | 28/09/2010 | 23 | 1633.7 | 0.82±0.06 | 1.56±0.04 |
| 88727.09 | Abrolhos Bank | F | N | 19/09/2009 | 64 | 5704.83 | 1.03±0.04 | 1.08±0.01 |
| 96380.1 | Barra Grande region | F | Y | 23/09/2010 | 20 | 1378.69 | 0.8±0.07 | 1.26±0.04 |
| 111868.11 | Barra Grande region | M | N | 10/10/2011 | 19 | 1497.41 | 0.94±0.07 | 1.18±0.02 |
| 111871.12 | Abrolhos Bank | F | Y | 2/11/2012 | 170 | 8626.14 | 0.59±0.03 | 1.5±0.02 |
| 112702.12 | Abrolhos Bank | M | N | 20/10/2012 | 33 | 2134.59 | 0.76±0.05 | 1.68±0.02 |
| 112712.12 | Abrolhos Bank | M | N | 26/10/2012 | 24 | 2089.92 | 1.03±0.09 | 1.58±0.04 |
| 112714.12 | Abrolhos Bank | M | N | 25/10/2012 | 8 | 339.92 | 0.49±0.08 | 1.83±0.02 |
| 120947.12 | Abrolhos Bank | M | N | 25/10/2012 | 10 | 440.29 | 0.54±0.1 | 1.66±0.02 |
| 121189.12 | Abrolhos Bank | M | N | 20/10/2012 | 312 | 20016.54 | 0.74±0.03 | 1.66±0.01 |
| 121192.12 | Abrolhos Bank | M | N | 27/10/2012 | 19 | 1512.56 | 0.95±0.07 | 1.25±0.01 |
| 121193.12 | Abrolhos Bank | F | Y | 25/10/2012 | 36 | 3384.23 | 1.1±0.07 | 1.28±0.03 |
| 121195.12 | Abrolhos Bank | F | Y | 20/10/2012 | 8 | 408.83 | 0.59±0.1 | 1.65±0.04 |
| 121196.12 | Abrolhos Bank | M | N | 19/10/2012 | 9 | 36.51 | 0.05±0.01 | 1.71±0.01 |
| | | **Total (n=92)** | | | **34 ± 4.8*** | **1917.32 ± 289.09*** | **0.66 ± 0.01*** | **1.46 ± 0.004*** |

**Table S5.2.** Summary of the tracking dataset of humpback whales equipped in Western Australia and main characteristics of breeding movements based on switching State space model (SSSM) positions estimated every 12h. Stars indicate that mean values were computed on all location values.

| Whale Id | Region | Tag location | Sex | Calf | Tagging date | Tag longevity (days) | Travelled distance (km) | Mean observed speed (m/s) | Mean B - mode |
|---|---|---|---|---|---|---|---|---|---|
| 40616 | North West Cape | Exmouth | Female | Y | 22/08/2005 | 9 | 174.87 | 0.26±0.04 | 1.78±0.01 |
| 53360 | North West Cape | Ningaloo Reef | Female | Y | 20/07/2011 | 20 | 1340.35 | 0.78±0.05 | 1.07±0.01 |
| 53398 | North West Cape | Ningaloo Reef | Male | Y | 7/07/2011 | 47 | 2513.58 | 0.63±0.03 | 1.06±0.02 |
| 60665 | North West Cape | Exmouth | Male | Y | 25/08/2005 | 10 | 431.45 | 0.59±0.11 | 1.5±0.03 |
| 60669 | North West Cape | Exmouth | Female | Y | 22/08/2005 | 12 | 467.33 | 0.47±0.11 | 1.85±0.02 |
| 86582 | Kimberley region | Broome | Male | N | 28/07/2008 | 28 | 1487.11 | 0.61±0.05 | 1.15±0.01 |
| 86583 | Kimberley region | Broome | Male | N | 1/08/2008 | 23 | 1359.44 | 0.69±0.07 | 1.53±0.03 |
| 86584 | Kimberley region | Broome | Male | N | 28/07/2008 | 25 | 1187.15 | 0.55±0.04 | 1.74±0.02 |
| 86587 | Kimberley region | Broome | Male | N | 28/07/2008 | 26 | 1279.34 | 0.58±0.05 | 1.41±0.03 |
| 96382 | Kimberley region | Pender Bay | Female | Y | 2/09/2009 | 108 | 5077.62 | 0.59±0.03 | 1.48±0.03 |
| 96384 | Kimberley region | Camden Sounds | Female | Y | 27/08/2009 | 25 | 1532.93 | 0.71±0.06 | 1.12±0.02 |
| 96389 | Kimberley region | Pender Bay | Female | Y | 3/09/2009 | 34 | 2484.8 | 0.88±0.06 | 1.22±0.04 |
| 96391 | Kimberley region | Beagle Bay | Female | Y | 6/09/2009 | 36 | 2062.82 | 0.67±0.05 | 1.36±0.02 |
| 96399 | Kimberley region | Buccaneer | Female | Y | 30/08/2009 | 10 | 502.29 | 0.57±0.08 | 1.23±0.01 |
| 96400 | Kimberley region | Buccaneer | Female | Y | 30/08/2009 | 74 | 2948.75 | 0.53±0.04 | 1.74±0.03 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 96407 | Kimberley region | Pender Bay | Female | Y | 4/09/2009 | 8 | 321.94 | 0.47±0.08 | 1.38±0.03 |
| 96408 | Kimberley region | Buccaneer | Female | Y | 30/08/2009 | 19 | 822.78 | 0.51±0.06 | 1.61±0.03 |
| 96411 | Kimberley region | Pender Bay | Female | Y | 4/09/2009 | 8 | 492.7 | 0.8±0.1 | 1.18±0.03 |
| 98107 | North West Cape | Ningaloo Reef | Female | N | 18/07/2011 | 28 | 1782.4 | 0.74±0.05 | 1.43±0.02 |
| 98111 | North West Cape | Ningaloo Reef | Male | N | 13/07/2011 | 30 | 1628.49 | 0.62±0.04 | 1.56±0.05 |
| 98118 | North West Cape | Ningaloo Reef | Female | Y | 23/07/2011 | 29 | 1131.15 | 0.47±0.05 | 1.15±0.02 |
| 98121 | North West Cape | Ningaloo Reef | Female | Y | 21/07/2011 | 11 | 686.16 | 0.75±0.1 | 1.05±0.01 |
| 98123 | North West Cape | Ningaloo Reef | Male | N | 10/07/2011 | 22 | 1324.59 | 0.7±0.05 | 1.67±0.02 |
| 98126 | North West Cape | Ningaloo Reef | Female | N | 9/07/2011 | 24 | 950.2 | 0.45±0.06 | 1.21±0.01 |
| 98127 | North West Cape | Ningaloo Reef | Male | N | 20/07/2011 | 28 | 1415.43 | 0.58±0.05 | 1.06±0.01 |
| 98140 | North West Cape | Ningaloo Reef | Male | N | 16/07/2011 | 45 | 2494.72 | 0.65±0.04 | 1.36±0.03 |
| | | | **Total (n=26)** | | | **28 ± 4.27*** | **1458 ± 205*** | **0.62 ± 0.01*** | **1.32 ± 0.08*** |

**Table S5.3.** Summary of the tracking dataset of humpback whales equipped in Eastern Australia and main characteristics of breeding movements based on switching State space model (SSSM) positions estimated every 12h. Stars indicate that mean values were computed on all location values.

| Whale ID | Region | Tag location | Sex | Calf | Tag date | Tag longevity (days) | Travelled distance (km) | Mean observed speed (m/s) | Mean B-mode |
|---|---|---|---|---|---|---|---|---|---|
| 88730 | Eastern coast | Evans Head, NSW | Male | N | 28/06/2009 | 45 | 2710.85 | 0.7±0.04 | 1.41±0.02 |
| 88734 | Eastern coast | Evans Head, NSW | Female | N | 26/06/2009 | 26 | 1596.32 | 0.72±0.07 | 1.43±0.03 |
| 88736 | Eastern coast | Evans Head, NSW | Male | N | 29/06/2009 | 15 | 1043.09 | 0.8±0.11 | 1.22±0.03 |
| 88737 | Eastern coast | Evans Head, NSW | Male | N | 29/06/2009 | 21 | 1555.68 | 0.86±0.07 | 1.15±0.02 |
| 88742 | Eastern coast | Evans Head, NSW | Male | N | 27/06/2009 | 21 | 1305.63 | 0.7±0.08 | 1.25±0.02 |
| 88747 | Eastern coast | Evans Head, NSW | Male | N | 24/06/2009 | 14 | 880.22 | 0.73±0.07 | 1.21±0.03 |
| 88750 | Eastern coast | Evans Head, NSW | Male | N | 26/06/2009 | 30 | 1456.6 | 0.56±0.07 | 1.61±0.03 |
| 88751 | Eastern coast | Evans Head, NSW | Male | N | 27/06/2009 | 22 | 1302.58 | 0.72±0.06 | 1.17±0.02 |
| 88754 | Eastern coast | Evans Head, NSW | Female | N | 28/06/2009 | 60 | 3887.92 | 0.76±0.04 | 1.3±0.02 |
| 88755 | Eastern coast | Evans Head, NSW | Male | N | 25/06/2009 | 41 | 1925.89 | 0.54±0.05 | 1.62±0.04 |
| 88756 | Eastern coast | Evans Head, NSW | Male | N | 29/06/2009 | 26 | 1583.21 | 0.71±0.07 | 1.7±0.03 |
|  |  |  | **Total (n=11)** |  |  | **29 ± 4*** | **1750 ± 258*** | **0.7 ± 0.02*** | **1.4 ± 0.011*** |

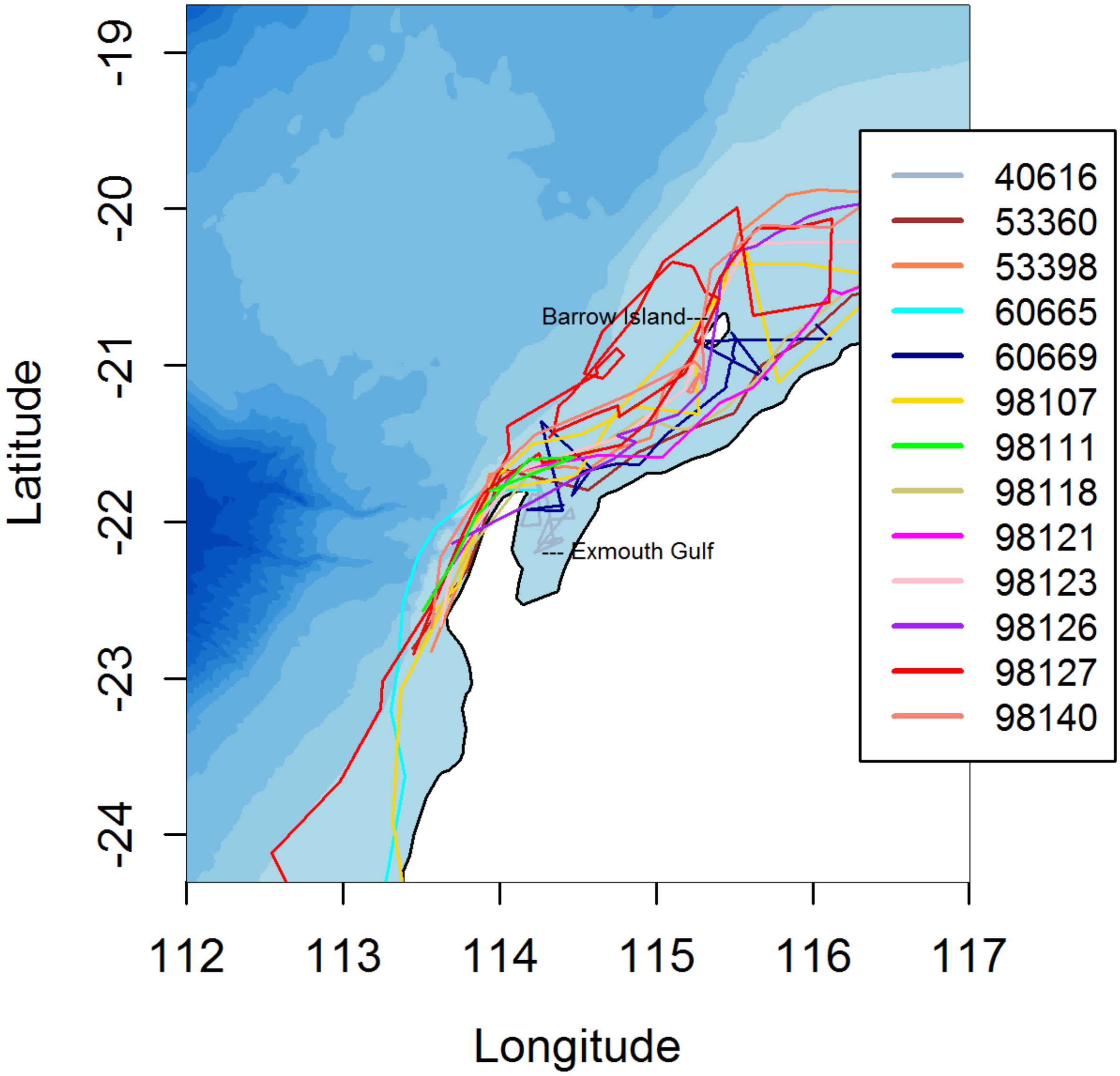

**Figure S5.1.** Trajectories of satellite tracked humpback whales tagged in the North West Cape (Western Australia, BSD-WAC) zoomed on the Barrow Island region.

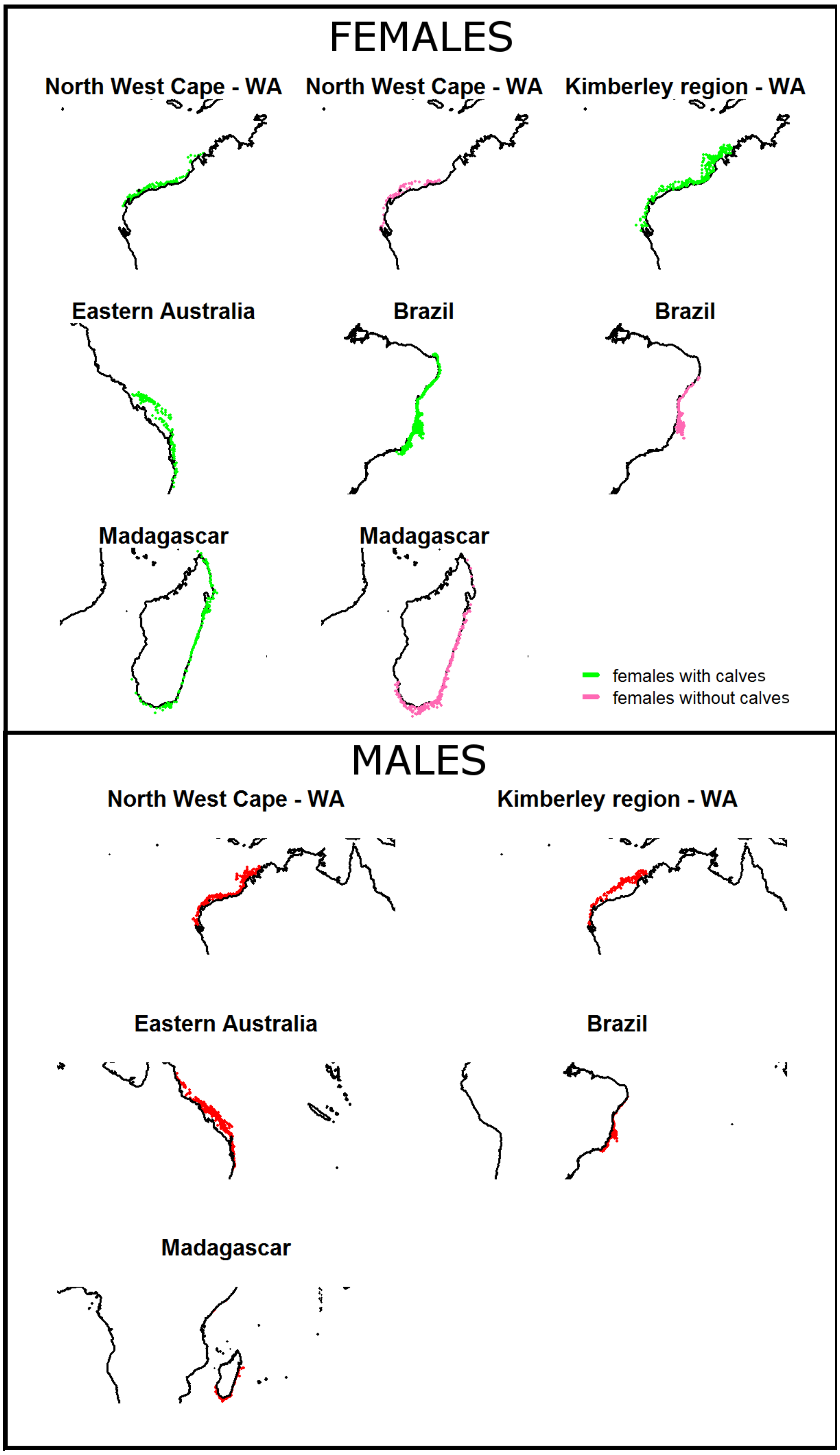

**Figure S5.2.** Estimated locations of females with calves (green), females without calves (pink), and males (red) from the Western Australia (WA, North West Cape and Kimberley regions), Eastern Australia, Brazil and Madagascar breeding grounds.

**Table S5.4.** Summary of whale behavioral mode and whale observed swimming speed during coastal movements for females with calves and females without calves in each breeding ground. Mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| | **B-mode** | | | **Observed swimming speed (m/s)** | | |
|---|---|---|---|---|---|---|
| | **Females with calves (FC)** | **Females without calves** | **FC vs FWC** | **Females with calves (FC)** | **Females without calves** | **FC vs FWC** |
| **Madagascar** | 1.32 ± 0.02 (n=6) | 1.18 ± 0.01 (n=5) | p=0.3 | 0.8 ± 0.8 (n=6) | 0.81 ± 0.04 (n=5) | p=0.3 |
| **Brazil** | 1. 55 ± 0.01 (n=54) | 1.23 ± 0.01 (n=6) | **p=0.02** | 0.5 ± 0.01 (n=54) | 0.7 ± 0.03 (n=6) | p=0.3 |
| **North West Cape** | 1.44 ± 0.03 (n=5) | 1.47 ± 0.04 (n=2) | p=0.9 | 0.6 ± 0.04 (n=5) | 0.8 ± 0.06 (n=2) | p=0.5 |

**Table S5.5.** Summary of environmental variables for each Brazilian coastal track. Values are presented as mean ± se. Distance from shore is the average of distances between closest positive bathymetric value and each whale position. Stars indicate that mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| **Whale Id** | **Sex** | **Bathymetry (m)** | **Slope (°)** | **Distance from shore (km)** | **Current speed (m/s)** | **Sea surface temperature (°C)** |
|---|---|---|---|---|---|---|
| 7617.05 | F | 46±3.03 | 0.15±0.02 | 64.62±6.14 | 0.13±0.01 | 25.75±0.07 |
| 7618.05 | F | 11±1.06 | 0.16±0.02 | 24.27±0.52 | 0.16±0.01 | 26.02±0.02 |
| 10946.05 | F | 66±27.33 | 1.23±1.03 | 75.16±27.55 | 0.14±0.03 | 26.28±0.1 |
| 20162.03 | M | 92±24.28 | 0.91±0.4 | 51.26±5 | 0.18±0.02 | 24.15±0.19 |
| 20687.03 | F | 30±3.26 | 0.28±0.1 | 37.98±4.13 | 0.26±0.04 | 25.4±0.35 |
| 21791.03 | F | 38±2.78 | 0.11±0.02 | 38.5±5.15 | 0.23±0.05 | 24.77±0.21 |
| 21800.03 | F | 44±1.74 | 0.15±0.01 | 62.28±2.33 | 0.24±0.02 | 25.97±0.06 |
| 21809.03 | F | 34±2.76 | 0.12±0.02 | 28.35±3.04 | 0.38±0.06 | 24.44±0.38 |
| 21810.03 | M | 92±22.1 | 1.07±0.44 | 42.07±3.59 | 0.17±0.02 | 23.72±0.35 |
| 24640.03 | F | 35±5.97 | 0.18±0.03 | 39.79±7.68 | 0.2±0.02 | 25.06±0.06 |
| 24641.05 | F | 41±5.3 | 0.14±0.04 | 55.59±11.36 | 0.1±0.01 | 26.01±0.11 |

| Whale Id | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|
| 24642.03 | F | 40±1.45 | 0.18±0.03 | 47.04±2.14 | 0.21±0.02 | 26.15±0.06 |
| 26712.05 | F | 41±7.83 | 0.68±0.38 | 72.17±14.85 | 0.16±0.02 | 25.9±0.05 |
| 27258.05 | F | 28±1.67 | 0.11±0.01 | 28.15±1.81 | 0.14±0.01 | 25.81±0.07 |
| 27259.03 | F | 38±2.37 | 0.15±0.03 | 31.85±4.29 | 0.21±0.03 | 24.34±0.37 |
| 27259.05 | F | 38±2.91 | 0.16±0.02 | 53.73±4.27 | 0.12±0.01 | 25.77±0.08 |
| 27261.05 | F | 31±1.74 | 0.1±0.01 | 37.17±2.21 | 0.18±0.01 | 25.86±0.06 |
| 27261.07 | F | 33±2.32 | 0.14±0.02 | 50.21±3.84 | 0.22±0.02 | 24.37±0.07 |
| 33000.05 | F | 61±7.63 | 0.33±0.15 | 63.01±5.66 | 0.14±0.01 | 24.89±0.23 |
| 33001.06 | F | 44±10.23 | 0.58±0.41 | 85.43±30.94 | 0.28±0.09 | 24.47±0.16 |
| 37229.05 | F | 47±6.92 | 0.16±0.02 | 49.25±10.08 | 0.12±0.03 | 25.88±0.1 |
| 37231.05 | F | 84±19.5 | 0.87±0.31 | 76.73±7.69 | 0.13±0.01 | 25.63±0.08 |
| 37231.07 | M | 38±3.69 | 0.19±0.07 | 54.83±6.89 | 0.07±0.01 | 24.42±0.09 |
| 37234.05 | F | 60±12.66 | 0.43±0.23 | 43.78±6.02 | 0.12±0.03 | 25.37±0.22 |
| 37234.06 | F | 32±3.76 | 0.12±0.02 | 21.93±2.48 | 0.27±0.03 | 24.64±0.11 |
| 37236.06 | F | 32±2.66 | 0.13±0.03 | 35.67±1.91 | 0.39±0.05 | 24.73±0.13 |
| 37286.07 | F | 49±12.02 | 0.51±0.37 | 42.31±3.71 | 0.19±0.02 | 23.63±0.16 |
| 37288.07 | F | 42±2.61 | 0.1±0.01 | 52.4±3.87 | 0.2±0.02 | 23.47±0.25 |
| 42521.07 | F | 31±2.96 | 0.18±0.04 | 35.42±2.1 | 0.14±0.01 | 24.19±0.08 |
| 42525.07 | F | 31±2.77 | 0.11±0.02 | 35.79±3.27 | 0.1±0.02 | 24.5±0.09 |
| 50682.06 | F | 31±3.13 | 0.2±0.06 | 30.76±3.57 | 0.3±0.03 | 24.49±0.09 |
| 50682.07 | F | 35±5.64 | 0.25±0.07 | 41.37±3.58 | 0.17±0.01 | 24.66±0.05 |
| 50686.07 | F | 69±16.43 | 0.57±0.22 | 68.09±6.16 | 0.16±0.02 | 24.31±0.08 |
| 50687.07 | F | 62±20.31 | 0.63±0.35 | 58.59±7.84 | 0.08±0.01 | 24.45±0.12 |
| 60004.07 | M | 16±0.68 | 0.08±0.01 | 15.64±1.52 | 0.18±0.02 | 21.29±0.67 |
| 81123.09 | F | 48±32.08 | 0.67±0.55 | 17.87±2.72 | 0.17±0.04 | 24.66±0.82 |

| **Whale Id** | **Sex** | **Bathymetry (m)** | **Slope (°)** | **Distance from shore (km)** | **Current speed (m/s)** | **Sea surface temperature (°C)** |
|---|---|---|---|---|---|---|
| 81125.09 | M | 74±29.92 | 1.19±0.64 | 19.38±3.03 | 0.08±0.01 | 24.46±0.76 |
| 81126.09 | F | 39±10.91 | 0.86±0.29 | 15.04±3.01 | 0.19±0.06 | 25.29±0.4 |
| 84480.12 | F | 52±4.4 | 0.29±0.1 | 49.82±2.93 | 0.18±0.01 | 24.94±0.1 |
| 84497.1 | F | 85±13.33 | 1.3±0.43 | 68.34±6.04 | 0.13±0.01 | 24.25±0.07 |
| 87632.12 | F | 62±9.36 | 0.39±0.12 | 48.25±3.43 | 0.18±0.02 | 24.73±0.13 |
| 87759.08 | M | 59±12.04 | 0.97±0.56 | 115.41±11.35 | 0.12±0.02 | 24.47±0.13 |
| 87761.08 | M | 113±23.91 | 2.12±0.62 | 41.03±13.25 | 0.14±0.04 | 23.4±0.5 |
| 87762.08 | M | 85±20.24 | 1±0.29 | 53.71±14.35 | 0.13±0.03 | 23.82±0.48 |
| 87763.08 | F | 49±6.07 | 0.59±0.17 | 42.82±3.94 | 0.14±0.01 | 24.18±0.24 |
| 87764.08 | F | 64±7.97 | 0.81±0.21 | 37.92±2.69 | 0.22±0.02 | 24.6±0.19 |
| 87765.08 | F | 64±13.95 | 0.97±0.31 | 42.97±8.63 | 0.1±0.01 | 22.37±0.64 |
| 87766.08 | M | 42±4.86 | 0.42±0.13 | 30.86±3.98 | 0.11±0.01 | 23.91±0.27 |
| 87768.08 | F | 73±10.7 | 1.31±0.26 | 27.38±1.78 | 0.24±0.02 | 25.8±0.18 |
| 87768.11 | F | 94±14.74 | 0.92±0.23 | 80.24±5.6 | 0.14±0.01 | 24.43±0.11 |
| 87769.11 | F | 142±29.3 | 2.11±0.73 | 84.57±13.01 | 0.15±0.02 | 23.67±0.48 |
| 87770.08 | M | 76±32.27 | 1.17±0.68 | 12.9±1.38 | NA±NA | 24.11±0.75 |
| 87773.08 | F | 62±9.03 | 0.27±0.07 | 32.54±3.36 | 0.2±0.01 | 22.31±0.38 |
| 87773.1 | M | 35±7.61 | 0.46±0.22 | 38.87±7.48 | 0.11±0.02 | 23.85±0.52 |
| 87773.11 | F | 56±8.11 | 0.29±0.09 | 41.36±3.4 | 0.14±0.01 | 23.62±0.27 |
| 87774.09 | F | 43±5.04 | 0.34±0.09 | 44.36±2.8 | 0.19±0.01 | 25.3±0.18 |
| 87774.11 | M | 36±3.33 | 0.4±0.14 | 33.4±3.89 | 0.2±0.02 | 22.64±0.61 |
| 87775.08 | F | 43±3.69 | 0.26±0.06 | 59.57±7.21 | 0.13±0.01 | 24.38±0.08 |
| 87775.12 | F | 43±11.39 | 0.34±0.19 | 62.15±15.07 | 0.11±0.01 | 25.22±0.1 |
| 87776.08 | F | 96±23.07 | 1.13±0.49 | 103.58±8.82 | 0.08±0.01 | 24.4±0.13 |
| 87776.11 | F | 41±10.81 | 0.54±0.26 | 26.95±3.41 | 0.13±0.01 | 24.08±0.49 |

| **Whale Id** | **Sex** | **Bathymetry (m)** | **Slope (°)** | **Distance from shore (km)** | **Current speed (m/s)** | **Sea surface temperature (°C)** |
|---|---|---|---|---|---|---|
| 87777.1 | F | 43±10.5 | 0.4±0.15 | 35.27±3.89 | 0.19±0.01 | 24.06±0.37 |
| 87778.08 | M | 49±4.25 | 0.2±0.07 | 51.38±2.8 | 0.27±0.02 | 23.95±0.12 |
| 87781.1 | F | 100±31.13 | 2.1±1.09 | 61.96±10.72 | 0.14±0.02 | 24.24±0.25 |
| 87783.09 | F | 59±16.24 | 1.15±0.35 | 10.25±1.07 | - | 23.98±0.79 |
| 87783.11 | F | 41±2.46 | 0.2±0.02 | 57.13±3.82 | 0.17±0.02 | 24.11±0.24 |
| 88724.1 | F | 34±7.94 | 0.36±0.24 | 17.44±2.64 | 0.23±0.02 | 23.03±0.93 |
| 88726.1 | F | 71±11.86 | 0.62±0.25 | 72.53±8.37 | 0.13±0.02 | 23.92±0.29 |
| 88727.09 | F | 76±13.63 | 1.35±0.41 | 36.99±4.26 | 0.07±0.01 | 25.39±0.32 |
| 96380.1 | F | 34±12.52 | 0.44±0.19 | 31.81±8.25 | 0.19±0.02 | 23.76±0.54 |
| 111868.11 | M | 63±12.54 | 0.59±0.27 | 29.1±3.56 | 0.16±0.02 | 22.5±0.42 |
| 111871.12 | F | 70±10.51 | 0.69±0.25 | 86.47±6.23 | 0.13±0.01 | 25.05±0.03 |
| 112702.12 | M | 49±3.73 | 0.3±0.12 | 60.14±2.99 | 0.2±0.01 | 24.79±0.11 |
| 112712.12 | M | 50±6.22 | 0.16±0.02 | 41.51±4.19 | 0.17±0.02 | 23.18±0.83 |
| 112714.12 | M | 19±2.71 | 0.12±0.02 | 27.6±2.92 | 0.12±0.01 | 25.48±0.1 |
| 120947.12 | M | 24±4.41 | 0.14±0.02 | 32.6±4.55 | 0.12±0.01 | 25.19±0.07 |
| 121189.12 | M | 28±2.58 | 0.13±0.02 | 39.24±4.9 | 0.22±0.03 | 24.57±0.12 |
| 121192-1.12 | M | 69±27.08 | 0.51±0.32 | 81.42±18.51 | 0.09±0.02 | 25.34±0.14 |
| 121189-2.12 | M | 33±2.99 | 0.14±0.03 | 48±6.25 | 0.21±0.03 | 24.56±0.11 |
| 193.12 | F | 75±14.63 | 0.61±0.24 | 56.3±7.48 | 0.16±0.02 | 23.75±0.55 |
| 121195.12 | F | 83±22.72 | 1.04±0.46 | 82.2±9.93 | 0.15±0.02 | 24.75±0.12 |
| 121196.12 | M | 10±1.44 | 0.07±0.01 | 8.04±1.72 | - | 25.05±0.27 |
|  | **Females (n=60)** | **51 ± 1** | **0.5 ± 0.03** | **46.1 ± 0.7** | **0.2 ± 0.00** | **24.8 ± 0.04** |
|  | **Males (n=22)** | **50 ± 3** | **0.5 ± 0.05** | **41.1 ± 1.4** | **0.2 ± 0.01** | **23.8 ± 0.11** |

| Whale Id | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|
| | **Total (n=82)** | **51 ± 1.15** | **0.5 ± 0.02** | **45.3 ± 0.6** | **0.2 ± 0.003** | **24.6 ± 0.04** |

**Table S5.6.** Summary of environmental variables for each coastal track of Australian west coast. Values are presented as mean ± se. Distance from shore is the average of distances between closest positive bathymetric value and each whale estimated position. Stars indicate that mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| Whale Id | Region | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| 40616 | North West Cape | Female | 12 ± 1.5 | 0.08 ± 0.02 | 7.6 ± 0.94 | 0.3 ± 0.02 | 21.8 ± 0.38 |
| 53360 | North West Cape | Female | 29 ± 6.7 | 0.14 ± 0.04 | 12.85 ± 1.78 | 0.3 ± 0.05 | 22.6 ± 0.46 |
| 53398 | North West Cape | Male | 38 ± 3.02 | 0.18 ± 0.04 | 22.79 ± 2.22 | 0.4 ± 0.07 | 23.9 ± 0.24 |
| 60665 | North West Cape | Male | 247 ± 91.11 | 0.8 ± 0.28 | 22.68 ± 4 | 0.2 ± 0.03 | 21.9 ± 0.27 |
| 60669 | North West Cape | Female | 16 ± 9.16 | 0.08 ± 0.02 | 6.55 ± 0.67 | 0.2 ± 0.02 | 22.4 ± 0.1 |
| 86582 | Kimberley region | Male | 131 ± 20.6 | 0.51 ± 0.23 | 50.03 ± 6.53 | 0.2 ± 0.04 | 23.1 ± 0.23 |
| 86583 | Kimberley region | Male | 97 ± 14.53 | 0.19 ± 0.02 | 51.53 ± 6.47 | 0.3 ± 0.03 | 25.1 ± 0.1 |
| 86584 | Kimberley region | Male | 152 ± 28.98 | 0.41 ± 0.12 | 63.46 ± 9.24 | 0.2 ± 0.03 | 24.6 ± 0.11 |
| 86587 | Kimberley region | Male | 253 ± 26.16 | 0.41 ± 0.08 | 84.99 ± 6.37 | 0.2 ± 0.04 | 24.3 ± 0.08 |
| 96382 | Kimberley region | Female | 19 ± 1.74 | 0.07 ± 0.01 | 11.41 ± 1.06 | 0.2 ± 0.01 | 23.5 ± 0.31 |

| Whale Id | Region | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| 96384 | Kimberley region | Female | 24 ± 3.01 | 0.16 ± 0.04 | 12.38 ± 1.92 | 0.5 ± 0.07 | 24.6 ± 0.47 |
| 96389 | Kimberley region | Female | 50 ± 6.29 | 0.11 ± 0.03 | 20.85 ± 2.6 | 0.2 ± 0.02 | 23.1 ± 0.4 |
| 96391 | Kimberley region | Female | 50 ± 7.9 | 0.14 ± 0.04 | 26.18 ± 4.63 | 0.2 ± 0.02 | 23.1 ± 0.46 |
| 96399 | Kimberley region | Female | 51 ± 13.13 | 0.07 ± 0.01 | 42.41 ± 10.5 | 0.3 ± 0.02 | 25.7 ± 0.55 |
| 96400 | Kimberley region | Female | 32 ± 2.76 | 0.07 ± 0.01 | 22.29 ± 2.23 | 0.3 ± 0.04 | 25.7 ± 0.32 |
| 96407 | Kimberley region | Female | 46 ± 5.89 | 0.12 ± 0.03 | 15.54 ± 1.81 | 0.2 ± 0.04 | 26.3 ± 0.57 |
| 96408 | Kimberley region | Female | 34 ± 4.55 | 0.11 ± 0.02 | 21.51 ± 3.71 | 0.4 ± 0.04 | 25.2 ± 0.42 |
| 96411 | Kimberley region | Female | 34 ± 5.2 | 0.09 ± 0.02 | 19.93 ± 5.74 | 0.2 ± 0.03 | 24.4 ± 1.13 |
| 98107 | North West Cape | Female | 60 ± 10.32 | 0.34 ± 0.08 | 9.73 ± 1.41 | 0.1 ± 0.02 | 22.3 ± 0.41 |
| 98111 | North West Cape | Male | 89 ± 17 | 0.3 ± 0.08 | 43.28 ± 7.38 | 0.2 ± 0.03 | 23.8 ± 0.24 |
| 98118 | North West Cape | Female | 19 ± 3.35 | 0.1 ± 0.03 | 9.7 ± 0.92 | 0.1 ± 0.02 | 21.7 ± 0.37 |
| 98121 | North West Cape | Female | 43 ± 11.99 | 0.33 ± 0.13 | 9 ± 1.27 | 0.1 ± 0.02 | 21.5 ± 0.66 |
| 98123 | North West Cape | Male | 43 ± 4.52 | 0.19 ± 0.05 | 18.29 ± 1.43 | 0.2 ± 0.03 | 23.6 ± 0.18 |
| 98126 | North West Cape | Female | 33 ± 5.31 | 0.19 ± 0.08 | 13.8 ± 1.54 | 0.1 ± 0.01 | 22.7 ± 0.18 |
| 98127 | North West Cape | Male | 141 ± 15.14 | 0.45 ± 0.06 | 19.26 ± 2.15 | 0.1 ± 0.01 | 23.5 ± 0.1 |
| 98140 | North West Cape | Male | 43 ± 7.81 | 0.25 ± 0.1 | 16.82 ± 1.89 | 0.3 ± 0.04 | 22.9 ± 0.35 |
|  | **North West Cape** | **Females (n=7)** | **30 ± 3** | **0.2 ± 0.03** | **10.5 ± 1** | **0.2 ± 0.01** | **22.2 ± 0.1** |

| Whale Id | Region | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| | **North West Cape** | **Males (n=6)** | **74 ± 7** | **0.3 ± 0.03** | **23.4 ± 1.5** | **0.3 ± 0.02** | **23.4 ± 0.1** |
| | **North West Cape** | **Total (n=13)** | **56 ± 4** | **0.2 ± 0.02** | **18.3 ± 1** | **0.2 ± 0.02** | **22.9 ± 0.1** |
| | **Kimberley region** | **Females (n=9)** | **36 ± 2** | **0.1±0.01** | **20 ± 1** | **0.3 ± 0.01** | **24.3 ± 0.2** |
| | **Kimberley region** | **Males (n=4)** | **159 ± 12** | **0.4±0.07** | **62.5 ± 4** | **0.3 ± 0.02** | **24.2 ± 0.1** |
| | **Kimberley region** | **Total (n=13)** | **80 ± 5** | **0.2±0.03** | **35.2 ± 2** | **0.3 ± 0.01** | **24.2 ± 0.1** |

**Table S5.7.** Summary of environmental variables for each Australian coastal track of east coast. Values are presented as mean ± se. Distance from shore is the average of distances between closest positive bathymetric value and each whale position. Stars indicate that mean values were computed on all location values whereas mean values used in statistical tests were computed by individual.

| Whale Id | Region | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| 88730 | Eastern coast | Male | 59 ± 9 | 0.3 ± 0.05 | 32.8 ± 2 | 0.4 ± 0.05 | 22.9 ± 0.18 |
| 88734 | Eastern coast | Female | 54 ± 7 | 0.2 ± 0.03 | 28.5 ± 4 | 0.5 ± 0.05 | 22 ± 0.25 |
| 88736 | Eastern coast | Male | 59 ± 5 | 0.2 ± 0.09 | 32.5 ± 4 | 0.4 ± 0.04 | 21.7± 0.49 |
| 88737 | Eastern coast | Male | 97 ± 13 | 0.3 ± 0.07 | 47.1 ± 4 | 0.4 ± 0.05 | 22.7 ± 0.22 |
| 88742 | Eastern coast | Male | 56 ± 3 | 0.2 ± 0.04 | 31.02 ± 3 | 0.4 ± 0.04 | 22.5 ± 0.32 |
| 88747 | Eastern coast | Male | 69 ± 10 | 0.4 ± 0.2 | 34.5 ± 4 | 0.2 ± 0.02 | 21.7 ± 0.52 |
| 88750 | Eastern coast | Male | 49 ± 3 | 0.1 ± 0.01 | 21 ± 2 | 0.5 ± 0.05 | 22.5 ± 0.2 |

| Whale Id | Region | Sex | Bathymetry (m) | Slope (°) | Distance from shore (km) | Current speed (m/s) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|
| 88751 | Eastern coast | Male | 63 ± 12 | 0.3 ± 0.07 | 22.2 ± 2 | 0.5 ± 0.07 | 22.2 ± 0.22 |
| 88754 | Eastern coast | Female | 104 ± 12 | 0.2 ± 0.04 | 44.9 ± 3 | 0.3 ± 0.02 | 21.9 ± 0.18 |
| 88755 | Eastern coast | Male | 98 ± 12 | 0.3 ± 0.05 | 48.3 ± 4 | 0.4 ± 0.03 | 22.6 ± 0.12 |
| 88756 | Eastern coast | Male | 50 ± 3 | 0.2 ± 0.04 | 27.6 ± 3 | 0.4 ± 0.05 | 22 ± 0.23 |
| | | **Females (n=2)** | **86±8** | **0.2 ± 0.03** | **38.9 ± 3** | **0.4 ± 0.03** | **21.9 ± 0.15** |
| | | **Males (n=9)** | **68±3** | **0.2 ± 0.02** | **33.9 ± 1** | **0.4 ± 0.02** | **22.4 ± 0.08** |
| | | **Total (n=11)** | **72±3** | **0.2 ± 0.01** | **35.1 ± 1** | **0.4 ± 0.01** | **22.3 ± 0.07** |

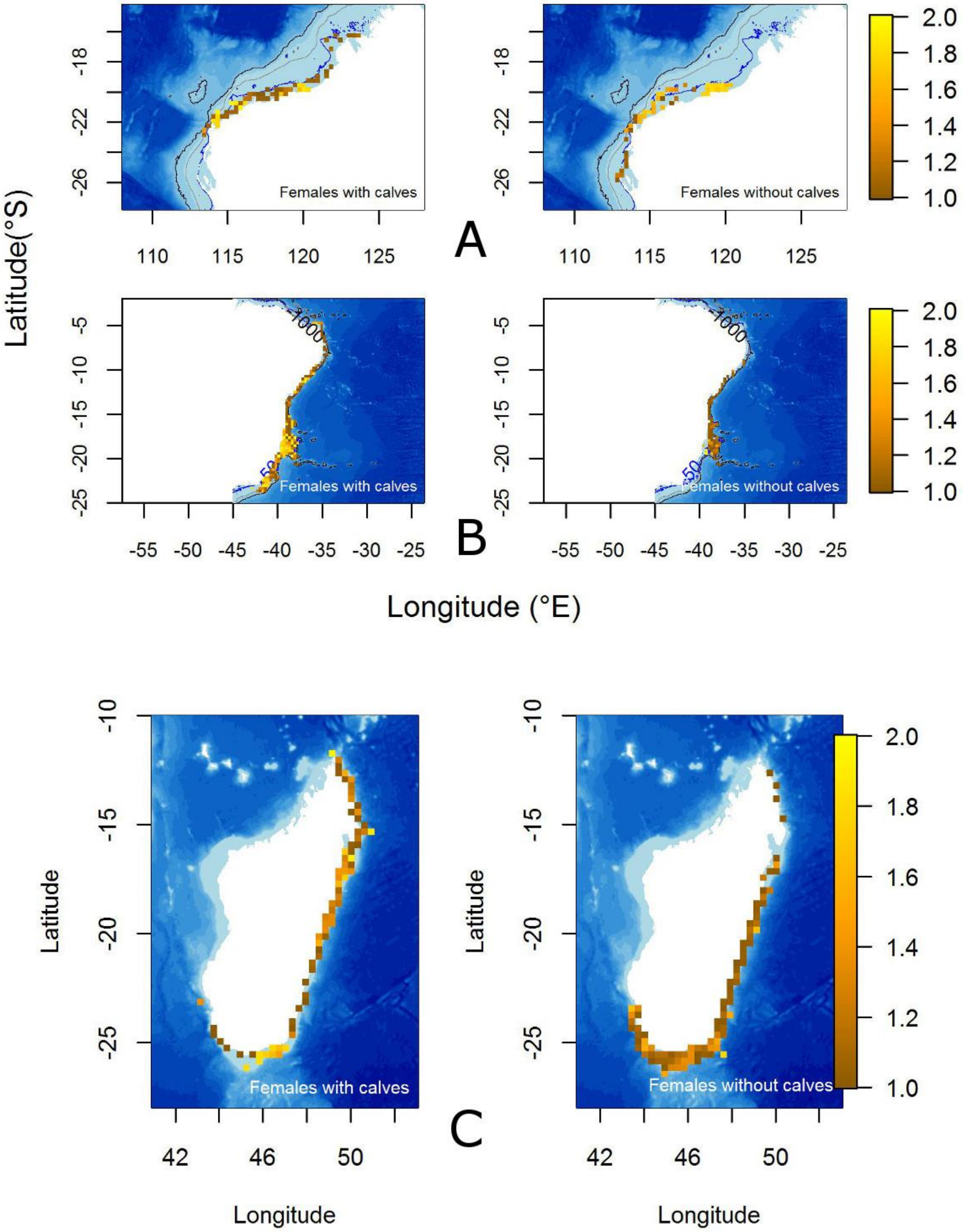

**Figure S5.3.** Averaged B-mode into 0.3x0.3° grid cell for both female with claves' and females without calves' coastal tracks from the different breeding areas: Eastern Australia (A), Brazil (B), and Madagascar (C).

# CHAPITRE VI – DISCUSSION GENERALE ET PERSPECTIVES

*Aquarelle de Caroline Jacques*

# CHAPITRE VI – DISCUSSION GENERALE ET PERSPECTIVES

## I. DISCUSSION GENERALE

### A. SYNTHESE DES RESULTATS

#### 1. RAPPEL DES OBJECTIFS DE LA THESE

Les baleines à bosse présentent une stratégie de reproduction sur capital (Stearns 1992). Ainsi, en période de reproduction, leur distribution ne sera pas influencée par la disponibilité en ressources. Il s'agissait, dans cette thèse, d'étudier les déplacements et l'utilisation d'habitats des baleines à bosse qui viennent se reproduire à Madagascar en fonction du sexe et du statut reproducteur et de les comparer avec d'autres sites de reproduction de l'hémisphère Sud comprenant l'Australie de l'Est et de l'Ouest et le Brésil, pour tenter de dégager un schéma général de l'utilisation de l'habitat de cette espèce lors de cette période clé de leur cycle annuel. Pour cela, nous avons tenté de quantifier l'influence des paramètres environnementaux sur la distribution des baleines en fonction du sexe et à différentes échelles spatiales et d'évaluer l'influence relative des conditions environnementales locales. Afin d'acquérir des nouvelles données sur l'écologie de la reproduction et de prédire les caractéristiques des habitats de reproduction, il est indispensable de décrire les déplacements des individus et leurs préférences environnementales. Les baleines à bosse migrent chaque année vers des zones de reproduction très côtières fréquemment soumises à une pression anthropique importante (activités industrielles ou touristiques). Caractériser leurs déplacements et déterminer les paramètres qui influencent leur distribution est crucial pour la protection de leurs habitats de reproduction et pour mieux répondre aux enjeux de gestion et de conservation de cette espèce.

#### 2. UTILISATION DE LA TELEMETRIE SATELLITAIRE

Les baleines à bosse ont été largement étudiées pendant la période de reproduction, pendant laquelle elles sont généralement observées à proximité des côtes. Les données sont en général collectées dans les eaux côtières ou depuis des postes d'observations terrestres, et plus rarement lors de survols aériens. Cependant, ces méthodes ne nous permettent pas de suivre les baleines au cours de leurs déplacements individuels et de déterminer quels habitats elles exploitent pendant toute la durée de la reproduction. Depuis les 20 dernières années, la télémétrie a permis d'améliorer considérablement nos connaissances sur les migrations, les mouvements individuels et l'utilisation de l'habitat des grandes baleines. Cette approche est particulièrement utile pour l'étude d'espèces hautement migratrices telles que les baleines à bosse dont la répartition géographique est très étendue et qui les conduisent à utiliser des habitats très différents (Mate et al. 2007a, Gales et al. 2010, Zerbini et al. 2011, Kennedy et al. 2013, Garrigue et al. 2015) Dans ce travail de thèse, l'utilisation de cette approche a donc permis d'apporter de nouvelles informations sur les déplacements individuels et l'utilisation d'habitats des baleines à bosse de l'hémisphère Sud.

## 3. A PETITE ECHELLE SPATIALE : LE CANAL DE SAINTE MARIE

Bien que la présence de baleines à bosse autour de l'île Sainte Marie soit connue depuis longtemps, ayant notamment stimulé le développement du « whale-watching[3] » depuis la fin des années 80 (Hoyt 1996, 2000, O' Connor S et al. 2009), aucune étude scientifique n'a été publiée sur cette population à l'exception de Faria et al. (2013) rapportant la naissance d'un baleineau dans les eaux du canal de Sainte Marie. Le chapitre 3 de cette thèse s'intéresse à la distribution et l'utilisation de l'habitat des groupes sociaux au cours de la saison dans une zone d'étude encore peu étudiée.

Dans notre étude, l'analyse du taux de rencontre (observations/heure) annuel des baleines à bosse dans le canal de Sainte Marie nous a permis de mettre en évidence une variation interannuelle significative du taux de rencontre global des groupes et du taux de rencontre des groupes avec baleineaux. Bien que nous n'ayons pu estimer l'abondance de la population globale ni celle des groupes par des méthodes standards, nos résultats suggèrent que la variabilité interannuelle du taux de rencontre dépend fortement du nombre de

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[3] Le « whale-watching » se définit comme l'observation des cétacés dans leur milieu naturel. Il est généralement associé à une activité touristique à but lucrative

femelles avec un baleineau. Ceci nécessiterait une étude plus approfondie mais ouvre néanmoins une nouvelle piste de recherche.

Dans le canal de Sainte Marie, les baleines à bosse sont présentes durant tout l'hiver de juin à septembre avec un pic d'abondance entre juillet et août. L'observation de différents types de groupes sociaux et la présence de chants communément constatés dans la zone témoignent que le canal est utilisé comme une zone de reproduction. En dehors des Comores, la proportion de groupes avec baleineaux (33%) dans notre zone d'étude est notamment plus élevée ou égale que celle observée dans d'autres régions du Sud-Ouest de l'océan Indien (e.g. 14.8%, Mozambique, Findlay et al. 1994, 33.4% La Réunion, Dulau-Drouot et al. 2012) ou d'autres zones de reproduction de l'hémisphère Sud (e.g. 17% Equateur, Scheidat et al. 2004, 13% Nouvelle Calédonie, Garrigue et al. 2001). En revanche il est interessant de noté que dans l'archipel des Comores et à Mayotte, cette proportion est beaucoup plus élévée (68.6% Comores, Kiszka et al. 2010, 73%, Ersts et al. 2006) et que le sex ratio dans la région des Comores est biaisé en faveur des femelles suggérant que cette zone de reproduction (cf. sous-stock C2) est utilisée préfrérentiellement par les femelles gestantes ou accompagnées d'un baleineau. De plus, la première observation de la naissance d'un baleineau reportée à Sainte Marie appuie l'idée que la région est particulièrement favorable aux couples mère-baleineau. Nous montrons que la saison de reproduction se caractérise par deux grandes périodes séparées temporellement d'un mois. La première est marquée par l'abondance de groupes sans baleineaux et la seconde par l'abondance des groupes avec baleineaux. Ceci est en adéquation avec l'existence d'une ségrégation temporelle en fonction de la classe d'âge, du sexe et du statut reproducteur des individus durant la migration, et selon laquelle les femelles gestantes seraient notamment les dernières à migrer depuis les zones d'alimentation, arrivant en seconde partie de saison sur les zones de mises bas. Ainsi, les contraintes énergétiques associées au stade de reproduction (i.e. gestation, allaitement) influencent probablement la distribution spatiale mais aussi temporelle des femelles en gestation lors de la migration ou sur les sites d'hivernage (Craig & Herman 1997, Craig et al. 2003).

Dans notre étude, les groupes avec baleineaux sont observés plus fréquemment dans des eaux de plus faibles profondeurs que les groupes sans baleineaux et particulièrement les femelles suitées (< 20 m). De plus, le nombre d'escortes présentes dans les groupes avec baleineaux diminue avec la distance à la côte. Il est notamment admis qu'à petite échelle spatiale, la structure sociale et le statut reproducteur jouent un rôle dans la répartition spatiale des baleines à bosse (Smultea 1994, Craig & Herman 2000, Ersts & Rosenbaum 2003). A Hawaii, le nombre d'escortes augmente avec la profondeur (Craig et al. 2014). On peut penser que la présence de plusieurs escortes entraine une compétition entre mâles pour la femelle et que les zones de faibles profondeurs et plus proche des côtes seront alors moins favorables aux comportements reproducteurs. Ainsi, la profondeur est un paramètre important pour les baleines à bosse en général et les femelles suitées en particulier. Dans notre étude, il a été aussi observé que les plus grandes proportions de groupes avec baleineaux et sans baleineaux étaient observés dans la gamme de profondeur comprise entre 20 et 30 m. Le canal de Sainte Marie ayant un faible gradient de profondeurs, les différents types de groupes partagent probablement un même type d'habitats. Une autre étude, réalisée dans le canal de 'Au'au à Hawaï indique que les groupes avec baleineaux ne montrent pas de ségrégation spatiale avec les autres types de groupes et utilisent des eaux moins profondes (40-60 m), plus loin de la côte (4-6 km) et sur des fonds plus accidentées (Cartwright et al. 2012). La présence de nuisances près de la côte (port de Lahaina, trafic maritime élévé) dans cette zone d'étude pourrait expliquer que les couples femelle-baleineau éviteraient les zones côtières dans cette région. Par conséquent, les couples mère-baleineau et possiblement les autres types de groupes pourraient avoir une flexibilité de réponse dans le choix des habitats utilisés, même si au vu de nos résultats à Madagascar et des tendances observées dans la plupart des études publiées, on peut penser que l'éloignement de la côte des mères-baleineaux observé à Hawaï reste une exception reflétant une réponse d'évitement des nuisances d'origine humaine. Située entre la côte malgache et l'île Sainte Marie, le canal de Sainte Marie, constitue pour les baleines à bosse une zone particulièrement abritée. De plus, l'extension du plateau continental au Nord-Est de Madagascar se traduit par la présence dans le canal d'eaux de très faibles profondeurs particulièrement recherchées par les femelles accompagnées de leurs petits. Aussi, la faible largeur du canal (30 km) et la langue de terre formant un entonnoir (7 km) au centre de celui-ci explique certainement la densité relativement importante de baleines à bosse dans le canal de Sainte Marie durant la période de reproduction. Par sa configuration géographique particulière et ses faibles profondeurs, le canal de Sainte Marie représente un site d'étude unique. Des comparaisons photographiques de nageoires caudales intra et inter-annuelles sont actuellement en cours afin de quantifier la fidélité aux sites des individus. Dans un futur proche, des comparaisons avec d'autres sites de reproduction du sud-ouest de l'océan Indien comme par exemple la baie d'Antongil ou de l'île de la Réunion seront réalisées afin d'approfondir nos connaissances sur les échanges entre les sous-populations du stock C.

## 4. DEPLACEMENTS DES BALEINES A BOSSE DANS LA ZONE DE REPRODUCTION DE MADAGASCAR

A Madagascar, les baleines à bosse sont présentes tout autour de l'île pendant l'hiver, cependant leur distribution et leurs déplacements restaient mal documentés. La région dont la population est la plus connue est la baie d'Antongil située au nord de Sainte Marie sur la côte Est de l'île dont les données photographiques et génétiques ont servi à estimer la taille de la population de Madagascar (Rosenbaum et al. 1997, Cerchio et al. 2009, Jackson et al. 2015). Dans ce contexte, une des questions posée était : quels sont les déplacements des baleines à bosse fréquentant les eaux malgaches en période de reproduction ? Nous avons mis en évidence par le suivi télémétrique satellitaire que les baleines à bosse se déplaçaient sur de longues distances en peu de temps, pouvant parcourir des distances de 100 km/j. Elles se déplaçent le long du plateau continental de la côte Est et Sud de Madagascar mais également vers d'autres sites (e.g. côte Est africaine) transitant par des eaux plus profondes (Cerchio et al. In prep, **annexe A**) Les individus équipés à Sainte Marie ont exploité préférentiellement le centre de la côte Est de Madagascar alors que les individus équipés près d'Anakao se sont déplacés préférentiellement le long de la côte Sud et Sud-Est, ce qui semble indiquer l'utilisation d'habitats relativement distincts en période de reproduction (Cerchio et al. In prep, **annexe A**). Certains individus, dont des femelles avec un baleineau, ont également quitté Madagascar dans différentes directions atteignant pour certaines la côte Est africaine (i.e. Somalie et Kenya). Aussi, les femelles ont montré des déplacements moins localisés que les mâles ce qui suggère des stratégies de reproduction différentes (Cerchio et al. In prep, **annexe A**).

## 5. INFLUENCE DES PARAMETRES ENVIRONNEMENTAUX SUR LES DEPLACEMENTS DES BALEINES A BOSSE A MADAGASCAR : DIFFERENCES ENTRE MALES ET FEMELLES

La bathymétrie est un paramètre essentiel qui a été retenu dans la majorité des modèles statistiques évalués dans le chapitre 4. Au contraire, la témpérarure de surface ne semble pas être déterminante localement car c’est un paramètre qui agit probablement à plus grande échelle, comme par exemple sur la distribution des cétacés dans les zones d’alimentation (e.g. Tynan et al. 2005). Durant la période de reproduction, nous avons montré que les baleines à bosse se déplacent principalement sur le plateau continental mais également en milieu océanique. Lors des déplacements côtiers, les femelles passent plus de temps dans les eaux inférieures à 200 m de profondeur que les mâles. Néanmoins, les déplacements localisés des femelles sont associés à des habitats plus profonds et plus loin de la côte que ce qui avait été supposé. Dans cette étude, bien que le statut reproducteur des femelles n’ait pas été pris en compte dans les modèles et que la différence de comportements ne soit pas significative entre les femelles avec baleineau et les femelles sans baleineau, on peut néanmoins supposer d’après la littérature (Craig & Herman 2000, Ersts & Rosenbaum 2003, Félix & Botero-Acosta 2011, Craig et al. 2014) et par les résultats du chapitre 4, que le statut reproducteur est un facteur déterminant dans la sélection d’habitats chez des femelles. A l’inverse de ce qui est suggéré pour les femelles avec baleineau, les femelles sans baleineaux disposées à se reproduire pourraient exploiter davantage les zones plus profondes, situées plus au large, qui permettent une meilleure manœuvrabilité dans les comportements de reproduction (Smultea 1994, Elwen & Best 2004). Une autre hypothèse possible serait l’évolution du comportement des femelles suitées tout au long de la croissance du baleineau sur le site d’hivernage, se traduisant par des déplacements plus fréquents et sur de plus longues distances, plus loin des côtes et dans des zones plus profondes au fur et à mesure de la croissance du jeune. Les femelles avec baleineau pourraient ainsi exploiter à la fois des zones côtières de faibles profondeurs mais aussi des zones plus profondes. Par ailleurs, bien que ce résultat soit surprenant, les mâles ne semblent pas montrer de préférences d’habitats particulières bien qu’ils diminuent leur vitesse de nage dans des zones moins profondes. Les femelles et les mâles augmentent leur vitesse dans les zones de plus faibles courants suggérant que la vitesse du courant n’influence pas les déplacements d’individus. Bien que les femelles accompagnées d’un baleineau puissent sélectionner des zones calmes et protégées afin de réduire les dépenses énergétiques du baleineau (Taber & Thomas 1982, Whitehead & Moore 1982, Corkeron & Connor 1999, Rayment et al. 2015), les mâles ou les femelles sans baleinaux impliqués dans des activités de reproduction sont probablement moins sélectifs dans leur choix d'habitats.

Bien que les déplacements en milieu océanique soient associés à des habitats plus profonds, les individus (femelles et mâles non dissociés par manque de données) se déplacent lors de la migration de façon plus erratique dans les eaux les moins profondes, de faible courant ou les eaux plus riches en chlorophylle telles que le mont sous-marin des Walters Shoals ou le plateau continental des îles Crozet lors de la migration. De plus, il était intéressant de constater qu'en milieu océanique les vitesses moyennes de nage des baleines à bosse étaient supérieures aux vitesses rencontrées du courant, ce qui m'a amenée à tenter de quantifier l'influence du courant sur la vitesse et la direction des déplacements. Notre étude a ainsi montré que la vitesse du courant de surface ne semblait pas être un facteur majeur dans le déplacement des baleines à bosse. Cependant, elles semblent suivre la même direction que le courant lorsque celui-ci est fort comme lorsqu'elles quittent Madagascar par le Nord ou par le Sud. Alors que de nombreuses études existent sur l'influence du courant sur les déplacements de différentes espèces marines comme les tortues, peu ont été conduites sur les mysticètes (Carey et al. 1990, Klimley 1993, McConnell et al. 2002, Luschi et al. 2003, Stark et al. 2005, Ream et al. 2005, Gaspar et al. 2006, Lambardi et al. 2008, Chapman et al. 2011, Fossette et al. 2012). Les données issues de suivis satellites ont révélé que pendant leur migration, les baleines étaient capables de se déplacer dans des couloirs migratoires restreints sur le plan spatial en gardant un cap constant sur plusieurs centaines de kilomètres (Mate et al. 2007a, Horton et al. 2011, Zerbini et al. 2011, Kennedy et al. 2013), utilisant probablement une stratégie de complète compensation (modification de leur direction de nage par rapport à la direction du courant) pour maintenir un cap constant Cepedant, il est également suggéré que cette statégie, utilisée généralement par les espèces migratrices, ne soit pas maintenue constamment et qu'elles ajustent leurs déplacements aux conditions environnementales locales (Chapman et al. 2011). Ainsi, notre étude révèle notamment que pendant les trajets océaniques réalisés durant la période de reproduction (e.g. entre sites de reproduction), les individus peuvent à la fois utiliser une stratégie de compensation ou suivre la direction du courant quand celui-ci est fort. Par ailleurs, le but des déplacements n'étant pas le même, il est possible que les stratégies d'orientation des individus soient plus flexibles aux conditions environnementales locales que pendant la migration. Pour arriver au bon moment (e.g. pic annuel de la ressource, synchronisation du cycle hormonal au cycle saisonnier) et à bonne destination, les baleines à bosse doivent être précisent et constantes dans leurs trajectoires de migration alors que durant la période de reproduction, on peut supposer que les déplacements sont plus aléatoires. Ceci peut suggèrer que la stratégie de déplacements des baleines à bosse est dynamique dans le temps et dans l'espace ajustant celle-ci selon leurs comportements, leurs destinations et l'environnement local.

## 6. ZONES DE REPRODUCTION DE L'HEMISPHERE SUD : DEPLACEMENTS ET UTILISATION DE L'HABITAT A DIFFERENTES PERIODES DE LA SAISON

### *A) SCHEMA DE DEPLACEMENTS*

Dans le chapitre 5, notre étude révèle que la distribution spatiale varie selon la période de la saison, entre les sites étudiés et selon le sexe. Nos résultats montrent qu'en début et milieu de saison, les mâles sur les côtes Est et Ouest australiennes tendent à se diriger directement vers des sites reconnus comme des zones de reproduction principales : Sud de la grande barrière de Corail et région de Kimberley (Jenner et al. 2001, Smith et al. 2012). A l'inverse, sur la côte Ouest australienne, les femelles avec et sans baleineaux transitent par différentes zones entre le golfe d'Exmouth et la région de Kimberley ce qui indiquerait l'existence de zones de repos le long des routes migratoires Nord et Sud. Lors de la migration vers le nord les femelles empruntent deux principaux corridors ; celles sans baleineaux tendent à emprunter des corridors plus au large, le long de l'île de Barrow tandis que celles avec baleineaux longent la côte ce qui suggère, encore une fois, des différences dans les déplacements et le choix d'habitats en fonction du statut reproducteur.

En milieu de saison à Madagascar, il semble que certaines régions soient associées à des comportements de reproduction ou de repos (faible vitesse, changement de direction (Cerchio et al. In prep , **annexe A**) mais il n'est pas clairement identifié si ces zones sont des destinations finales ou des arrêts le long de la route migratoire (IWC. 2011, Cerchio et al.

2009). Les femelles avec ou sans baleineaux se déplacent sur de longues distances en peu de temps alors que les mâles se déplacent de façon plus erratique dans différentes zones. Cela suppose des stratégies de reproduction différentes où les mâles vont chercher à multiplier les opportunités de se reproduire dans des zones favorables (Cerchio et al. *In prep*). A Madagascar, les femelles avec baleineau semblent se concentrer dans la partie centrale de la côte Est et à la pointe Sud-Est alors que les femelles sans baleineaux se déplacent davantage le long de la côte suggérant également des différences dans les déplacements selon le statut reproducteur.

En fin de saison sur la côte brésilienne, les femelles et les mâles sont concentrés dans la région d'Albrolhos Bank, zone principale de reproduction de la population de l'Est de l'océan Atlantique Sud. Ce schéma est comparable à ce qui est observé plus tôt dans la saison sur les côtes australiennes. Néanmoins à la différence de celles-ci, la côte brésilienne n'a pas été identifiée comme un corridor de migration (Zerbini et al. 2006, IWC 2011b) et pourrait expliquer que les déplacements des individus soient plus localisés et probablement associés à des activités de reproduction et d'allaitement.

### *B) HABITATS UTILISES*

Notre étude comparative entre les zones de reproduction confirme que la bathymétrie est un facteur clé dans la distribution spatiale des baleines à bosse. Présents généralement dans des zones de faibles profondeurs (< 200 m), les mâles de manière générale tendent néanmoins à utiliser des zones plus profondes que les femelles. Lors de la migration vers le nord (plus tôt dans la saison), sur la côte Ouest de l'Australie, ils empruntent un chemin à l'ouest de l'île de Barrow, île située à environ 50 km des côtes australiennes mais également un corridor situé plus près de la côte. Nous avons aussi noté que lors de la migration vers le nord, les femelles effectuaient des déplacements localisés lorsqu'elles se trouvaient près de la côte mais également dans des zones plus profondes ce qui suggère une certaine variabilité du type d'habitats utilisés. En effet, comme les mâles, les femelles utilisent deux corridors, un situé plus au large le long de l'île de Barrow et un le long de la côte. Bien que les femelles avec baleineau semblent préférer les habitats côtiers et peu profonds, il semble que les femelles utilisent des habitats plus variés que de ce qui était attendu.

En fin de saison, lors de la migration vers le sud, les femelles accompagnées d'un baleineau descendent le long de la côte tandis que les mâles empruntent des corridors situés plus au large à de plus grandes profondeurs (> 200 m). Cette variabilité dans le type d'habitats utilisés par les mâles et les femelles sur la côte ouest australienne peut donc notamment s'expliquer par la combinaison de déplacements associés à la migration et des déplacements associés à des périodes de reproduction ou de repos. Nos résultats soulignent que, plus tard dans la saison, les individus du Brésil effectuent des déplacements plus localisés, à des vitesses moyennes plus faibles que les individus des autres sites alors que les balises ont été déployées plus tard dans la saison. De plus, au Brésil, les femelles avec baleineau montrent aussi des déplacements plus erratiques et sont présentes plus fréquemment dans des zones peu profondes et proches des côtes que les femelles sans baleineau. Ceci appui notre hypothèse que les femelles avec baleineau sont plus sélectives dans leurs habitats que les femelles sans baleineaux, préférant généralement les eaux de faibles profondeurs et relativement proche des côtes (Craig & Herman 2000, Ersts et al. 2006, Félix & Botero-Acosta 2011, Craig et al. 2014). Des différences de distribution liées au statut reproducteur ont aussi été observées chez d'autres cétacés (baleine franche australe : Payne 1986, Elwen & Best 2004, lagénorynque obscur : Weir et al. 2008).

## B. COMPARAISON AVEC LA DISTRIBUTION ET L'HABITAT DES BALEINES FRANCHES AUTRALES EN PERIODE DE REPRODUCTION

Les baleines à bosse ne sont pas les seules parmi les grandes baleines à migrer dans les eaux chaudes des basses latitudes pour se reproduire et mettre bas. Cependant, elles sont les plus intensément étudiées et celles dont les zones de reproduction, principalement côtières, sont les mieux connues. En effet, mysticète de taille intermédiaire, cette espèce peut tirer partie des habitats côtiers (e.g. zones calmes, faibles profondeurs, risque de prédation moins élevé). En comparaison, ces mêmes habitats peuvent présenter des contraintes (e.g. comportements, déplacements) pour les espèces de plus grande taille telles que la baleine bleue ou le rorqual commune qui vont être présentes plus au large. Ainsi, leurs zones de reproduction sont plus difficiles à identifier et encore mal connnues.

Parmi les grandes baleines, les baleines franches sont celles dont les schémas de migration et d'utilisation d'habitat en hiver se rapprochent le plus de ceux observés chez les baleines à bosse. Dans le cas des baleines franches australes, les populations les mieux documentées sont celles d'Argentine (péninsule de Valdès)/Brésil, d'Afrique du Sud et d'Australie/Nouvelle Zélande (Brownell et al. 1986, IWC 1998b, Patenaude et al. 2007). A grande échelle, certaines zones de reproduction sont identifiées plus au sud (e.g. Argentine, Sud de l'Australie) que celles des baleines à bosse indiquant que les préférences thermiques des baleines franches tendent à être moins restreintes que celles des baleines à bosse (Rasmussen et al. 2007). De nombreuses régions étant aussi communes aux deux espèces, certaines aires de distribution se chevauchent ce qui suggèrent l'existence d'habitats favorables aux deux espèces (e.g. Brésil, Afrique du Sud) (IWC 1998b). Bien qu'historiquement Madagascar n'ait pas été identifiée comme une zone de reproduction majeure pour les baleines franches australes, quelques observations ont été reportées notamment dans la Baie d'Antongil et à Sainte Marie (Richards & Du Pasquier 1989, International Whaling Commission 1998, Rosenbaum et al. 2001). Dans cette thèse, nous avons montré que le sexe des baleines à bosse et le statut reproducteur des femelles influent sur leurs déplacements et les habitats utilisés en période de reproduction ce qui est aussi observée chez les baleines franches (Burnell 2001). La ségrégation spatiale entre les groupes avec un baleineau et les autres groupes, les premiers étant présents plus proche de la côte et dans des eaux moins profondes que les autres groupes, est semblable à ce qui est généralement observé chez les baleines à bosse (Rayment et al. 2015). Aussi, les femelles accompagnées d'un baleineau sont plus sélectives dans leur choix d'habitats que les femelles sans baleineau (Rayment et al. 2015). Il est d'ailleurs intéressant de noter que les femelles suitées et les sub-adultes semblent passer plus de temps sur un site donné que les mâles et les femelles sans baleineau, qui se déplaceraient davantage entre les différents sites de reproduction (Burnell 2001, Rowntree et al. 2001)

Les baleines franches comme les baleines à bosse sont communément observées le long des côtes et près des îles dans des eaux peu profondes. Durant la période de reproduction, les baleines franches australes cessent également de s'alimenter et par conséquent leur distribution n'est pas influencée par la distribution des proies (Tormosov *et al.* 1998, Best & Schell 1996). A petite échelle, les deux espèces sont toutes les deux influencées par la bathymétrie (Payne 1986, Elwen & Best 2004, Rayment et al. 2015). Les baleines franches ont aussi une préférence pour les fonds à pente douce et à substrats meubles (Payne 1986, 1995). Bien que les modèles de notre étude n'aient pas retenu la pente comme facteur déterminant, les baleines à bosse exploitent aussi des zones caractérisées par des pentes douces (e.g. Smith et al. 2012). Les zones calmes, à l'abri du vent et de la houle, sont aussi privilégiées par les baleines franches et particulièrement les couples mère-baleineau (Payne, 1995, Elwen & Best. 2004, Rayment et al. 2015). Bien que nos modèles n'aient pas révélés de préférences particulières pour les zones à faibles courants, notre étude réalisée dans le canal de Sainte Marie indique que celui-ci est situé dans une zone à faible courant. De plus d'après la littérature, les baleines à bosse sont généralement observées dans des zones abritées (Whitehead & Moore, 1982, Smultea 1994, Félix et Botero-Acosta. 2011). Chez les deux espèces, les femelles avec leurs petits sont observées plus fréquemment dans les eaux de plus faible profondeur et plus proches de la côte que les autres groupes. Néanmoins, la ségrégation géographique de couples mère-baleineau et des autres groupes serait plus importante chez les baleines franches que chez les baleines à bosse. Chez ces dernières, les couples mère-baleineau sont peu fréquemment observés dans des groupes reproducteurs et la présence d'escorte n'est pas été reportée (Cassini & Vila 1990). Chez les baleines à bosse, les mâles utilisent différentes stratégies de reproduction ciblant les femelles accompagnées de baleineaux et les femelles sans baleineaux ce qui explique probablement une ségrégation spatiale moins forte entre les différents groupes ; on pourra observer plus au large des couples mère–baleineau dans des groupes compétitifs ou accompagnés d'une escorte. En effet, à la différence des baleines à bosse, de plusieurs études ont montré que chez les différentes espèces de baleines franches l'ovulation n'était pas post-natale, les femelles ne donnant naissance à un petit que tous les 2 à 4 ans (Bannister 1990, Best 1990, Payne et al. 1990, Knowlton et al. 1994, Best et al. 2001, Cooke et al. 2001). En comparaison des baleines à bosse, les femelles n'étant pas sexuellement réceptives après la mise bas (Best 1994, Cooke et al. 2003, Brandão et al. 2010), l'hypothèse que les couples mère-baleineau de baleines franches choisissent les eaux côtières de faibles profondeurs pour éviter le harcèlement des mâles n'est pas évidente. En Afrique du Sud, il a été observé que les comportements reproducteurs des baleines franches mâles n'étaient dirigés que sur vers femelles juvéniles (Best et al. 2003). Par ailleurs, l'absence d'observations des femelles dans les zones de reproduction l'année précédente la mise bas, suggère que l'accouplement a lieu dans des zones encore inconnues (Payne 1986, Best et al. 2003). Ainsi, d'autres facteurs environnementaux et/ou sociaux que ceux opérant chez la baleine à bosse influencent probablement la distribution des baleines franches en période de reproduction comme le choix d'une zone protégée pour leur petit (Rayment et al. 2015).

## C. PERSPECTIVES

A l'issue de cette thèse, plusieurs perspectives d'approfondissement de certains résultats mais aussi des nouvelles voies à explorer peuvent être proposées :

### 1. AMELIORATION DE LA METHODE DE SUIVI TELEMETRIQUE

Bien que l'utilisation de balises satellitaires nous ait permis d'augmenter considérablement nos connaissances sur les déplacements des baleines à bosse, la durée d'émission de ces balises (entre 20 et 40 jours en moyenne chez cette espèce dans de nombreuse études (Mate et al. 1998, 2007a, Garrigue et al. 2010, Hauser et al. 2010, Zerbini et al. 2011, Kennedy et al. 2013, 2014, Willson et al. 2014) ne permet pas d'obtenir des trajets complets (un aller-retour). Plusieurs raisons ont été identifiées pour expliquer cela (cf. chapitre 2) mais l'évolution de la technologie et notamment du système d'ancrage pourrait permettre d'augmenter le temps de fixation de la balise (Kennedy 2013, Robbins et al. 2013).

### 2. ACQUISITION DE DONNEES A PLUS HAUTE RESOLUTION

Dans cette étude nous avons utilisé des balises Argos qui nous permettent de collecter des positions pouvant avoir une précision maximum de quelques centaines de mètres mais dont la fréquence et la régularité sont limitées. Néanmoins, pour étudier le comportement des individus à plus fine échelle, il serait intéressant de déployer des balises Argos, associées à un système GPS afin d'obtenir des positions plus précises (quelques mètres) et plus nombreuses (e.g. toutes les 30 secondes) (Hazel 2009, rorqual commun, Mate 2009, Sims et al. 2009, Costa et al. 2010, cachalot, Mate & Urban 2010) afin d'approfondir l'analyse des déplacements individuels et des zones côtières préférentiellement utilisées qui peuvent être associées à des menaces locales potentielles .

### 3. ESTIMATION D'ABONDANCE RELATIVE DE LA POPULATION DE SAINTE MARIE PAR UNE METHODE STANDARDISEE

Dans le cadre de cette thèse, nous avons calculé le taux de rencontre annuel dans les eaux du canal de Sainte Marie. Une méthode standardisée communément utilisée pour calculer une estimation d'abondance dans les études sur les cétacés pourrait venir compléter utilement notre évaluation. Cette méthode repose sur le comptage, à partir d'un bateau ou d'un avion, le long de routes prédéfinies (transect linéaire) (Findlay et al. 1994, Moore et al. 2000, 2002, Andriolo et al. 2010).

### 4. SUIVI INTERANNUEL DE LA DISTRIBUTION SPATIAUX-TEMPORELLE DES GROUPES SOCIAUX DANS LE CANAL DE SAINTE MARIE

Lors de cette étude, nous avons analysé cinq années de données opportunistes dans le canal de Sainte Marie. Des variations interannuelles dans les taux de rencontre des groupes avec baleineaux et sans baleineau ont été notées mais sans que l'on puisse en identifier les causes en raison d'une série temporelle trop courte. Une série temporelle plus longue (i.e. décennale ou multi décennale) pourrait permettre de relier ces variations avec de possibles changements des paramètres physiques de l'océan liés à la variabilité climatique à plus grande échelle, dans la zone du sud-ouest de l'océan Indien (e.g. température de surface) mais aussi dans les zones d'alimentation associées (e.g. étendue de la glace de mer, (Nicol 2006).

## 5. PREDICTION D’HABITATS UTILISES ET MISE EN PLACE D’AIRES MARINES PROTEGEES

Des menaces potentielles et actuelles pèsent sur les habitats côtiers peu profonds de Madagascar incluant la présence d’une forte activité minière sur la côte est (environ 100 km au sud du canal de Sainte Marie) et des tests sismiques, réalisés ou à venir, visant l’exploitation de pétrole sur les côtes Ouest et Eest de l’île (https://www.offshoreenergytoday.com/tag/madagascar/,http://www.spectrumgeo.com/press-release/new-seismic-agreement-with-madagascars-omnis,http://www.huffingtonpost.com/jackie-savitz/exxonmobil-seismic-explor_b_3996608.html, Clarke 2010, Brown 2014, Cerchio et al. 2015). Ainsi, une perspective de ce travail de thèse serait l’application de modèles prédictifs de distribution d’habitats (e.g. GLM, GAM, Maxent) dans le but de prédire les zones clés utiles à des plans de gestion et de conservation et notamment à la définition d’Aires Marines Protégées autour de Madagascar (Johnston et al. 2007, Smith et al. 2012). Il serait néanmoins nécessaire d’augmenter la taille du jeu de donnée en réalisant de nouvelles campagnes de déploiement de balises dans les zones étudiées dans cette thèse

## 6. DEPLACEMENTS ET SELECTION D’HABITATS DES FEMELLES EN FONCTION DU STATUT REPRODUCTEUR

Les femelles en post-oestrus sont facilement dissociables des mâles par la présence d’un baleineau. Ainsi de manière générale, la majorité des études porte sur les femelles accompagnées de nouveaux-nés. Mais qu’en est-il des comportements, des déplacements et des préférences d’habitats des femelles sans baleineaux venues se reproduire (en oetrus) ? Le dimorphisme sexuel entre les mâles et les femelles étant peu prononcé, il est difficile de distinguer une femelle d’un mâle en l’absence de baleineau. Cependant, il est parfois possible de le faire par les comportements des individus mâles dans un groupe reproducteur. La femelle se trouvera le plus souvent à l’avant du groupe et dictera sa direction. Une grande partie de notre étude s’est concentrée sur les déplacements et les préférences d’habitats chez les mâles et les femelles (sexe confirmé pas analyse génétique) Nous avons également mis en évidence de possibles différences dans le comportement et l’habitat utilisé en fonction de l’état reproducteur des femelles lorsque l’échantillonnage était suffisant. Cependant, il serait intéressant d’équiper de balises un plus grand nombre de femelles sans baleineaux (e.g. identifiées dans les groupes compétitifs ou par photo-identification) afin d’inclure dans nos modèles le statut reproducteur et d’étudier plus en détail comment celui-ci influence la sélection d’habitats chez les femelles.

## 7. MONT SOUS-MARIN DES WALTERS SHOALS : QUI ? QUAND ? COMMENT ?

La récente découverte de l’utilisation régulière des monts sous-marins par les baleines à bosse amène à se questionner sur l’utilisation et l’importance de ces habitats océaniques pour cette espèce (Garrigue et al. 2010, 2015, Kennedy et al. 2014). En Nouvelle Calédonie ou encore à La Réunion, des observations visuelles et le suivi de baleines équipées de balises Argos ont révélé l’utilisation de monts sous-marins (Dulau-Drout et al. *In prep*, Garrigue et al 2010, 2015). Des comportements de reproduction et la présence de baleineaux sur certains de ces sites laissent penser qu’ils constituent des zones de reproduction ou des zones de repos le long de la migration (Garrigue et al. 2015). Néanmoins, par manque de données cela n’est pas clairement défini. Des observations de baleines à bosse, incluant des couples mère-baleineau avaient déjà été reportées avant notre étude sur les hauts fonds situés au sud du plateau de Madagascar et notamment sur le mont sous-marin des Walters Shoals entre septembre et décembre (Collette & Parin 1991, Best et al. 1998). Dans notre étude, un seul individu femelle a visité le mont sous-marin des Walters Shoals avant de revenir à Madagascar. La présence de baleines dans cette région reste cependant peu documentée. Située à environ 750 km au sud de Madagascar, les Walters Shoals sont difficiles d’accès et l’étude des baleines de cette région exigerait des moyens logistiques et financiers importants. Bien qu’une campagne de recherche en haute mer serait extrêmement utile pour récolter des données visuelles (i.e. comportements, type de groupes, nombre d’individus), l’utilisation de gliders (planeur-sous-marin autonome) équipés d’un capteur acoustique pourrait être une méthode alternative intéressante pour détecter dans un premier temps la présence d’activités vocales et si possible, la présence des mâles chanteurs.

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# ANNEXES

# ANNEXE A

# Satellite tagging of humpback whales off Madagascar reveals breeding habitat insights and long range movements within the Southwest Indian Ocean

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## ABSTRACT

Humpback whales wintering in the Southwest Indian Ocean are thought to exhibit population substructure with the primary subdivision occurring between Madagascar and east Africa. To investigate movements and connectivity through the region, breeding behavior and habitat utilization, 23 whales were satellite tagged, twelve off northeast Madagascar and eleven off southwest Madagascar during peak breeding season in 2012 and 2013, respectively. Mean tag duration was 24.2 days (3-58 days) and twelve females generally had longer duration deployments as compared to ten males. No individuals remained near the tagging sites and several whales displayed extensive long-range movements in short periods of time. Considering movements around Madagascar, whales tagged in the northeast tended to spend time on a 500km stretch of the central east coast, whereas whales tagged in the southwest tended to spend time on the south and southeast coasts, with little overlap between the animals from the different regions within the tag duration timeframe. Considering whales that departed Madagascar waters, three females and one male tagged in the northeast travelled on similar north-westerly trajectories, two of which travelled to the east African coast off Kenya and Somalia. Southerly movements included a female tagged in the northeast that travelled to Walters Shoals and a female tagged in the southwest that travelled to the Crozet Islands. Despite these long range movements in relatively short periods, no whale travelled to the northwest coast of

Madagascar, Mozambique, or the Mascarene Islands, where breeding aggregations are well documented. These results suggest that there may be more interchange between Madagascar and central-east Africa than previously thought, and whales off east and west Madagascar may not use the same habitat within breeding seasons. We applied a switching State-Space Model to estimate behavioral modes of “transiting” (consistent/directional movement, B-mode approaching 1.0) vs. “localized” (variable/non-directional movement, B-mode approaching 2.0). A GLMM analysis of B-mode indicated that females were more likely to display transiting behavior compared to males (mean B-mode females=1.28, males=1.64; $p = 0.029$). This suggests male mating strategy may involve a higher degree of localized searching, whereas females travel more extensively during breeding season.

## INTRODUCTION

Humpback whale migratory and breeding ecology – Humpback whales (Megaptera novaeangliae) globally are seasonal breeders, and with few exceptions populations migrate yearly between high latitude feeding regions in summer, and low latitude breeding regions in winter. Migrations are typically extensive and latitudinal migratory movements of several thousand kilometers have been documented in multiple ocean basins. The details of the mating system has been debated, but is generally agreed to be polygynous, with elements of lekking and male dominance (Herman & Tavolga 1980, Clapham 1996, 2000, Cerchio et al. 2005). Females reproduce on average once every two to three years and likely have a short estrus period (Chittleborough 1958, 1965; Clapham & Mayo 1990; Glockner-Ferrari & Ferrari 1990), resulting in a severely skewed operational sex ratio (Clapham 2000). Gestation lasts one year with both conception and parturition generally occurring during a five month period centered in winter, thus in a breeding region females can be subdivided into two reproductive classes: relatively high fecundity adult females without calves (termed "non-parous females" throughout) that have migrated solely for the purpose to become fertilized; and partum or post-partum females with a calf of the year (termed "mothers" throughout), that have relatively low fecundity since only a small fraction of females give birth in consecutive years. Males exhibit alternative mating tactics while on the breeding grounds, including a male-limited acoustic display or song (Payne & McVay 1971), intense physical competition among groups of males for single estrous females in "competitive groups" (Tyack & Whitehead 1983), and "escorting" of mothers with a calf of the year (despite their relatively low fecundity). Molecular paternity analysis has indicated polygyny with a slight but significant skew in reproductive success among males, and that males engaged in different tactics do attain reproductive success, i.e., success does not appear to be severely skewed towards a single tactic (Cerchio 2003, Cerchio et al. 2005).

Population Distribution in the Southwest Indian Ocean (SWIO) - Humpback whales in the southern hemisphere are distributed in circumpolar high latitudes during the austral summer, and migrate to low latitude breeding areas in the austral winter. The International Whaling Commission (IWC) currently designates seven breeding stocks (populations) labeled

A through G, from the western South Atlantic eastward to the eastern South Pacific (IWC 1998, 2007). The breeding population that winters in the SWIO is sub-divided into four designated sub-stocks (Figure 1); these are distributed in the eastern African coastal waters of South Africa to Kenya (C1), off the islands of the Mozambique Channel (C2), in the coastal waters of Madagascar (C3), and off the Mascarene Islands (C4) (IWC 2007). Modern whaling of humpback whales in the SWIO began in 1908 and expanded rapidly thereafter, depleting the population with an estimated 19,000 whales taken up until 1963 (Findlay 2001). Different catch histories in C1 (South Africa/Mozambique, where there was early depletion prior to 1915) as compared to C3 (Madagascar, where catches remained relatively high) were the first evidence of population structure in the region (Best 1994, Findlay 2001).

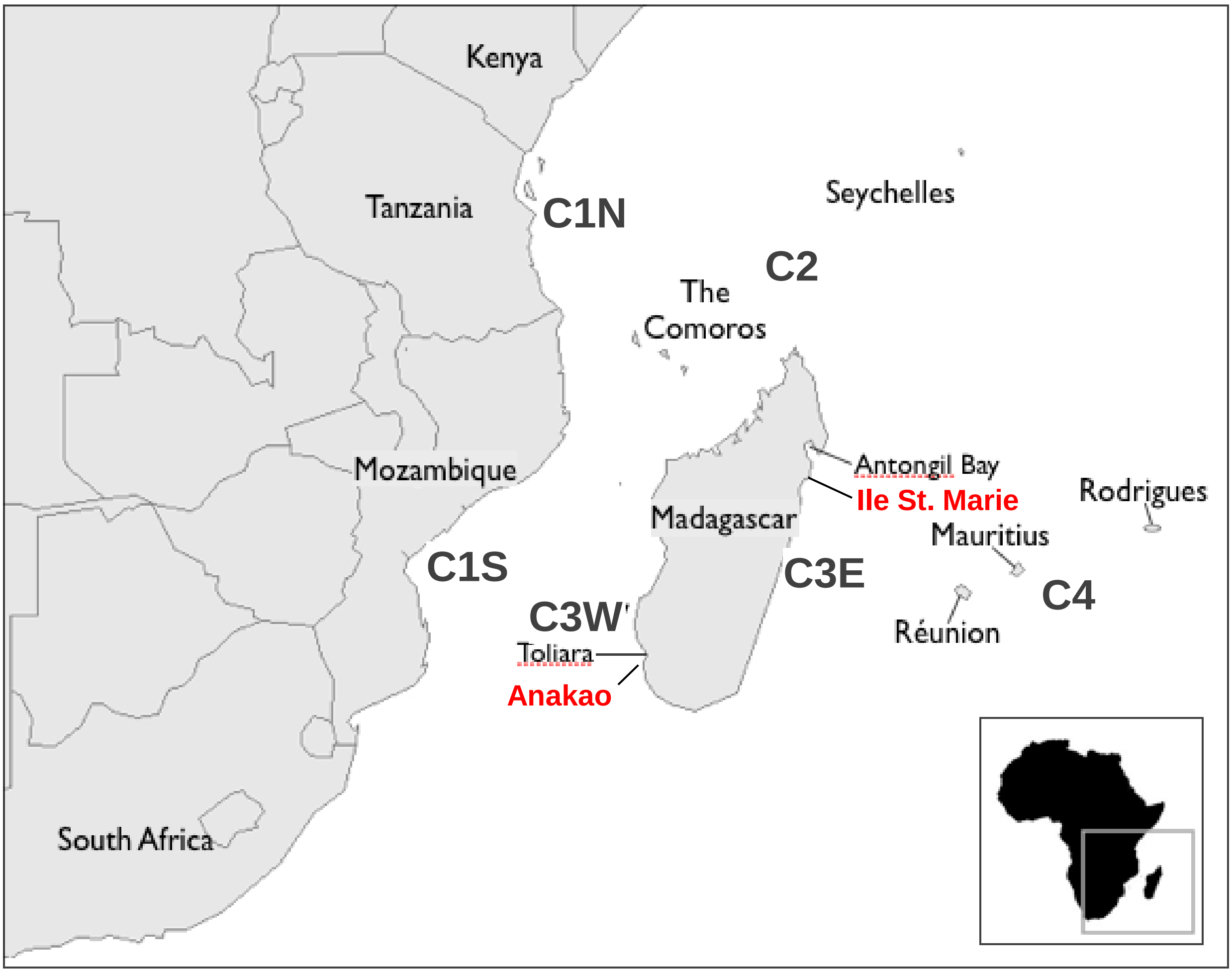

Figure 1. Map of the Southwest Indian Ocean indicating the key sub-stocks in Humpback whale Breeding Stock C (C1 = East Africa Mainland, C2 = Comoros and Seychelles Islands, C3 = Madagascar, and C4 = Mascarene Islands) and locations of Ile Saint Marie and Anakao, from which satellite tagging of humpback whales was conducted.

In the C1 sub-region, humpback whales utilize the east coast of South Africa as a migratory corridor from southern feeding grounds to a wintering ground in the coastal waters of Mozambique, with apparent lower concentrations of whales distributed along the coasts of Tanzania and Kenya (Findlay et al 2011a, 2011b, Amir et al. 2012). The relationship of whales in the southern range (Mozambique, C1S) with the northern range (Tanzania, Kenya, C1N) is uncertain. In the C2 sub-region, humpback whales occur around the Comoros Islands, including Mayotte, and in lesser concentrations around the Seychelles Islands from Aldabra to the Mahe plateau (Kiszka et al. 2010, Ersts et al. 2009). The characteristics of the population in the Comoros Islands is unusual for a humpback breeding ground, with apparent late season peak in abundance and a strong bias towards mothers with calves, suggesting that this may be primarily a nursing area (Ersts et al. 2009). In the C3 sub-region, humpback whales are distributed around the entire island of Madagascar. Most information comes from the northeast in Antongil Bay which, along with the nearby Ile Saint Marie, hosts concentrations of whales throughout the season displaying all breeding behaviors (Rosenbaum et al. 1997, Ersts and Rosenbaum 2003, Cerchio et al. 2009, Vely et al. 2009). Recapture rate in Antongil Bay is relatively low and apparent residency is short, suggesting a large population continuously moving through the area (Cerchio et al. 2009). Concentrations of whales are also known in the southeast and along most of the west coast, best documented in the southwest around Toliara where encounter rate is similar to Antongil Bay (Cerchio, pers. observ.). The relationship of east coast and west coast animals is unknown (i.e., the same or a sub-divided population). In the C4 sub-region, humpback whales are distributed around Reunion, Mauritius and Rodrigues, but appear to be a relatively recent arrival to the islands. Studies conducted in Reunion from 2004-2010 demonstrated a significant increase in sighting rate after 2008, suggesting a possible range expansion from other areas in the SWIO (Dulau-Drouot et al. 2012). Within-year recapture rate is relatively high with long apparent residency times, as compared to Antongil Bay in C3 (Dulau-Drouot et al. 2011). This suggests that this group may be relatively small and resident; however whales sighted early in the season seem to be more transient.

Population Structure and Movements - Population genetic studies indicate a strong significant differentiation between C1 and C3 at both mitochondrial and nuclear microsatellite loci; however, this differentiation is less pronounced than between the SWIO and adjacent stocks in the Southeast Atlantic and Southeast Indian Oceans (Rosenbaum et al. 2009). Converse to the C1-C3 relationship, there is no significant differentiation between C2 and C3 (Rosenbaum et al. 2009). Similarly, capture-recapture studies indicate low probability of exchange of individuals between C1 and C3 (Cerchio et al. 2008), and apparently greater exchange between C2 and C3 (Ersts et al. 2011); and between C3 and C4 (Dulau et al. 2011). Despite significant population structure and low probability of interchange based on capture-recapture analyses, long-term gene flow rates and effective migrants per generation have been estimated for C1-C3 (Rosenbaum et al 2009).

Thus current information suggests that humpback whales are heterogeneously distributed throughout the SWIO, and there is distinct population structure between at least sub-populations in the C1 and C3 sub-regions. The relationship of C2 and C4 is less clear, however it is possible that each may have greater interaction with C3, and perhaps represent range expansions from C3. Alternatively, due to its proximity in the Mozambique Channel, C2 may have more interaction with C1 than currently known, and may thus act as a conduit for exchange of animals (and genes) between C1 and C3. Migratory corridors and pathways to and throughout the region are completely unknown, as are whether different animals, or animals from the same sub-region, consistently use similar pathways. All of these unknown elements carry consequence for our understanding of population status (i.e., abundance and growth rate), delineation of sensitive habitat, and management and protection of the population.

## Methods

Tag Technology and Deployment - Implantable satellite tags have been used to remotely monitor movements of various large whale species, including humpback whales (Zerbini et al. 2006, 2011, Dalla Rosa et al 2008, Garrigue et al 2010, Hauser et al 2010). The tags used in this study were Wildlife Computers (Redmond, WA, USA) SPOT 5 transmitters custom-designed within implantable cylinder housings. The anchoring systems used corresponded to a modified version of the Gales et al. (2009) design. Tags are designed to penetrate to a maximum of 290mm into the dorsal surface of the whale, generally just forward and to the side of the dorsal fin, and to anchor within the variable muscle and connective tissue matrix (the fascia) that underlies the blubber. Tag retention is maintained by passively deployed sets of barbs. All external components of the tag are built from surgical-quality stainless steel. Tag deployment was carried out from the bow of a small boat at distances of 3-5m using a tagging pole (Heide-Jorgensen et al. 2003; Zerbini et al. 2006) or a modified pneumatic tagging device (Heide-Jorgensen et al 2001, Gales et al., 2009).

Sampling Design – Of priority interest in this study were movements of whales during the breeding season, and the resultant implications for stock structure and breeding behavior, with lower priority given to return migration routes and destinations in feeding areas. For this reason we chose to tag during the height of breeding season, as opposed to late season which would maximize potential for migratory movements and increased tag duration, but miss within region movements. Tagging was conducted off the northeast coast of Madagascar, from Ile Saint Marie in 2012, and the southwest coast, from Anakao in 2013 (see Figure 1). These regions were known to have high densities of humpback whales during the breeding season.

In choice of tagging subject, we attempted to target equal proportions of adult females and adult males, in order to evaluate differences between the sexes. We attempted to target both post-partum females (mothers with a young calf of the year) and non-parous females (an estrous female that has migrated to the breeding grounds solely to mate, as opposed to give birth) in equal proportions, since it is expected that reproductive status may affect intra-regional movements as well as timing of migratory behavior. In the field, adult males and females are essentially impossible to distinguish based upon morphological characteristics alone, presenting a challenge for this targeted sample design. Post-partum females are readily distinguished from males because they are accompanied by a calf in close association. In some circumstances a non-parous female can be distinguish based upon behavioral queues when the female is the focus of competition between males in a "competitive group" (Tyack and Whitehead 1983, Clapham et al. 1992). In a typical competitive group, a female, termed the "Nuclear Animal" (NA), is closely guarded by an adult male, termed the "Principal Escort" (PE), while a number of additional males, termed "Secondary Escorts" (SE), follow the pair; some Secondary Escorts will make attempts to supplant the Principal Escort, through which behavior they are distinguished as "Challengers" (CH). Typically the different roles can be diagnosed through observation of position in the group and behaviors, and thus with adequate observation, inference about apparent sex can be made for both non-parous females (NAs) and adult males (PEs, SEs and

CHs). Since the competition among males in competitive groups can be intense and very physical, there was distinct concern that tags placed on such males could be damaged, shortening the duration of the tagging event. We further attempted to tag males and females in associated pairs, either as the “NA” and “PE” in a competitive group, or as a mother and her escort in a mother/calf/escort trio. Tagged whales were biopsied using standard biopsy equipment (crossbow with biopsy dart) and photographed for individual identification using tail flukes (when possible) and dorsal fins. Whole genomic DNA was extracted from biopsy skin tissue samples using the DNeasy Blood and Tissue Kit (Qiagen), and the sex of whales was confirmed using simultaneous PCR amplification of SRY and ZFX/ZFY gene fragments (Jayasankar et al 2008).

Data Collection and Analysis - Transmitters were programmed to optimize data collection while in the breeding grounds (for detailed assessment of movement), while maximizing tag longevity during migration after departure from the breeding grounds. Accordingly, tags were duty-cycled in 2012 to be on 6 hours during day (07h to 13h local) and 6 hours at night (19h to 01h local), and then increased in 2013 to be on 9 hours during day (05h to 14h local) and 9 hours at night (17h to 02h GMT), with a limit of 400 and 700 transmissions/day, respectively. Tags (Mold 177) were scheduled to transmit every day for the first 3 months after deployment and no tag lasted longer than this duration. Location data were obtained from Service ARGOS by instruments on satellites from NOAA and the European Organization for the Exploration of Meteorological Satellites. These satellites complete 14 passages over the earth in a 24-hour period and are ‘in view’ for 9-12 minutes per passage. Positions are calculated based on the ‘Doppler shift principle’, and recent processing techniques provide position-specific error assignment, increased precision and number of estimated locations.

Raw location data for each tagged whale provided by service ARGOS included for each position: date and time of position, position in latitude and longitude, number of messages received contributing to position, a location class defined by increasing number of messages and decreasing uncertainty from Z, B, A, 0, 1, 2 and 3, and an estimate of spatial elliptical error in meters. Prior to analysis, we removed all data with location classes of Z (the least accurate), and applied a speed filter that removed all locations that resulted in a leg speed greater than 12 km/hr (Garrigue et al. 2010), in order to remove the most likely erroneous positions.

We fitted a behaviorally switching state-space model, SSSM, (Jonsen et al. 2003, 2005, 2007, Breed et al. 2009), that estimates model parameters by Markov Chain Monte Carlo (MCMC) to the locations of each tagged whale using software R v.2.11.1 (R Core Team) and WinBUGS v1.4 (Bayesian inference Using Gibbs Sampling Project). SSSMs simultaneously solve a model of observation error and a mechanistic model of animal movement (Jonsen et al. 2005), and thus yield better estimates of both the satellite locations and the uncertainty in those locations than raw tracking data. This is because the SSM draws on all of the data and the animal's behavior (e.g., speed and turning angles from the satellite track) to predict the probability of an animal being found at a certain location (Jonsen et al. 2003, 2005). In order to make data comparable between the two years and combine years for a comparison of sexes, 2013 data was sub-sampled to match the 6hr-on/6hr-off duty cycle of 2012 data prior to running the SSSM. We estimated locations and associated credible intervals twice a day, once during the day and once at night, equivalent to a 12 hour time step. Behavioral state was classified on the basis of two parameters, mean turning angle (θ) and autocorrelation in speed and direction (γ). We ran two MCMC chains for 50,000 iterations, including a burn-in of 20,000, and further thinned the iterations by 30 to reduce autocorrelation; the retained iterations were used to estimate the mean and variance for each location and behavioral parameter. Thus the posterior distribution for each parameter is based on 1000 samples from each chain resulting in a total of 2000 independent samples. The two behavioral states were differentiated by a separation of the values of the two parameters (θ and γ), resulting in "B-mode" state values of 1 or 2 for each iteration, and a mean B-mode calculated for each estimated position across all iterations. We nominally referred to the two states as 'transiting', highly directional (turning angles near 0°) and consistent long-distance movements, likely representing transits through breeding habitat or between distinct breeding habitats (B-mode state of 1); and 'localized', more variable movements with a higher rate of acute turning angles (near 180°), likely representing searching behavior or meandering within breeding habitats (B-mode state of 2). Spatial distribution of behavioral states were evaluated by plotting the standardized mean of B-modes on a 0.3° grid, so that each grid cell contained a mean of individual means for all positions in that cell.

Linear mixed-effects models (Pinheiro and Bates, 2000; Zuur et al., 2009) were used to evaluate the influence of diel period (day and night), Julian day, tagging day, sex, and region on the SSSM-estimated behavioral mode using package nlme (Pinheiro et al., 2015) with R open-access statistical software (v. 3.2.0, R Core Team, 2015). The response variable (behavioral mode) was logit-transformed prior to analysis, 'tagged individuals' were used as a random effect, and an ARMA(2,0) autocorrelation structure to account for lack of temporal independence within telemetry data for each whale. Choice of the best correlation structure and model selection followed the procedures outlined in Zuur et al. (2009). Nested models were fit using maximum likelihood (ML), candidate models were ranked using the Akaike Information Criterion (AIC), and the most supported model was then fitted using restricted maximum likelihood (REML) (Zuur et al., 2009).

## Results

Tag Results Summary - Twelve humpback whales were satellite tagged off Ile Saint Marie, Madagascar, between July 24 and August 3, 2012, and eleven humpback whales were tagged off Anakao, Madagascar, between July 16 and 28, 2013. Whales were chosen as tagging targets in the field based upon apparent sex and behavioral subclass. Tagged whales consisted of seven males and five females in St. Marie and three males and seven females in Anakao, confirmed by molecular sexing, and one of unknown sex in Anakao for which a biopsy was not obtained (Table 1). Among males, one whale was tagged as a Solo animal, three were tagged as members of Pairs of adults, three were tagged as Principal Escorts (PE) and one as a Secondary Escort (SE) in competitive groups, and one tagged as the Escort (Esc) to a Mother-calf group. Among females, five post-partum females were tagged as Mothers, and seven non-parous females were tagged, three as Nuclear Animals (NA) in competitive groups, one as an apparent NA in a non-competitive group (based on positions of other whales) and three in Pairs of adults. We thus succeeded in tagging a cross section of sexes, reproductive classes and behavioral subclasses, with relatively equal representation of sexes despite the relatively small sample size.

Table 1. Summary data from 23 humpback whales satellite tagged off Madagascar, at sites in the northeast, Ile St. Marie (SM) and southwest, Anakao (AO).

| Tag | Site | Subclass | Sex | Tag Date | Days Trans | # Raw Locs | # Filt. Locs | # SSSM Est Locs | Filt Track Dist (km) | Filtered Mean Spd (km/hr) | Mn B-Mode w/ Sth Migr | Mn B-Mode w/o Sth Migr |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | SM | Solo | M | 24-Jul-12 | 32 | 123 | 101 | 31 | 3250 | 4.3 | 1.30 | |
| 2 | SM | CG | M | 30-Jul-2012 | 31 | 231 | 204 | 61 | 1947 | 1.9 | 1.88 | |
| 3 | SM | Pair | M | 30-Jul-2012 | 20 | 169 | 144 | 40 | 1551 | 2.2 | 1.65 | |
| 4 | SM | Mom | F | 31-Jul-2012 | 25 | 58 | 51 | 25 | 2261 | 1.8 | 1.52 | |
| 5 | SM | Esc | M | 31-Jul-2012 | 5 | 21 | 18 | N/A | 489 | 1.7 | N/A | |
| 6 | SM | Pair | M | 31-Jul-2012 | 10 | 71 | 60 | 19 | 689 | 1.7 | 1.80 | |
| 7 | SM | Mom | F | 31-Jul-2012 | 13 | 102 | 88 | 26 | 1187 | 2.1 | 1.05 | |
| 8 | SM | CH/PE | M | 1-Aug-2012 | 3 | 21 | 17 | N/A | 112 | 1.3 | N/A | |
| 9 | SM | NA | F | 1-Aug-2012 | 58 | 368 | 300 | 115 | 5631 | 3.3 | 1.21 | 1.24 |
| 10 | SM | Mom | F | 1-Aug-2012 | 30 | 222 | 200 | 60 | 2444 | 2.5 | 1.32 | |
| 11 | SM | PE | M | 3-Aug-2012 | 15 | 104 | 85 | 29 | 1018 | 1.7 | 1.67 | |
| 12 | SM | NA | F | 3-Aug-2012 | 23 | 196 | 174 | 45 | 2549 | 3.8 | 1.04 | |
| 13 | AO | Pair | U | 16-Jul-2013 | 15 | 206 | 183 | 31 | 1388 | 4.1 | 1.32 | |
| 14 | AO | Pair | F | 17-Jul-2013 | 21 | 8 | 6 | N/A | 759 | 1.6 | N/A | |
| 15 | AO | Pair | F | 17-Jul-2013 | 42 | 473 | 432 | 84 | 3729 | 4.2 | 1.22 | |
| 16 | AO | Pair | F | 17-Jul-2013 | 2 | 13 | 9 | N/A | 73 | 3.8 | N/A | |
| 17 | AO | Pair | M | 17-Jul-2013 | 34 | 480 | 444 | 67 | 2639 | 3.8 | 1.50 | |
| 18 | AO | PE | M | 21-Jul-2013 | 23 | 307 | 280 | 44 | 1652 | 3.6 | 1.73 | |
| 19 | AO | SE | M | 21-Jul-2013 | 8 | 85 | 81 | 10 | 737 | 4.6 | 1.58 | |
| 20 | AO | Mom | F | 23-Jul-2013 | 23 | 269 | 247 | 35 | 1766 | 4.0 | 1.08 | |
| 21 | AO | NA | F | 25-Jul-2013 | 17 | 129 | 116 | 33 | 1221 | 4.1 | 1.53 | |
| 22 | AO | NA? | F | 27-Jul-2013 | 57 | 786 | 696 | 104 | 4341 | 3.7 | 1.37 | 1.65 |
| 23 | AO | Mom | F | 28-Jul-2013 | 52 | 807 | 765 | 103 | 3191 | 3.3 | 1.37 | |

Mean tag transmission duration was 24.2 days (+/- s.d. 16.1, range 2-58) for all whales, and when segregating by sex, 30.1 days (+/- 18.1, range 2-58) for females and 17.9 days (+/-11.6, range 3-34) for males. In two cases, the tag stopped transmitting for an extended period of days during the total transmission duration, resulting in a gap of 16 days during the 32 day duration for Tag 1 (a Solo male), and a gap of 12 days during the 25 day duration for Tag 4 (a Mother). In order to estimate total track distance for these two tags, the shortest navigable distance was measured from the location where the tags stopped transmitting to the location where they commenced transmitting again (and added to distances of track segments to obtain values reported in Table 1); for State-Space Modeling of these individuals, the different temporal segments for each tag were modeled separately. Total number of raw locations per tag ranged from 8 to 807, and speed filtering reduced locations by 5% to 31% (Table 1). Filtered track lengths ranged from 73km for the shortest duration tag (Tag 16, Female, 2 days) to 5,631km for the longest duration tag (Tag 9, Female, NA, 58 days).

Description of Movements - The locations and tracks for tagged individuals are grouped by sex in Figure 2**,** and shown separately for each individual in Supplemental material Figure S1A-W, using the speed filtered location data. In some cases a location occurred on land when an animal was traveling close to the coast; this was an unavoidable limitation of the data and associated error, and we chose not to delete these locations because despite the obvious inaccuracy, they still provide information on the complete track of the individual. No individuals remained in the immediate vicinity of the tagging sites for more than one to three days. The types of movements observed can generally be categorized into four subclasses: (1) movement along the central east coast of Madagascar, primarily from St Marie, (2) movement along the south and southeast coast of Madagascar, primarily from Anakao, (3) northbound movements and departure from Madagascar, only from St Marie and (4) southbound movements and departure from Madagascar, from both St Marie and Anakao. Descriptions of movements in each category are as follows (with Tag numbers referring directly to Table 1 and Figure S1):

(1) Central East Coast Movements: Five males (Tags 2, 3, 6 ,8, 11) tagged off Ile St. Marie in 2012 spent the entire duration (ranging from 3 to 29 days) along an approximately 500km stretch of the Madagascar central east coast south of Ile St. Marie, not previously

recognized as active breeding habitat. Three females (Tags 9, 10, 12) also spent time in the similar stretch of coast south of Ile St. Marie, but traveled more extensively during relatively similar amounts of time as the five males. One female, a mother (Tag 10) first traveled steadily north approximately 640km to the north tip of Madagascar, and over 22 days traveled back south approximately 1,000km, with some meandering off the central east coast region. Two other females (Tags 9, 12) also transited through this central east coast region en route to depart Madagascar from the south, described below. Only 2 individuals tagged off Anakao in 2013, both mothers and the only mothers tagged off Anakao, traveled up the east coast of Madagascar into this region; one (Tag 20) continued past Ile St. Marie to the north until the tag locations became erratic and the tag stopped transmitting, and the other (Tag 23) reversed direction about 140km south of Ile St. Marie and traveled back to the southeast corner of Madagascar before the tag ceased transmitting.

(2) South and Southeast Coast Movements: One female tagged as an NA off St. Marie in 2012 (Tag 9) moved directly to the south and lingered for six days on the Madagascar Plateau off Cap St. Marie (the most southern point of Madagascar), before more extensive southerly movements described below. This was the only whale tagged off St. Marie to visit this region. Conversely, all but one individual tagged off Anakao in 2013 that transmitted for more than a few days travelled southerly to the south coast and southwest coast of Madagascar (Tags 14, 15, 17-23). A non-parous female tagged in a pair (Tag 15) traveled around the south to the southeast corner of Madagascar (approximately 600km) and then 400km up the east coast in 15 days, reversed direction and traveled all the way back to Anakao before reversing direction again and repeating the same general path before the tag stopped transmitting after a total 42 days while she was still on the Madagascar Plateau. A male tagged in a pair (Tag 17) followed a similar pattern travelling to approximately the same point up the southeast coast before turning back south and eventually departing Madagascar on a southeasterly direction before the tag stopped transmitting after 34 days. Two males (Tags 18,19) and a non-parous female (Tag 21) also traveled to the south coast and meandered on the Madagascar Plateau to varying degrees during 23, 8 and 17 days, respectively. Another non-parous female (Tag 19), traveled to the same area and lingered for 19 days, before more extensive southern migration movements described below.

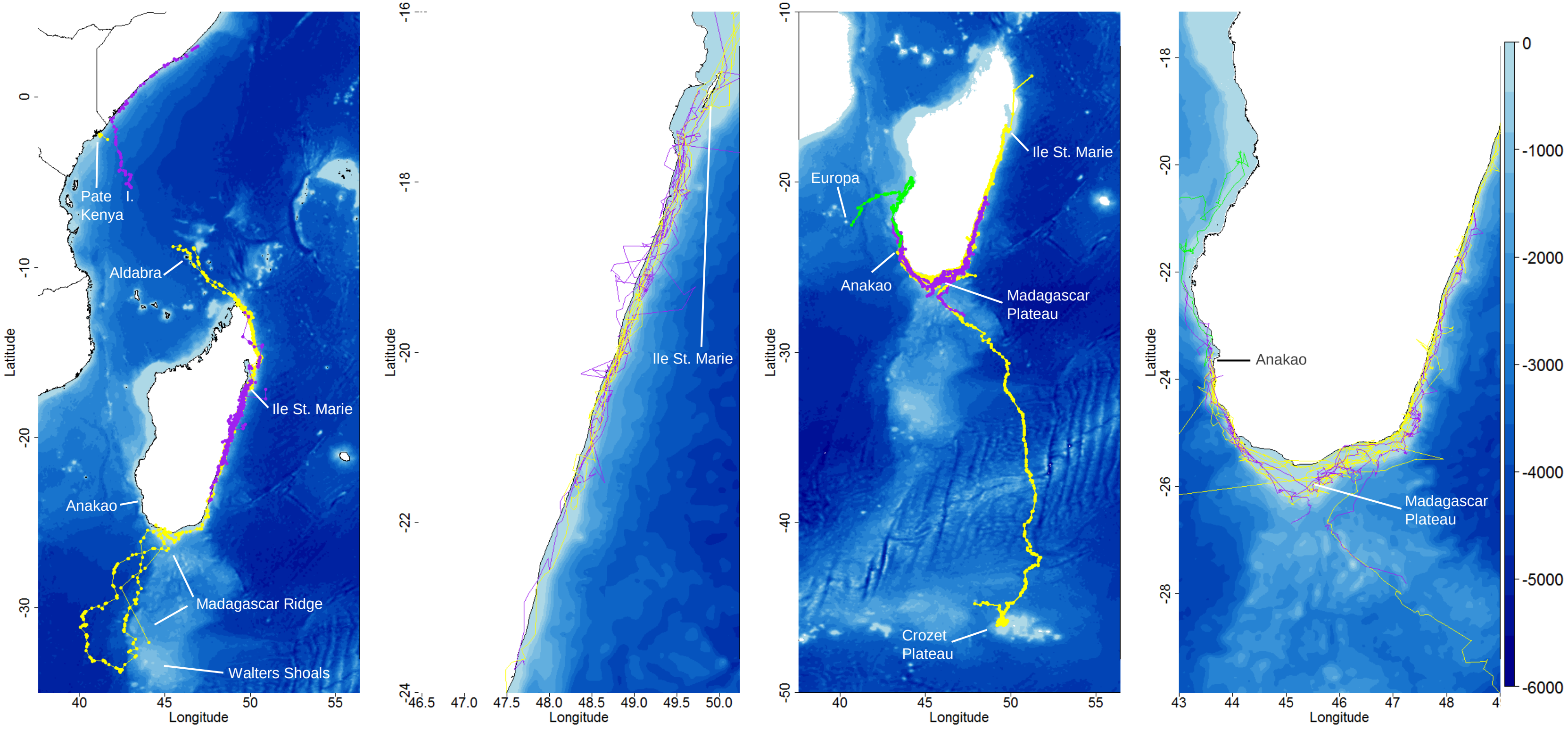

Figure 2. Tracks of all tagged whales, from Ile St. Marie in the northeast during 2012 (A) with detail of movements on central east coast (B), and from Anakao in the southwest during 2013 (C) with detail of movements on south and southeast coasts (D). Each track is represented by dots for speed filtered locations (see text for description), and a line connecting temporally consecutive locations (legs). Females are represented in yellow, males in violet, and a single whale of unknown sex in green. Separate figures for each individual are presented in Supplementary material Figure S1.

(3) Northbound Movement: Five animals, two males and three females, traveled north from Ile St. Marie, four of which departed Madagascar on similar northwesterly trajectories. Two females (a mother, Tag 7, and NA, Tag 12) travelled north ultimately to a location beyond Aldabra Atoll when the tags stopped transmitting, traveling approximately 450km in 4 days, and 500km in 3 days, respectively, after departing Madagascar. The NA (Tag 12) appeared to linger around Aldabra for one day before continuing to the northwest. It is noteworthy that both of these females appeared to pass through the Aldabra region, and were steadily moving to the northwest when the tags stop transmitting. This represents over 1,100km covered in 13 days for the Tag 7 mother, and over 2,300km in 23 days for the Tag 12 female.

Two individuals, a male and a female, traveled to the central African coast, but in both cases the tag did not transmit for the entire transit, so the path can only be inferred. A mother (Tag 4) travelled approximately 600km north in 8 days to the north tip of Madagascar before the tag temporally stopped transmitting. The tag began to report again after 12 days, when the mother was approximately 15km off Pate Island, on the north coast of Kenya. The shortest navigable distance between the two end locations is 1,497km, so it is likely that she moved steadily on a direct course during the 12days that would have followed the path of the females Tag 7 and 12 past Aldabra. She then remained within 50km for 5 days before transmissions ceased; the total transit covered over 2,100km in 25 days. A male tagged as a solo (Tag 1) travelled north 110km to the mouth of Antongil Bay before the tag temporally stopped transmitting. The tag began to report again after 16 days, when the male was approximately 390km off the coast of Kenya at latitude 5º18.9’S. The shortest navigable distance between the two end locations is 1,540km, so it is likely that he moved steadily on a direct course during the 16days, again following the same path of the three females past Aldabra. He then proceeded on a somewhat meandering course covering 450km in 8 days and joining the African coast in south Somalia at 1º25.9’S. Thereafter he moved steadily north up the Somalia coast for 750km in 5 days, crossing the equator before the tag stop transmitting at 2º59.9’N. During 32 days he covered over 2,800km (over 3,120km of trackline) ending within 1,200km of the Gulf of Aden.

(4) Southbound Movement - An adult female tagged off St. Marie as an NA (Tag 9) traveled south immediately after tagging, traveling a somewhat meandering course along

the coast approximately 1,200km in 21 days to the south tip of Madagascar. She lingered on the Madagascar Plateau off Cap St. Marie for 6 days, before departing Madagascar on a meandering southwesterly course west of the Madagascar ridge for 13 days, to the west edge of Walters Shoals approximately 900km south of Madagascar. She then turned north and returned to Madagascar following the west edge of the Madagascar ridge for 9 days, lingered for 3 days off Cap St. Marie, and finally moved south again 700km before the tag stopped transmitting. In total she covered over 5,600 km in 58 days.

A non-parous female tagged off Anakao in a non-competitive group of three whales (Tag 22), moved immediately to the south coast of Madagascar where she lingered on the Madagascar Plateau for 19 days before departing Madagascar waters to the south on August 15. She followed somewhat meandering path for 24 days before arriving on the Crozet Island Plateau, approximately 2,200 km south of Madagascar. She lingered on the western edge of the plateau approximately 50km west of the Crozet Islands for 10 days before departing in a north-northwesterly direction; the tag stopped transmitting two days later.

Aside from these four general movement categories, one whale of unknown sex tagged in Anakao (Tag 13) traveled on a somewhat meandering path 470km north of Anakao over 10 days, before turning back south and departing the coast of Madagascar on a southwesterly course. The tag stopped transmitting after another 5 days and 380km when the whale was off Europa Island. This was the only case both of a whale moving north up the west coast, and departing Madagascar across the Mozambique Channel.

Behavioral Observations of Tagged M-F Pairs - On three occasions an associated male and female were tagged in the same group, all off St. Marie: once as a Mother and Escort (Tags 4 and 5, respectively), and twice as a PE to a NA in two different competitive groups (Tags 8 and 9, and Tags 11 and 12). In the case of the Mother and Escort, the pair appeared to remain together for the entire period of the time that both tags were transmitting (5 days, the period of the shorter duration male Tag 5). In both cases of the PE and NA paired tag events, the two whales appeared to remain together for first 24 hours after tagging, but then diverged on distinctively separate paths thereafter. In addition to these three pairs that were tagged within the same pod, there were two whales tagged separately off Anakao that appeared to join and travel together many days after the tagging event. A male tagged in a pair on July 17, 2013 (Tag 17) and a non-parous female tagged in a non-competitive group on July 27, 2013 (Tag 22) following very different paths during the first 30 and 20 days of the tags' duration, respectively. Then on August 16, they appear to converge about 40km off the edge of the Madagascar Plateau and tightly follow the same positions, course and timing for three days and 285km until Tag 17 stopped transmitting on August 19. Although it is impossible to determine if they were associated due to error in tag positions, it appears possible if not likely they were.

State-Space Modeling Results – A switching space-state model (SSSM) was applied to each tags' data to infer behavioral states of transiting *vs* localized movements. Two estimated locations were generated per day (daytime position and nighttime position) based on all filtered locations, and for each estimated location a B-mode parameter value was estimated as an average of the 2000 iterations retained from the MCMC procedure. Tags that provided less than 10 days of data (Tags 5, 8, 14, 16) were not considered, and only the longer segment of those tags that had a large gap in transmission (Tags 1, 4) was considered.

Females on average displayed a lower B-mode value, 1.27 (1.30 when removing southward migration tracks), as compared to males, 1.64, suggesting that females engaged primarily in directional transiting movement, whereas males displayed more localized and meandering movement. Average B-modes were similar for animals tagged at either site, 1.44 for St. Marie, and 1.42 for Anakao (1.45 and 1.46, respectively, when removing southward migration tracks). Spatial plots of the standardized mean B-modes clearly show an overall distinction between sexes when comparing all females (Figure 3A) with all males (Figure 3B), with male movements strongly skewed toward localized, and female movements strongly skewed towards transiting. Females tended to display areas of more localized movement along the central east coast region and south/southeast coast region (Figure 3C) where males were displaying the highest degree of localized movements (Figure 3D). Thus, although females are moving through these regions in a more transiting fashion than males, they tended more towards localized movements than when documented moving outside of these regions. The movements of whales that left Madagascar mostly conformed to transiting behavior, as might be expected. Exceptions to this include male Tag 1, which displayed a period of localized movement approximately 300km off the Tanzania coast (Figure 3B), female Tag 9 that display localized movement as the most southern extent of her track in the vicinity of Walters Shoals, and female Tag22 that displayed localized movement as the most southern extent of her track on the Crozet Plateau (Figure 3A).

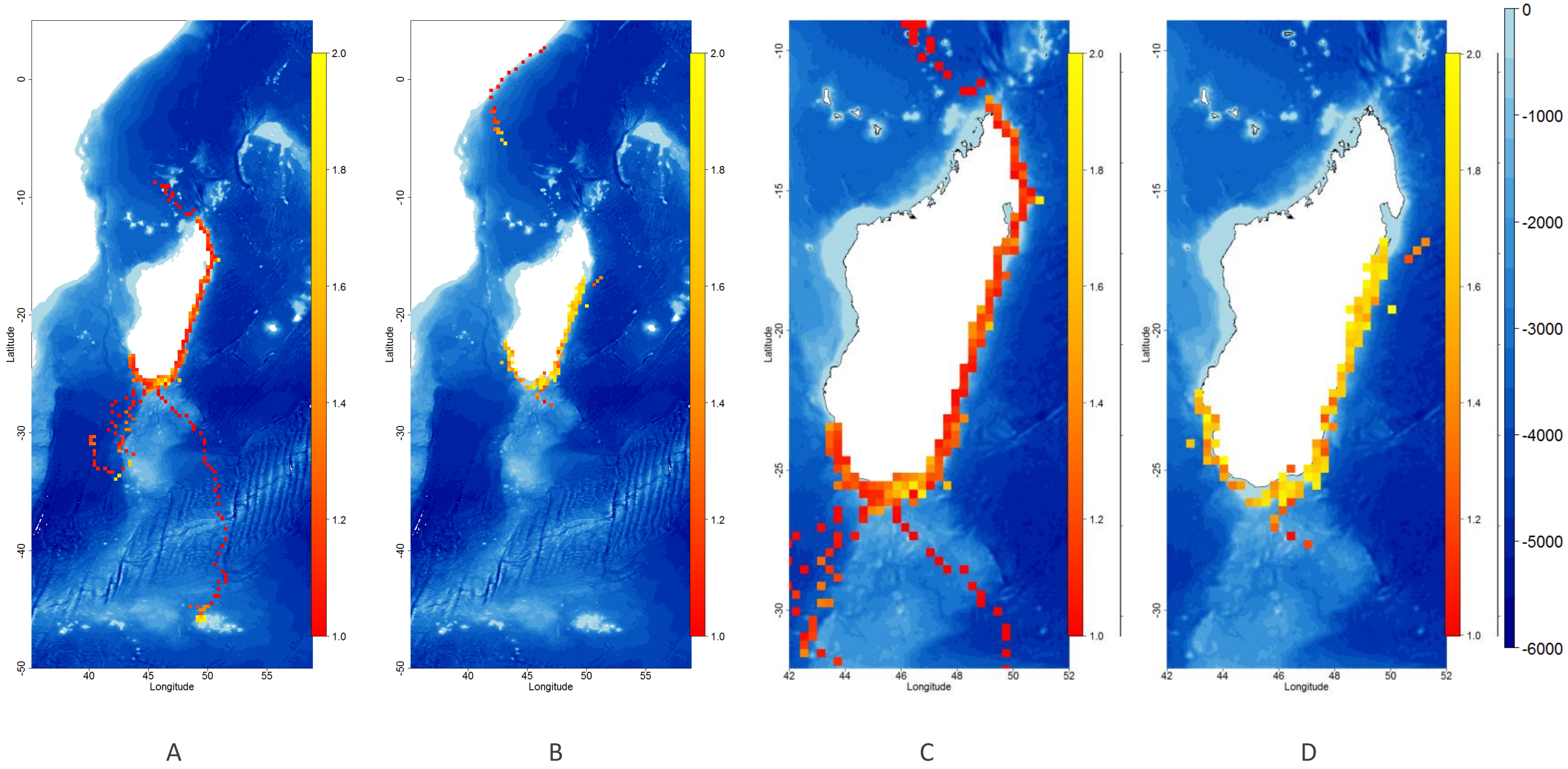

Figure 3. Maps showing spatial distribution of switching state-space model B-mode values, represented as standardized mean values in 0.3deg grid. Shown are all females (A) and all males (B) for the entire range of tracks, and details off the east and south coasts of Madagascar for all females (C), and all males (D). B-mode is represented on a color gradient from red (1.0) = transiting movement, to yellow (2.0) = localized movement.

Before linear mixed effects models were applied to assess variables influencing behavioral state, portions of tracks for those animals that departed Madagascar from the south were trimmed, because these were interpreted as southward migratory movements and we sought to assess movements while in the breeding area. The most supported linear mixed-effect model (Table 2) indicated that sex was the only variable to significantly influence the behavioral states of the tagged whales in their breeding grounds off Madagascar. Model coefficients indicated that male behavioral states are significantly larger than females (Table 3, Figure. 4), which is consistent with the hypothesis that males moved slower and in a more meandering fashion than females during the breading season.

Table 2. Top three linear mixed effect models selected using AIC for humpback whale behavioral state in the breeding grounds off Madagascar (df = degrees of freedom, AIC = Akaike Information Criterion, TagDay = tagging day, DielPer = diel period).

| Model | df | AIC | ΔAIC |
|---|---|---|---|
| Sex | 6 | 1992.12 | 0.00 |
| Sex + TagDay | 7 | 1993.74 | 1.62 |
| Sex + DielPer | 7 | 1993.90 | 1.78 |

Table 3. Estimates of the fixed-effect coefficient in the most supported mixed-effects model for humpback whale behavioral state in the breeding grounds off Madagascar (SE = standard error, df = degrees of freedom).

| Parameter | Estimate | SE | df | t-value | p-value |
|---|---|---|---|---|---|
| Intercept | -0.434 | 0.162 | 842 | -2.678 | 0.0075 |
| Sex | 0.608 | 0.253 | 16 | 2.396 | 0.0291 |

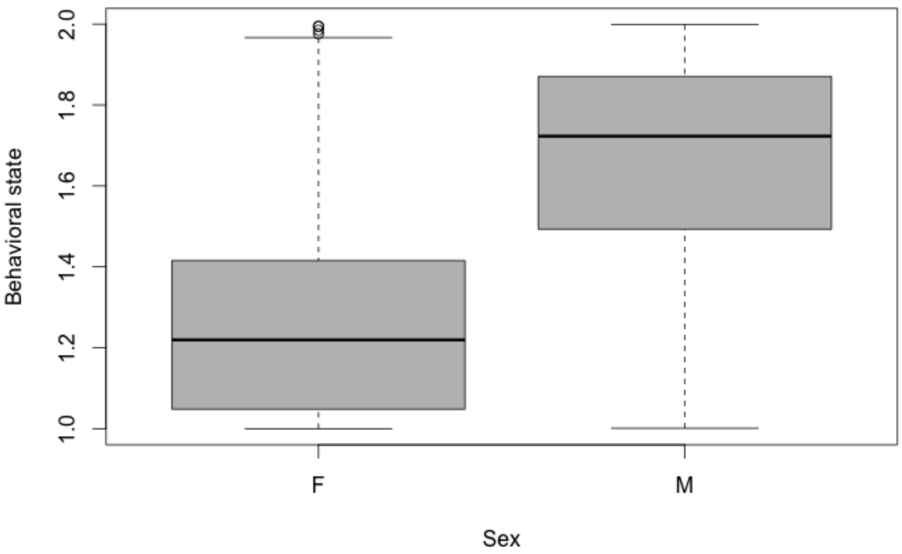

Figure. 4 – Boxplot showing distribution of behavioral states of female (F) and male (M) humpback whales in the breeding grounds off Madagascar.

## Discussion

In this study we used satellite telemetry in the southwest Indian Ocean to elucidate movements of humpback whales throughout the region during the height of the breeding season. Our results have suggested some new and unexpected information concerning exchange of individuals through the region, and population structure, as well as breeding behavior and definition of breeding habitat. Our sample is still small with only 23 tagged individuals, and tag duration was relatively short, so interpretations should be viewed with these caveats in mind. However, despite these constraints our sample of individuals displayed a remarkable variety of movement patterns, with consistency among multiple individuals for several different patterns, and some dramatic and unexpected movements in relatively short periods.

Implications for Population Movements and Structure – Several long distance movements within the SWIO were documented over relatively short periods of time by at least one male and four females, all tagged off Ile St. Marie. Probably the most surprising result was the documentation of two individuals, a male (Tag 1) and a mother (Tag 4), that made it to the central east coast of Africa.  In addition, two other individuals, another mother (Tag 7) and a non-parous female (Tag 12), left Madagascar moving in the same general direction, and had passed Aldabra Atoll by the time the tags had stopped transmitting. It is at least possible, if not likely, that these individuals continued on the same course towards the same general destinations off the African coast.

This movement to the east African coast suggests greater interchange of C1 and C3 sub-populations than previously inferred with population genetic and capture-recapture data. Population genetic data using both mtDNA and nuclear microsatellite markers indicated significant differentiation between samples of whales from C1 and C3 (Rosenbaum et al. 2009). Similarly, a photographic mark-recapture comparison of long-term (2000-2006) samples indicated significant demographic segregation of whales from both areas: although 2 recaptures were discovered between C1 and C3, permutation modeling indicating this was significantly fewer than expected and mixing was not random (Cerchio et al. 2008). It is important to note that in both these genetic and photographic comparisons with C3, the C1 sample was collected in the southern portion of the range, in South Africa (migratory corridor) and southern Mozambique (C1S). The movements we documented with satellite telemetry were direct to the extreme northern portion of the range, Kenya and Somalia (C1N). There is currently no information regarding the relationship of whales that aggregate in the opposite ends of the C1 range, or whether C1S and C1N animals are mixing. Therefore, it is possible that there may be two completely different migratory streams to the east coast of Africa, one that follows the coastline (and represents a genetically and demographically distinct sub-population from whales that visit Madagascar) and a second that passes through the central West Indian Ocean, passing through Madagascar waters en route. Based on these tagging results, along with population genetic and recapture analyses taken collectively, population substructure and interchange appears to be more complex than previously considered, and should be taken into account when developing future recovery models.

In addition to the new perspectives that these results infer for substock mixing, novel information was obtained on travel routes through the region. Virtually nothing is known about the paths that whales take throughout the West Indian Ocean, beyond the coastal movement along South Africa (Findlay et al. 2011a,b), and scant information from the

Mozambique channel based on a few acoustic recordings of song (Best et al. 1998). Here we have documented a route of travel from Madagascar to Kenya/Somalia through the Seychelles Islands. As stated, our sample is small, but it is noteworthy that fully 33% (4 of 12) of whales tagged off Ile St. Marie in 2012 departed Madagascar on the same northwesterly trajectory, suggesting that this may be a prominent movement pattern. This has particular relevance with the recent expansion of petroleum industry activities in the region, and the conservation need to define both important breeding habitat and movement corridors. In regards to the choice of route that these whales navigated, their course follows the direction of the predominant current moving west-northwest from the tip of Madagascar (Lutjeharms 2006), but departs that current as they crossed to the north of Aldabra. Therefore it appears that the whales maybe using the current to assist their long-range movements for part of the transit to east Africa, but not for the entire route. The role of currents on the trajectory of these tagged whales is assessed in detail by Trudelle et al. (in review), suggesting that although currents are not a major determinant of whales' course, they did tend to orient in the direction of the strongest currents encountered.

In regards to the destinations of these whales, aggregations of breeding humpback whales are known from Tanzania and Kenya (Findley et al 2011b, Amir et al. 2012), and there are historical observations of whales along the Somali coast during the Austral breeding season (T. Collins, pers. comm.). The movement of a male up the Somali coast, across the equator and into Northern Hemisphere waters up to 3ºN latitude, is of particular consequence. Movements of whales from the Southern Hemisphere across the equator into breeding areas in the low latitudes of the Northern Hemisphere has been documented in at least two other ocean basins (eastern South Atlantic, Rosenbaum & Mate 2006; eastern South Pacific, Rassmussen et al. 2007) and was predicted by modeling of physical oceanographic characteristics (Rassmussen et al. 2007). However, this particular movement in the West Indian Ocean would not be predicted by the oceanic regimes described in Rassmussen et al. (2007). Furthermore, this has potential implications for our understanding of the Northern Indian Ocean population of humpback whales in the Arabian Sea. To the best of our knowledge, the Arabian Sea population is completely isolated from the populations in the Southern Hemisphere, as documented through strong genetic differentiation (Rosenbaum et al. 2009, Pomilla et al. 2014), lack of any photographic recaptures (Minton et al. 2009), small population size and atypical migratory and breeding behavior (Minton et al. 2011). The male tagged in this study had traveled over 2,800km in 32 days and when the tag stopped transmitting, was within only 1,200km of the horn of Africa and the Gulf of Aden. It is most unfortunate in this case that the tag did not continue transmitting in order to determine his ultimate destination, or at what point he slowed and turn back south. Given what we know about the Arabian Sea population, and about humpback whale behavior in general (specifically the asynchrony of breeding cycles between Southern and Northern Hemisphere populations), we find it unlikely that this animal would have made it into the range of the Arabian Sea animals. Estimates of gene flow and divergence times, as well as clustering analyses, suggest that the Arabian Sea population has likely originated from the Southern Indian Ocean, but has been isolated for approximately 70,000 years, has significantly reduced genetic diversity and the lowest gene flow estimates among all population comparisons conducted to date (Rosenbaum et al. 2009, Pomilla et al. 2014).

Despite these long range movements in relatively short periods, no whale traveled to the northwestern coast of Madagascar, Mozambique, the Comoros Archipelago, or the Mascarene Islands, where breeding aggregations are well documented. This may simply be a matter of sample size or timing of tagging, and larger samples along with tagging at different times of the season, may reveal a greater variety of movements and destinations. At least one whale tagged off Anakao during our study started to cross the Mozambique Channel before the tagged stopped transmitting, so there is clearly the potential for movement to Mozambique. Fossette et al (2014) tagging late in the breeding season in the Comoros Archipelago documented several whales moving to the west coast of Madagascar and therefore mixing between these regions within a breeding season, at least towards the end of the season during southward migration. In a satellite telemetry study off the Island of Reunion, a majority of whales tagged during peak season moved west after tagging to the east coast of Madagascar (Dulau et al. *in prep*); therefore it appears that there is in fact extensive exchange between the Mascarene Islands and Madagascar, however movement may be in only one direction.

Southern migration movements – Although it was a deliberate choice to deprioritize detection of southern migration with our timing of tagging, we expected to increase the probability of documenting a southward migration in choosing to tag non-parous females despite the relative early season. Non-parous females have been documented with shorter residency times on the breeding grounds, and it is logically expected that once a female becomes impregnated, there is little reason to remain in low latitudes; returning to high latitude feeding grounds as soon as possible would appear a reasonable strategy. Two tagged whales displayed what can be considered southward migratory movements and both were non-parous females. The movement of a female (Tag 22) to the Crozet Islands Plateau likely represents a southward migration to feeding habitat, and the localized movement behavior indicated by the SSSM suggests a stop for feeding behavior. Since the tag stopped transmitting it is not clear whether this represented a short stop on the way to other feeding grounds, however the animal did leave the Crozet Plateau before the tag stopped transmitting. Fossette et al (2014) also documented a migratory transit to the Crozet Plateau from the Comoros Archipelago, so it appears that this may be a relatively common feeding destination or stopover on the way to other feeding grounds for Madagascan humpback whales.

The movements of the non-parous female Tag 9 was particularly unexpected and difficult to explain with our current understanding of breeding behavior. This female was tagged off Ile St. Marie as a Nuclear Animal in a competitive group that was actively being defended by dominant (PE) male. After tagging this female did move south, and began what appeared to be the start of her migration; why she stopped and returned to Madagascar is a matter of speculation. Perhaps she was in fact fertilized, however the pregnancy failed and thus she returned to once again search for mates. Chittleborough (1958) documented cases of multiple ovulations within a season through examination of ovaries, suggesting that females can have multiple estrus due to failure of fertilization or early failure of pregnancy. An alternative explanation is that the viable breeding habitat extends down the Madagascar Ridge to the Walters Shoals area, however, we might expect to document other whales exhibiting the same movement pattern. Another alternative explanation is that the Walters Shoals area represents feeding habitat and the female temporarily left the breeding habitat in order to make a short trip to feed.

Implications for Breeding Behavior and Habitat Definition – The tracks of tagged whales and results of the state-spaced models suggest that the central east coast of Madagascar represents important breeding habitat for humpback whales tagged off Ile St. Marie, whereas the south and southeast coasts represent important breeding habitat for whales tagged off Anakao. Given what is known about the distribution of whales in

Madagascar, with aggregations of breeding whales in Antongil Bay/Ile Saint Marie in the northwest, and regular sightings off Fort Dauphin in the southeast and off Anakao in the southwest, it was expected that whales would at least transit through the central east coast region; however our results indicate that whales are not simply transiting through the area, but rather utilizing it as breeding habitat. This was not previously recognized, largely due to a lack of research effort in the region and absence of data. This is of consequence for conservation efforts in the region, due to the recent development of mining industry activities in Tamatave, located within the stretch of coast utilized by these tagged whales. Existing information for the east coast comes primarily from efforts in Antongil Bay (Rosenbaum et al. 1997, Ersts and Rosenbaum 2003, Cerchio et al. 2009) and Ile St. Marie (Vely et al. 2009). Cerchio et al. (2009) noted from photographic mark-recapture data in Antongil Bay, 2000-2006, few individuals were recaptured within a season and residence times inferred by recaptures were short, suggesting that animals are transiting through Antongil Bay and utilizing a larger area. This is congruent with the results obtained from our satellite tagging. Interestingly, no tagged individuals were documented entering into Antongil Bay, despite its close proximity to the tagging location, Ile St. Marie. Prior to tagging on St. Marie, three days (July 21-23, 2012) were spent in Antongil Bay with no sightings of humpback whales, despite extensive documentation of high densities of whales in the Bay during this period in previous years (Cerchio et al. 2009). Therefore, there may exist some degree of variation between years, or a recent shift in distribution patterns.

Of particular interest is the minimal amount of overlap between individuals tagged off Ile St. Marie and Anakao, and the lack of movement to the mid- and northwestern coast of Madagascar, despite such movements representing much shorter transits than documented by our long-range movements. Although there was some overlap between the tracks of a few whales tagged in Ile St. Marie and Anakao, whales tagged off Ile St. Marie largely favored the central east coast of Madagascar, whereas those tagged off Anakao tended to favor the south and southeast coasts. Those whales that did cross into the other tagging areas favored region were females (particularly mothers) that tended to show more transiting movement in general. It appears that whales coming to either side Madagascar may not use the same breeding habitat within a season, or possibly movement patterns may vary substantially at different points in the season, and whales may move between east and west Madagascar at other times (i.e., earlier or later in the breeding season, similarly to as documented from the Comoros Archipelago to Madagascar in late season, Fossette et al. 2014).

There appears to be a distinction between how the central east coast and south/southeast coast regions were utilized by males and females, and key differences in movement patterns between the sexes in general. Males displayed more variable and localized movement in the range, perhaps as a result of searching for mates. Females overall tended to transit through the breeding habitat, covering more distance in shorter periods of time, and traveling greater distances overall. However, despite this transiting tendency, female movement in the central east coast and the south/southeast coast regions (where males from Ile St. Marie and Anakao, respectively, were displaying strongly localized movement) appears less direct, tending more towards localized movement themselves, perhaps as a consequence of the presence of males actively searching for mates. This difference between males and females suggests varying mating strategies between the sexes, with males focusing more effort prospecting the local area for females. Conversely, females may be covering more distance in an effort to expose themselves to a higher number of males. A lek mating system has been suggested for humpback whales (Herman and Tavolga 1980, Clapham 1996, 2000, Conner et al 2000), which would infer aggregations of males displaying through song, and females moving through aggregations assessing male displays and ultimately exerting female choice (Höglund and Alatolo 1995). The movement patterns described here are largely congruent with expectations based on the lek hypothesis, particularly when considering an expansive breeding habitat (the central east coast, or the Madagascar Plateau) as large-scale aggregating sites for males through which females move to assess potential mates. Therefore, contrary to classical leks (as in ground birds, Höglund and Alatolo 1995) where the lekking arena is relatively small, localized and fixed, the lek for humpback whales might be very large, as well as mobile, as suggested by Clapham's (1996) "floating lek" proposal. It is noteworthy that no clear distinction was apparent between mothers and non-parous females, with examples of both traveling extensive distances in transiting mode. The sample is too small to draw conclusions, and further data is required before relevant comparisons can be made between reproductive classes.

Associations among individual humpback whales on the breeding grounds, including between potentially courting males and females, are thought to be transient in nature

(Mobley and Herman 1985, Clapham 1996, 2000). Among three male-female pairs tagged in this study, two associations appeared to last no more than one day; this was not surprising as in both cases the association was between an NA and PE within Competitive Groups, and thus subjected to disruption by competing males. In the third case, an Escort to a Mother, the association appeared to be prolonged for at least 5 days before the tagged male stopped transmitting. In addition, a male and female not tagged together appeared to join post tagging and remain together for several days. Andriolo et al. 2014 found similar periods of association (5 and 4 days) from two of four pairs tagged off Brazil, and also documented pairs apparently coming back together post tagging. Cerchio (2003), in a molecular paternity assessment off the Revillagigedos Archipelago, Mexico, found two cases in which mated male-female pairs were sighted together during the year in which the female was impregnated over the course 3 and 9 days, respectively, for an association in a Competitive Group and an association in a Pair. Therefore, although associations on breeding grounds are clearly fluid, and long-term associations may be rare or absent, it is likely that medium-term associations over at least several days may be important in courtship behavior and reproductive success, and more common than currently realized.

Future Work and Perspectives – This first effort of tracking whales from Madagascar using satellite telemetry has provided new information and some unexpected results. It is clear that there is much more to be learned about this population and region. Tagging during the height of the breeding season provided key results with implications on interchange in the region that would not have been obtained otherwise. The composition of our sample of individuals suggests that it is possible to deliberately target a representative sample across the different sexes and reproductive classes. Future satellite tagging effort should focus on increasing the samples size in each subclass, allowing comparisons across subclasses. Given the documented movement patterns, future tagging should also be done in different areas, repeating the tagging in northeast and southwest regions, and adding in particular on the northwest coast of Madagascar to which we documented no movements. Increasing the available information on movement patterns of humpback whales throughout the southwest Indian Ocean will provide valuable guidance for future research and conservation efforts, identifying new areas where further work is warranted, and defining important habitat that should be protected as extractive industry and coastal development in the region increases.

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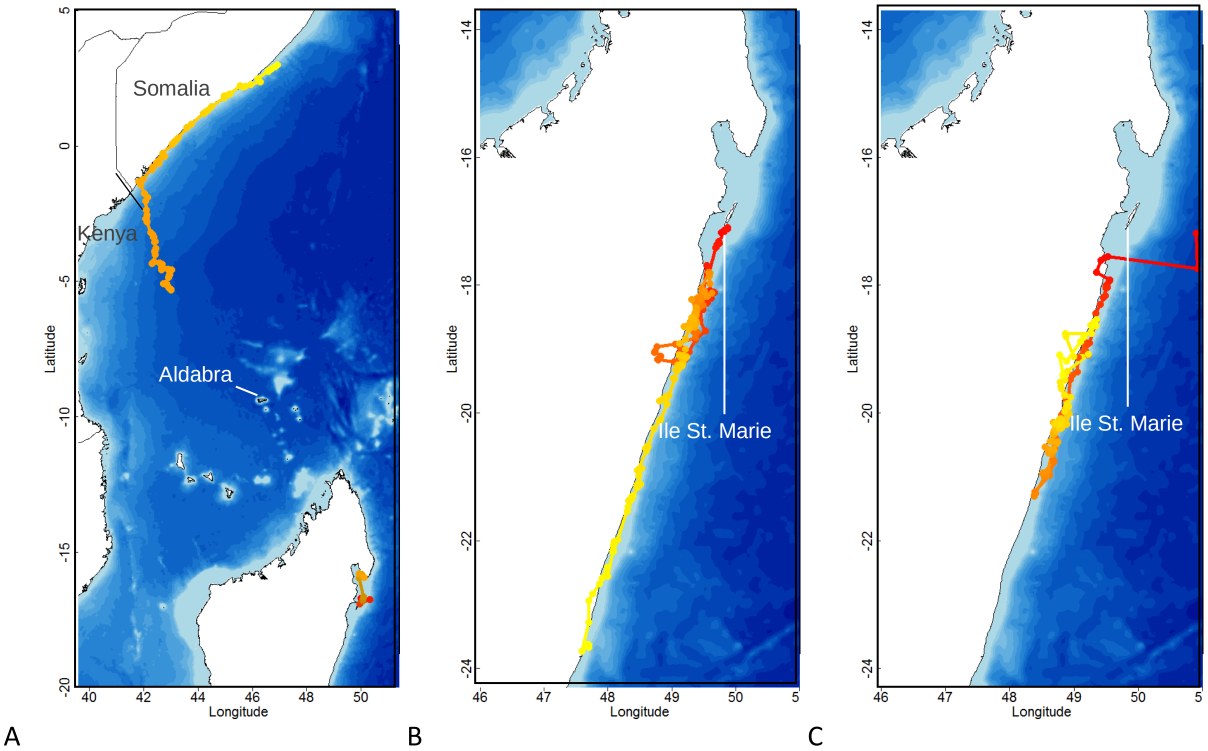
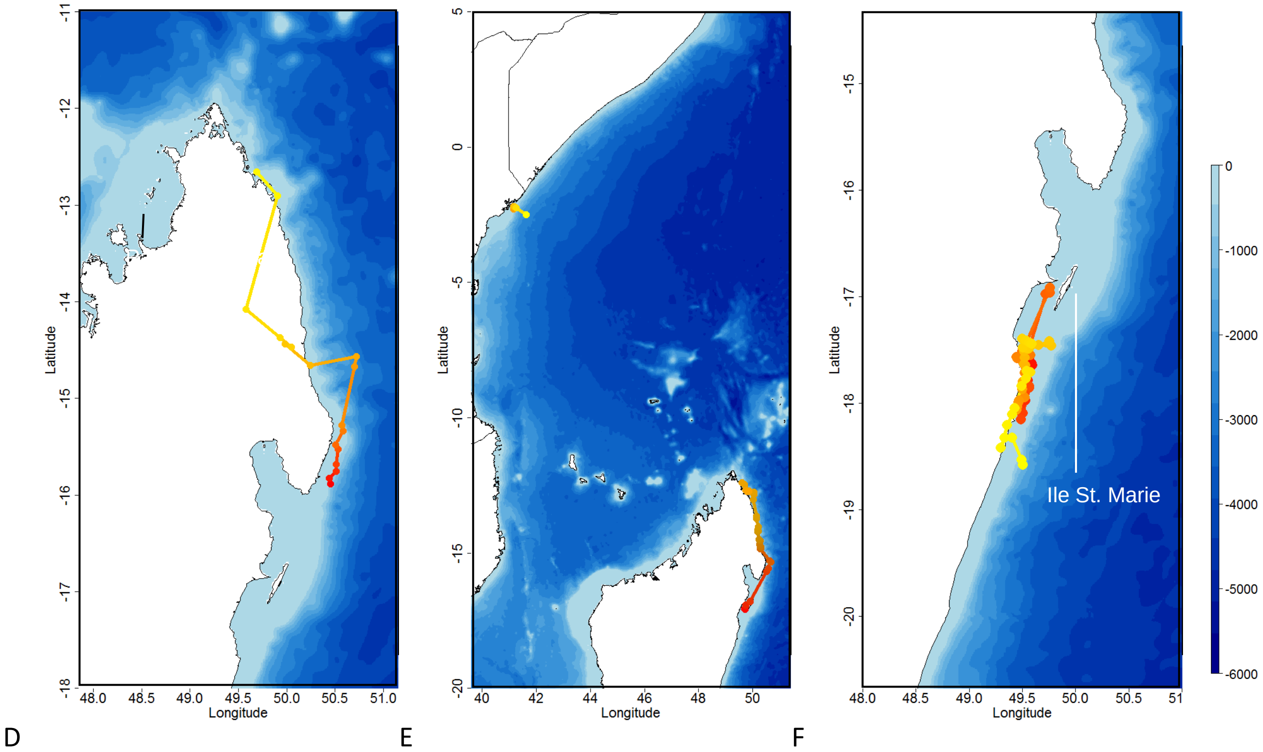
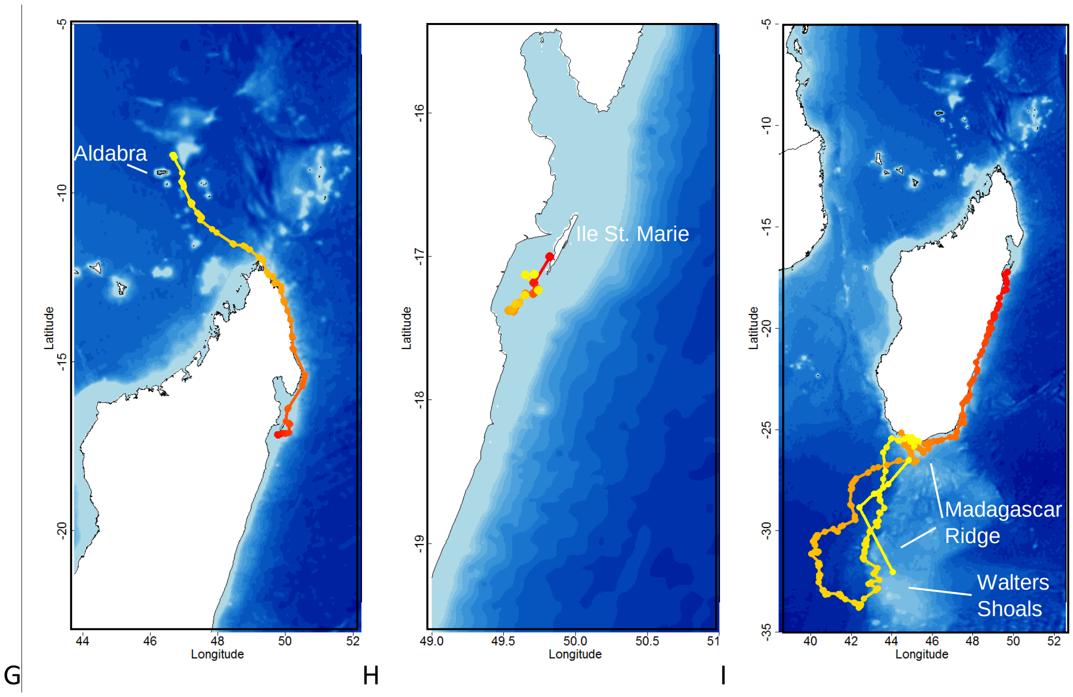


Tag 1 – M, Solo    Tag 2 – M, in CG    Tag 3 – M, in Pair

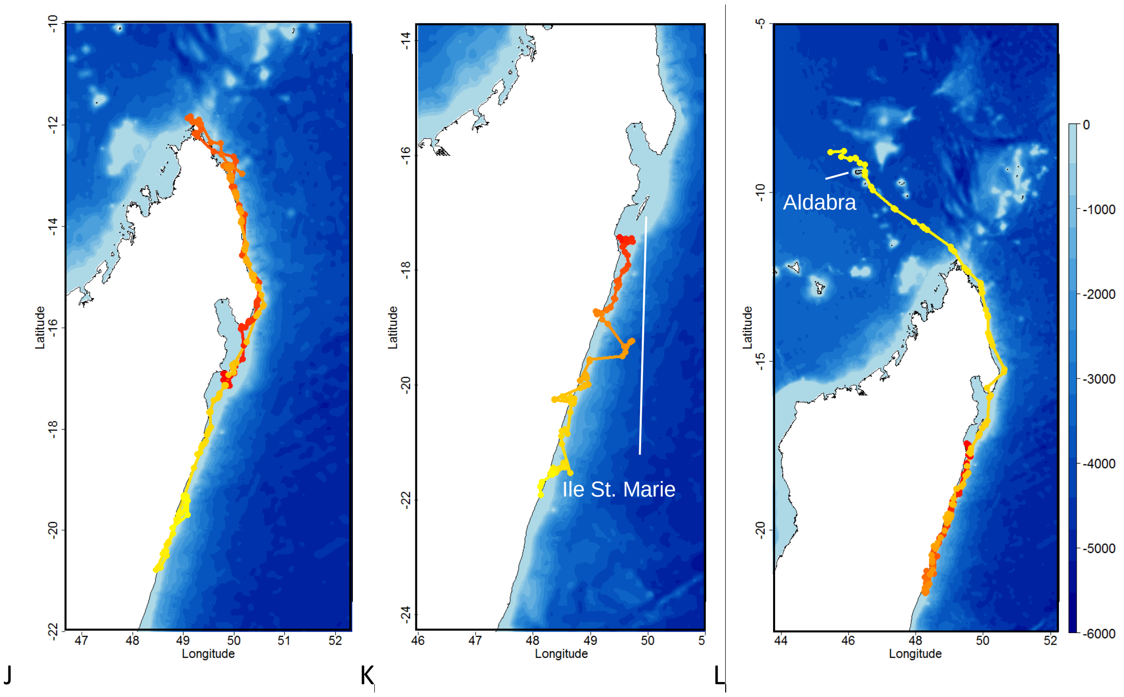


Tag 4 – F, Mother    Tag 5 – M, Esc    Tag 6 – M, in Pair

Figure S1A-W. Tracks for each humpback whale satellite tagged off Madagascar, Tags 1-12 from Ile St. Marie in the northeast, and Tags 13-23 from Anakao in the southwest. Each track is represented by dots for speed filtered locations (see text for description), and a line connecting temporally consecutive locations (legs). Temporal progression is represented with a continuous color gradient, from the first initial location after tagging in red to the final location with last tag transmission in yellow.

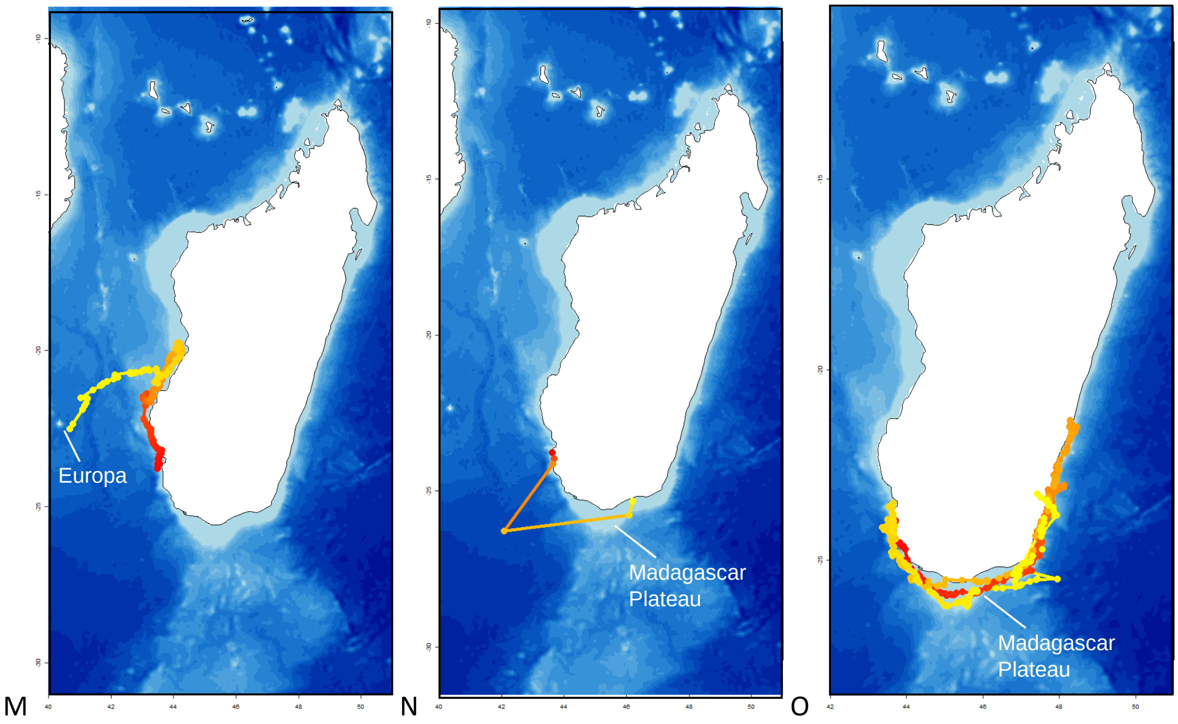


Tag 7 – F, Mother Tag 8 – M, CH/PE Tag 9 – F, NA



Tag 10 – F, Mother Tag 11 – M, PE Tag 12 – F, NA

Figure S1A-W (continued). Tracks for each humpback whale satellite tagged off Madagascar, Tags 1-12 from Ile St. Marie in the northeast, and Tags 13-23 from Anakao in the southwest. Each track is represented by dots for speed filtered locations (see text for description), and a line connecting temporally consecutive locations (legs). Temporal progression is represented with a continuous color gradient, from the first initial location after tagging in red to the final location with last tag transmission in yellow.



Tag 13 – Unk sex, in Pair

Tag 14 – F, in Pair

Tag 15 – F, in Pair

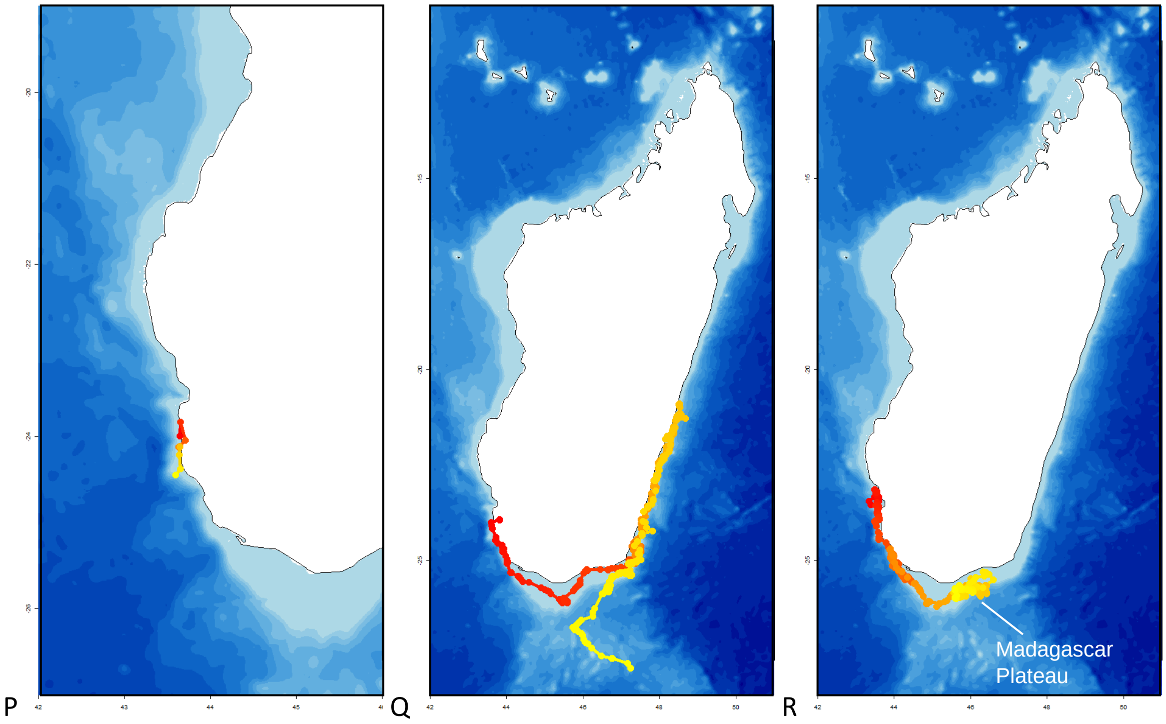
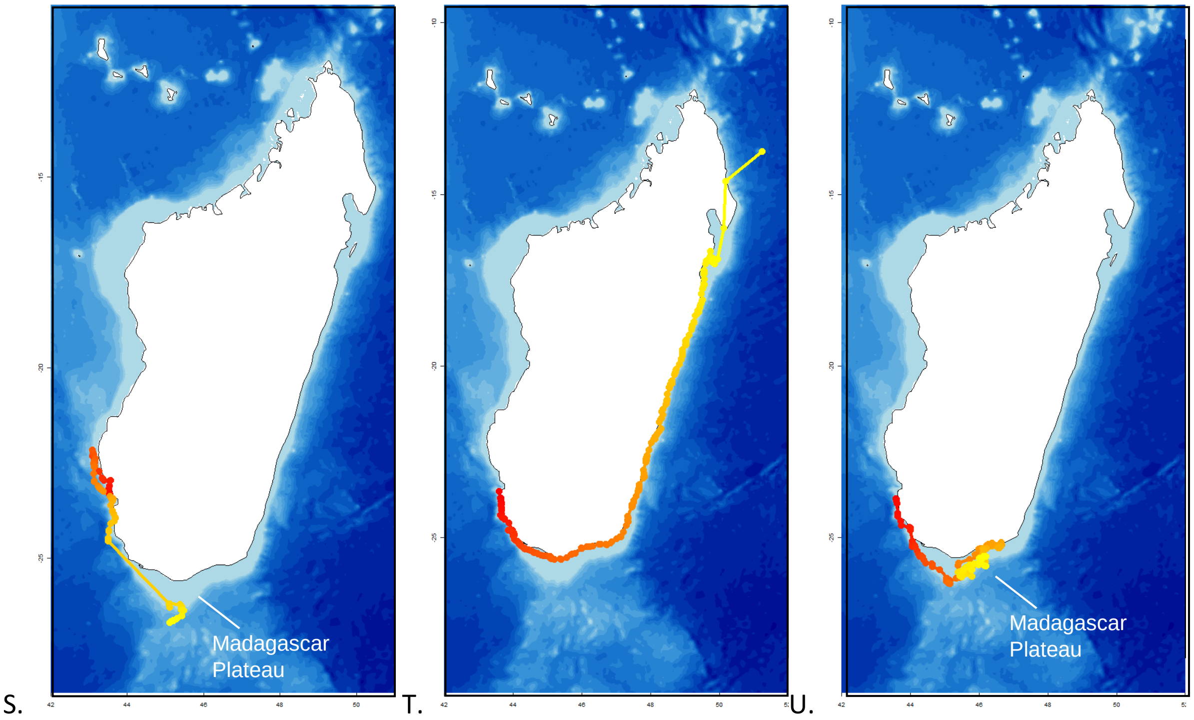


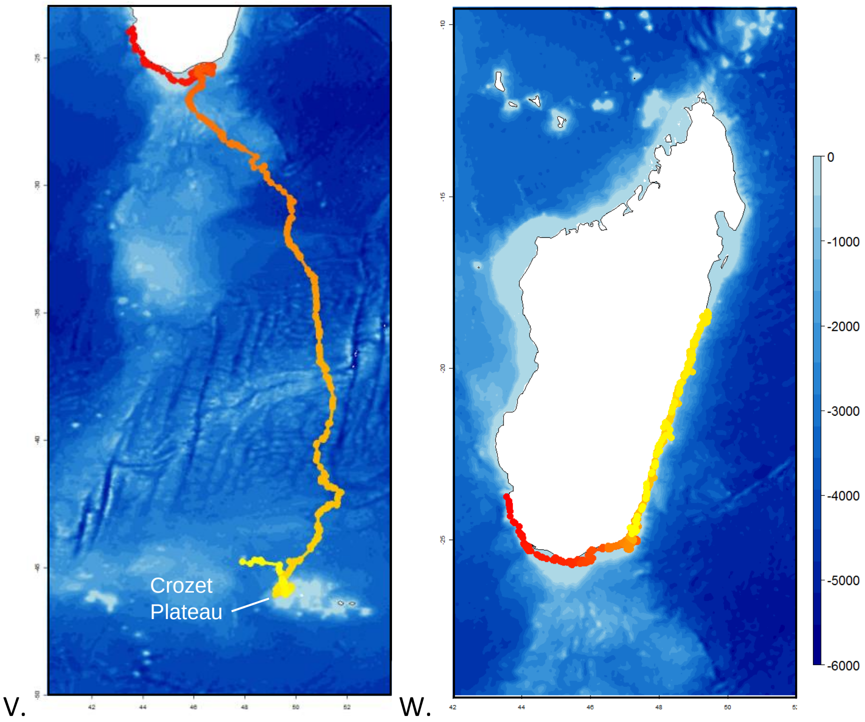
Figure S1A-W (continued). Tracks for each humpback whale satellite tagged off Madagascar, Tags 1-12 from Ile St. Marie in the northeast, and Tags 13-23 from Anakao in the southwest. Each track is represented by dots for speed filtered locations (see text for description), and a line connecting temporally consecutive locations (legs). Temporal progression is represented with a continuous color gradient, from the first initial location after tagging in red to the final location with last tag transmission in yellow.



Tag 19 – M, SE

Tag 20 – F, Mother

Tag 21 – F, NA

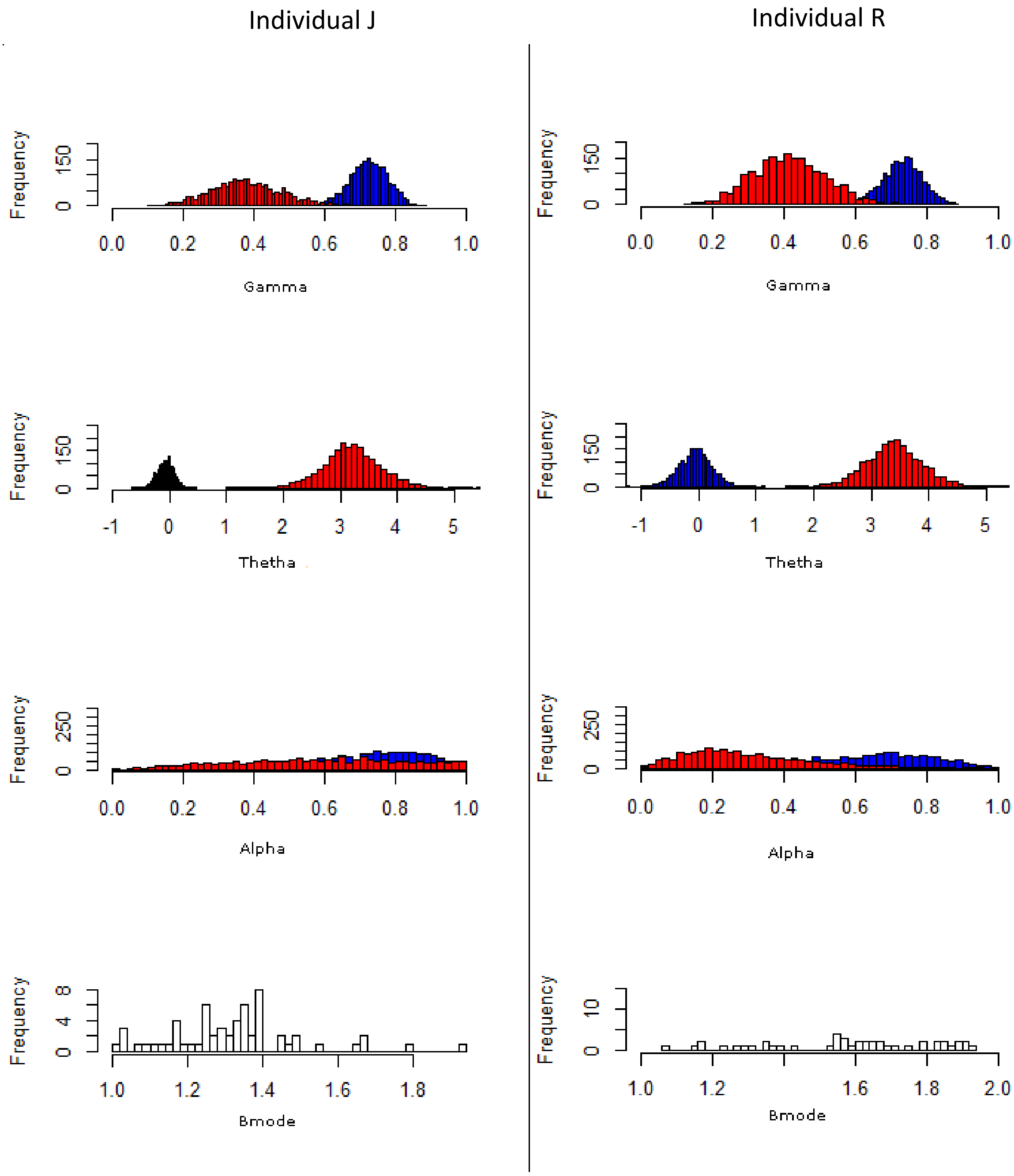


Tag 22 – F, NA?

Tag 23 – F, Mother

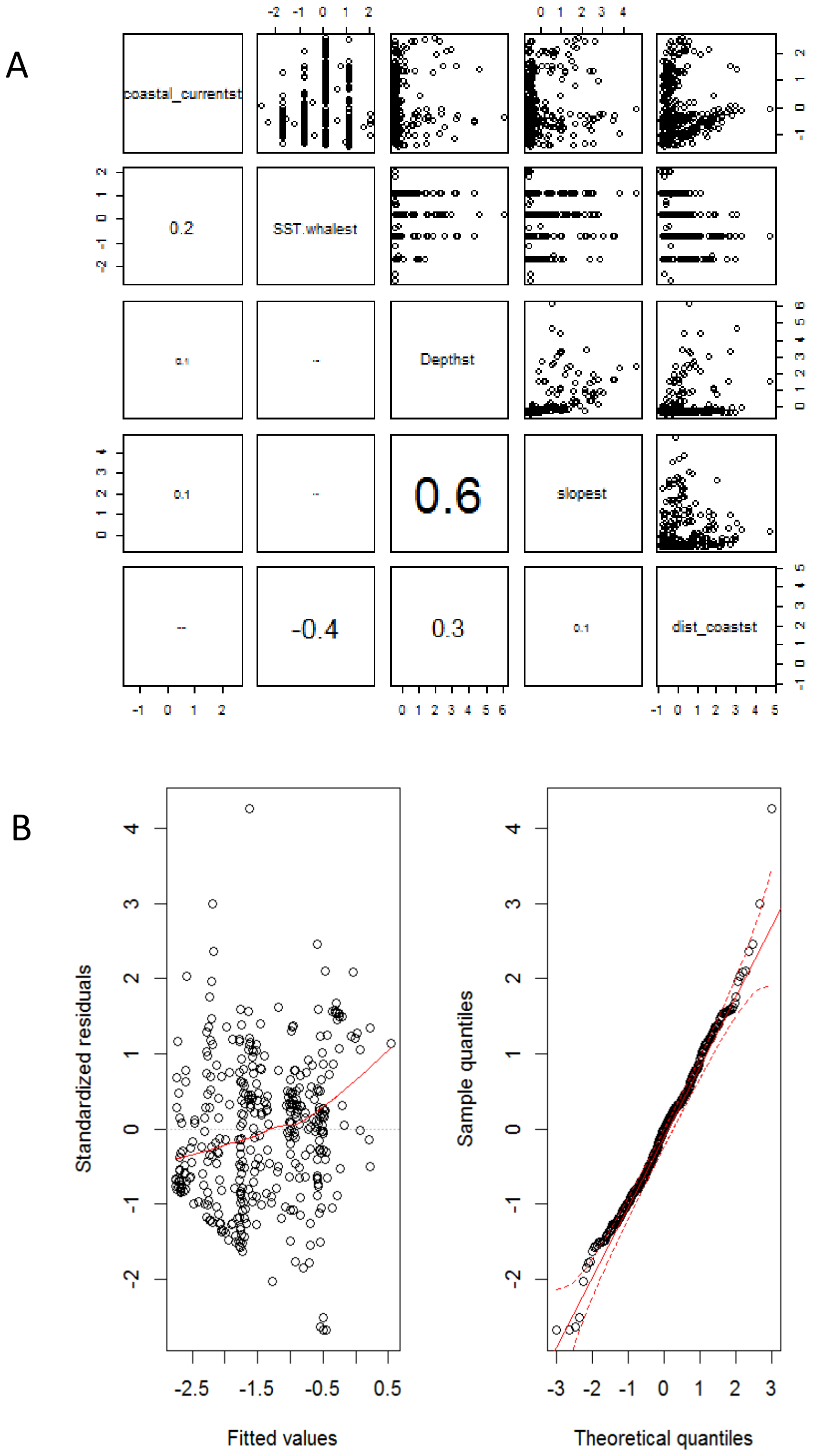
Figure S1A-W (continued). Tracks for each humpback whale satellite tagged off Madagascar, Tags 1-12 from Ile St. Marie in the northeast, and Tags 13-23 from Anakao in the southwest. Each track is represented by dots for speed filtered locations (see text for description), and a line connecting temporally consecutive locations (legs). Temporal progression is represented with a continuous color gradient, from the first initial location after tagging in red to the final location with last tag transmission in yellow.

# ANNEXE B



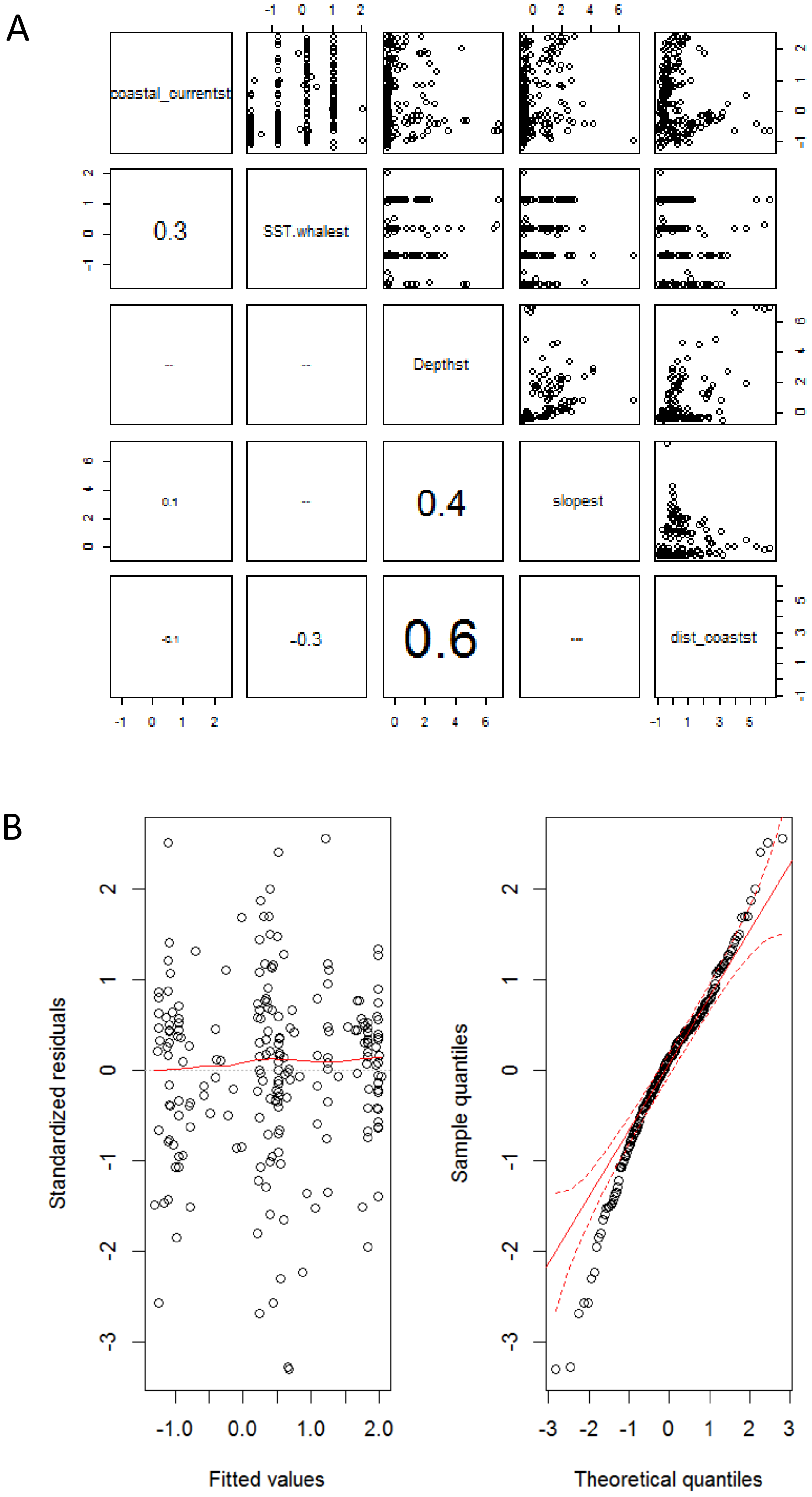
Switching State Space Model (SSSM) outputs for individuals J and R. Frequency histographams of the estimated parameters, γ (gamma, the move autocorrelation) and $\theta$ (theta, the mean tun angle in radians), α (probability of switching from one state to another anoe) and the behavioral mode (bmode). Blue and red colours indicate the two behavioral modes (1 and 2).

# ANNEXE C



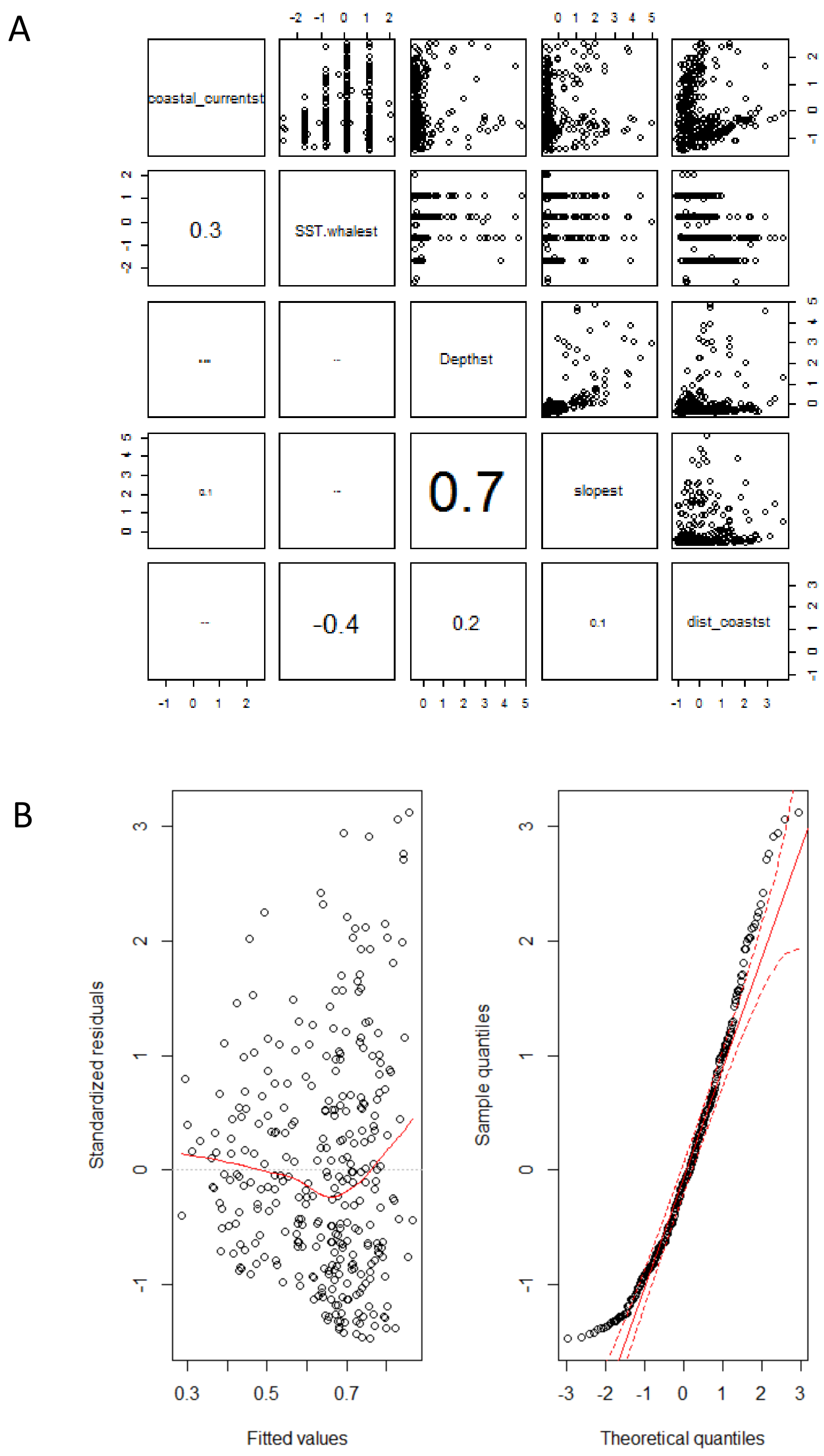
(A) Multi-panel scatterplot for female coastal data (behavioral mode). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE D



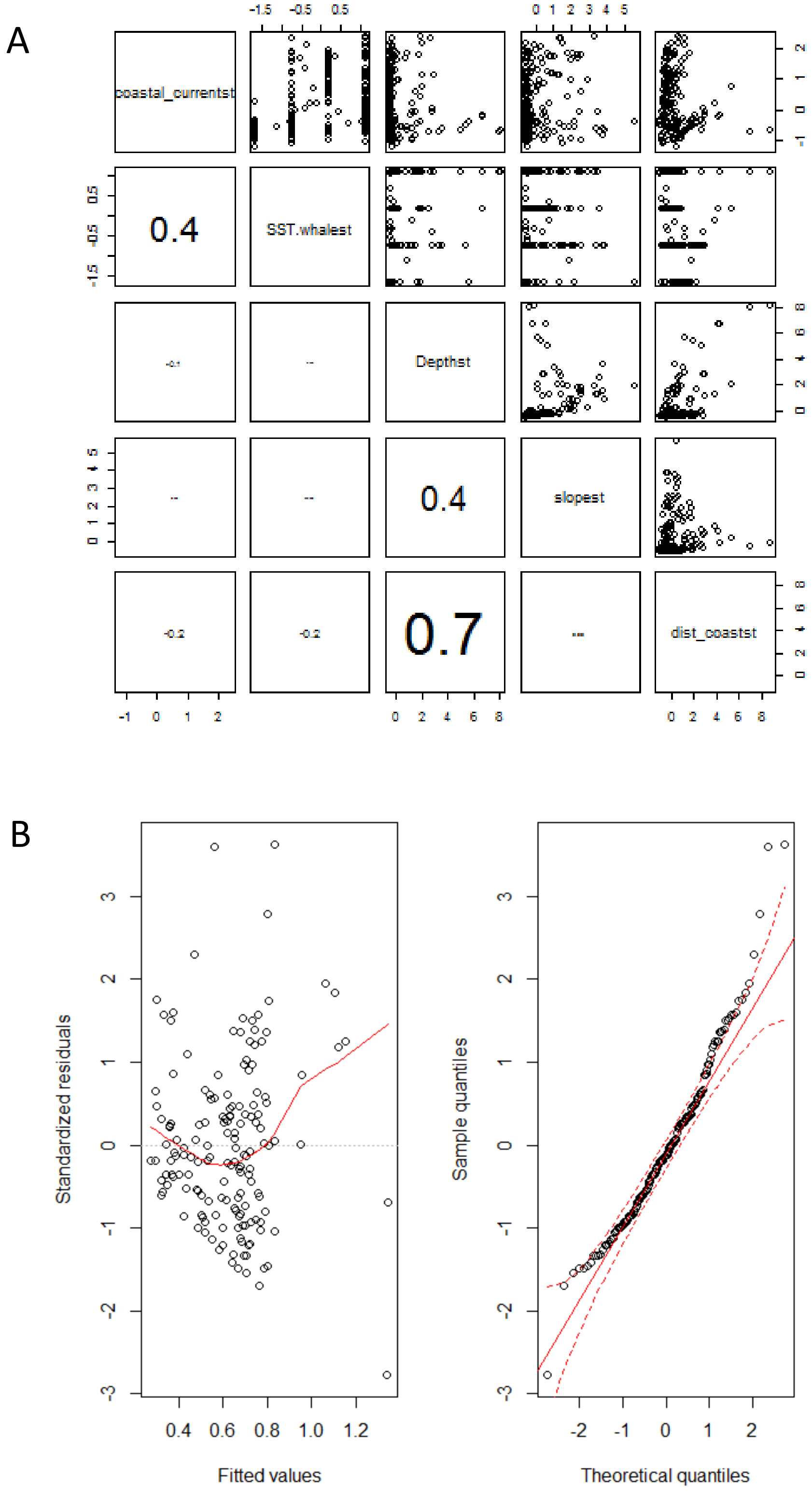
(A) Multi-panel scatterplot for male coastal data (behavioral mode). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE E



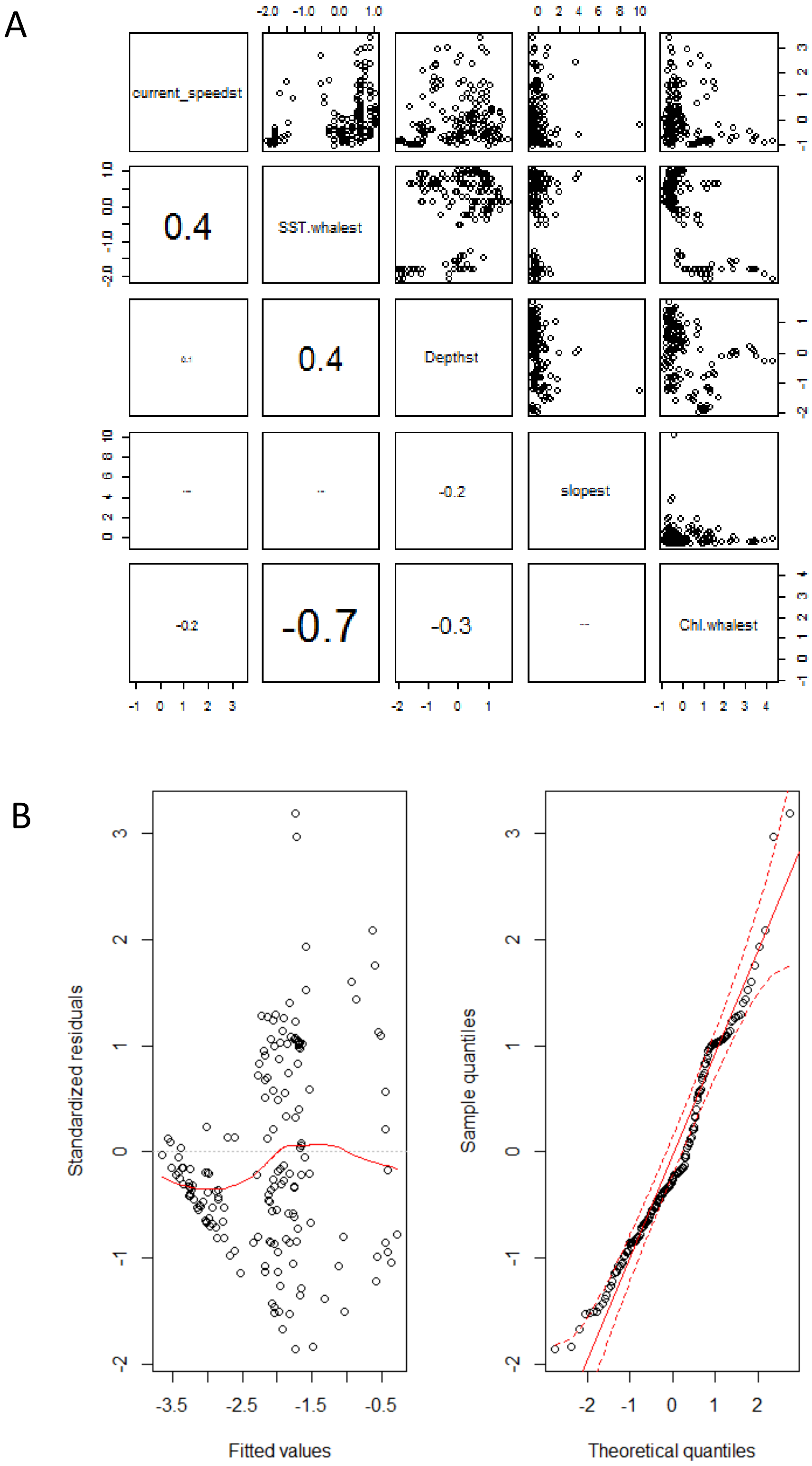
(A) Multi-panel scatterplot for female coastal data (swimming speed). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE F



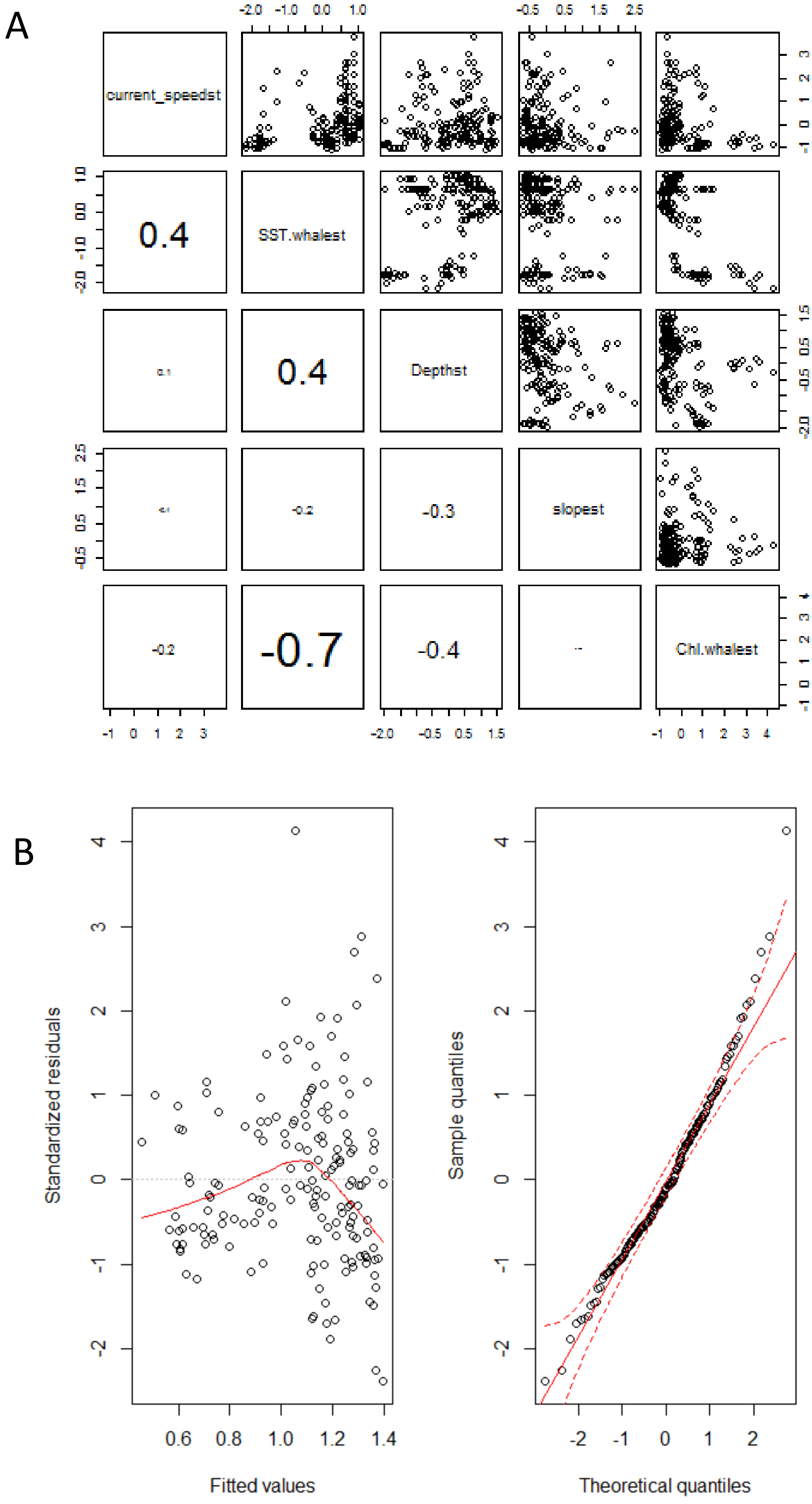
(A) Multi-panel scatterplot for male coastal data (swimming speed). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE G



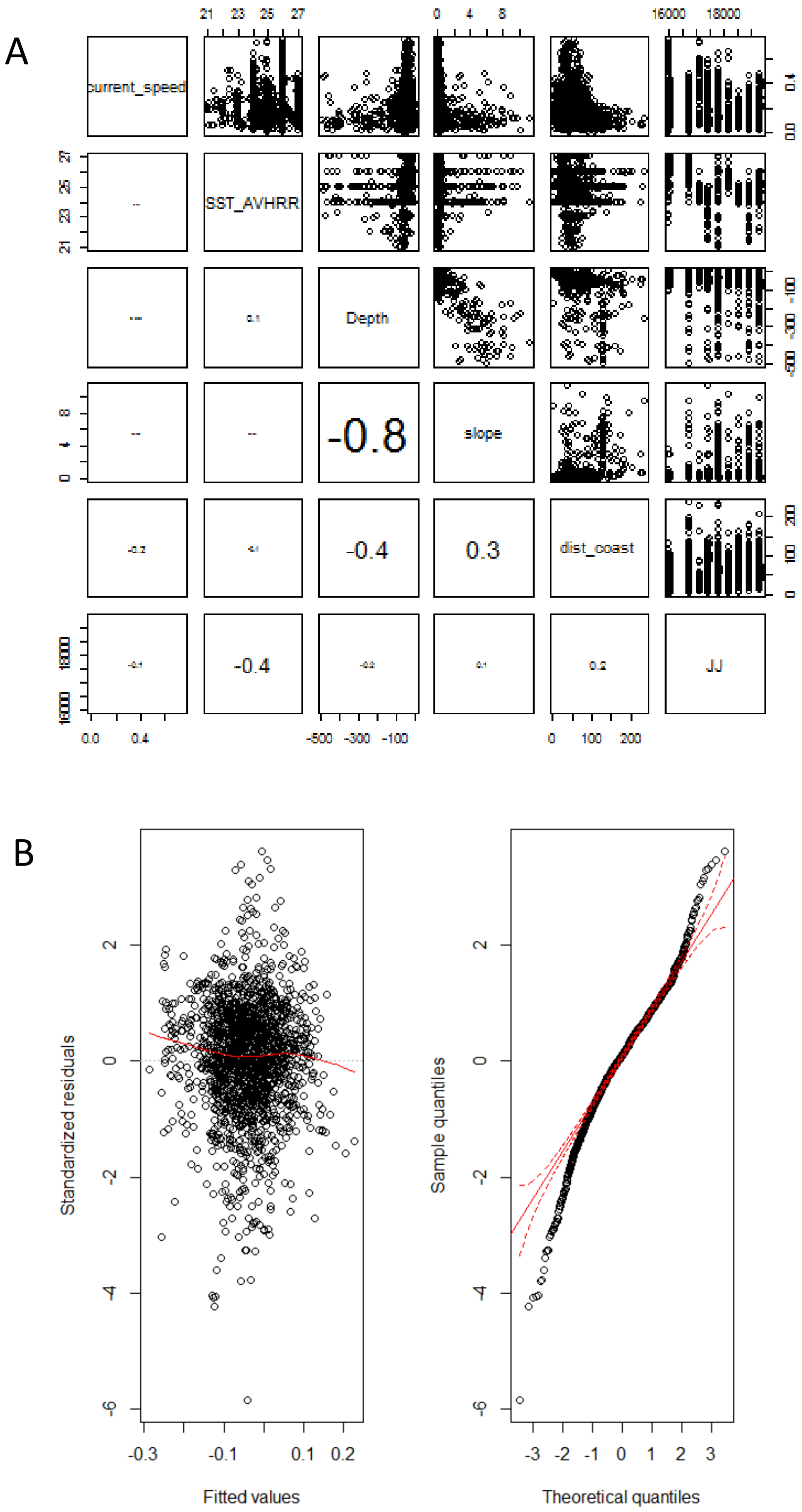
(A) Multi-panel scatterplot for oceanic data (behavioral mode). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, CHL), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE H



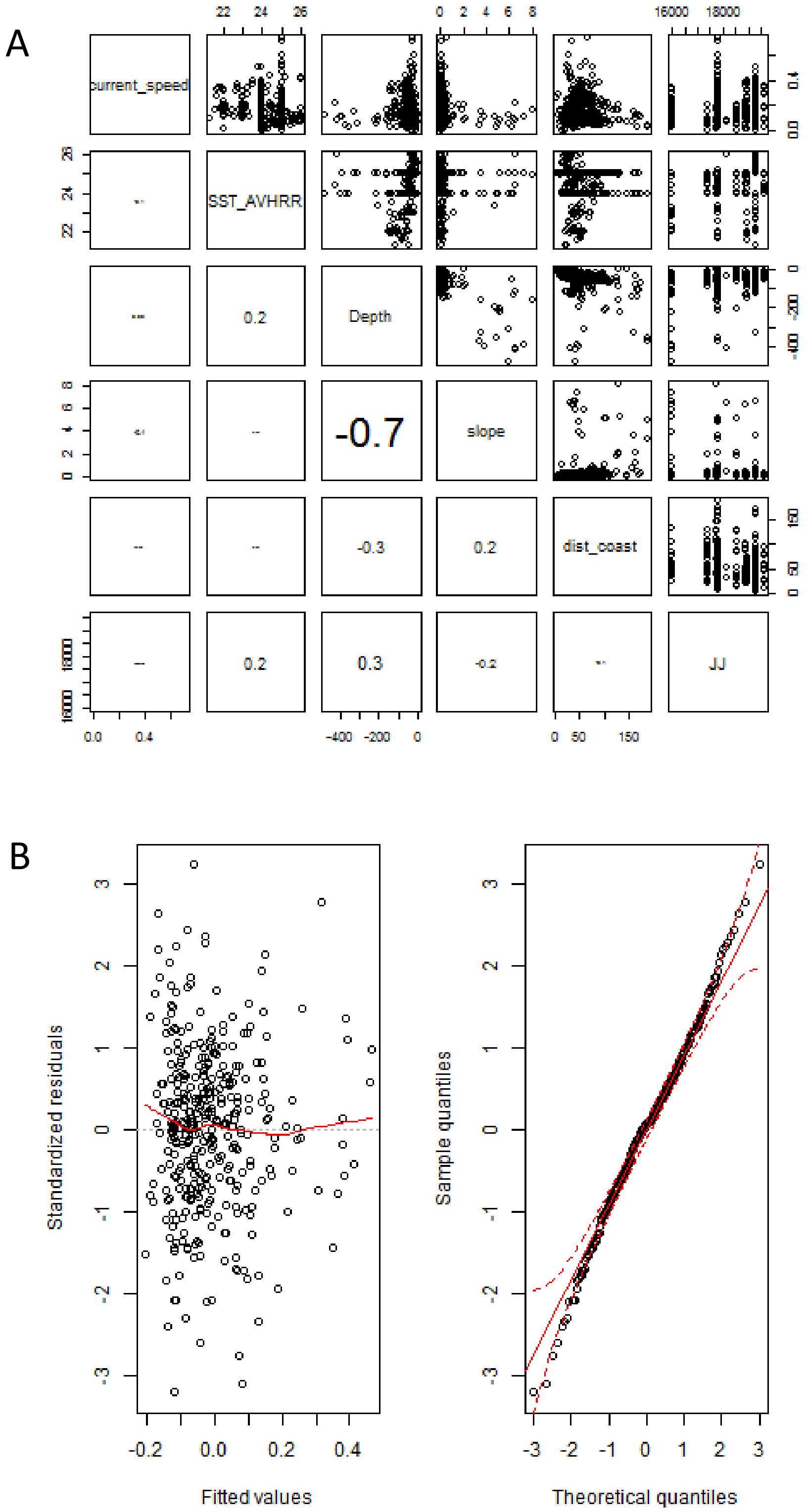
(A) Multi-panel scatterplot for oceanic data (swimming speed). The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, CHL), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE I



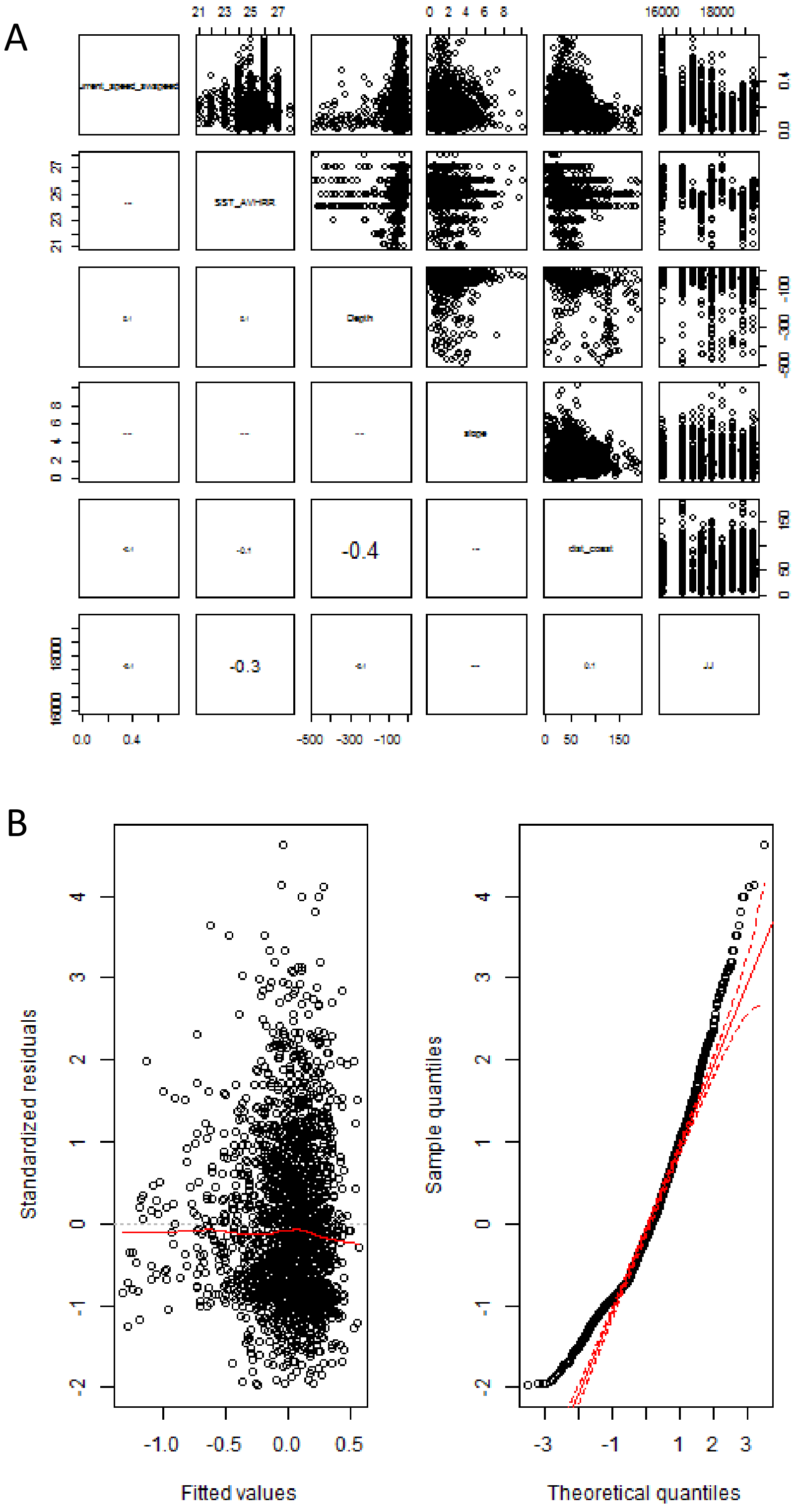
(A) Multi-panel scatterplot for female coastal data (behavioral mode) from BSA. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE J



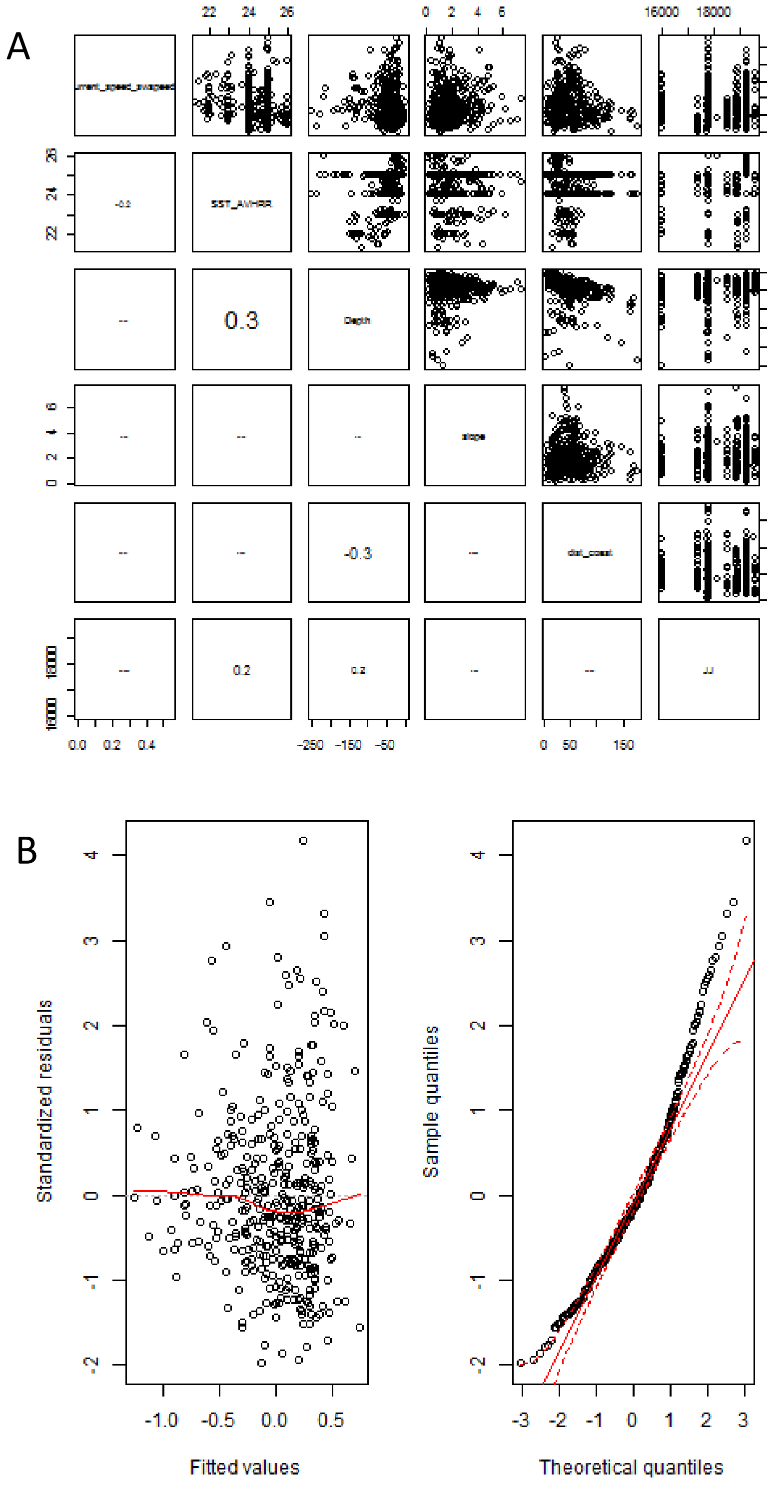
(A) Multi-panel scatterplot for male coastal data (behavioral mode) from BSA. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE K



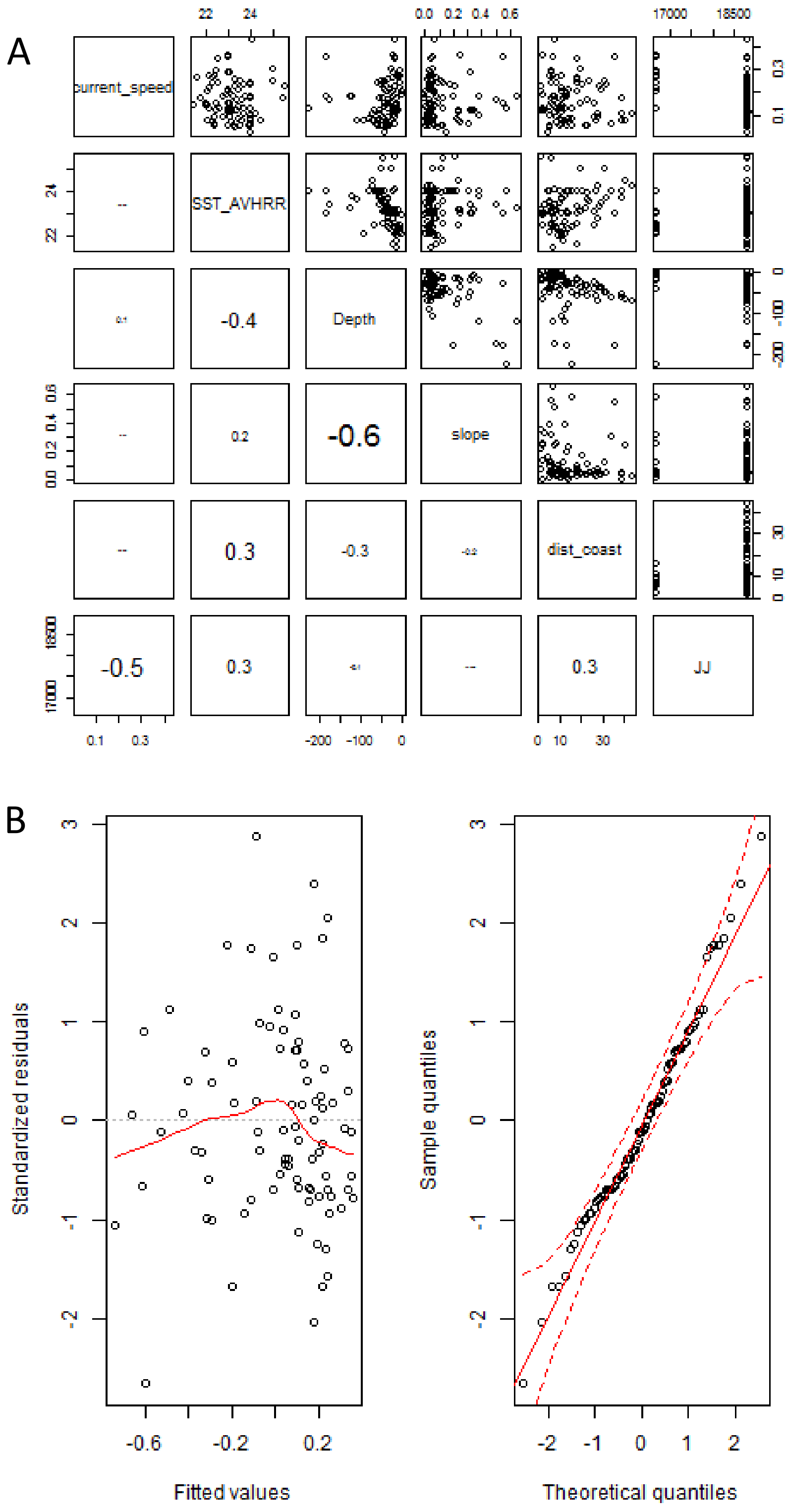
(A) Multi-panel scatterplot for female coastal data (swimming speed) from BSA. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE L



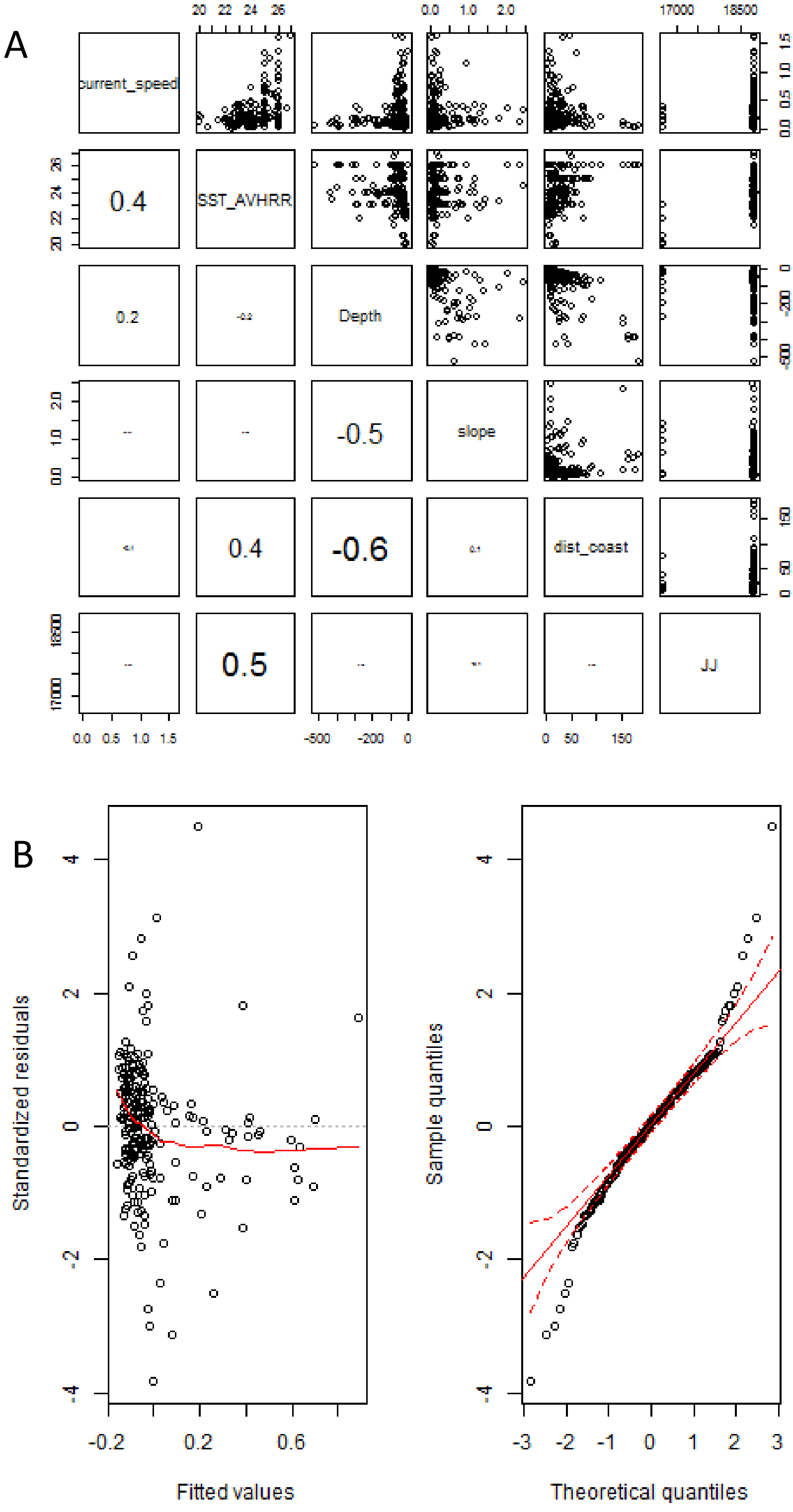
(A) Multi-panel scatterplot for male coastal data (swimming speed) from BSA. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE M



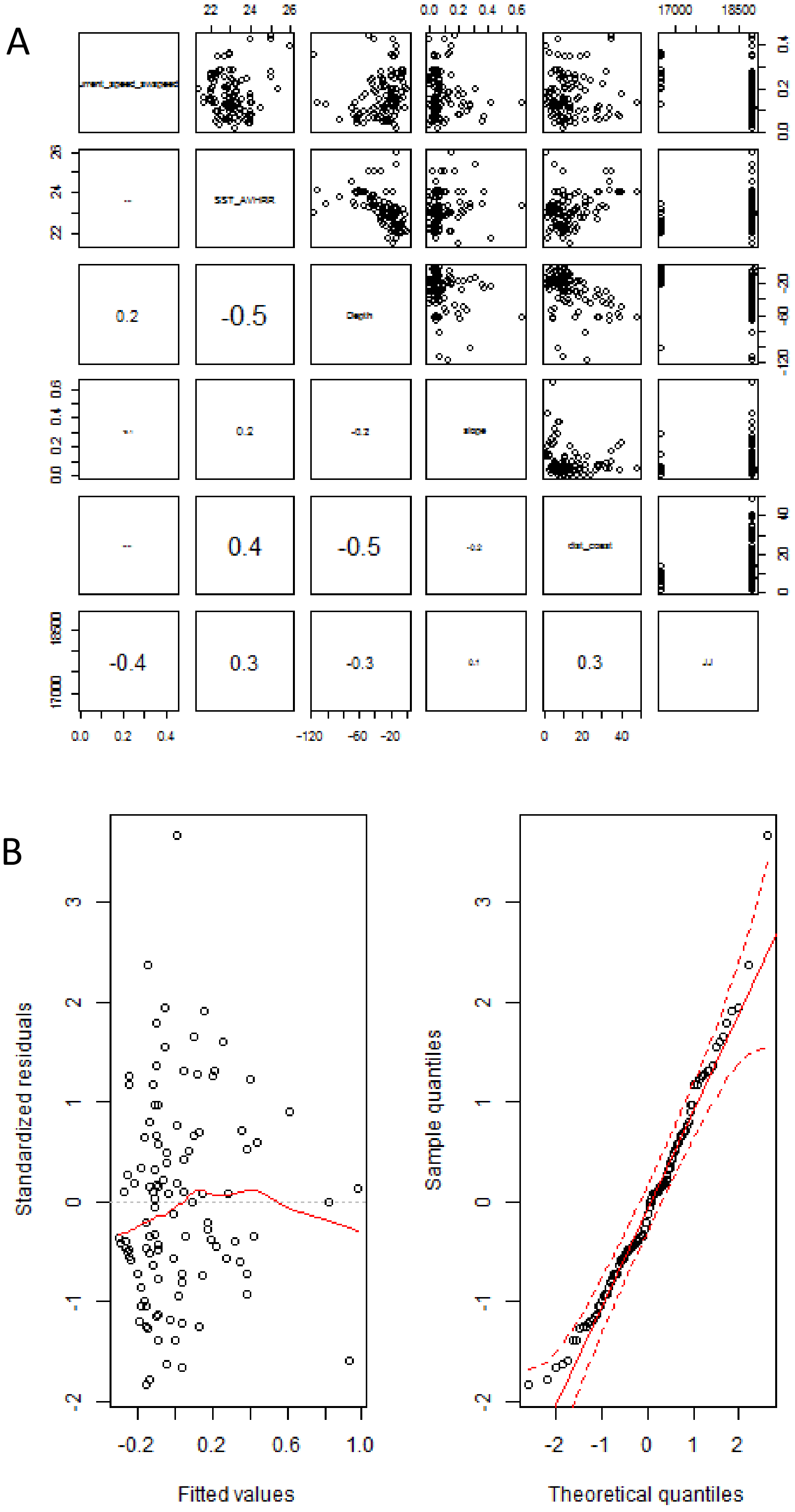
(A) Multi-panel scatterplot for female coastal data (behavioral mode) from BSD-WAC. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE N



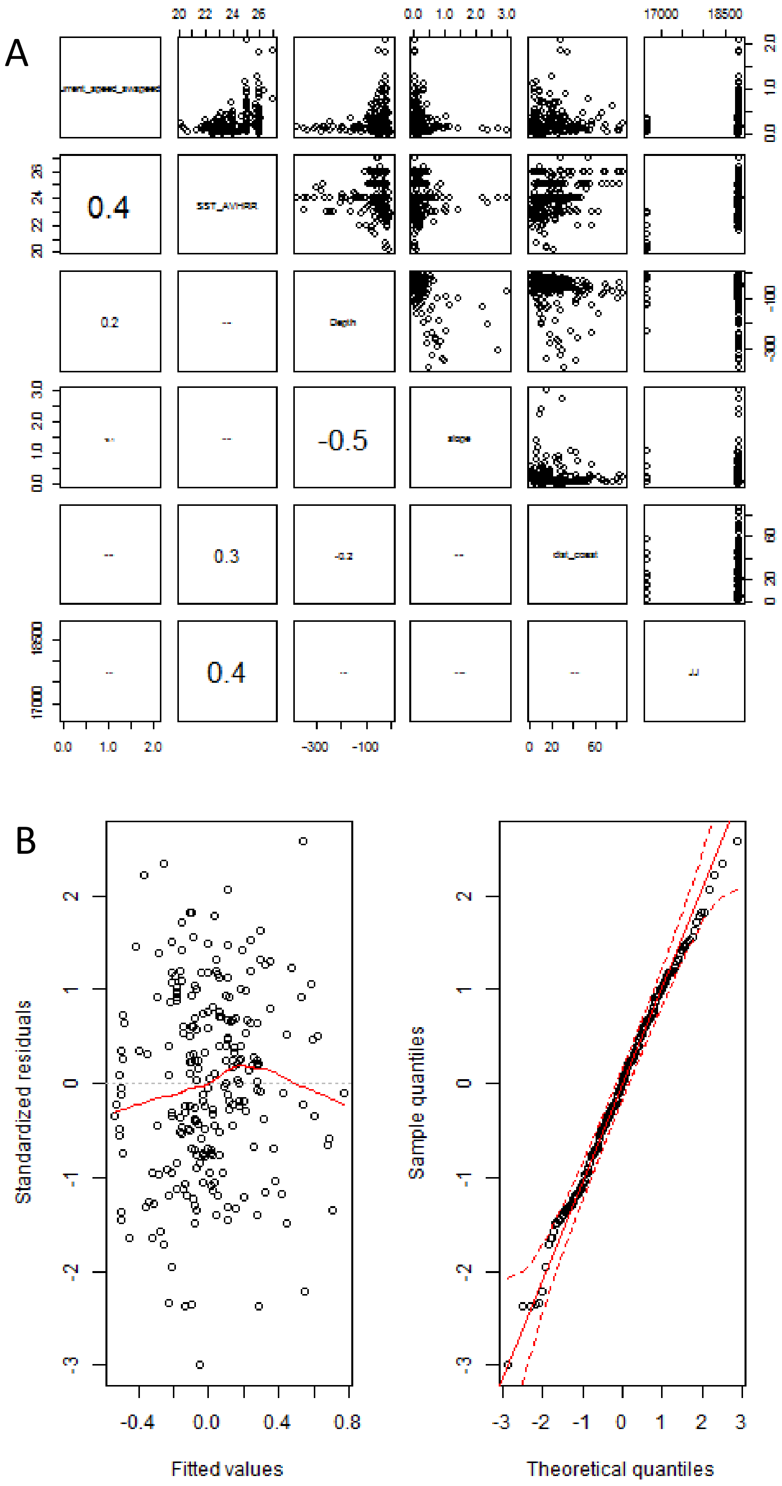
(A) Multi-panel scatterplot for male coastal data (behavioral mode) from BSD-WAC. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE O



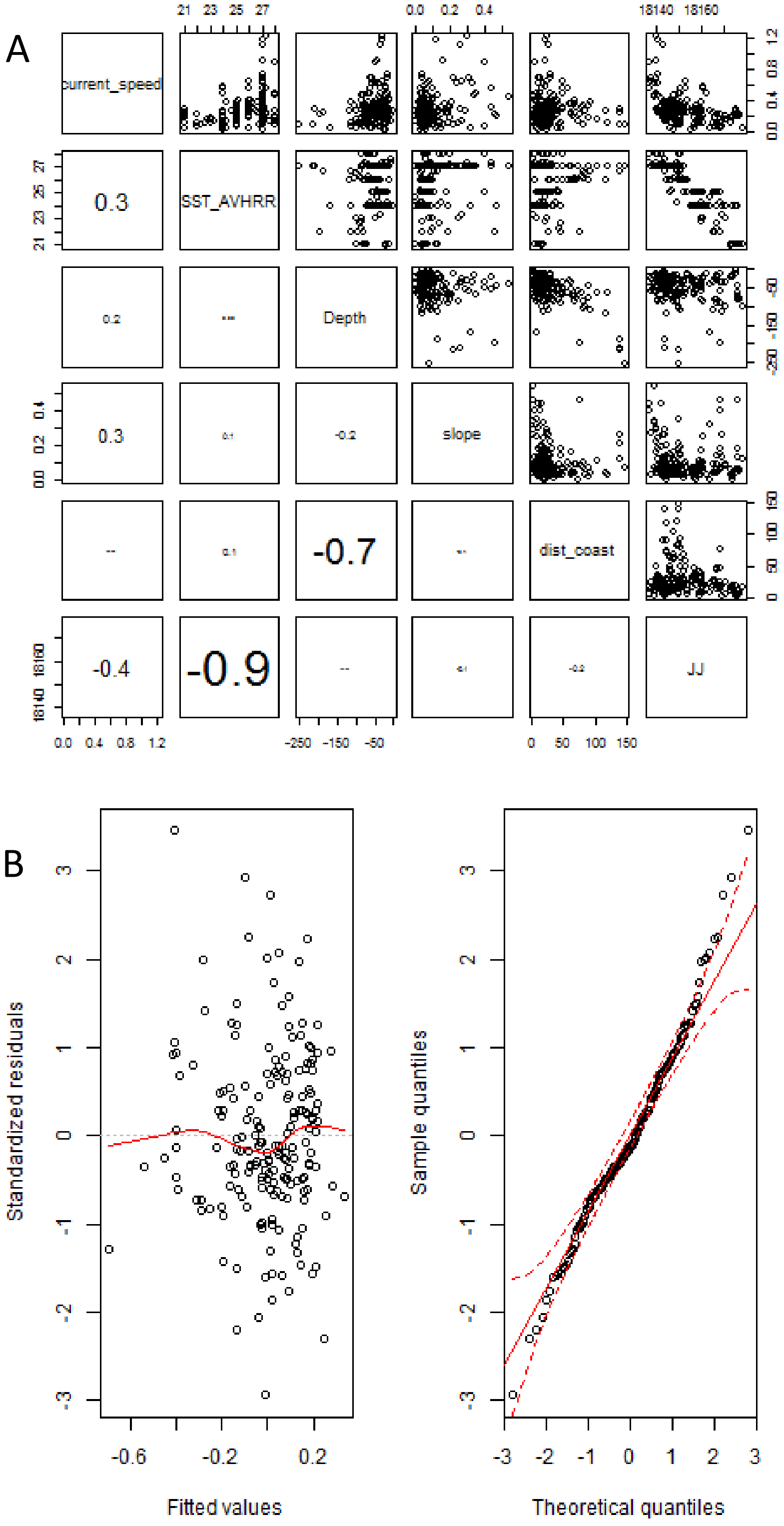
(A) Multi-panel scatterplot for female coastal data (swimming speed) from BSD-WAC. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE P



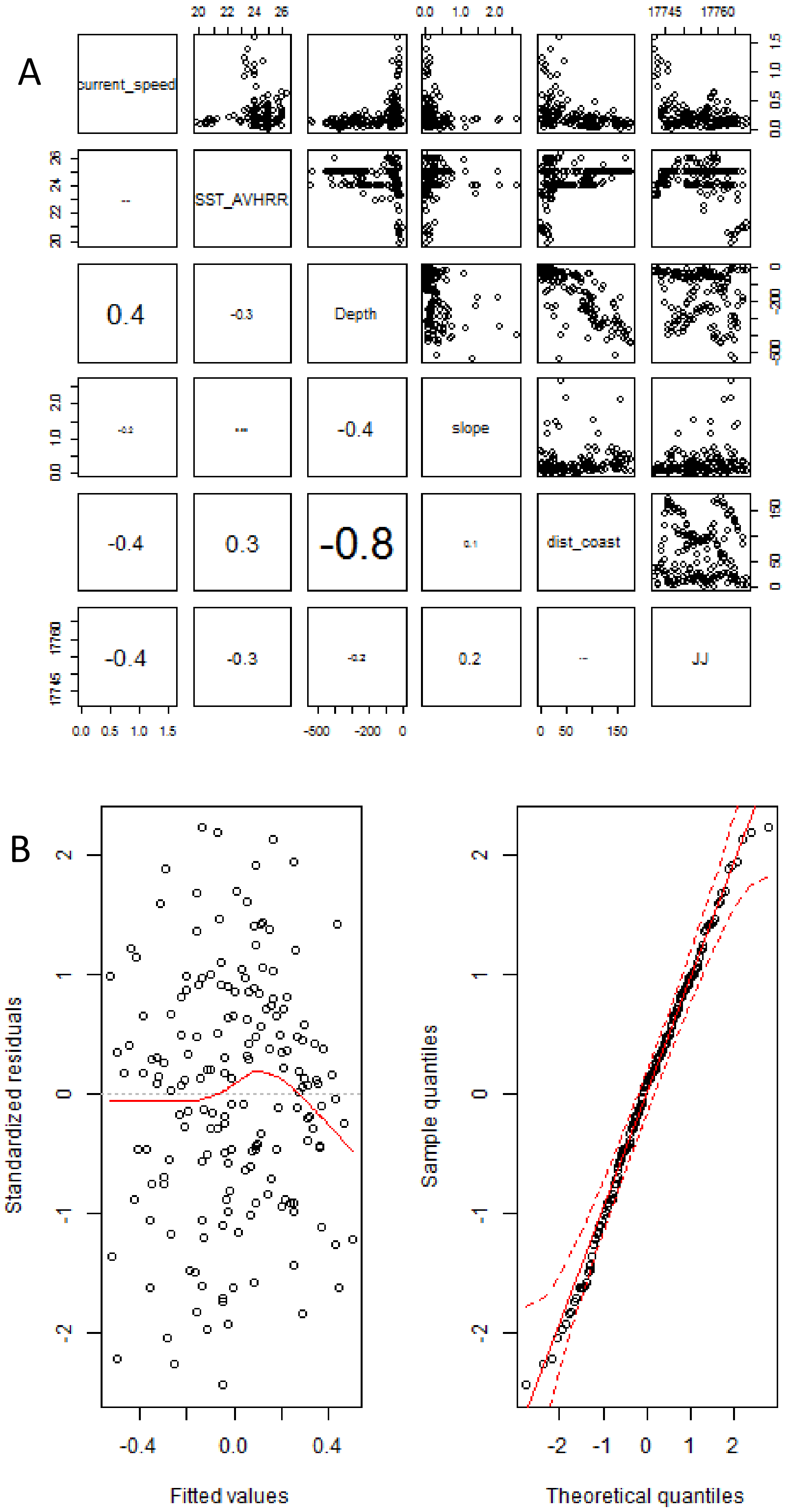
(A) Multi-panel scatterplot for male coastal data (swimming speed) from BSD-WAC. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE Q



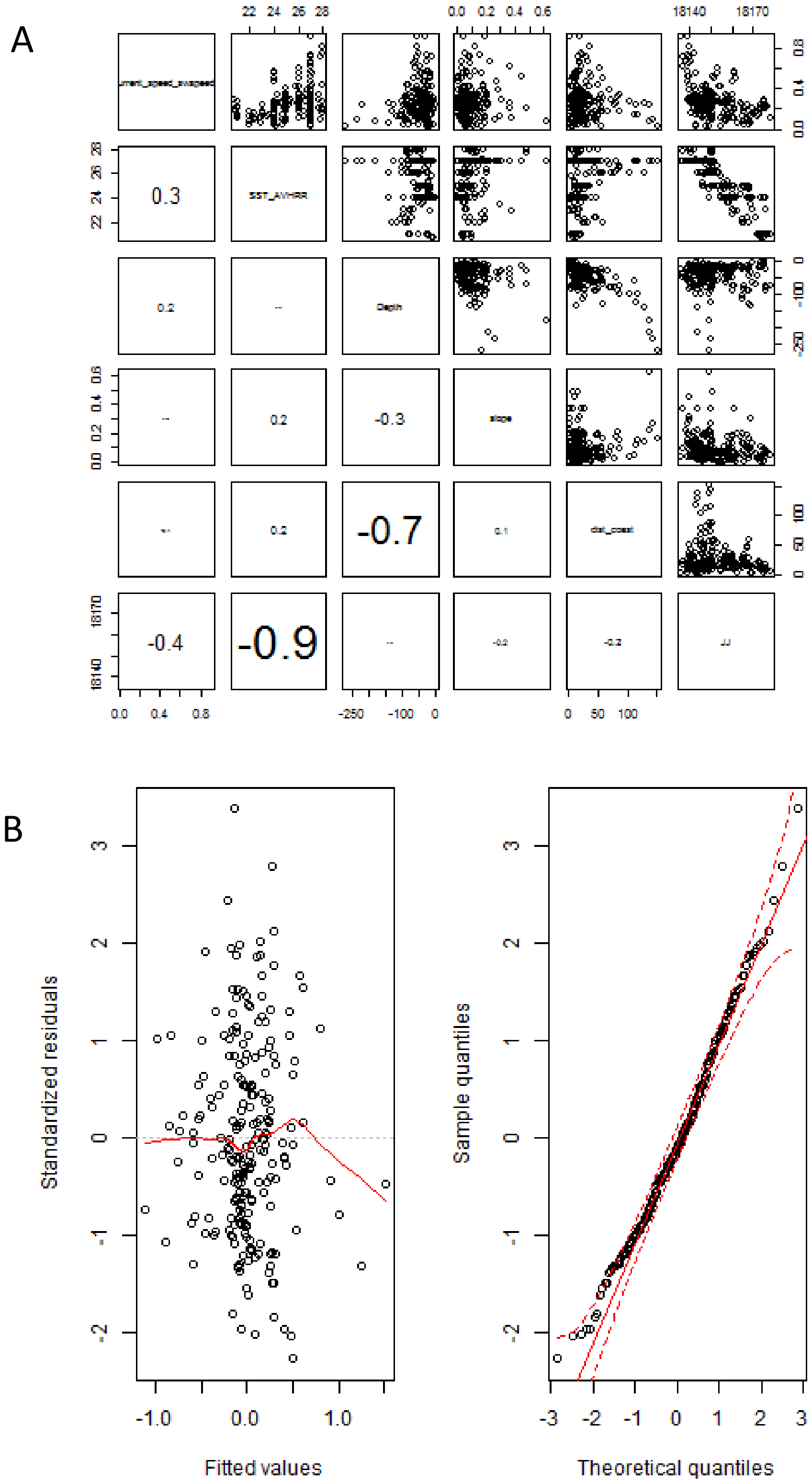
(A) Multi-panel scatterplot for female coastal data (behavioral mode) from BSD-WAK. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE R



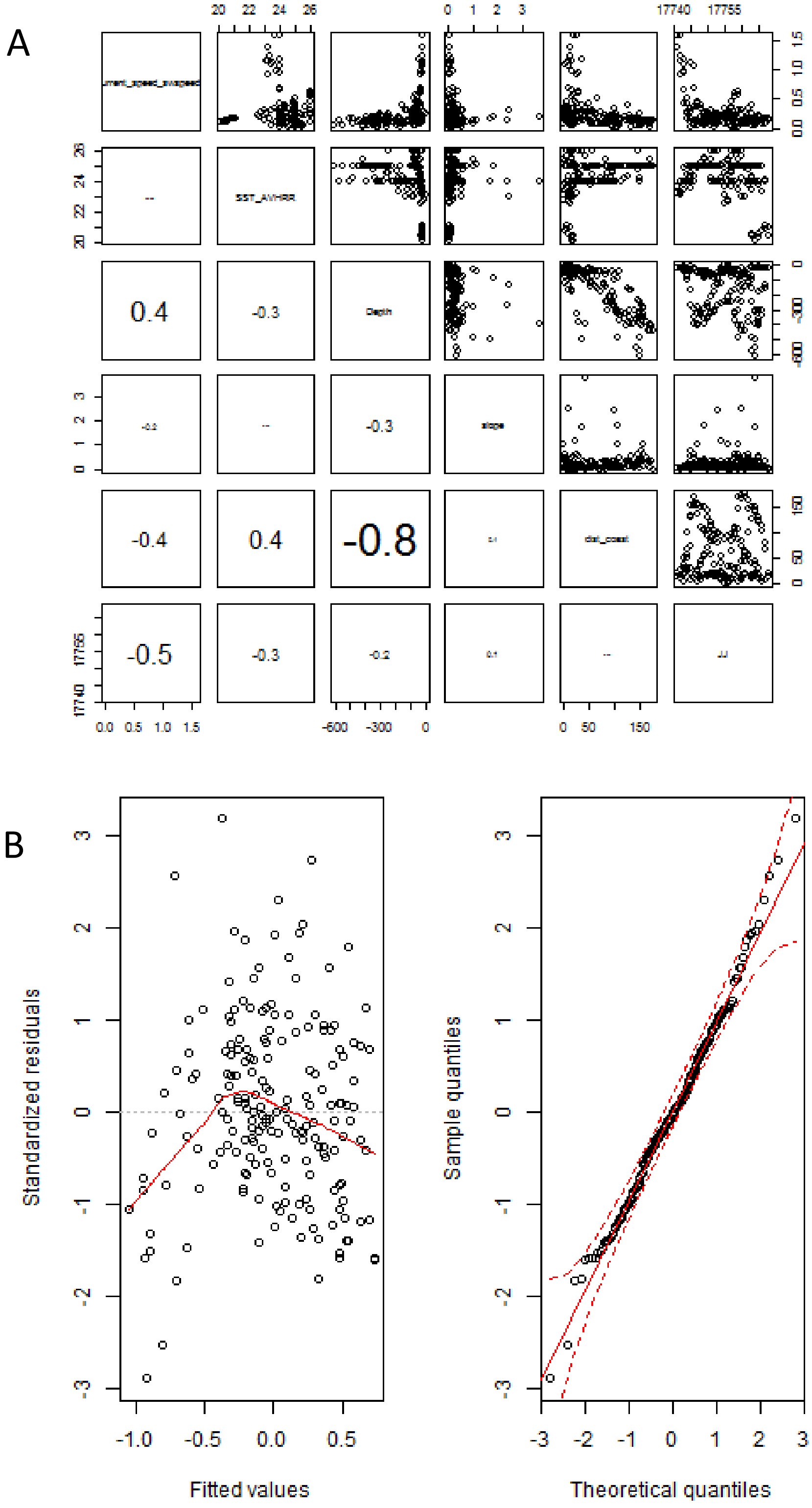
(A) Multi-panel scatterplot for male coastal data (behavioral mode) from BSD-WAK. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE S



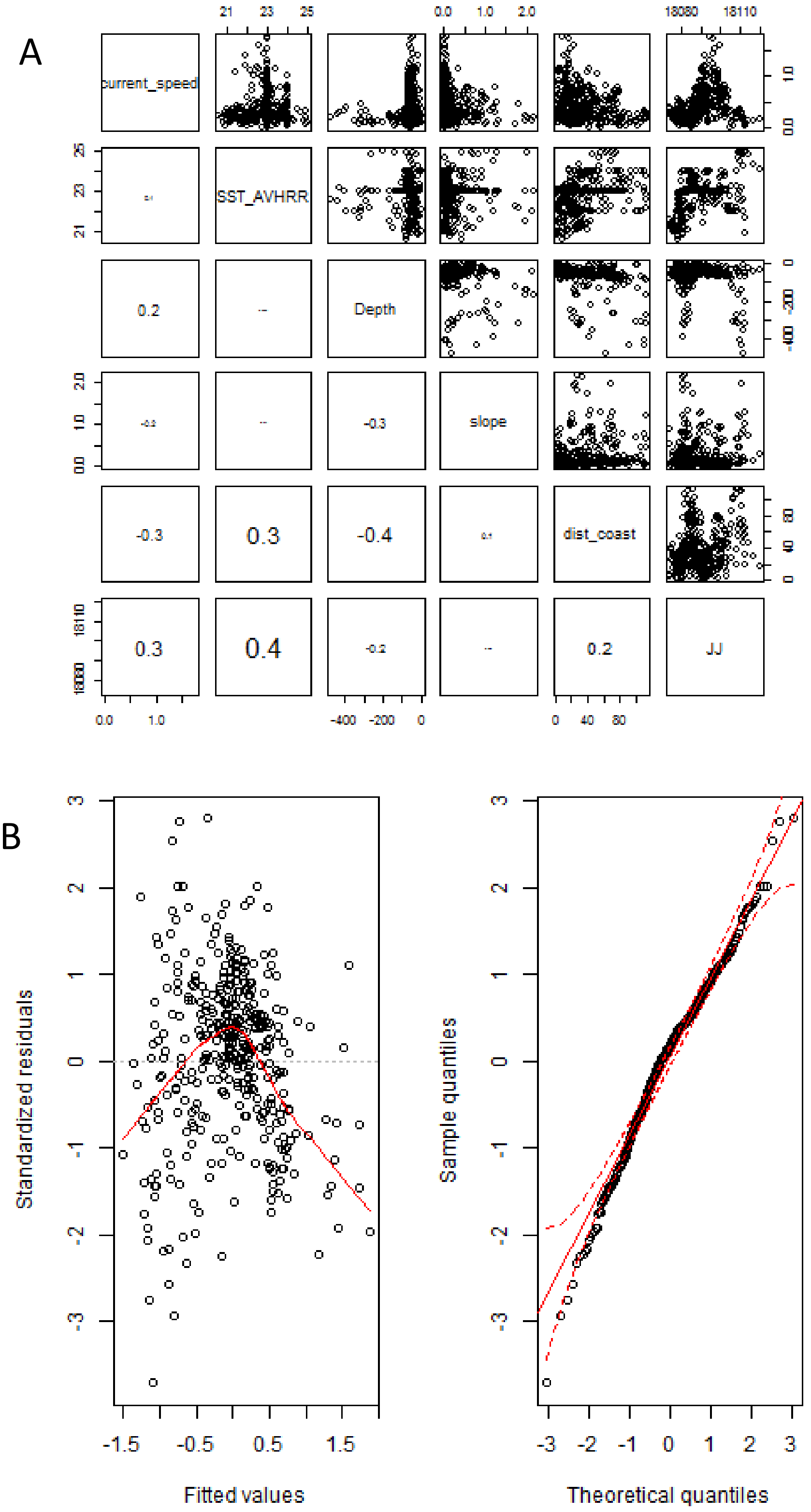
(A) Multi-panel scatterplot for female coastal data (swimming speed) from BSD-WAK. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE T



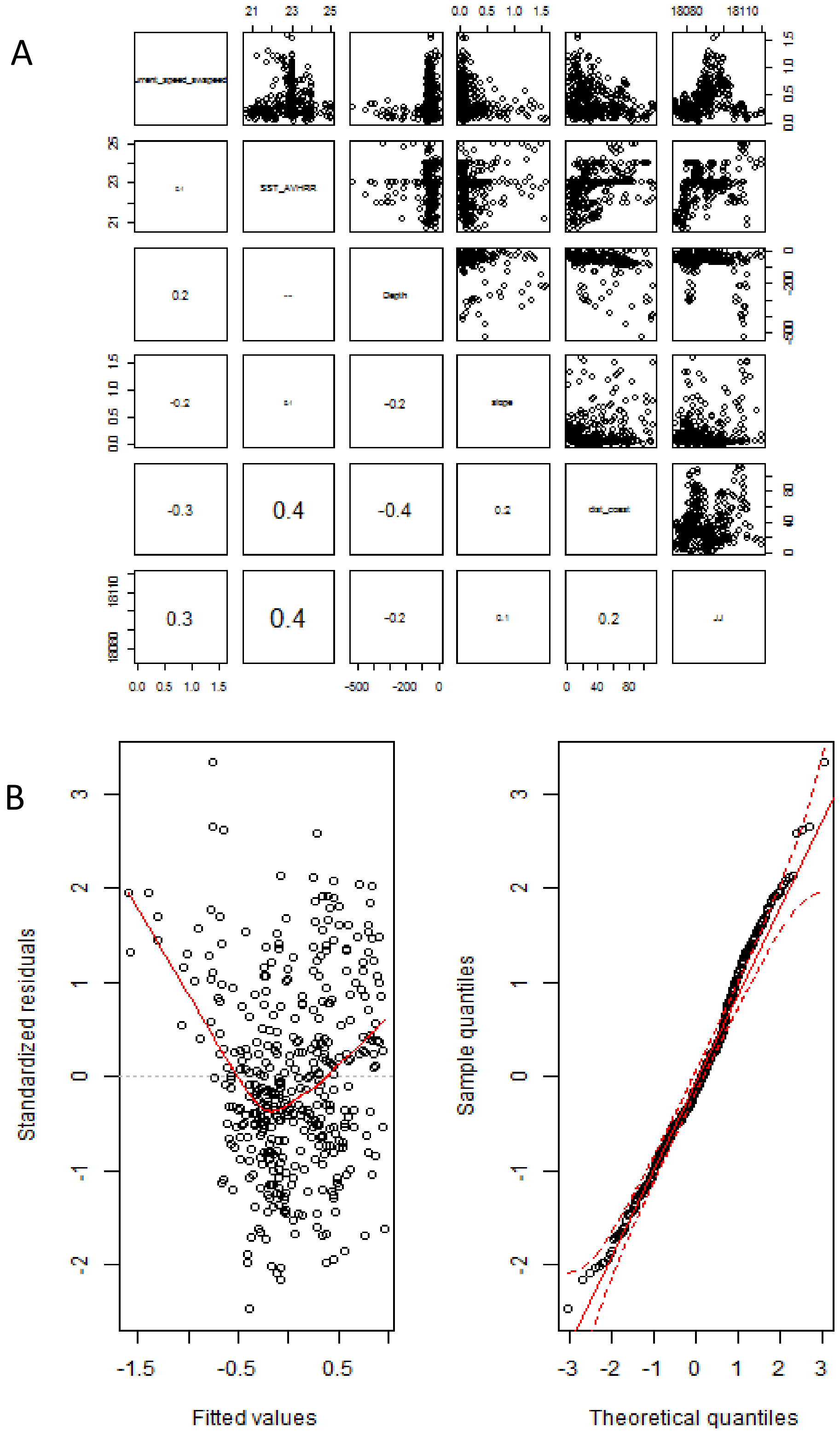
(A) Multi-panel scatterplot for male coastal data (swimming speedode) from BSD-WAK. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower/left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE U



(A) Multi-panel scatterplot for male coastal data (behavioral mode) from BSE1. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

# ANNEXE V



(A) Multi-panel scatterplot for male coastal data (swimming speed) from BSE1. The upper/right panels show pairwise scatterplots between each explanatory variable (current speed, STT, Depth, slope, distance from shore), and the lower⁄left panels contain Pearson correlation coefficients (B) Standard model validation graphs are: residuals versus fitted values to verify homogeneity and (left) and a QQ plot of the residuals for normality (right) of the most parsimonious model (LLM).

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ÉCOLE DOCTORALE
Signalisation
et réseaux intégratifs
en biologie (BIOSIGNE)

# Distribution et préférences d'habitats des baleines à bosse de l'hémisphere Sud en période de reproduction

Mots clés : Baleines à bosses, océan Indien, reproduction, distribution, habitat, télémétrie satellitaire.

L'étude des déplacements des baleines à bosse (*Megaptera novaeangliae)* en relation avec les paramètres environnementaux permet d'apporter des informations précieuses sur leur distribution et leurs préférences d'habitats. Grâce à des données d'observations opportunistes collectées dans le canal de Sainte Marie (Nord-Est de Madagascar) et des données de télémétrie collectées pour cette étude (25 baleines équipées de balises Argos), cette thèse a pour objectif l'étude des déplacements et de l'utilisation de l'habitat des baleines à bosse de Madagascar en fonction du sexe et du statut reproducteur. Des variables physiographiques et océanographiques (mesurées par satelllite) ont été extraites sous chaque position. Un schéma général d'utilisation de l'habitat en période de reproduction a également été proposé à partir de données de télémétrie provenant de différentes zones de reproduction de l'hémisphère Sud: le Brésil (n=81 individus), l'Australie de l'Ouest (n=26) et l'Australie de l'Est (n=11). Dans le canal de Sainte Marie, nos résultats ont montré une ségrégation temporelle d'un mois avec une première partie de saison dominée par les groupes avec baleineaux et une seconde dominée par les groupes sans baleineaux (Chapitre III). La profondeur influence la distribution des groupes sociaux avec une préférence des couples mère-baleineau pour les plus faibles profondeurs (< 20 m). Le long de la côte de Madagascar, les déplacements localisés des femelles sont associés à des habitats plus profonds et plus éloignés de la côte que ce qui avait été supposé (Chapitre IV). En revanche, les mâles ne semblent pas montrer de préférences d'habitats particuliers bien qu'ils diminuent leur vitesse de nage dans les zones peu profondes. En zone océanique, les individus se déplacent de façon plus erratique dans les eaux les moins profondes, de faible courant ou les plus riches en chlorophylle a. La vitesse du courant de surface ne semble pas être un facteur majeur dans le déplacement des baleines à bosse. Cependant, elles semblent suivre la même direction que celui-ci lorsque ce dernier est fort. Notre étude comparative entres les zones de reproduction a montré que la distribution spatiale varie selon la période de la saison, entre les sites étudiés et selon le sexe (Chapitre V). En début et fin de saison, les mâles se déplacent de manière plus directe et exploitent des zones plus au large que les femelles, notamment celles avec baleineau. Au pic de la saison, les mâles et les femelles effectuent des déplacements plus localisés. La prise en compte des différences dans la variabilité spatio-temporelle des mâles et des femelles en zone de reproduction apparait être une nécessité pour mieux comprendre l'écologie des baleines à bosse et contribuer à la conservation de l'espèce.

# Distribution and habitat preferences of Southern Hemisphere humpback whales during the breeding season

Keywords: Humpback whales, Indian Ocean, breeding, distribution, habitat, satellite telemetry.

Of key importance for the comprehension of humpback whales' (Megaptera novaeangliae) distribution patterns and habitat use is to quantify how ecological and environmental factors affect the distribution of animals, which requires knowledge on dispersal movements of individuals. Using an opportunistic sightings dataset collected in the Sainte Marie Channel (Northeast of Madagascar) and satellite telemetry data acquired for this study (25 tagged whales), the aim of this thesis was to study the movements and the habitat use of humpback whales in Madagascar during the breeding season, according to sex and reproductive status. Physiographic and oceanographic variables (measured by satellite) were extracted under each position. A general distribution pattern of habitat use during the breeding season was also proposed based on additional humpback whales tracks from others breeding grounds of the Southern Hemisphere: Brazil (n=81 individuals), the Western Australian coast (n=26), and the Eastern Australian coast (n=11). In the Sainte-Marie Channel, groups without calves dominated the first 30 days of the breeding season, followed by an increase in groups with calves (Chapter III). Water depth influenced the distribution of social groups with mother-calf pairs more frequently found in relatively shallow water (0-20 m). Along the coast of Madagascar, over the shelf, females showed localized behavior in deep water and at large distances from shore suggesting that their breeding habitat extends beyond the shallow coastal waters (Chapter IV). Males' active swimming speed decreased in shallow waters, but we found no influence of environmental parameters on males' movements. In oceanic habitats, both males and females showed localized behaviors in shallow waters and high surface chlorophyll-a concentrations. The active swimming speed accounts for a large proportion of the whale observed speed while observed direction of tagged whales tending to be closer to the current direction when the current intensity was high. Our comparative study between breeding areas showed that the spatial distribution varies according to the period of the season, between the studied sites, sex and breeding status (Chapter V). Early and late in the season, males moved more directly and in more offshore areas than females, especially females with calves. At the peak of the season, both males and females performed more localized movements than at the other periods. Accounting for differences in the spatio-temporal variability of the distribution of males and females in the breeding grounds seems a necessity to better understand the humpback whales ecology and contribute to the species conservation.

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