Distribution of cetaceans and seabirds in tropical oceans : roles of physiographic, oceanographic and biological factors

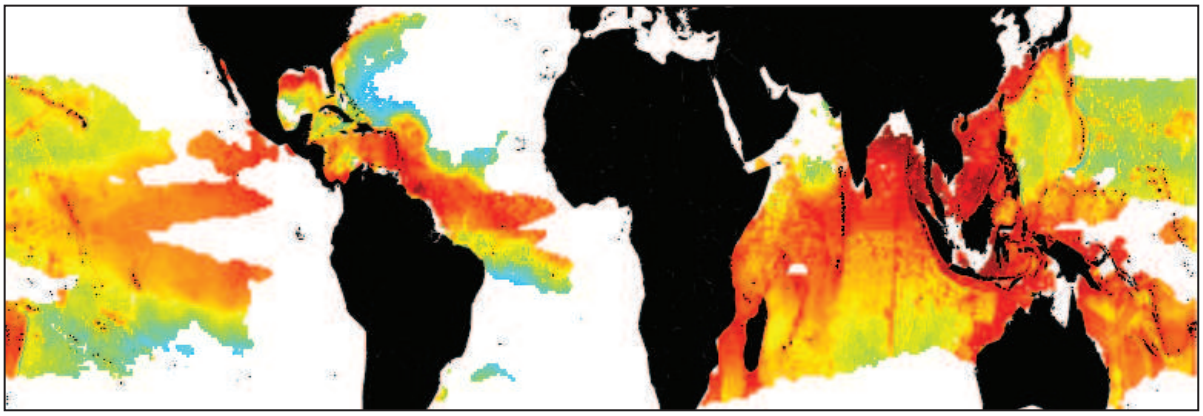
Laura Mannocci

UNIVERSITÉ DE LA ROCHELLE

Ecole Doctorale Sciences pour l'Environnement Gay Lussac

Distribution des cétacés et oiseaux marins dans les océans tropicaux: rôles des facteurs physiographiques, océanographiques et biologiques

Distribution of cetaceans and seabirds in tropical oceans: roles of physiographic, oceanographic and biological factors



Thèse présentée par Laura MANNOCCI

Soutenue le 03 décembre 2013

pour l'obtention du grade de Docteur de l'Université de La Rochelle

Discipline : Biologie de l'environnement, des populations, écologie marine

JURY :

Christophe GUINET	Directeur de Recherche, CEBC Chizé, Président du jury
Lisa BALLANCE	Directrice de recherche, NOAA La Jolla, Rapporteur
Phillip HAMMOND	Professeur, Université de St Andrews, Rapporteur
Vincent RIDOUX	Professeur, Université de La Rochelle, Directeur de thèse
Frédéric MENARD	Directeur de recherche, IRD Sète, Examinateur
Patrick LEHODEY	Chargé de recherche-HDR, CLS Argos Toulouse, Invité
Pascal MONESTIEZ	Directeur de recherche, INRA Avignon, Invité

UNIVERSITÉ DE LA ROCHELLE

ÉCOLE DOCTORALE Gay-Lussac

Littoral, Environnement et SociétéS (LIENSs)
UMR CNRS 7266 / Université de La Rochelle

Distribution des cétacés et oiseaux marins dans les océans tropicaux: rôles des facteurs physiographiques, océanographiques et biologiques

Distribution of cetaceans and seabirds in tropical oceans: roles of physiographic, oceanographic and biological factors

Thèse présentée par Laura MANNOCCI

Soutenue le 03 décembre 2013
pour l'obtention du grade de Docteur de l'Université de La Rochelle
Discipline : Biologie de l'environnement, des populations, écologie marine

JURY :

Christophe GUINET	Directeur de Recherche, CEBC Chizé, Président du jury
Lisa BALLANCE	Directrice de recherche, NOAA La Jolla, Rapporteur
Phillip HAMMOND	Professeur, Université de St Andrews, Rapporteur
Vincent RIDOUX	Professeur, Université de La Rochelle, Directeur de thèse
Frédéric MENARD	Directeur de recherche, IRD Sète, Examinateur
Patrick LEHODEY	Chargé de recherche-HDR, CLS Argos Toulouse, Invité
Pascal MONESTIEZ	Directeur de recherche, INRA Avignon, Invité

Remerciements

Je voudrais d'abord remercier sincèrement Vincent Ridoux pour m'avoir embarquée dans cette histoire un peu folle de guildes et de mers chaudes et pour m'avoir soutenue tout au long de cette aventure. Merci d'avoir toujours cru en moi, surtout quand moi je n'y croyais plus ! Merci de m'avoir fait confiance et de m'avoir donné la chance de travailler sur un tel sujet !

Je voudrais également remercier chaleureusement Pascal Monestiez pour m'avoir fait découvrir le monde des géostatistiques au détour d'un séjour à Avignon. Merci d'avoir répondu patiemment à mes questions et de m'avoir aiguillée dans mes choix méthodologiques tout au long de ma thèse. Merci à l'équipe BioSP pour avoir accueillie une doctorante un peu atypique !

Merci à Christophe Guinet, Frédéric Ménard, Pascal Monestiez et Patrick Lehodey d'avoir accepté de faire partie de mon jury, merci à Lisa Ballance et Phillip Hammond d'avoir accepté d'évaluer cette longue thèse.

Merci à Henri Weimerskirch, Pascal Monestiez, Frédéric Ménard, Patrick Lehodey et Paco Bustamante pour avoir participé aux débats de mon comité de thèse, pour m'avoir conseillée et orientée dans les bonnes directions.

Merci à Patrick pour nous avoir accueillis à CLS Argos et donné l'opportunité d'exploiter son petit bijou de SEAPODYM.

Merci à Henry pour pour m'avoir fait bénéficier de ses connaissances immenses sur l'écologie des oiseaux tropicaux.

Merci à Jean Claude Thibault, Matthieu Le Corre et Sébastien Jaquemet pour leur aide précieuse sur les colonies d'oiseaux.

Merci à Jérome Spitz pour avoir initié l'aventure énergétique et avoir toujours répondu présent pour une discussion en passant dans le couloir !

Merci à Amandine, Maxime et Charlotte pour avoir mis du votre dans cette histoire. Merci Amandine pour ton entrain à placer des colonies d'oiseaux sur des cartes, merci Max

pour ton coté agro et tes fonctions sous R, merci Charlotte pour ta motivation à rechercher des patrons proies-prédateurs !

Merci à Benoit Simon-Bouhet et à Eric Pante, les « Messieurs R du labo », pour avoir accepté de relever les défis numériques que je leur posais !

Merci à Séverine Alvain pour m'avoir donné l'opportunité de travailler sur les sorties de son modèle PHYSAT.

Merci à Géraldine Lassalle, Cédric Cotté et Matthieu Authier pour leurs conseils techniques et statistiques au long de ces trois ans.

Merci à Cécilia Pignon-Mussaud pour sa disponibilité pour répondre à mes questions sur ArcGIS.

Merci à l'Agence des Aires Marines Protégées et au Ministère de l'Ecologie pour m'avoir apporté son soutien financier qui m'a permis de participer à la campagne aérienne en Polynésie, à la conférence de la SMM en Floride et aux workshops Distance Sampling en Ecosse.

Merci à Olivier, Ghislain et Sophie pour m'avoir offert la chance de participer à cette aventure polynésienne qui m'a permis de découvrir la réalité du terrain, les espèces locales et les paysages époustouflants vus de là-haut. Merci Sophie pour ton aide avec Distance Sampling et ArcGIS, merci Olivier pour avoir répondu à mes questions techniques sur les survols et merci Ghislain pour tes apports naturalistes. J'espère avoir fourni un travail à la hauteur du votre pour collecter ces données exceptionnelles !

Cette thèse n'aurait pas pu avoir lieu si toute une armada d'observateurs, de pilotes et de techniciens ne s'était pas investie pour observer et survoler du bleu aux trois coins des tropiques ! Alors merci à vous tous !

Merci à mes deux compagnes de bureau et généticiennes, Marie et Amélia, pour avoir partagé la grotte avec moi, avec ou sans chauffage, avec ou sans ventilateur, avec ou sans possibilité de sortir ! Merci d'avoir crée cette ambiance de travail qui m'a permis de rester concentrée jusqu'à la fin… Merci de vos conseils et de votre soutien jusqu'au bout !

Merci aux anciens doctorants, en particulier Jérôme, Hélène, Paula, Tiphaine, Flore, Matthieu pour m'avoir fait tenir bon et réaliser que c'était possible !

Un merci tout particulier à Emeline, pour son soutien sur les mois de la fin et ses conseils de grande sœur de thèse !

Merci aux companions de LIENSs : Marie, Alice, Aurélie, Céline, David, Méra, Luc, Camille, Thomas, Caio… Merci pour ces moments passés ensemble et les soirées détente de l'été… Plein de courage pour celles et ceux qui sont sur la route de la thèse !

Un merci tout particulier à David pour m'avoir soutenue (et nourrie !) dans les moments durs des dernières semaines !

Merci à toute l'équipe de l'UMS PELAGIS pour son accueil dans les premiers mois de ma thèse, son intérêt à suivre mon travail et sa sympathie depuis mon M2.

Spéciale dédicace à la dream team PELAGIS du rallye, à l'homme dauphin et aux filles à plumes et à fleurs, pour cette après midi à sillonner les rues de La Rochelle qui restera mémorable ! On la tient cette deuxième place !

Retour du coté de la Polynésie et clin d'oeil à tous les observateurs et les pilotes, merci pour cette aventure qui était aussi humaine ! Dédicace à la golden team de Tubai !

Parce qu'il n'y a pas que la thèse dans la vie, merci aux potes de plongée, d'apnée, de planche et de cata pour m'avoir fait oublier un peu tout ça et partager ces activités aquatiques qui me sont chères !

Je voudrais enfin remercier de tout cœur ma famille pour m'avoir encouragée depuis le début à poursuivre ce rêve fou… Merci pour votre soutien tout au long de mes études.

Le mot de la fin est pour toi, Olivier, merci d'avoir toujours cru en moi depuis la prépa, merci pour tous ces moments d'évasion des Highlands à Telegraph Cove, du Montana au Mercantour, de la Corsica Nazione à Plitvitce, qui m'ont permis de faire le plein d'énergie tout au long de ces trois ans.

Table of contents

Foreword

This work came into existence with the REMMOA (*Recensement des mammifères marins et autres mégafaunes pélagiques par observation aérienne*) aerial surveys for the census of pelagic megafauna, funded by the French Agency for Marine Protected Areas (*Agence des Aires Marines Protégées*, AAMP) and the French Ministry for Ecology, Sustainable Development and Energy (*Ministère de l'Ecologie, du Développement Durable et de l'Energie*, MEDDE). The REMMOA surveys were implemented by the *PELAGIS* Observatory, the joint service unit of CNRS and University of La Rochelle dedicated to monitoring seabird and marine mammal populations in French waters and maintaining the corresponding data base system. The present work would have been impossible to conduct without the financial support of AAMP and MEDDE and the investment of many people, from survey preparation, to on-board observation and data cleaning. The general aims of the REMMOA surveys, as defined by AAMP, were to provide public marine conservation agencies with standardized background information on pelagic top predator distribution throughout all tropical regions of the French Exclusive Economic Zone in order to inform their management and monitoring policies. The present research proposes to go beyond this applied framework and the technical reports prepared for AAMP, and therefore to analyze these data in a more general framework of fundamental ecology.

Publications and international conferences

Peer-reviewed articles presented in the dissertation

Mannocci, L, Monestiez, P, Bolaños-Jiménez, J, Dorémus, G, Jeremie, S, Laran, S, Rinaldi, R, Van Canneyt, O, Ridoux, V (2013). Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic. *Journal of Marine Systems* 111–112: 208–222

Mannocci, L, Laran, S, Monestiez, P, Dorémus, G, Van Canneyt, O, Watremez, P, Ridoux,V (2013). Predicting top predator habitats in the Southwest Indian Ocean. *Ecography* 36: 001–018.

Mannocci, L, Catalogna, M, Dorémus, G, Laran, S, Massart, W, Monestiez, P, Van Canneyt, O, Watremez, P, Ridoux, V. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre. In revision in *Progress in Oceanography*.

Lambert, C, **Mannocci, L**, Lehodey, P, Ridoux, V. Predicting cetacean habitats from their energetic needs and the distributions of their prey in two contrasted tropical regions. To be submitted to *Marine Ecology Progress Series*.

Mannocci, L, Monestiez, P, Spitz, J, Ridoux V. Generic relationships of cetaceans with the quality of their habitats in tropical oceans. In preparation.

Other peer-reviewed articles

Mannocci, L, Dabin, W, Augeraud-Véron, E, Dupuy, J-F, Barbraud, C, Ridoux, V (2012). Assessing the impact of bycatch on dolphin populations: the case of the common dolphin in the eastern North Atlantic. PLoS ONE 7(2): e32615. doi:10.1371/journal.pone.0032615.

International conferences

Mannocci, L, Dorémus, G, Laran, S, Spitz, J, Van Canneyt, O, Ridoux, V. Do odontocetes with higher energy requirements select more productive habitats? A comparative study in the Southwest tropical Indian Ocean. Poster presentation. *19th Biennial Conference on the Biology of Marine Mammals*, November 27-December 2, 2011, Tampa (Florida).

Mannocci, L, Dabin, W, Augeraud-Véron, E, Dupuy, JF, Barbraud, C, Ridoux, V. Assessing the impact of bycatch on common dolphin in the eastern North Atlantic. Poster presentation. *25th Annual Conference of the European Cetacean Society*, March 21-23, 2011, Cadiz (Spain).

List of abbreviations

ANN: Artificial neural network

BMR: Basal metabolic rate

CARS: CSIRO Atlas of Regional Seas

CCA: Canonical correspondence analysis

CHL: Chlorophyll concentration

CSP: Central South Pacific

DVM: Diel vertical migration

EACC: East African coast current

EEZ: Exclusive economic zone

ENFA: Ecological niche factor analysis

ENSO: El niño Southern oscillation

ETP: Eastern tropical Pacific

ESW: Effective strip width

FMR: Field metabolic rate

FP: French Polynesia

GAM: Generalized additive model

GEBCO: General physiographic chart of the ocean

GLM: Generalized linear model

GOM: Gulf of Mexico

MaxEnt: Maximum entropy

MPA: Marine protected area

NBC: North Brazilian current

NEC: North Equatorial current

NECC: North Equatorial countercurrent

NEMC: Northeast Madagascar current

NPP: Net primary production

OFT: Optimal foraging theory

ROMS: Regional ocean model system

SC: Somali Current

SCANS: Small cetacean abundance in the North Sea

SDM: Species distribution model

SE: Southeast United States

SEAPODYM: Spatial Environmental population dynamics model

SEC: South Equatorial current

SECC: South Equatorial counter current

SEMC: Southeast Madagascar current

SLA: Sea level anomaly

SST: Sea surface temperature

STCC: Subtropical countercurrent

SWIO: Southwest Indian Ocean

WTA: Western tropical Atlantic

Chapter I. General introduction

Photo credit: Olivier Van Canneyt

1) Top predators in the marine environment

a) Occupying the top of pelagic food webs

Marine top predators, also named apex predators, are large marine vertebrates which occupy the highest trophic levels of pelagic food webs, representing the end point of energy and material fluxes (Estes et al. 2001). They include marine mammals, seabirds, large teleosts and sharks. Top predators inhabit pelagic waters where food is patchily distributed (Ashmole 1971, Platt 1972) and spatio-temporal variability is large (Richardson and Poloczanska 2008). In this challenging environment, they need to develop optimal strategies of resources and habitats utilization to optimize their foraging success. Yet, it is expected that the optimization of foraging success represents a strong selection pressure on these organisms. Minimizing predation risk, the other selection pressure, is probably a lower pressure for the vast majority of top predators (Pimm et al. 1991). However, it must not be ignored for cetaceans in waters inhabited by super-predators such as sharks and killer whales (Heithaus and Dill 2006), and in the presence of vulnerable individuals (calves, wounded animals) (Jefferson et al. 1991). Nevertheless, the optimization of foraging success seems a crucial driving force of strategies of resources and habitats utilization by top predators.

b) The hierarchical structure of the marine environment

If optimization of foraging success is the principal force driving habitat selection, top predators are expected to follow the spatial distribution of their prey (Morris 1987). Top predators forage at mid-trophic levels, most often on small schooling pelagic fish, cephalopods and crustaceans (micronekton), which represent a critical link between plankton and higher-trophic levels. The marine environment is characterized by a hierarchical structure where prey patches at small spatial scales are nested within larger patches (Russell et al. 1992, Fauchald et al. 2000, Fauchald 2009). For example, Murphy et al. (1988) highlighted different levels of aggregation in krill distribution. It is first congregated in swarms at a scale of 10s of meters; swarms are congregated in patches at a scale of kilometers, and patches are then congregated into concentrations over 100s of kilometers. To forage successfully, top predators must respond to the complex heterogeneity of their environment at a range of spatial scales (Russell et al. 1992, Fauchald et al. 2000, Fritz et al. 2003, Fauchald and Tveraa 2006).

Abundance of prey in a given water mass may result from both local production (through primary and subsequent secondary production), or from the concentration of organisms produced elsewhere (Hunt et al. 1999). Vertical gradients of temperature affect the structure of the water column; this results in an important discontinuity (the thermocline). Typically, a well-lit and nutrient-poor upper layer lies above a poorly-lit and nutrient-rich deeper layer. Primary production requires both light and nutrients. It is thus largely conditioned by hydrodynamic processes such as eddies and upwellings which bring up nutrients to the euphotic layer (Longhurst and Pauly 1987).

Hunt and Schneider (1987) identified hydrodynamic processes at five nested spatial scales: the mega scale (>3000 km), the macro scale (1000-3000 km), the meso scale (100-1000 km), the coarse scale (1-100 km) and the fine scale (1 m to 100s of m) (Figure I-1). Increasing spatial scales are associated with increasing time scales. Large-scale features change over fairly long time scales and are more predictable compared to the ephemeral small scale features. Top predator distributions mirror hydrodynamic processes at this range of scales of organization.

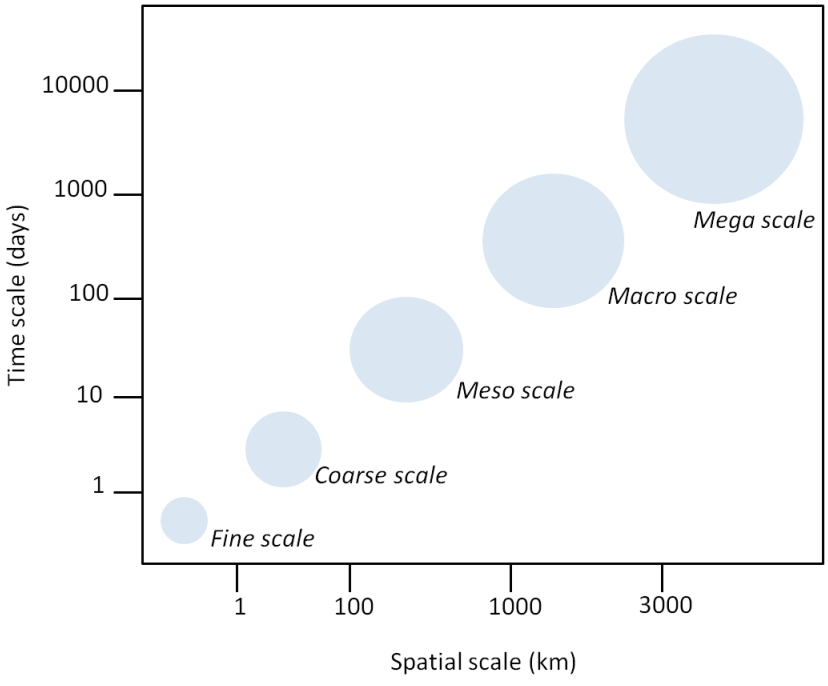


Figure I-1: Time-space plot representing the hierarchical structure of the marine environment. At-sea surveys are used to study top predators associations with oceanographic processes at the mega, macro and meso scales, telemetry is mostly used to relate predator to meso and coarse scale features, while direct observations can be relevant at the fine scale.

Distinct data collection methods can be used to highlight these scale-specific associations. At-sea surveys (either ship-based or airborne), when conducted over broad spatial domains, are useful for studying predator associations with features at the mega (Sydeman et al. 2010), macro (Ballance et al. 1997) and meso scales (Davis et al. 2002). Telemetry is relevant for demonstrating predator dependence on hydrodynamic features at the meso and coarse scales (Weimerskirch et al. 2004). When environmental measurements are acquired *in vivo* by instrumented animals, their associations with fine-scale features can be demonstrated (Xing et al. 2012). Alternatively, direct observations are relevant for the identification of predator responses to fine-scale features (Ridoux 1987).

At the mega scale, top predator distributions reflect biogeographic domains. For example, Reygondeau et al. (2011) partitioned tunas and billfishes across the global ocean into well-defined communities corresponding to Longhurst's biogeochemical provinces (Longhurst 2007). Hyrenbach et al. (2007) studied seabird communities along an extensive productivity gradient in the Southern Indian Ocean. Pursuit divers and divers were more abundant in the sub-Antarctic domain, whereas plunge divers dominated in subtropical waters.

At the macro scale, top predators associate with specific water masses. In the eastern tropical Pacific (ETP), spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) occurred predominantly in the countercurrent ridge, whereas common dolphins (*Delphinus spp*) were mostly associated with the Costa Rica Dome. The position of the thermocline closer to the surface makes both regions distinct biological habitats for top predators (Ballance et al. 2006). Seabirds also showed specific associations with water masses in the ETP. Piscivorous seabirds were associated with deep and strong thermoclines, while planktivorous preferred water masses characterized by weak and shallow thermoclines and cooler surface temperatures (Vilchis et al. 2006).

At the meso scale, top predators are known to track features such as eddies. Eddies are large (often hundreds of kilometers in diameter) and long-lived (from weeks to months) features of the world's oceans. They enhance primary production by bringing up nutrients in the euphotic layer (Oschlies and Garçon 1998, Vaillancourt et al. 2003), and concentrate mesopelagic organisms (Olson and Backus 1985). This fertilizing effect is especially important in the relatively unproductive tropical waters (McGillicuddy et al. 1998, Oschlies and Garçon 1998). For example, in the Mozambique Channel, frigatebirds and tunas foraged

at the periphery of mesoscale eddies (Weimerskirch et al. 2004, TewKai and Marsac 2010), where micronekton is known to aggregate (Sabarros et al. 2009).

At the coarse scale, top predators associate with frontal systems. For example, in the Bering Sea, short-tailed albatrosses (*Phoebastria albatrus*) were closely associated with fronts occurring at the edge of the continental shelf, a highly productive habitat also referred to as the "Green Belt" (Piatt et al. 2006). Intensive tidal mixing, as well as transverse circulation and eddies bring up nutrients into the euphotic zone, enhancing primary and secondary production. Fishes and squids respond to these favorable feeding conditions, and the abundance of prey species in turn attracts large numbers of seabirds and marine mammals (Springer et al. 1996).

At the fine scale, top predators associate with local and short-lived processes such as Langmuir circulation cells. Langmuir circulation develops when wind blows steadily over the sea surface, causing the formation of vortices rotating in opposite directions and parallel to the wind. Langmuir cells are known to concentrate materials, including phytoplankton (Evans and Taylor 1980). For instance, around the Aleutian Islands, the surface feeding fulmars were associated with Langmuir cells (Ladd et al. 2005).

c) Multi-scale foraging strategies

Top predators have developed multi-scale strategies to forage in the hierarchical marine environment (Fauchald et al. 2000). They demonstrate a hierarchy of decisions, decreasing in scale from foraging area selection to prey selection. A predator first searches for large-scale patches by travelling long distances with a low turning frequency. Once within a large-scale patch, it searches for smaller patches by increasing its turning rate and reducing its travel distances (Fauchald 1999, Fauchald et al. 2000). This has been described as area-restricted search (ARS) (Fauchald and Tveraa 2003). Pinaud and Weimerskirch (2005) studied the habitat selection in a long-ranging central place forager, the yellow-nosed albatross (*Thalassarche carteri*) (Figure I-2). Birds leaved their colony with a particular direction to reach the predictable and productive large-scale features of the Agulhas current. Once there, they exhibited an ARS behavior around the productive cyclonic eddies to locate prey aggregations. At each spatial scale, seabirds seem to cope with the heterogeneity of their environment by using a specific type of movement (Weimerskirch 2007).

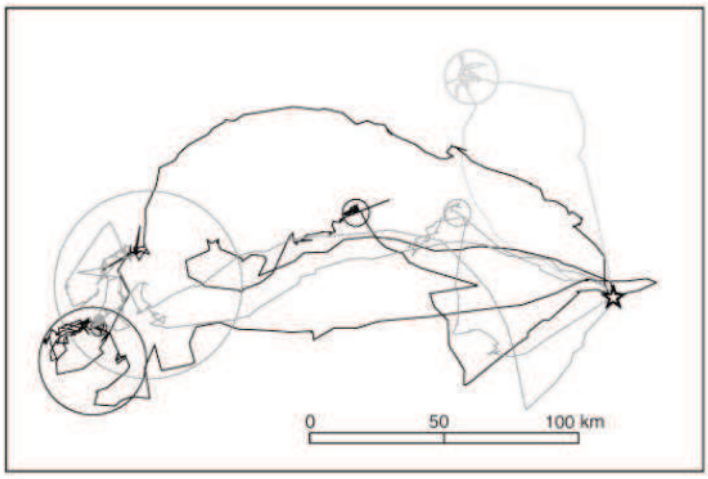


Figure I-2: Foraging trips of five albatrosses from their colony, from Pinaud and Weimerskirch 2005. The circles highlight the areas where birds adopted an ARS behavior.

At the largest spatial scales, especially the mega and macro scale, top predator distributions primarily reflect the physical features of the environment (Hunt and Schneider 1987). Because large-scale physical features are more predictable, learning probably plays an important role in the selection of general foraging areas (Bonadonna et al. 2001, Davoren et al. 2003a, Hunt et al. 1999). At the fine and coarse scales, top predator distributions are mainly controlled by the interplay of social interaction and foraging behavior (Hunt and Schneider 1987). For seabirds, the observation of sub-surface predators (Au and Pitman 1986), as well as the observation of foraging activities of congeners (local enhancement, Davoren et al., 2003a), are efficient ways of locating resource patches. In addition, through the use of echolocation, toothed cetaceans can obtain an assessment of prey patches in their neighboring environment (Au 2009). Consequently, spatial patterns of top predators appear to be formed by the interaction of environmental, ecological and behavioral factors, operating at specific spatial and temporal scales (Fauchald 2009).

When it comes to prey selection and capture within a patch, patch and prey characteristics become essential. Notably, the depth of the patch and local density of prey within a patch are important cues for the perception of resource profitability (Benoit-Bird et al. 2013). Information on prey becomes critical if we want to shift from studies correlating top predator distributions with their environment to studies examining more causal relationships at the origin of the observed patterns.

2) From food quality to habitat quality

a) The optimal foraging theory

A central principle of the optimal foraging theory (MacArthur and Pianka 1966, Pyke et al. 1977) is that foraging behavior has been shaped by natural selection in a way that individuals tend to maximize their fitness. According to this theory, a predator has to maximize the energy gained from prey acquisition, while minimizing the energy spent in searching for the prey. Thus, the optimal strategy at the individual level should be to locate and exploit the prey patches with the highest net energetic return from foraging (Kenney et al. 2001). Since the foraging theory is behind strategies of resources selection (Boyce and McDonald 1999), it is important to study these strategies in light of the costs and benefits for the predator.

b) The importance of food quality

Recently, studies have highlighted the importance of food quality in the diet of some marine predators. A bioenergetic model, combining information on prey distribution and characteristics in the field and energetic needs of spinner dolphins, predicted that they should forage on large prey items of high energy density to meet their energetic needs (Benoit-Bird 2004). Similarly, a diet study showed that common dolphins (*Delphinus delphis*) selected high energy density prey to meet their energetically expensive life style, while ignoring abundant but poorly energetic prey species (Spitz et al. 2010). Indeed, food quality (in terms of energy density) can be a crucial factor for top predators, influencing their demography and population dynamics (Österblom et al. 2008). In the Gulf of Alaska, a shift from high-lipid to low-lipid prey in the diet of Steller sea lions (*Eumetopias jubatus*) was suggested to have led to a dramatic decline of the population (Trites and Donnelly 2003). This has been referred to the junk-food hypothesis (Rosen and Trites 2000). Other studies provided further evidence of this phenomenon in the North Sea, the switch to less energy rich prey species, linked to complex modifications of the food web, has led to drastic breeding failures in seabirds (Wanless et al. 2005, 2007) and perhaps displacement of marine mammals (Hammond et al. 2013). However, all top predators do not have the same sensitivity to the quality of their food; species characterized by high energetic costs of foraging appear to be the most sensitive (Furness and Tasker 2000, Österblom et al. 2008).

c) Energetic costs of living may govern strategies of resources selection

Spitz et al. (2012) investigated the quality of the diets of cetaceans in the Northeast Atlantic in relation to their metabolic costs of living, estimated from indicators of muscle performance (muscle mitochondrial density and lipid content). The metabolic cost of living represents the energy needed to fulfill the daily requirements of an organism. The authors found that costs of living governed prey selection with respect to their quality. The common dolphin (*Delphinus delphis*) and harbor porpoise (*Phocoena phocoena*) had high costs of living and fed on high quality prey. Conversely, the sperm whale (*Physeter macrocephalus*), pygmy sperm whale (*Kogia breviceps*) and Cuvier's beaked whale (*Ziphius cavirostris*) had the lowest costs of living and were characterized by a low quality diet. It follows that cetaceans with high costs of living may be constrained to target high quality prey to sustain themselves, while less active cetaceans may meet their needs by feeding on low quality prey. This seems consistent with the predicted tradeoff between the cost of prey capture and the benefit of prey acquisition, ultimately determining the fitness of the predator (MacArthur and Pianka 1966, Pyke et al. 1977).

d) Energetic costs of living may govern strategies of habitats utilization

We can postulate that the optimal foraging theory underlies predator strategies of habitats utilization. Hence, strategies of resources selection at the individual scale can be extrapolated to strategies of habitats utilization. Similarly, the costs of living of predators may govern their strategies of habitats utilization and they should distribute themselves among habitats with respect to their quality. Energetically costly predators may be constrained to select the highest quality habitats to meet their high energetic requirements, whereas less active predators would be able to satisfy their needs by exploiting either high or low quality habitats.

The idea that energetic constraints may shape the utilization of habitats is not new. It was first noted by Ainley (1977) for seabirds across the Pacific, where the habitats of polar and tropical communities reflected their feeding methods and flight characteristics. It is now well known that diving seabirds with an expensive foraging strategy are absent from the oligotrophic tropical waters, where surface feeding seabirds, characterized by a more economical foraging strategy, dominate (Smith and Hyrenbach 2003, Hyrenbach et al. 2007). Similarly, otariids, which have an expensive foraging strategy, are found in highly productive

regions whereas the less energy demanding phocids also inhabit low productivity areas (Costa 1993). In the ETP, Ballance et al. (1997) showed that seabirds were structured along a productivity gradient according to their costs of flight. Red footed boobies (*Sula sula*) and masked boobies (*Sula dactylatra*), with high costs of flight, occupied the highest quality habitats, whereas sooty terns (*Sterna fuscata*), with more economical flights, occupied the lowest quality habitats (*i.e.* with low primary productivity). This phenomenon was also documented in terrestrial systems. Mueller and Diamond (2001) studied five species of mice originating from very different habitats and noticed a correlation between their metabolic rates and the primary production of their habitats, high metabolism mice occupying the most productive habitats.

In order to investigate top predator strategies of habitats utilization with respect to their costs of living, the next step is to find relevant descriptors of habitat quality.

3) Describing habitat quality in the marine environment

Habitat can be defined as the set of environments meeting a species' ecological requirements and tolerances (Looijen 1995). Here, we are interested in pelagic habitats from the meso to the mega scales, which are appropriate when collecting top predator data from at-sea surveys (Figure I-1). Ultimately, habitat quality may be seen as the ability of the environment to provide suitable conditions for the survival, reproduction and persistence of the study population (Block and Brennan 1993).

a) Distal *versus* proximal descriptors of habitat quality

Following Austin (2002), we can distinguish distal and proximal descriptors of habitat quality according to their position in the chain of processes from the descriptor to its impact on predators. The most proximal descriptor of habitat quality would be the most directly causal. In the case of marine predators, the abundance of mid-trophic level organisms is a proximal descriptor of habitat quality. Prey fields are very difficult to document over extensive stretches of oceans. However, since prey availability is conditioned by a series of biogeochemical and physical processes that promote primary production and the concentration of organisms (Hunt et al. 1999), a description of these features is useful for

characterizing habitat quality. In contrast to mid-trophic levels, the biomass of lower-trophic levels is readily available from satellite measures of ocean color. Primary production is stimulated by dynamic features such as mesoscale eddies, fertilizing the euphotic layer (Oschlies and Garçon 1998, Vaillancourt et al. 2003). Eddies can be easily identified from sea level anomalies detected by satellites. Enhanced biological production is also associated with static bathymetric features like continental shelves, where physical forcing promotes the upwelling of nutrient-rich waters and the retention of organisms (Springer et al. 1996). Although these static features represent distal descriptors of habitat quality, they are easily derived from bathymetric data and relevant for explaining top predator distributions. Relating top predators to a range of habitat quality descriptors would be useful to determine their relative contributions and influences on higher-trophic levels.

b) Ephemeral *versus* persistent descriptors of habitat quality

Hyrenbach et al. (2000) distinguished ephemeral (low predictability) from persistent (high predictability) oceanographic features. Studies that synoptically sampled environmental parameters and top predators have related their distributions to ephemeral features (Johnston et al. 2005, Ladd et al. 2005, Benoit-Bird and Au 2009). However, at the meso to the mega scale, habitat quality may be best described by persistent oceanographic features. To optimize their foraging success, predators may rely on their past experience and memory to locate persistent features in which foraging conditions are on average favorable (Davoren et al. 2003a, b). This is illustrated by site fidelity in seabirds foraging from a central place. Among 58 studied seabird sub-populations, Weimerskirch (2007) found that 91% of the birds returned consistently to the same particular mesoscale feature. Furthermore, in Kerguelen, black-browed albatrosses (*Thalassarche melanophrys*) were found to use the same foraging sites year after year (Weimerskirch et al. 1997). The consistent use of predictable areas was referred to as memory-based foraging strategy (Davoren et al. 2003a). Many top predators are known to exploit large-scale features of enhanced productivity, such as shelf edges, frontal zones and upwellings (Ballance et al. 2006, Weimerskirch 2007). Evaluating their responses to time-averaged habitat quality would allow investigating their dependence on recurring features of the environment.

4) The biological models: cetaceans and seabirds in tropical oceans

For this study, we relied on cetacean and seabird sighting data, obtained from aerial surveys conducted in three tropical regions.

a) Features of tropical oceans

The oceanic tropics represent the major, central portion of the world ocean, encompassing 50% of ocean surfaces. They comprise tropical (25-28°C), equatorial (20-28°C) and subtropical surface waters (19-28°C) (Longhurst and Pauly 1987). The "true tropics" have been defined by ornithologists as ocean areas with sea surface temperatures greater or equal to 23°C (including seasonally and year-round tropical waters) (Ashmole 1971, Ballance and Pitman 1999) (Figure I-3). In the tropics, although sunlight is abundant year-round, a strong permanent thermocline inhibits the vertical mixing of nutrients from deeper waters. Low rates of nutrients are partially compensated by a year-round growing season for phytoplankton and a deep euphotic layer. Nevertheless, net primary production and standing crops of photosynthetic autotrophs remain low. In addition, phytoplankton communities are characterized by a dominance of small cells (Longhurst and Pauly 1987). Compared to polar and temperate oceans, the tropics are characterized by a lower productivity, resulting in more patchy and less predictable food resources. In these challenging environments, strong selection pressures may exert on top predators for efficient foraging.

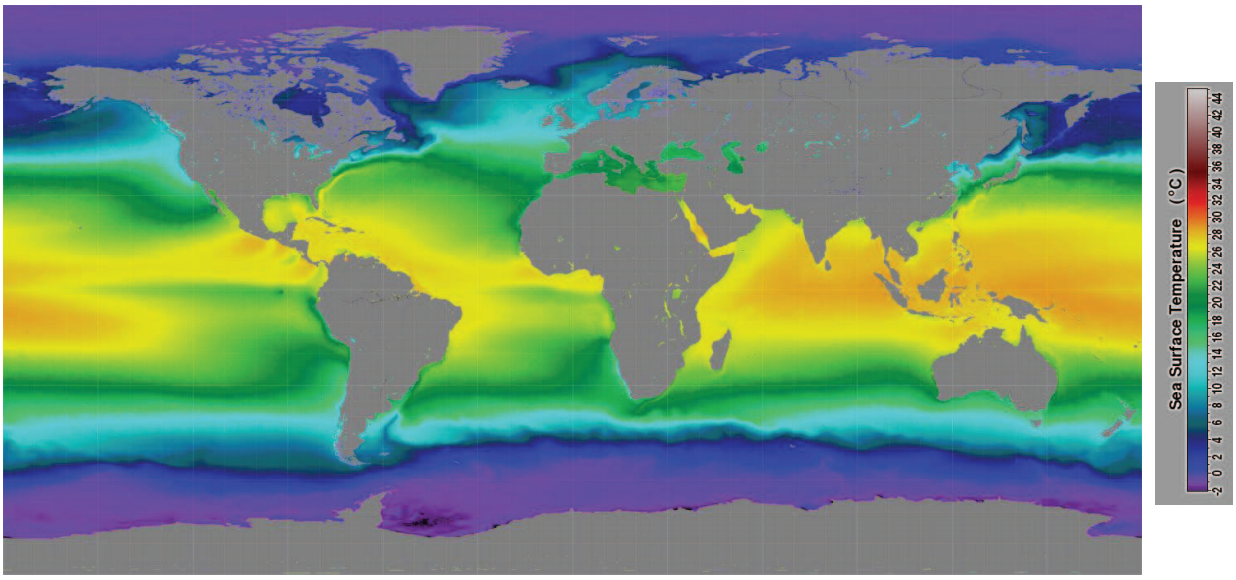


Figure I-3: Global sea surface temperatures from Ocean Color website. The "true tropics" are characterized by waters ≥ 23°C, excluding seasonal and year-round upwelling (Balance and Pitman 1999).

b) Ecological significance of cetaceans and seabirds

Cetaceans and seabirds are distinctive top marine predators. While cetaceans are fully aquatic through their life cycles, seabirds must return to their colonies during the breeding season to incubate and feed their chicks; they are referred to as central place foragers. In a sense, cetaceans also constitute central place foragers since they must travel between two important resources when foraging: oxygen in the atmosphere and food resources in the water column (Williams and Yeates 2004). The long dives of cetaceans are accomplished by a variety of adaptations including slowed heart rate, reduced oxygen consumption, and shunting blood to essential organs and tissues (Berta et al. 2006). Tropical seabirds show great adaptations for efficient flight (Hertel and Ballance 1999).

Significant ecological effects of cetaceans and seabirds are implied from their great abundance, high trophic status and the fact that some of them require significant proportions of primary production (Barlow et al. 2008). There is a large growing body of evidence for the ecological importance of these large consumers in the dynamics of marine food webs. Yet, their declines can generate large-scale cascading effects through reduced predation on mesoconsumers and indirect increase in the mortality of prey species (Heithaus et al. 2008). As a result, cetaceans and seabirds have been identified as keystones in some ecosystems, strongly influencing the abundances of other species and the ecosystem dynamics (Libralato et al. 2006).

c) Management rationale

Their generally large size, high trophic level and vast vital domains expose cetaceans and seabirds to many anthropogenic pressures. Cetaceans are threatened by fisheries, through accidental catch and depredation (Lewison et al. 2004, Read 2008), collisions (Laist et al. 2001), anthropogenic noise (Weilgart 2007), pollution (Aguilar et al. 2002) and global warming (Alter et al. 2010). For seabirds, the principal threat occurs at breeding sites as a result of alien invasive predators, human disturbance and habitat degradation. At sea, the main threats are commercial fisheries, through bycatch and overfishing and pollution (Croxall et al. 2012). These anthropogenic pressures generate additional mortality, alter survival and fecundity or disrupt the vital behaviors of these organisms, characterized by a low fecundity and low adult mortality, which severely limit their rate of recovery.

As charismatic large vertebrates, cetaceans and seabirds also constitute flagship species (Simberloff 1998) that can be the leading elements of the conservation of pelagic ecosystems. Owing to their large home ranges and high trophic levels, their effective conservation is considered beneficial to the larger system because they overlap a variety of species both horizontally as well as vertically through the food chain. This has been named the umbrella effect (Simberloff 1998, Caro and O'Doherty 1999)

Cetaceans and seabirds form one of the few components of pelagic biodiversity that can be readily seen from the surface of the oceans and therefore be surveyed across large oceanic regions. It is expected that their species assemblages reveal some of the major properties of the underlying ecosystems. In this respect, they are usually suggested as ecosystem composition indicators, since their presence or abundance can denote a particular habitat or biological community (Zacharias and Roff 2001). In addition, they have been referred to as sentinels of marine ecosystems, reflecting their underlying state and health, as a result of both anthropogenic and ecological factors (Burger and Gochfeld 2004, Piatt et al. 2007, Moore 2008). Cetaceans and seabirds are thus crucial for informing the management and conservation of pelagic ecosystems. As composition indicators, they can be used to determine areas or priorities for conservation. As sentinels, they can be used to assess conservation efforts once specific habitats or communities have been identified (Zacharias and Roff 2001).

5) Hypothesis, objectives and strategy of the thesis

a) General hypothesis and objectives

In the present dissertation, I hypothesize that top predator strategies of habitats utilization are in accordance with their general energetic constraints and that they should distribute among habitats with respect to their quality. Energetically costly predators may be constrained to select the highest quality habitats to meet their high energetic requirements, whereas less active predators would be able to satisfy their needs by exploiting either high or low quality habitats.

The first objective is to evaluate the response of cetaceans and seabirds with contrasting energetic costs of living to the spatial heterogeneity of habitat quality. I describe habitat quality by a range of physiographic, oceanographic and biological variables.

The second objective is to evaluate cetacean and seabird responses to contemporaneous *versus* averaged habitat quality.

Finally, the third objective is to highlight generic properties of cetacean distributions in tropical waters.

This study is mainly focused on fundamental research, although management implications will be discussed at the end of the dissertation (Chapter X).

b) Cetacean and seabird data

The REMMOA (*Recensement des Mammifères marins et autre mégafaune pélagique par observation aérienne*) surveys are multispecific aerial surveys implemented in the Exclusive Economic Zone (EEZ) of French overseas territories and in some adjacent EEZ of neighboring countries, from 2008 to present (Figure I-4). Sampling design was organized at several spatial levels. Three tropical regions were surveyed: the western tropical Atlantic (surveyed surface area: 175,000 km²), the Southwest Indian Ocean (1.4 million km²) and French Polynesia (1.75 million km²). In each region, sectors of contrasted oceanographic conditions were delimited. Within each sector, gross bathymetric strata (0-200 m: shelf, 200-2,000 m: slope, >2,000 m: oceanic) were sampled, within which transects were implemented. Data on the presence and abundance of cetaceans and seabirds, as well as on the associated

effort and detection conditions were collected following a standardized protocol. The present dissertation is entirely based on this aerial survey data.

I classified cetaceans and seabirds into energetic guilds on the basis of either direct metabolic measurements or indicators of their energetic costs from the literature.

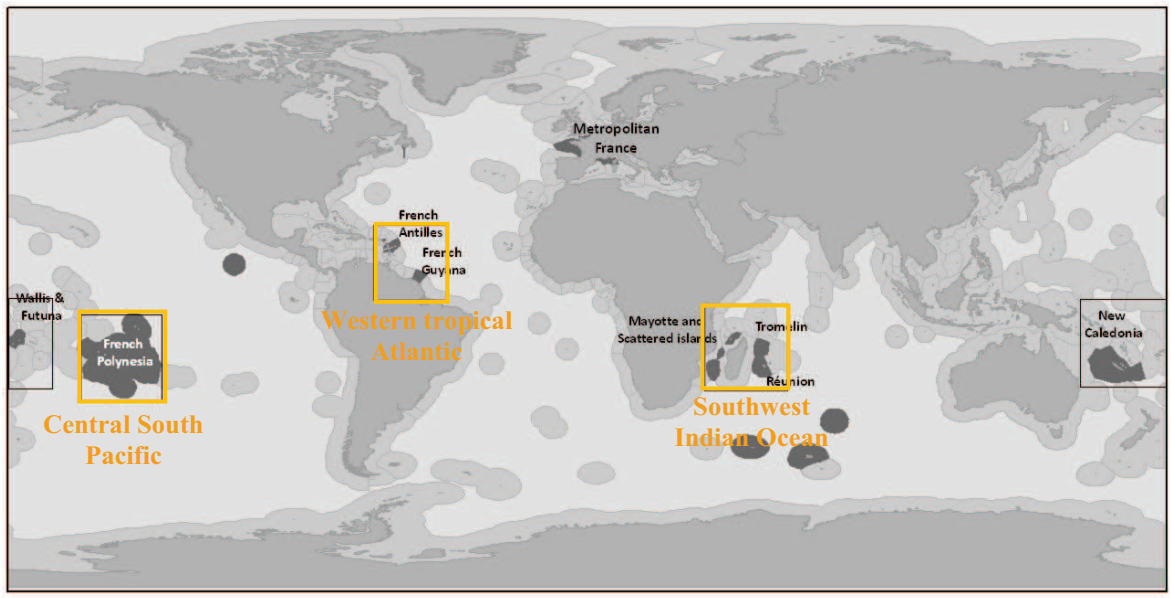


Figure I-4: The French EEZ (dark grey) stretches across all three oceans, between approximately 50°N and 50°S. It is highly fragmented and has a very large extent (11 million km²), 97% of which lie around overseas territories. The three regions sampled by the REMMOA aerial surveys are indicated in orange boxes. New Caledonia and Wallis and Futuna in the western South Pacific are to be surveyed in austral summer 2014-2015.

c) Habitat quality descriptors

I documented habitat quality using a variety of distal and proximal descriptors, from static to dynamic oceanographic features, and from lower to mid-trophic levels. Data on environmental variables were retrieved from satellite remote sensing, a global atlas of *in situ* measurements and model outputs. I described habitat quality at both contemporaneous and averaged temporal resolutions.

d) Analytical tools

I used habitat models to relate cetacean and seabird sightings to environmental variables and predict their spatial distributions. It is a correlative modeling approach in which sighting and environmental data are associated statistically and the resulting statistical

relationship is interpolated to the spatial domain of interest (Kearney 2006). I relied on sightings made on transects to successively provide predictions at the scale of the sector, the region and the circumtropical belt. Along this process, predictions were made to unsurveyed areas, but always within the range of environmental conditions sampled by the data (geographical rather than environmental extrapolation, Elith and Leathwick 2009).

e) From ecology to macroecology

In this dissertation, I shifted from ecological studies at the regional scale, to a macroecological study at the scale of the circumtropical belt (Figure I-5). Ecology is the study of the interactions that determine the distribution and abundance of organisms. Basically, it means answering three questions: (1) where does the organisms occur? (2) how many occur there? and (3) why? (Begon et al. 2006). Ecology mainly deals with description, and eventually tries to explain and predict the spatial patterns of organisms. As a first step, I attempted to describe, explain and predict cetacean and seabird distributions at the regional scale in the western tropical Atlantic, Southwest Indian Ocean and French Polynesia.

Macroecology is an approach to the field of ecology with distinctive characteristics (Brown 1995). Its aim is to understand the patterns and determinants of the broad scale distributions of species (Blackburn and Gaston 2003). However, beyond describing and explaining these patterns, macroecology seeks to reveal general laws and emergent properties which support the nature, structure and function of ecosystems (Kent 2005). In a second time, I searched for emergent properties that would govern cetacean distributions in tropical waters, in order to propose generic predictions in the circumtropical belt.

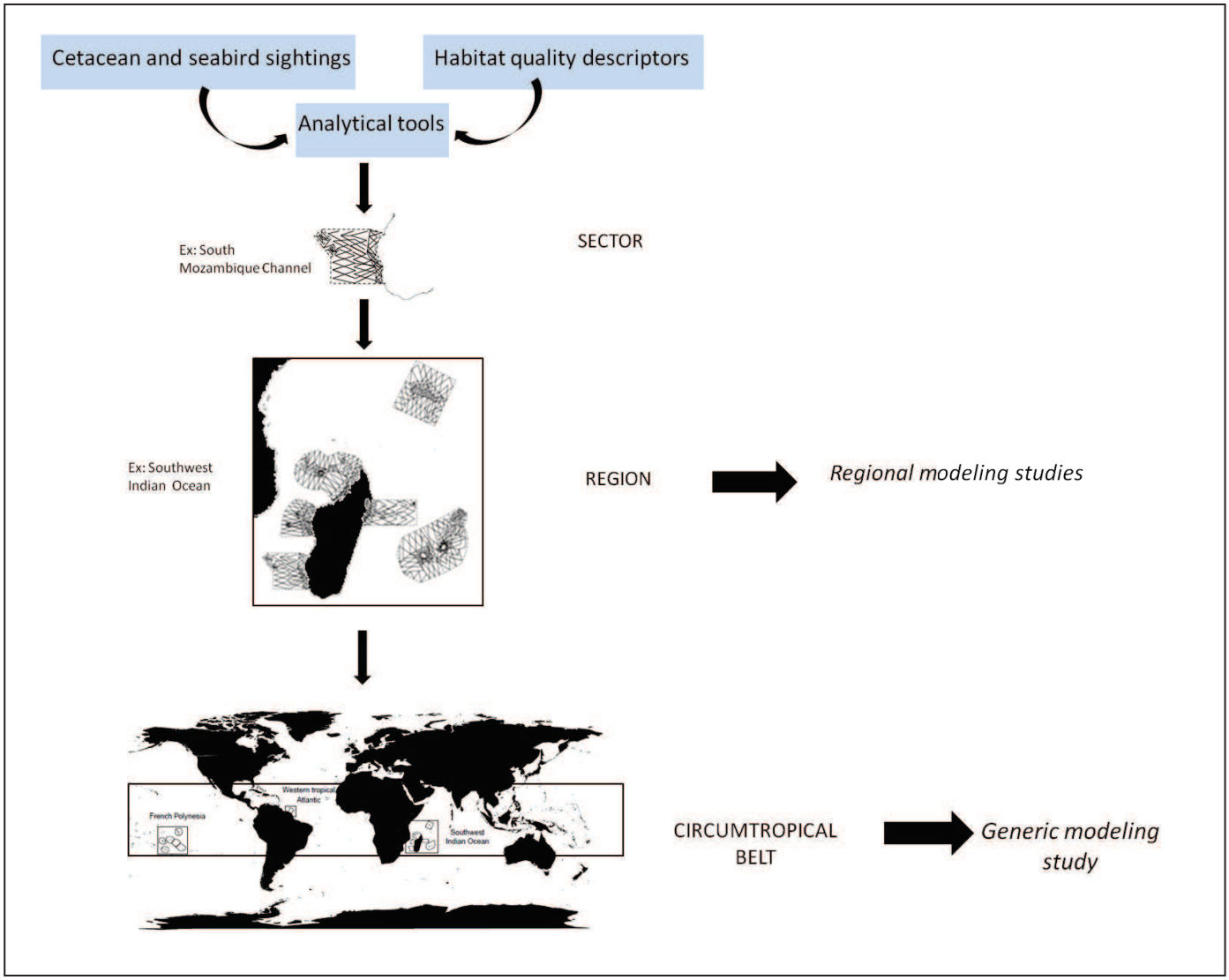


Figure I-5: Strategy of the dissertation highlighting the shift from ecological studies at the regional scale to a macroecological study at the circumtropical scale.

6) Outline of the dissertation

In **Chapter II**, I highlight the features of tropical oceans, describe the oceanographic characteristics of the study regions and define the energetic guilds.

Chapter III is a state-of-the art of species distribution modeling applied to cetaceans and seabirds, from data collection methods to environmental variables and statistical methods.

In **Chapter IV**, I present the general methodological choices.

Chapters V to VIII are related to four articles (published, in revision or in preparation) presented in the ANNEXES 1 to 4 (Table I-1). They concern regional modeling studies. In the dissertation, I retained a minimal introduction limited to the objectives of the study, the presentation of the core results and a short specific discussion. Elements of general interest are discussed in the general discussion. The implementation of the methods described in Chapter IV, as well as more descriptive results, are visible in the corresponding Annexes.

In **Chapter V,** the objective was to compare cetacean and seabird communities from two contrasting ecosystems in the western tropical Atlantic (the Antilles and Guiana), in terms of encounter rates, composition, relative abundance and spatial distribution.

In **Chapter VI**, I modeled the habitats of contrasting cetacean and seabird guilds in the Southwest Indian Ocean based on static and oceanographic variables. The first objective was to evaluate their responses to the spatial heterogeneity of habitat quality. This allowed to test the hypothesis in a large region characterized by three distinct oceanographic provinces. The second objective was to evaluate cetacean and seabird responses to contemporaneous *versus* averaged habitat quality.

In **Chapter VII**, the modeling approach was the same as in Chapter VI, but implemented in French Polynesia. The objectives were common with Chapter VI. This study allowed to test the hypothesis across a productivity gradient in an oligotrophic region.

In **Chapter VIII,** I modeled cetacean habitats from the distribution of their prey in both the Southwest Indian Ocean and French Polynesia. The objectives were (1) to model cetacean habitats from the simulated distribution of micronekton, and (2) to compare the results between the two regions. This gave the opportunity to investigate the central hypothesis, relying on more proximal descriptors of habitat quality.

Chapters IX is related to an article in preparation (Table I-1). It concerns a generic modeling study. The article is presented *in extenso* in the dissertation. I predicted cetacean habitats in a circumtropical envelope constructed from the three regional datasets and a variety of habitat descriptors representative of ecosystemic processes. The objectives were (1) to highlight emergent properties of cetacean distributions and (2) to provide spatial predictions in tropical waters of similar characteristics as the surveyed areas.

A general discussion, conclusions and perspectives are provided in **Chapter X.**

Table I-1: Overview of Chapters V to IX.

Chapter	**Chapter V: Cetacean and seabird communities from two contrasting ecosystems in the western tropical Atlantic.**	**Chapter VI: Predicting cetacean and seabird habitats in the Southwest Indian Ocean.**	**Chapter VII: Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre.**	**Chapter VIII: Predicting cetacean habitats from the distributions of their prey in two contrasted tropical regions.**	**Chapter IX: Generic relationships of cetaceans with the quality of their habitats in tropical oceans.**
Article	Published article presented in ANNEX 1	Published article presented in ANNEX 2	Article in revision presented in ANNEX 3	Article in preparation presented in ANNEX 4	Article in preparation presented *in extenso* the dissertation
Objective(s)	-Compare cetacean and seabird communities from two contrasted areas	-Response of cetaceans and seabirds to the spatial heterogeneity of habitat quality -Response to contemporaneous *versus* averaged habitat quality	-Response of cetaceans and seabirds to the spatial heterogeneity of habitat quality -Response to contemporaneous *versus* averaged habitat quality	-Model cetacean habitat from the distribution of their prey -Compare both regions	-Highlight generic properties of cetacean distributions -Provide circumtropical predictions
Sighting data	Aerial surveys in the Antilles and Guiana	Aerial surveys in the Southwest Indian Ocean	Aerial surveys in French Polynesia	Aerial surveys in the Southwest Indian Ocean and French Polynesia	Aerial surveys in Guiana, the Southwest Indian Ocean and French Polynesia
Habitat quality descriptors	_	Static and remotely sensed oceanographic variables	Static and remotely sensed oceanographic variables	Distribution of micronekton	Variety of static, physical, chemical, and biological variables
Analytical tools	Spatial models	Habitat models	Habitat models	Habitat models	Habitat models
Spatial scale of the predictions	Sector	Region	Region	Region	Circumtropical belt

Chapter II. Study regions and energetic guilds

Photo credit: Observatoire Pelagis / AAMP

1) Features of tropical oceans

a) Oceanic circulation

The main forces generating motion in the open ocean are: (1) the winds, which drive currents in the upper water layer by exerting a stress at the ocean surface and (2) pressure gradients, formed either through differences in sea surface height or horizontal differences in water density. In addition, the rotation of the Earth is at the origin of the Coriolis force, deviating waters to the left in the Southern Hemisphere and to the right in the Northern Hemisphere. It results in two types of motions: the Ekman transport and geostrophic currents (Ganachaud et al. 2010).

Ekman transport

Owing to the Coriolis force, the surface current flow is deviated perpendicular to the wind direction. It occurs on either side of the equator, where easterly trade winds cause southward water motion in the Southern Hemisphere (deviation 90° to the left of wind direction) and northward water motion in the Northern Hemisphere (deviation 90° to the right of wind direction). As a result, surface waters flow away from each other on both sides of the equator. Cool water is upwelled to compensate for this surface divergence. At the equator (no Coriolis force), surface waters flow in the same direction as the wind (Figure II-1).

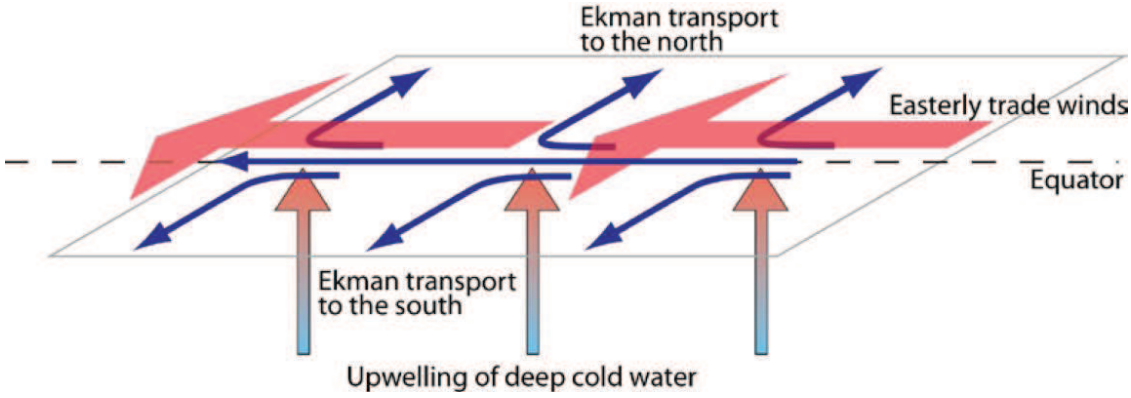


Figure II-1: Diagram representing the Ekman transport, from Ganachaud et al. 2010.

Geostrophic motion

When pressure differences occur, either from variations of sea surface height or horizontal differences in temperature or salinity, water flows 90° to the left of the gradient

from high to low pressure in the Southern Hemisphere (and to the right in the Northern Hemisphere). As a result, any horizontal change in water density is associated with a current flowing perpendicular to the front.

Ekman transport in surface layers and geostrophic flow in deeper layers combine to produce the surface and deep currents of the oceans. The current systems of tropical oceans are mirror images in both hemispheres, although circulation can be modified by land masses. Currents are determined by the Hadley circulation. Warm air rises at the equator, heat is transferred poleward to high altitudes and air descends in the subtropics, driving the permanent trade wind system that brings surface air back toward the equator. Hence, the general circulation of tropical surface waters is mainly determined by east-west currents. North Equatorial currents and South Equatorial currents are driven by the prevailing easterly trade winds and flow westward. Equatorial countercurrents and undercurrents flow contrary to the prevailing winds and maintain the geostrophic balance (Longhurst and Pauly 1987) (Figure II-2).

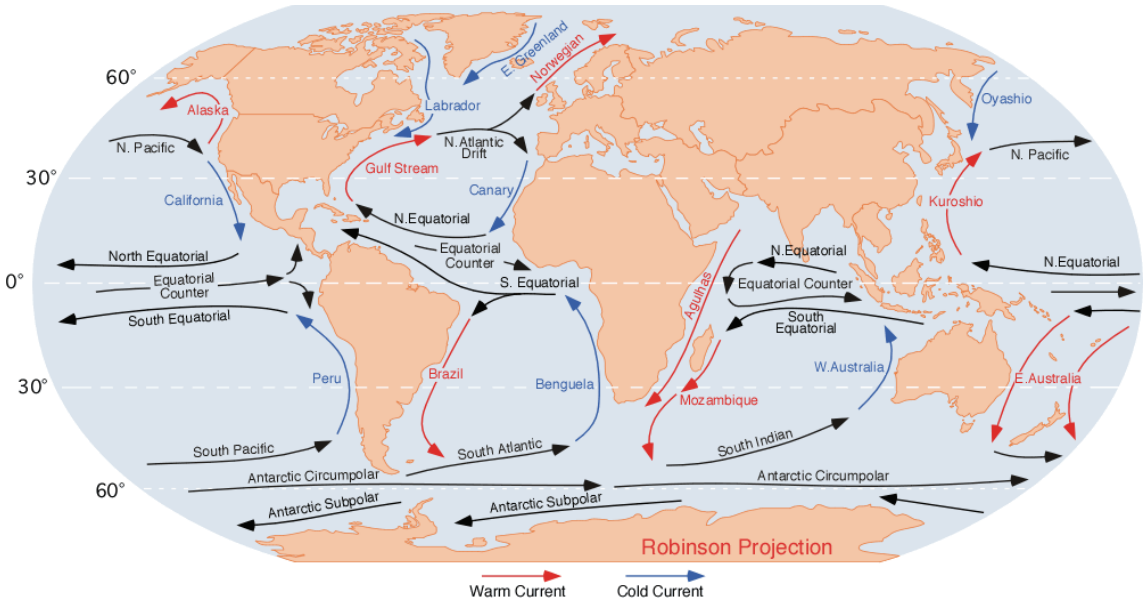


Figure II-2: Surface ocean currents, from Pidwirny 2006.

b) Vertical structure

Pelagic ecosystems can be considered as the most homogeneous living space of our planet, particularly in the tropics. Spatial heterogeneity is mostly restricted to vertical gradients of light, temperature and abundance of organisms, and horizontal gradients are generally weak. The thermocline represents the most important vertical discontinuity in the

open oceans. The warmer surface waters have lower density than the deeper cooler waters; these two layers meet at the thermocline where vertical gradients are the strongest (Longhurst and Pauly 1987). Temperature, and to a lesser extent salinity, have important effects on water density and create stratification. By stabilizing the water column, stratification inhibits the transfer of nutrients to the euphotic layer. Nevertheless, strong winds and evaporation cause mixing in the upper layer, weakening stratification. Turbulence and mixing homogenize the first tens of meters, resulting in a surface mixed layer (Ganachaud et al. 2010) (Figure II-3).

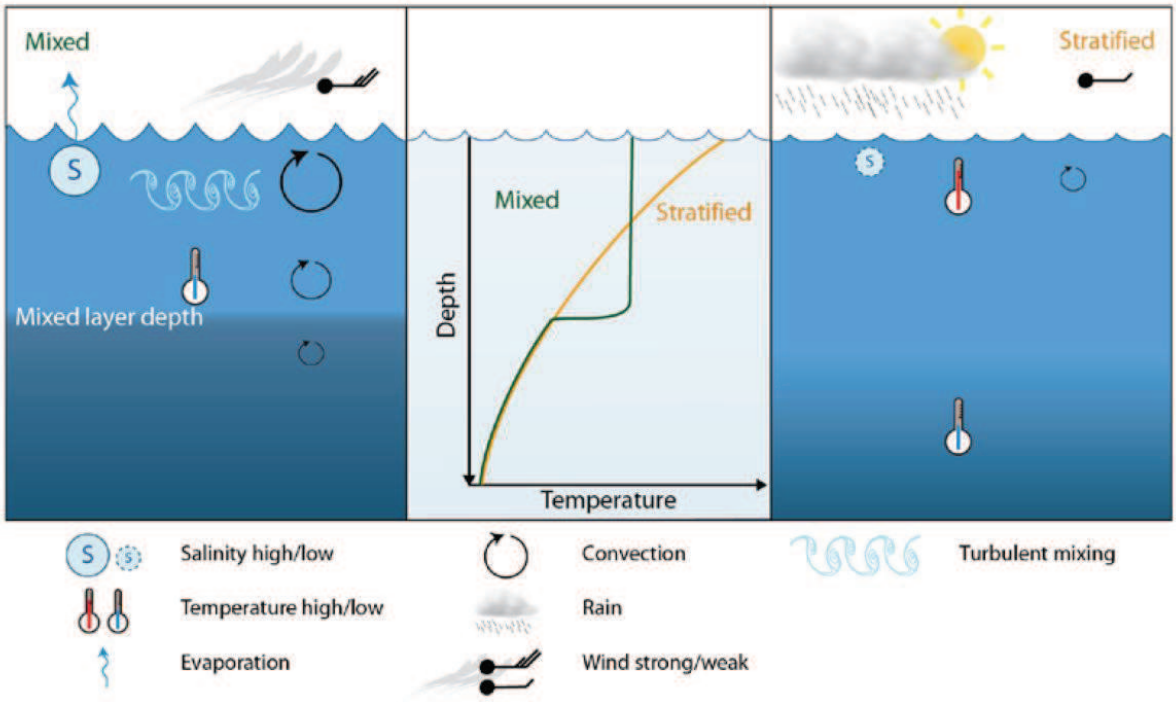


Figure II-3: Representation of a well formed mixed layer to the left and a stratified water column to the right, from Ganachaud et al. 2010. Corresponding temperature profiles are shown in the middle.

Primary production requires both light and nutrients. Tropical waters are characterized by a typical profile: a well-lit and nutrient-poor upper layer lies above a poorly-lit and nutrient-rich deeper layer. Thus, primary production critically relies on the transfer of nutrients to the euphotic zone by the interplay of three processes (Ganachaud et al. 2010):

Turbulence in the mixed layer

Strong mixing in the upper ocean can bring nutrient-rich waters from deeper layers to the euphotic zone. The extent of nutrient inputs depends on the depth of mixing relative to the depth of the nutricline. When the nutricline is shallow, mixing of the upper water column reaches down to nutrient-rich waters, transferring nutrients into the euphotic zone. When the

nutricline is deep, nutrients remain out of reach under the mixed layer. In oligotrophic waters, the mixed layer is fundamental as it determines the depth from which nutrients are delivered to surface waters to replenish the nutrient supply in the euphotic zone (Longhurst 2007).

Upwellings

Upwellings are formed when wind-driven surface currents move in opposite directions (equatorial upwelling) or when winds push surface water away from the coast (coastal upwelling). If upwelled waters originate from a sufficient depth, they deliver nutrients into the mixed layer.

Eddies

Eddies are large vortices extending from the surface to sometimes considerable depths. They are generated by instabilities of large scale flow and are associated with variations of currents, sea level and vertical structure of the water column. Their timescale ranges from weeks to months and their spatial scale, from tens to hundreds of kms. In the Southern hemisphere, cold cyclonic eddies depress the sea level and raise the thermocline temporarily, potentially making nutrients available for enhanced biological production in their center (Vaillancourt et al. 2003). In contrast, warm anticyclonic eddies slightly raise sea level and deepen the thermocline (Figure II-4). They are characterized by nutrient depleted waters in their center; however, local nutrient enrichment can occur at their outer edges (Biggs 1992). Rotation is reversed in the Northern Hemisphere. While the sea level rises/deepens of a few centimeters, thermocline is displaced of tens of meters (Longhurst and Pauly 1987).

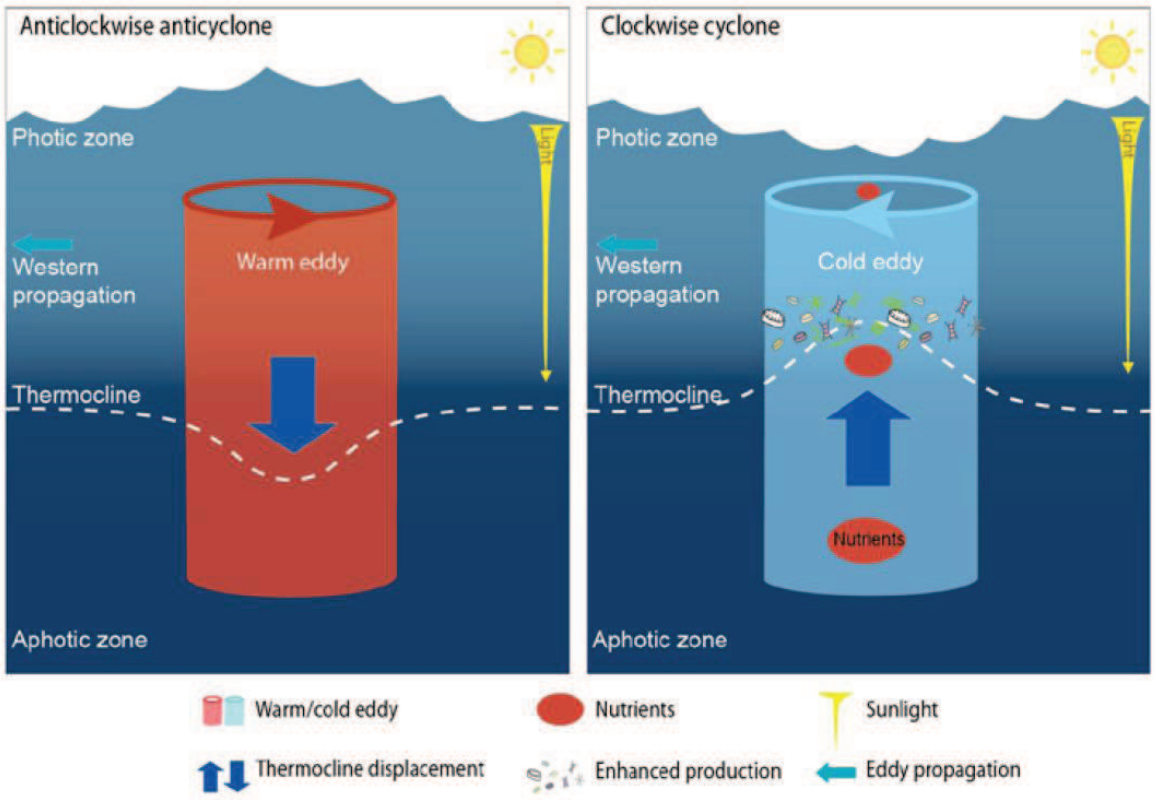


Figure II-4: Warm and cold eddies and their effects on the vertical structure of the water column (case of the Southern Hemisphere), from Ganachaud et al. 2010.

Closer to the coast, primary production is enhanced by nutrients inputs from coastal upwellings, shelf edge processes, and river discharge. Coastal upwellings typically occur at the subtropical eastern boundary coasts (*e.g.* Angola-Namibia, Peru-Chile, California-Mexico). They mainly originate from wind driven divergence of the Ekman layer from the coast and have a major impact on biological production. Vertical transport of nutrients also occurs at the edge of continental shelves where dynamic processes at the limit of oceanic and continental shelf water masses (under the influence of tidal mixing) generate frontal zones. Finally, river discharge can provide large quantities of nutrients. For example, the Amazon River discharge amounts to 2.10^5 m^{-3} s^{-1} and its plume extends far away from the Amazon delta, notably providing large quantities of silicates (Longhurst and Pauly 1987).

c) Primary production and pelagic food webs

Tropical oceans encompass 50% of total ocean surface and are characterized by relatively unproductive waters. Primary production, the generation of organic matter in the euphotic zone by phytoplankton from photosynthesis, is relatively low, as indicated by

surface chlorophyll concentration. This is particularly true within the vast subtropical gyres where chlorophyll concentration does not exceed 0.1 mg m^{-3} (Figure II-5).

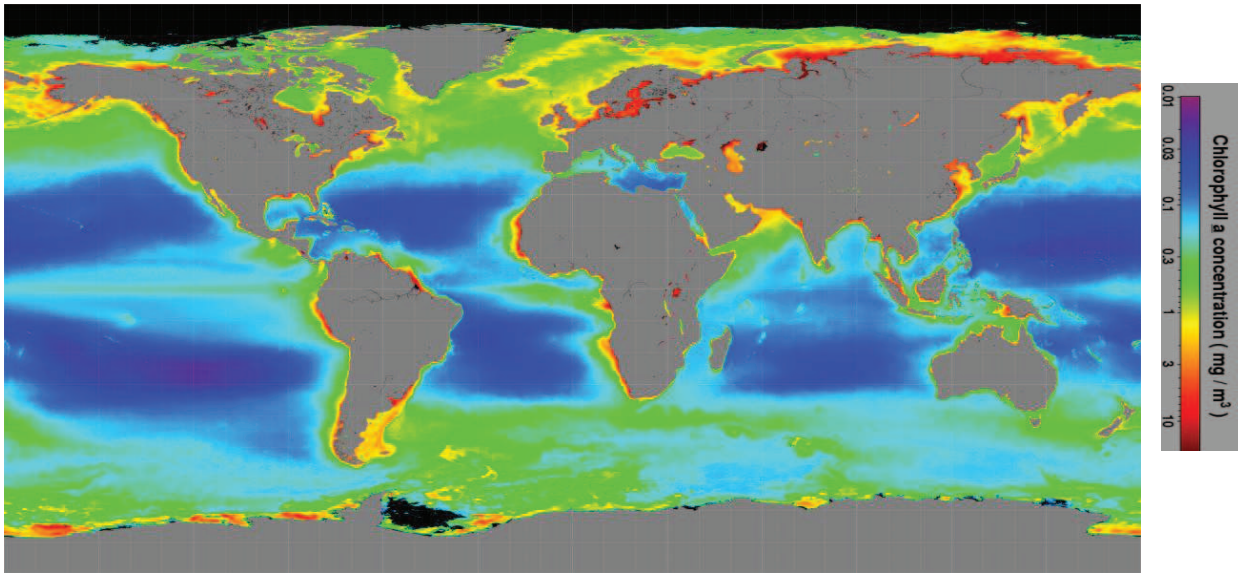


Figure II-5: Mean annual surface chlorophyll concentration, from Ocean Color website.

Primary production can be based on both regenerated and new nutrients. New nutrients are transferred from deeper layers into the euphotic zone by the physical processes described above. This is the basis of the classical herbivorous pathway. New production is supplemented by the uptake of dissolved nitrogen by diazotrophs such as unicellular or filamentous cyanobacteria (Karl et al. 2002). New nutrients are nitrates (NO_3), dinitrogen (N_2), soluble reactive phosphorus (SRP) and silicates. Regenerated nutrients are released in the euphotic zone though remineralization of exported organic matter (either particulate, from sinking of dead plants and animals or dissolved, from excretion) by heterotrophic bacteria and protozoans. This is termed the microbial pathway (Legendre and Le Fèvre 1995). Microbial and herbivorous pathways are intimately coupled (Figure II-6). Regenerated nutrients are mainly ammonia (NH_4) and SRP (Le Borgne et al. 2010). The oligotrophic tropical waters are dominated by regenerated production.

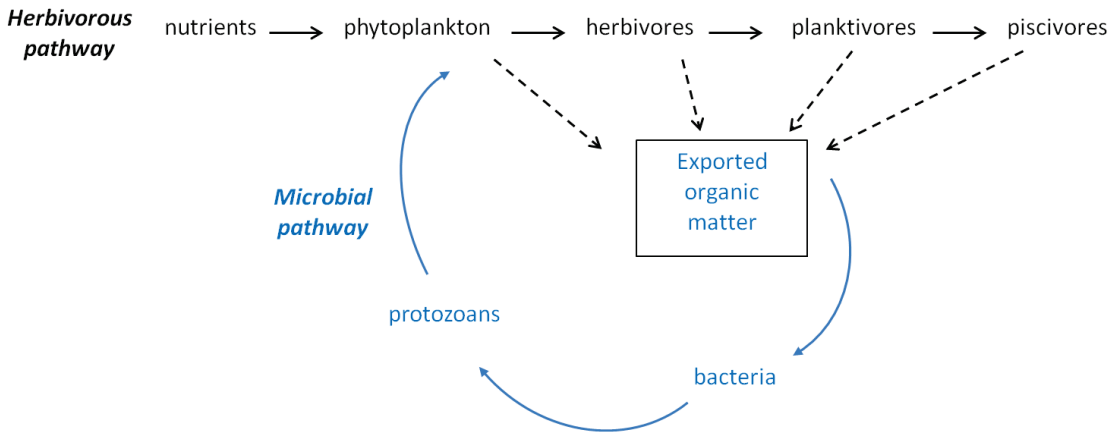


Figure II-6: Coupling between the microbial and herbivorous pathways, inspired form Lalli and Parsons 1997. Bacteria regenerate organic matter. They are consumed by planktonic protozoans, which are eaten by larger plankton, therefore transferring bacterial production to higher-trophic levels.

Primary production requires both macronutrients (nitrates, phosphates, silicates) and micronutrients such as iron, which is delivered by atmospheric dry and wet deposition. Iron is not soluble in water and interacts with organic ligands to form various dissolved organic complexes (Karl 2002). Nitrogen (in the form of ammonium or nitrate) is the main factor limiting primary production, although iron may also be limiting. The vertical structure of the water column determines the amount of new production relative to regenerated production in the euphotic zone (Le Borgne et al. 2010). The source of macronutrients influences phytoplankton composition. Diatoms usually dominate in areas of new primary production owing to their higher growth rate, whereas smaller phytoplankton dominates in areas of regenerated primary production (Officer and Ryther 1980).

The nature of macronutrients influences phytoplankton composition. Since diatoms require dissolved silicate to form their external shell, their growth is limited when the silicate to dissolved inorganic nitrogen ratio (known as the Redfield ratio, Redfield 1958) falls under 1:1. In this case, smaller phytoplankton such as flagellate algae, which only need nitrates and phosphates for their growth, dominates the community (Turner et al. 1998). Alvain et al. (2008) used a classification method to identify five major phytoplankton groups around the globe from the spectral shape of water leaving radiance of SEAWIFS ocean color sensor. In tropical waters, Prochlorococcus and Synechococcus, cyanobacterias < 5 µm in diameter, were largely dominant although some diatom blooms occurred coastally (Figure II-7).

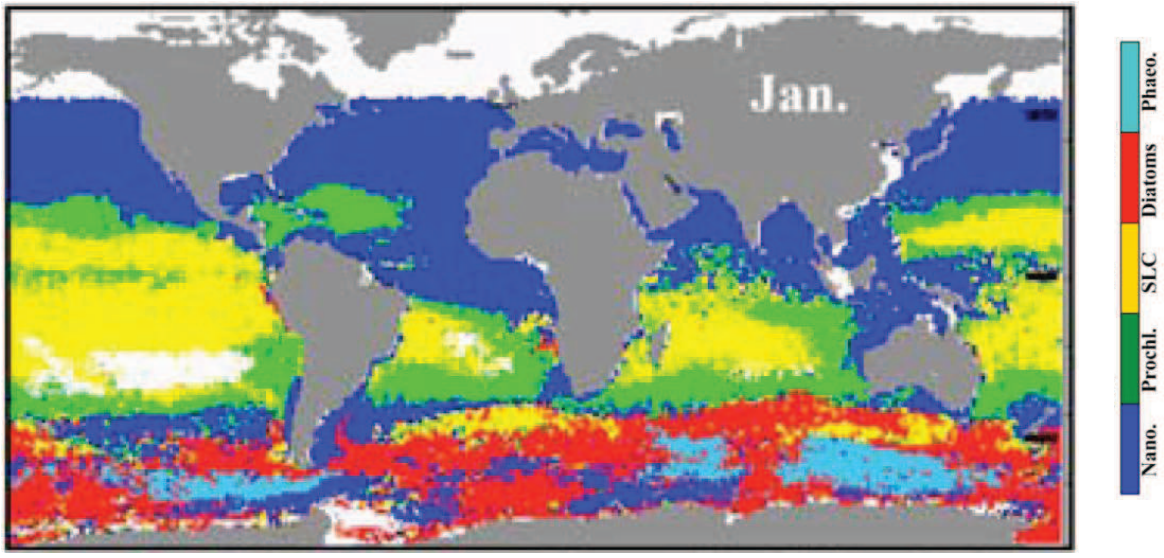


Figure II-7: Monthly climatology (January) of dominant phytoplankton groups (nanoeucaryotes, Prochlorococcus, Synechococcus (SLC), diatoms and phaeocystis-like), from Alvain et al. 2008.

Subsequently, phytoplankton size determines grazing zooplankton size. This leads to two broad categories of food chains depending on the dominant phytoplankton (Parsons and Lalli 2002) (Figure II-8).

Low energy food chains

Small phytoplankton, like autotrophic flagellates, is grazed by small zooplankton (such as heterotrophic flagellates and ciliates), which in turn is consumed by jellyfishes and other gelatinous plankton eaters. These food chains can lead to blooms of gelatinous plankters.

High energy food chains

Large phytoplankton, such as diatoms, is eaten by large zooplankton (like copepods), which in turn is consumed by fishes. These food chains are supported by fewer trophic levels and thus less energy losses. They are typically the basis for the production of top predators.

In addition to total primary production, it is also important to consider phytoplankton composition which indicates the "quality" of primary production rather than its quantity, and is at the basis of contrasting trophic pathways.

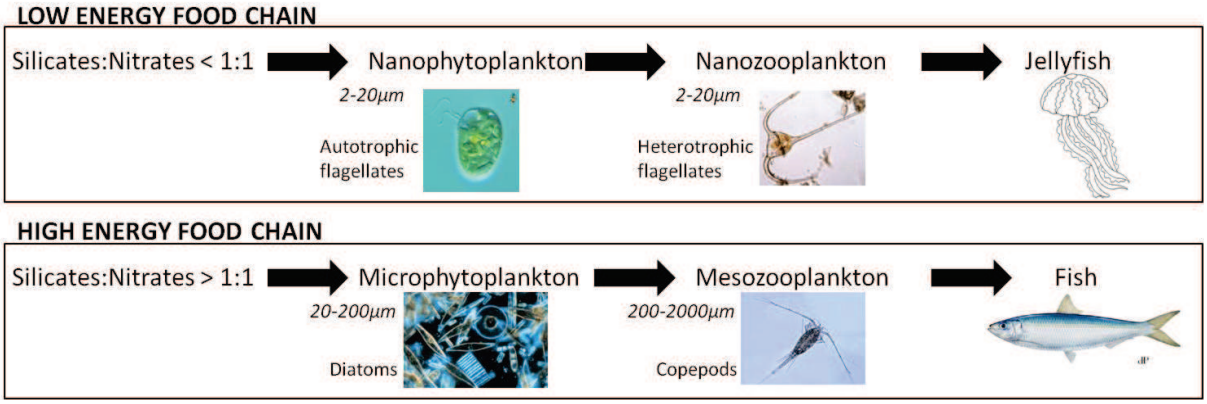


Figure II-8: Illustration of high and low energy food chains. High energy food chains are at the origin of the production of top predators.

Zooplankton and micronekton are secondary producers. Micronekton encompasses actively swimming fishes, crustaceans, and cephalopods, generally ranging from 1 to 10 cm (Blackburn 1968). Zooplankton and micronekton are characterized by diel vertical migrations (DVMs). They move towards the surface near sunset and descend to deeper layers near sunrise. DVMs are responsible for the production of moving deep scattering layers picked up by echosounders (Barham 1966). Micronekton migrates to the surface from waters as deep as 1000m, whereas zooplankton generally migrates from depths shallower than 400m. Some zooplankton and micronekton only undertake small-scale migrations or do not migrate at all (Le Borgne et al. 2010). As a consequence of DVMs, biomasses of zooplankton and micronekton differ in the water column between the night and the day (Hidaka et al. 2003). The main factors determining DVMs are search of food and avoidance of visuals predators (Stich and Lampert 1981). Andersen et al. (1997) observed a reduction of DVMs in eutrophic and mesotrophic areas compared to oligotrophic areas in the tropical Atlantic. They related this to the sensitivity of migrants to different light conditions, forcing them to dive deeper during daylight in the oligotrophic area to avoid visual predators. DVMs induce interrelations between the euphotic zone and deep ocean layers. Indeed, while in the euphotic zone organisms acquire their energy from phytoplankton production, fauna in deep ecosystems get their energy from the euphotic layer by the intermediate of vertical migrations (Legand et al. 1972). Many studies of cetacean and seabird feeding ecology (Harrison et al. 1983, Pauly et al. 1998) showed that their diets consisted of different categories of micronekton.

d) Temporal variability

Temporal variability in tropical oceans is often considered to be relatively weak. Nonetheless, it does exist and can be divided into within-year (seasonal) and between-year variability. The latter is the most important source of variability (Longhurst and Pauly 1987).

Within-year variability

Seasonality in the tropics is mostly driven by the passage of the atmospheric Intertropical Convergence Zone (ITCZ) across the equator twice a year, at the origin of the alternation of wet and dry seasons. This may induce a seasonal reversion of the currents. For example, in the Caribbean region, the North Equatorial current reverse in February-April, decreasing the influence of the Amazon River plume in the southern Caribbean. In the Indian Ocean, monsoon also causes a reversal of circulation, resulting in seasonal upwellings (*e.g.* along the Somali coast). Mesoscale eddies (time scales of weeks to months) can also cause within-year variability. In addition, the depth of the mixed layer can change seasonally, for instance as a result of the passage of tropical cyclonic storms. Overall, within-year changes in biological communities are small in the tropics. Seasonality may be greater in upwelling systems, with strong implications for fisheries (Longhurst and Pauly 1987).

Between-year variability

Between-year variability is the prominent source of temporal variability in tropical oceans. The El Niño–Southern Oscillation cycle (ENSO), alternating between warm El Niño and cold La Niña events, constitutes the dominant year-to-year signal. It originates in the tropical Pacific from ocean-atmosphere interactions. El Niño and La Niña last 12 to 18 months and occur every 2 to 7 years, in association with the Southern Oscillation, an atmospheric pressure event closely related to the strength of the Pacific trade winds. ENSO consequences are felt beyond the tropical Pacific through atmospheric teleconnections, affecting patterns of weather variability worldwide (McPhaden 2004, McPhaden et al. 2006).

In the neutral situation, prevailing trade winds push warm surface waters to the west of the Pacific, deepening the thermocline. This causes an upwelling of cold water in the eastern side of the Pacific with an elevation of the thermocline. The resulting east-west surface temperature gradient reinforces the east-west air pressure difference across the basin. This leads to a warmer and wetter atmosphere in the western side of the Pacific (Figure II-9a).

An El Niño event is produced when easterly winds weaken. It is characterized by anomalously warm sea surface temperatures in the central and eastern Pacific, as the result of warm water flowing eastward in the western Pacific and weakening of the upwelling. As surface temperatures warm to the east, convective cloudiness and rainfall migrate eastward, making the east wetter and the west drier (McPhaden 2004, Ashok and Yamagata 2009). Biological productivity is reduced in the otherwise highly productive equatorial cold tongue and coastal upwellings of the Americas. This affects the mortality, fecundity and distribution of marine mammals, seabirds and commercially important fish (Barber and Chavez 1983) (Figure II-9b). La Niña, the opposite phase of El Niño, is characterized by stronger trade winds, colder sea surface temperatures in the tropical Pacific, and heavy rainfall to the far western tropical Pacific. La Niña effects on global patterns of weather variability are roughly opposite to those of El Niño. Its impacts on ocean dynamics are grossly an exaggeration of the neutral situation (McPhaden 2004, Ashok and Yamagata 2009) (Figure II-9c).

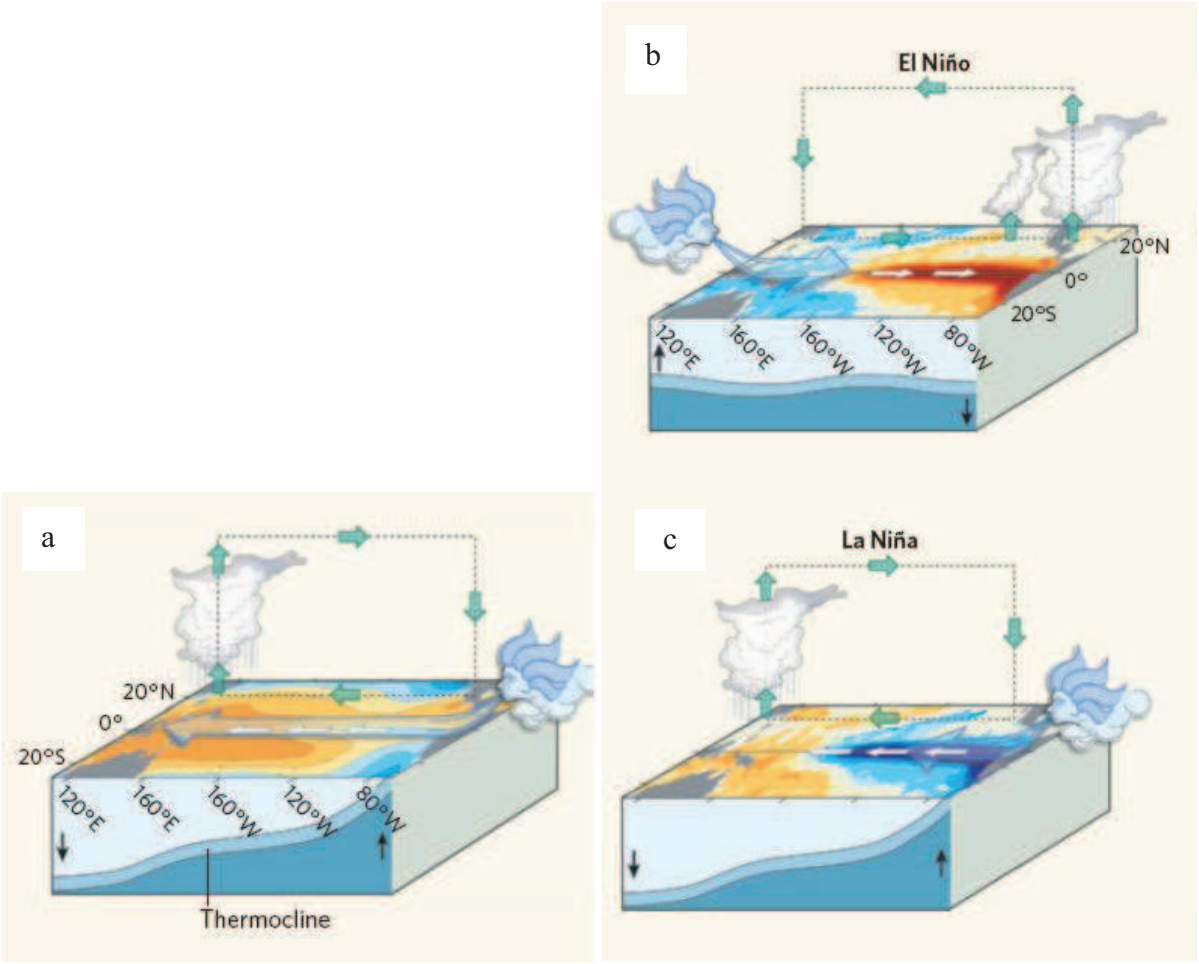


Figure II-9: Representation of neutral (a), El Niño (b) and La Niña (c) conditions, from Ashok and Yamagata 2009.

2) Study regions

Regions sampled as part of the REMMOA program include the western tropical Atlantic (French Caribbean and Guiana), the Southwest Indian Ocean and French Polynesia, in the central South Pacific. The three sampled regions belong to diverse biogeochemical provinces with specific environmental conditions (Longhurst 2007) (Figure II-10). French Caribbean and Guiana are situated in the Caribbean and the Guianas coastal provinces respectively. The Southwest Indian Ocean region lies at the intersection of the Eastern Africa coastal province, the Indian monsoon gyres province and the Indian South Subtropical gyre province. French Polynesia is entirely included in the South Pacific subtropical gyre province.

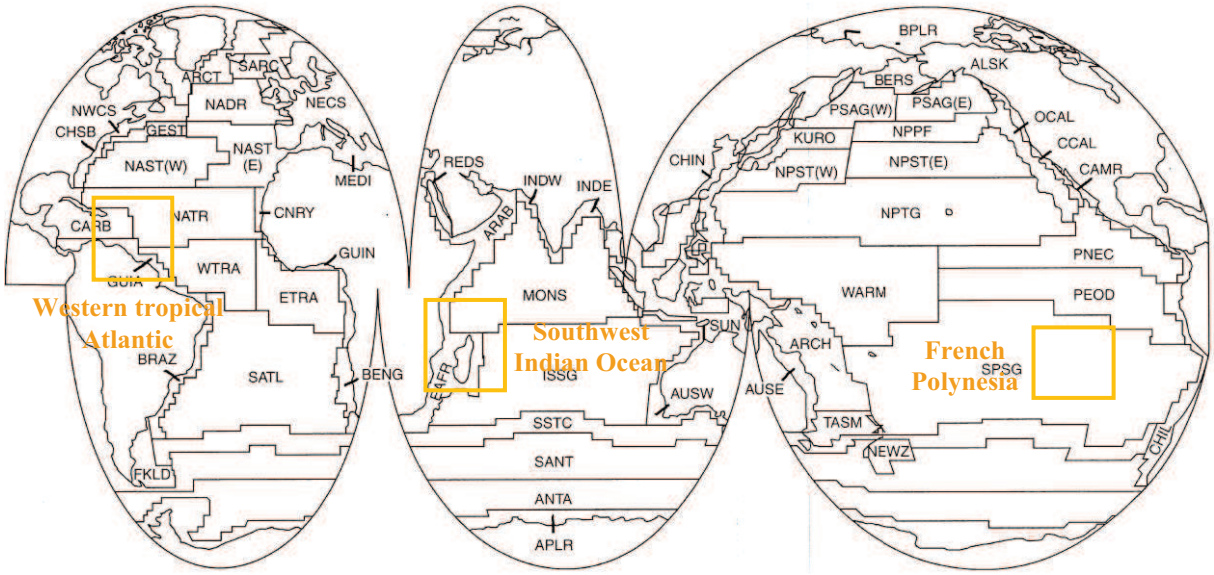


Figure II-10: The biogeochemical provinces of Longhurst (2007). Study regions are indicated in orange boxes.

a) Western tropical Atlantic

In Guiana, the French EEZ (4–9°N, 49–54°W), spanning 132,000 km², extends 200 NM into the Atlantic Ocean, including a broad continental shelf, a slope, which is wider on its western part, and an abyssal plain where depths reach 4500 m. Several rivers open into these waters (Approuague, Oyapock, and Maroni) that are under the influence of the Amazon River plume. As a consequence, extensive mudflats are present along the coast and coastal waters are highly turbid (Froidefond et al. 1988). Local oceanography is strongly influenced by the variability of river discharge which is maximum in May–June and minimum in November.

The Amazon plume is retroflected seaward into the North Equatorial countercurrent during boreal summer (July to December) when the North Brazilian current is at its strongest (Longhurst 2007) (Figure II-11). This results in large and persistent eddies moving into the open Atlantic. Moreover, wind-driven coastal upwelling occurs, as indicated by the presence of cool water in the upper 10 m (Gibbs 1980). Productivity is highly seasonal and maximal in the summer. However, chlorophyll biomass inferred from remote sensing may be unreliable since the color of the water in the river plumes is dominated by dissolved organic matters rather than chlorophyll light absorption (Hu et al. 2004).

The French EEZ in the Antilles (14–19°N, 57–64°W), spanning 143,000 km², extends from Guadeloupe and Martinique Islands, 200 NM into the Atlantic Ocean and 80 NM into the Caribbean Sea and northward around St Barthélemy and St Martin islands. These volcanic islands are characterized by narrow submarine shelves and a steep dropping of the sea floor, especially on their Caribbean side. Despite high biological productivity along the coasts, Caribbean pelagic waters are relatively oligotrophic and characterized by a permanent stratification (Longhurst 2007). The wind regime, influenced by the position of the Intertropical Convergence Zone, has a strong influence on oceanographic processes (Longhurst 2007). The southern Caribbean shelf resembles ecologically the Guiana shelf, with turbid waters from the Guyana current passing along the southern Caribbean (near Trinidad and Tobago) to form the Caribbean current (Johns et al. 1998) (Figure II-11). However, water entering the Caribbean through the Lesser Antilles arc is largely dominated by the flow from the North Equatorial current and its low surface chlorophyll concentration (Borstad 1982). There is a limited yet complex seasonal cycle, with annual and seasonal variability and chlorophyll maxima in both boreal winter and summer (the second possibly induced by the Orinoco discharge plume in the southeastern Caribbean) (Longhurst 2007).

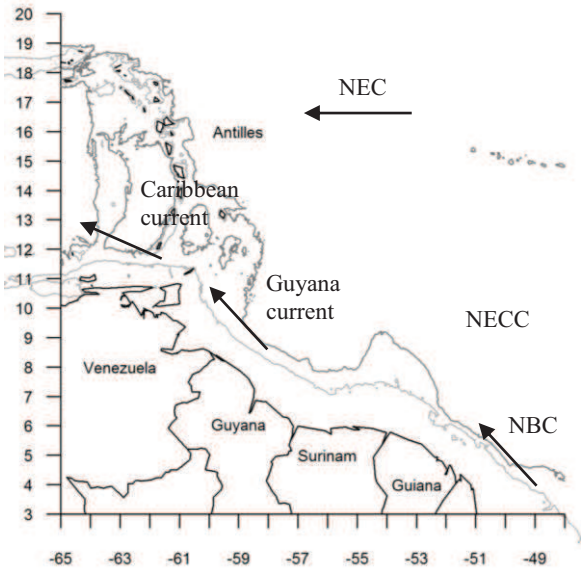


Figure II-11: Main currents in the western tropical Atlantic. The 200m (light grey) and 2,000m (dark grey) isobaths are provided. NEC: North Equatorial current, NECC: North Equatorial countercurrent, NBC: North Brazilian current.

b) Southwest Indian Ocean

The study region covers more than 1.4 million km², and encompasses the EEZ of the five countries of the Indian Ocean Commission: Comoros, Madagascar, Mauritius, Reunion (France) and the Seychelles, as well as waters around the Island of Mayotte and the Scattered Islands. The Indian Ocean is characterized by a seasonal reversal of the monsoon winds and of resulting surface currents (Tomczak and Godfrey 2003). During the Northwest monsoon (austral summer), the East African Coast current meets the Somali current and supplies the South Equatorial countercurrent flowing west-east (Figure II-12). The South Equatorial current (SEC) separates into two branches to the East of Madagascar at *c.* 17°S, generating the Northeast Madagascar current, which flows to the North of Madagascar, and the Southeast Madagascar current (Schott and McCreary 2001). The SEC forms a strong boundary between low nutrient subtropical waters in the South (around the Mascarene Islands) and richer waters to the North (Seychelles plateau) (New et al. 2005), where enhanced productivity is associated to mid-ocean shallow banks (Longhurst 2007).

The Mozambique Channel is characterized by an important mesoscale activity, notably in its central and southern part. A large and permanent anticyclonic eddy is present in the Comoros basin and then, along the coasts of Mozambique, a train of anticyclonic and cyclonic eddies (with diameters of 300 km and a frequency of 4 per year) propagate to the

South (Schouten et al. 2003, De Ruijter et al. 2004). High chlorophyll biomass is almost permanently associated with this eddy field, with slightly higher values in the Northwest monsoon. In addition, nutrient inputs from river discharge on the Northwest coast of Madagascar may induce coastal blooms (Longhurst 2007).

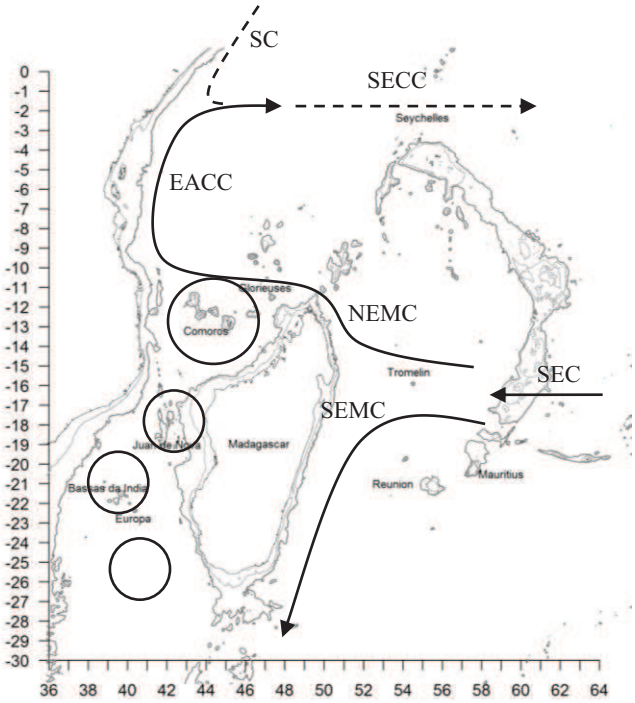


Figure II-12: Main currents in the Southwest Indian Ocean. Intermittent currents are indicated in dotted lines. Circles represent eddies. The 200m (light grey) and 2,000m (dark grey) isobaths are provided. EACC: East African Coast current, SC: Somali current, SECC: South Equatorial countercurrent, SEC: South Equatorial current, NEMC: Northeast Madagascar current, SEMC: Southeast Madagascar current.

c) French Polynesia

The study region encompasses more than 1.7 million km² in the EEZ of French Polynesia and extends over 20 degrees in latitude and longitude. It includes five archipelagos, grossly oriented northwest-southeastward. The largest Tuamotu archipelago comprises a high density network of islands and atolls. It is prolonged to its southeast by the more dispersed Gambier archipelago. The Society and Australs, as well as the Marquesas in the north, form three groups of steep islands separated by deep passages (Martinez et al. 2009).

The South Pacific anticyclonic system, resulting from the pressure difference between Easter Island and the western equatorial zone, is characterized by easterly trade winds that directly influence large-scale oceanic circulation (Rougerie and Rancher 1994,

Reid 1997). This westward flow is deviated by Ekman's rotation, generating a vast anticyclonic gyre. In the gyre, high evaporation induces the formation of hypersaline surface water which sinks in a downwelling process. This phenomenon prevents any upward transport of nutrients and generates a permanent decoupling between the oligotrophic euphotic layer and the nutrient-rich deep layer (Rougerie and Rancher 1994).

This basin-scale hydroclimate drives oceanic circulation in polynesian waters (Figure II-13), generating a strong spatial structuration of oceanographic features. To the north of the gyre, the South Equatorial current flows westward. The SEC follows a seasonal cycle: it strengthens during the austral winter and slows down during the austral summer, while the South Equatorial countercurrent appears (Martinez et al. 2009). The Marquesas form an important topographic obstacle to the SEC, creating turbulent mixing and advection, which, in combination with the iron enriched waters (from land drainage and hydrothermal supplies), creates an island mass effect (Signorini et al. 1999). Therefore, a significant enhancement of phytoplankton production occurs, and is an important contributor to the productivity of this otherwise oligotrophic region. Thus, around the Marquesas, the chlorophyll concentration is higher than 0.2 $mg.m^{-3}$ throughout the year and a seasonal bloom occurs between June and December (Martinez and Maamaatuaiahutapu 2004). As a result of dispersion by SEC, Chl *a* concentration is the highest on the lee side of the archipelago (Signorini et al. 1999). South of the Marquesas, a permanent countercurrent flows eastward in the summer (Martinez et al. 2009).

In southern French Polynesia (south of 17°S), the Subtropical countercurrent (STCC), flows eastward and is characterized by a strong eddy activity which creates westward and eastward perturbations, decreasing to the east. Eddy kinetic energy is maximum in the summer. The regional ocean modeling system highlighted two regions of strong eddy activity: south of 22°S (in the STCC) and north of 6-7°S (the northern part of the SEC); between these regions, mesoscale variability is weak (Martinez et al. 2009).

This oceanic circulation scheme is modified by aperiodic ENSO anomalies. During El Niño (as in 1997-1998), the SEC weakens while the SECC strengthens. During La Niña, due to the strengthening of trade winds, the SEC reinforces and the SECC moves to the southwest. La Niña related blooms are reported around the Marquesas (Martinez and Maamaatuaiahutapu 2004). In addition, during both episodes, the STCC appears to strengthen and the Marquesas countercurrent to disappear (Martinez et al. 2009).

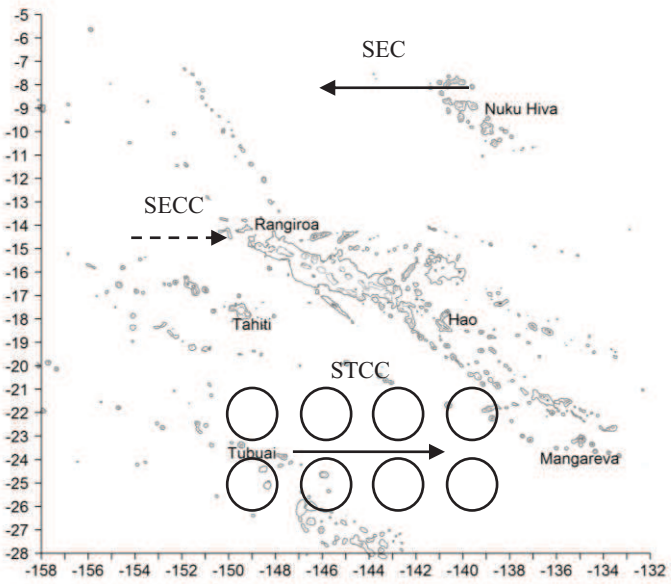


Figure II-13: Main currents in French Polynesia. Intermittent currents are indicated in dotted lines. Circles represent eddies. The 200m (light grey) and 2,000m (dark grey) isobaths are provided. SEC: South Equatorial current, SECC: South Equatorial countercurrent, STCC: Subtropical countercurrent.

3) Energetic guilds

I studied the distribution of a broad variety of top predators within these tropical regions. To deal with the issue of how cetaceans and seabirds with contrasting energetic requirements use pelagic habitats, I classified them into guilds on the basis of their likely relative costs of living, from either direct metabolic measurements or indicators of energetic costs available from the literature.

a) Seabird guilds

Seabirds are easy to observe and to capture in colonies, allowing a variety of metabolic measurements to be made. Basal metabolic rate (BMR) represents the minimal rate of energy expenditure under standard conditions. It is mostly obtained from measurements of oxygen consumption in animals placed within respirometry circuits. Field metabolic rate (FMR) represents the overall cost of daily activities (Ellis and Gabrielsen 2002). It is measured from the doubly labeled water which uses the turnover rate of isotopes of hydrogen (^{2}H or ^{3}H) and oxygen (^{18}O) to determine carbon dioxide (CO_2) production (Lifson and McClintock 1966). To classify seabirds into energetic guilds, I relied on the FMR/BMR ratio, referred to as sustained metabolic scope (Peterson et al. 1990), which is the capacity to

increase metabolism above resting levels. This ratio ranges from 2.8 to 4.2 in tropical seabirds (Ellis and Gabrielsen 2002) (Table II-1). From the most to the least energetically expensive life styles, I obtained the following guilds: tropicbirds, grey terns and noddies, boobies and petrels and shearwaters and the sooty tern. The FMR/BMR ratio was not available for frigatebirds and white terns, as no metabolic measurements exist for these guilds. However, the extremely low wing loading of frigatebirds (large wing area for a comparatively low body mass), suggests much reduced costs of flight (Weimerskirch et al. 2003). Hence, frigatebirds are considered here as the guild with the lowest cost of living. White terns have a wing loading similar to that of noddies (Hertel and Ballance 1999); thus, with respect to flight energetics, I assumed that they were similar to noddies (Figure II-14).

Table II-1: FMR/BMR ratios for tropical seabirds, reported in Ellis and Gabrielsen 2002.

Seabird species	FMR/BMR
White-tailed tropicbird *Phaethon lepturus*	4.2
Common tern *Sterna hirundo*	4.0
Brown noddy *Anous stolidus*	3.7
Wedge-tailed shearwater *Puffinus pacificus*	3.2
Red-footed booby *Sula sula*	3.1
Sooty tern *Onychoprion fuscatus*	2.8

b) Cetacean guilds

In contrast to seabirds, very few direct metabolic measurements exist for cetaceans (*e.g.* Yazdi et al. 1999). Thus, I relied on their diving performances, which are closely related to their capacity to save oxygen by reducing their energetic costs (Boyd 1997). The vast majority of cetaceans observed during the surveys (austral summer) were odontocetes; hence, the classification focuses on this suborder only, simply named cetaceans in the text. Although limited data are available for some species, sperm and beaked whales generally have remarkable abilities for breath-hold diving, reaching depths greater than 1000 m for durations of up to over one hour (Watkins et al. 1993, Tyack et al. 2006). They are considered to have the lowest energetic costs. Globicephalinae generally engage in fairly deep and long dives, as exemplified by the short-finned pilot whale (*Globicephala macrorhynchus*); however, this species, and perhaps other Globicephalinae, has also been reported to use burst and glide strategies when foraging (Aguilar de Soto et al. 2008). Therefore, Globicephalinae are

considered here to form an intermediate energetic guild. Conversely, Delphininae generally engage in shorter and shallower dives no deeper than 300 m (Hooker and Baird 2001, Klatsky et al. 2007) and their foraging tactic largely relies on active swimming, in particular for cooperative feeding (Benoit-Bird and Au 2009). Consequently, in this study Delphininae constitute the guild of cetaceans with the most costly lifestyle (Figure II-14). This classification is supported by indicators of the cost of living based on muscle performance as expressed by muscular mitochondrial density and lipid content (Spitz et al. 2012).

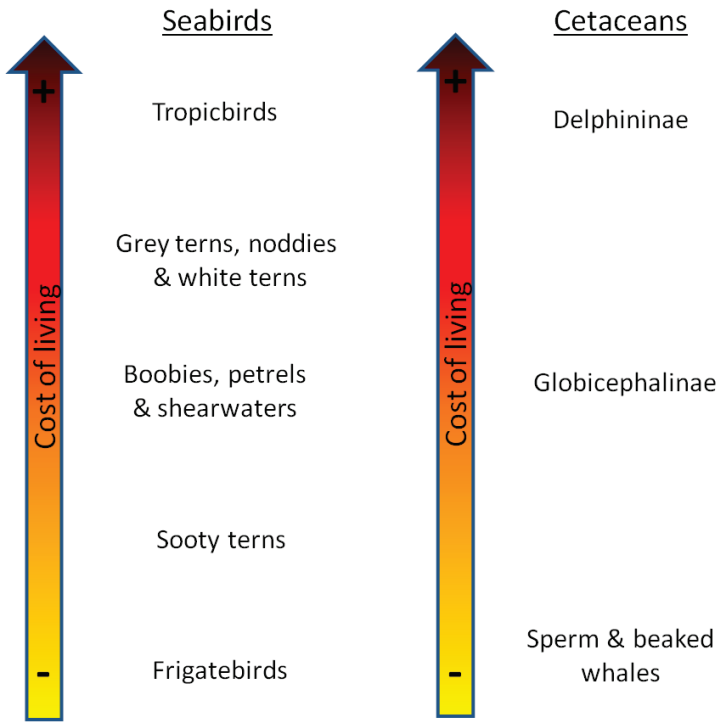


Figure II-14: Classification of seabird and cetacean guilds based on their likely relative costs of living.

The main species composing seabird and cetacean guilds are presented in Figure II-15 and Figure II-16 respectively.

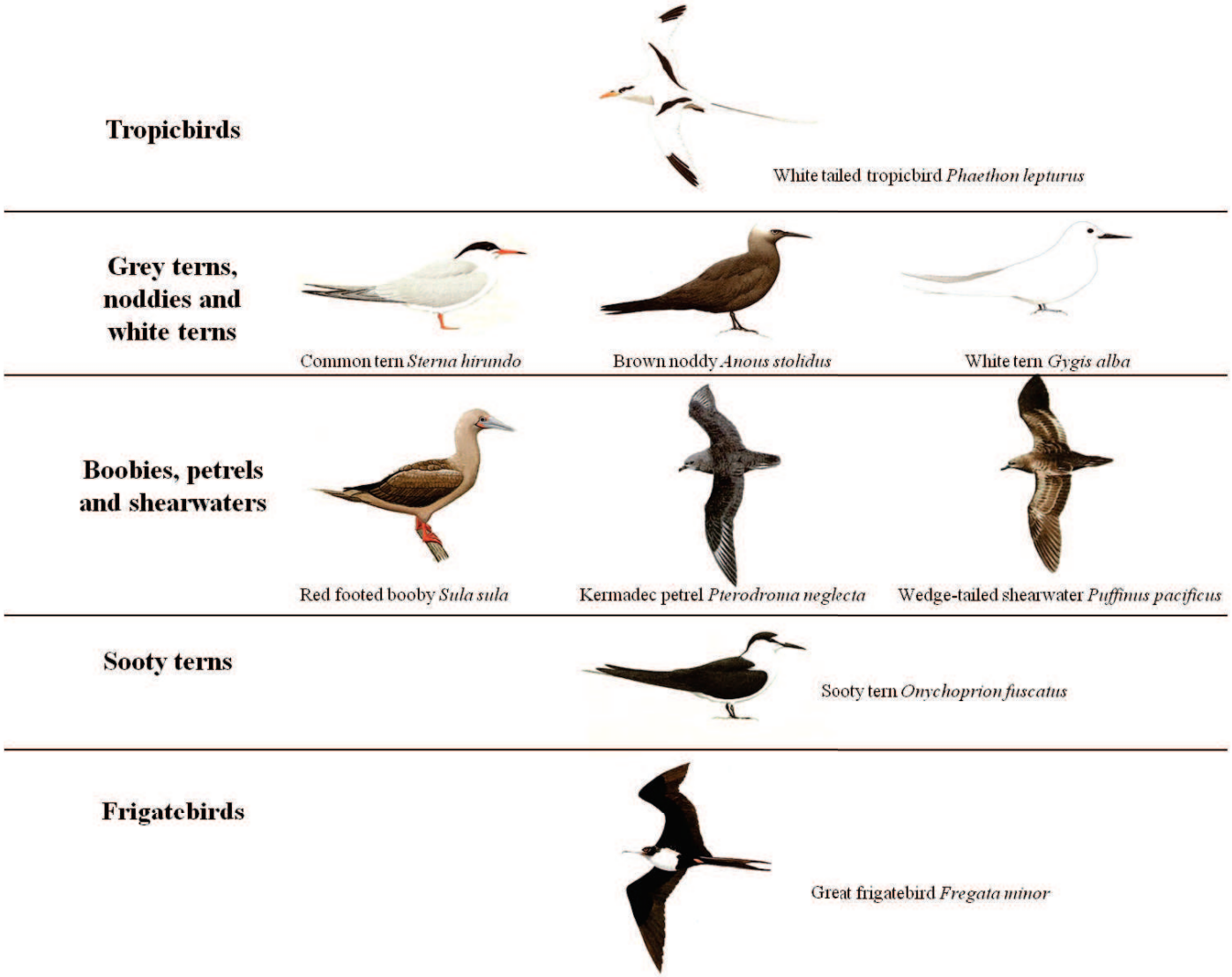


Figure II-15: Main species composing seabird guilds. Drawings from Hoyo et al. 1996 (authors: Ll. Sanz, F. Jutglar, I. Willis, J. Varela). Not to scale.

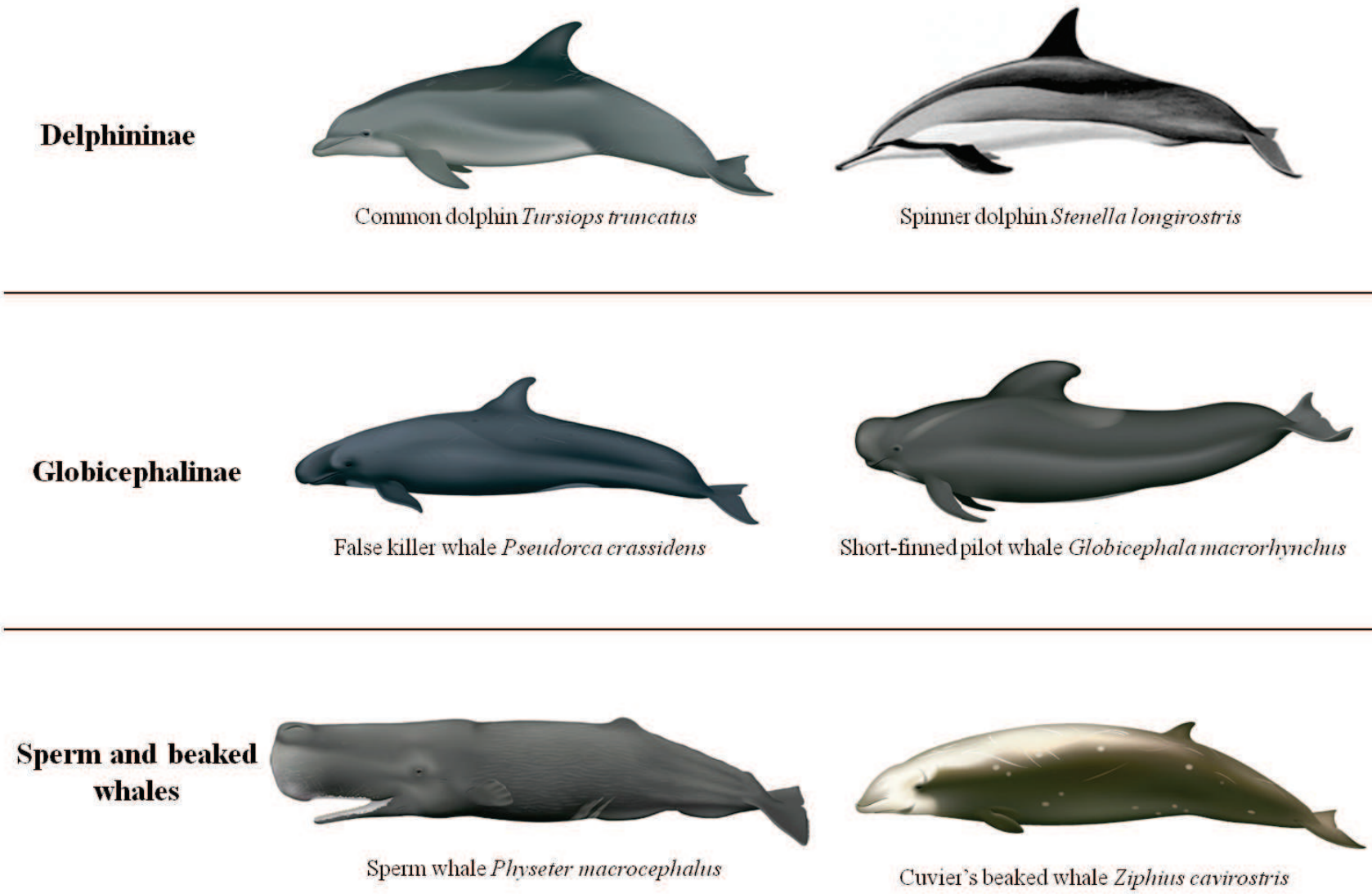


Figure II-16: Main species composing cetacean guilds. Drawings from Uko Gorter (http://www.ukogorter.com) and FAO (spinner dolphin only). Not to scale.

Chapter III. Modeling cetacean and seabird distributions: state-of-the-art

Photo credit: Sébastien Voillot

The framework of species distribution modeling can be described by the three following components: (1) an ecological model, representing the ecological theory being used or tested, (2) a data model, concerning the collection of data and (3) a statistical model, regarding the choice of the statistical methodology (Austin 2002). The success of the modeling exercise is determined by the interactions between these components (Figure III-1). This framework was initially developed for plant ecology in terrestrial ecosystems.

Challenges are inherent to studying top predators in their pelagic environments, with complications arising from survey preparation to development of predictive distribution models. Owing to their three-dimensional nature, their extensive range and their large spatiotemporal variability, logistical constraints are associated with the sampling of pelagic systems (Richardson and Poloczanska 2008). In addition, since most top predators are protected, the collection of data must be non intrusive and conform to legal constraints. Seabirds must return to land for breeding, making them more accessible during this period of their life cycle. Conversely, cetaceans spend most of their time below the surface, making their detection difficult and valid absences hard to determine (Praca et al. 2009). Finally, as wide ranging organisms, surveying these species and modeling their distribution must be performed over large spatial scales. These particularities must be considered in the modeling framework.

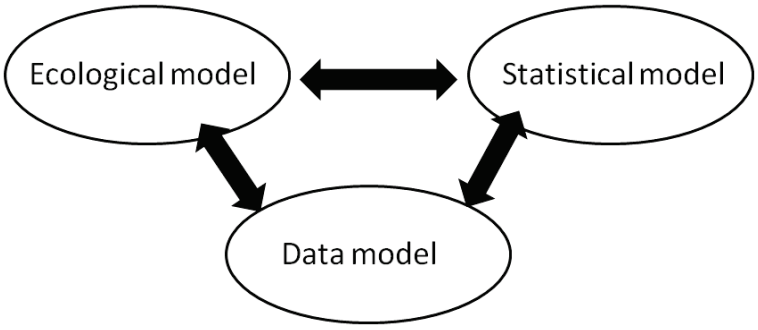


Figure III-1: Framework of species distribution modeling including three interacting components.

1) Ecological model

The ecological model encompasses assumptions on environmental predictors that potentially influence species distributions (Phillips et al. 2006). From a mechanistic point of view, we aim at predicting species distributions from ecological factors that are believed to be the causal driving forces of their distribution (Guisan and Zimmermann 2000). Austin (2002)

distinguishes proximal and distal predictors from their position in the chain of processes linking the predictor to its impact on the organism. Models based on proximal predictors are thought to be the most general and would therefore be applicable over large areas (Vaughan and Ormerod 2003). In practice, it is difficult to obtain sufficient information (notably sufficient coverage) for proximal variables (Austin 2002). Distal predictors potentially provide more robust predictions at coarse spatial scales (Pearson and Dawson 2003).

Top predators are likely to be dictated by availability of mid-trophic level organisms (Frederiksen et al. 2006, Barlow et al. 2009, Benoit-Bird et al. 2013), which constitute proximal predictors of their distributions. Since prey fields are often hard to measure directly, other variables easier to obtain like water depth or slope are commonly used. They represent distal predictors since they are not causally related with animal presence. I review the sources of data for environmental variables and present the main variable categories (from the most distal to the most proximal) for the study of cetaceans and seabirds (Figure III-2).

a) Sources of environmental data

Thanks to sensors carried aboard satellites, we can routinely document environmental conditions at the surface of the oceans at very short time intervals and very small spatial scales (Longhurst 2007). Sensors can be categorized as passive or active. Passive sensors detect the electromagnetic radiation reflected or emitted from natural sources. The measurement of chlorophyll biomass (referred to as ocean color) is based on the water-leaving radiance which depends on the absorption properties of marine components (pure seawater, suspended and dissolved constituents). It is measured by passive spectral radiometers such as Moderate Resolution Imaging Spectroradiometer (MODIS). Sea surface temperature is obtained from passive sensors like the Advanced Very High Resolution Radiometer (AVHRR), sensing in the visible and infrared, through measurement of a brightness temperature (Chassot et al. 2011). Active sensors detect reflected responses from irradiated objects. For example, TOPEX POSEIDON is an altimetry radar measuring the elevation of the ocean surface in relation to the geoid (Longhurst 2007).

Satellite remote sensing has become instrumental for environmental monitoring, with the limitations that clouds affect data acquisition and sub-surface phenomena cannot be described (Chassot et al. 2011). Many studies have successfully related cetacean (Jaquet et al. 1996, Moore et al. 2002) and seabird (Davies et al. 2010, Oppel et al. 2012) sightings with

remotely sensed variables. The contribution of satellite data in seabird habitat studies increased significantly in recent years (Tremblay et al. 2009).

In situ data can provide additional information on sub-surface conditions. Surface and sub-surface parameters can be measured simultaneously with the observation of top predators. They include chlorophyll, temperature, salinity, and parameters describing the water column structure such as thermocline depth or strength (Fiedler and Reilly 1994, Ferguson et al. 2006a, Vilchis et al. 2006, Santora et al. 2011). Some cruises have also sampled zooplankton, using continuous plankton recorders (Sydeman et al. 2010), and micronekton, from trawling (Santora et al. 2011) and acoustic surveys (Hazen and Johnston 2010). Unlike remote sensing, which provides an extensive two dimensional coverage of broad ocean areas, *in situ* data are limited to the sampled area and period (Becker et al. 2010). Nevertheless, their high temporal and spatial resolutions allow species-environment relationships to be modeled at finer scales.

Datasets have been compiled from *in situ* measurements at the global scale. For example, the General Bathymetric Chart of the Oceans (GEBCO) was generated from the compilation of bathymetric sounding datasets. In addition, the increasing availability of ocean property measurements, mainly from instrument profiles and autonomous profiling buoys, allowed the constitution of global climatologies such as CSIRO Atlas of Regional Seas (CARS) (Condie and Dunn 2006). CARS is a climatology of three dimensional properties, including ocean temperature, salinity, and nutrients. These global datasets have been used in biogeographic studies aimed at modeling top predator distributions at large spatial scales (Davies et al. 2010, Sequeira et al. 2012).

Numerical models provide another source of environmental variables. Ocean circulation models, such as the Regional Ocean Model System (ROMS), are three-dimensional models intended for simulating currents, biogeochemical cycles, and sediment movement. ROMS demonstrated its ability to reproduce large-scale structures of currents, as well as mesoscale characteristics at high spatial resolution (Penven et al. 2001, Lutjeharms et al. 2003). Models coupling physical to biological process at lower-trophic levels have also been developed. For instance, Pershing et al. (2009) used a coupled physical-biological model to determine North Atlantic right whale (*Eubalaena glacialis*) habitat relative to their principal prey. Furthermore, end-to-end ecosystem models, developed to represent entire marine ecosystems and their associated abiotic environment are promising. They are achieved

by coupling three sub-models describing the abiotic environment, nutrient and plankton dynamics and higher-trophic levels (Cury et al. 2008). They attempt to represent both bottom-up (physical) and top-down (biological) forces. The Spatial Environmental POpulation DYnamics Model (SEAPODYM) is a two dimensional physical-biological model at the ocean basin scale, initially developed for tunas in the Pacific Ocean (Lehodey et al. 2003, 2010). The quality of these model outputs may increase in the upcoming years thanks to the increasing amount of data available for model parameterization and assimilation.

b) Environmental variables

Physiographic variables

Physiographic variables are static descriptors, such as bottom depth, slope and geographic distances (distance to the shelf break, the coast, the nearest colony for seabirds). Bottom topography interacts with water circulation, influencing the availability of prey through processes of enrichment, concentration and retention (Bakun 1996). Distance to the colony reflects seabird constraints linked to central place foraging. Physiographic variables are commonly used in top predator modeling studies, perhaps because they are readily available and easily handled in Geographic Information Systems. Cañadas et al. (2002) found significant differences in cetacean distributions according to depth and slope in the Mediterranean Sea. Yen et al. (2004a) described seabird and cetacean habitats exclusively from bathymetric variables. Distance to the colony has been successfully used to model seabird habitats during the breeding season (Huettmann and Diamond 2001, Ford et al. 2004).

Physical variables

Variables characterizing physical oceanography are included in this category. It comprises winds (direction, velocity), which drive surface circulation patterns, sea level anomaly reflecting the mesoscale activity, as well as descriptors of water column structure (temperature and salinity profiles, mixed layer depth and thermocline depth). Physical variables may be relevant through their effects on the distribution of water masses, delimiting different oceanographic domains (Longhurst 2007). Cotté et al. (2011) highlighted the influence of oceanic circulation on the seasonal distribution of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea. TewKai and Marsac (2010) noted the importance of mesoscale features for spatial structuring of frigatebirds in the Mozambique Channel. Vilchis

et al. (2006) related seabird distributions in the ETP to the thermal structure of the water column.

Chemical variables

Chemical properties of oceanic waters encompass nutrient and dissolved oxygen contents. Nutrients, such as nitrates and silicates, are the main limiting factors for primary production (Longhurst 2007). The silicate:nitrate ratio (Redfield 1958) is a proxy for the nature of primary producers (Chapter II). Interestingly, in the North Sea, high porpoise densities were predicted in areas of low nitrate concentrations, indicating past phytoplankton blooms (Gilles et al. 2011). Areas of hypoxic waters may occur as a result of high productivity and subsequent strong decomposition. Low oxygen concentrations have notable effects on the distribution of marine organisms, including fishes and squids, vertically compressing their suitable habitat to the upper layer (Prince and Goodyear 2006, Stewart et al. 2012).

Biological variables

Top predators may be more causally related to biological variables, comprising lower (phytoplankton) and mid-trophic levels (micronekton). Surface chlorophyll concentration has been frequently used in cetacean (Jaquet et al. 1996, Ferguson et al. 2006a, Panigada et al. 2008) and seabird habitat studies (Weimerskirch et al. 2004, Louzao et al. 2006, Vilchis et al. 2006). It is a proxy for the biomass of primary producers. However, spatial and temporal lags between regions of high primary and high secondary production are common. Some studies highlighted the coherence between top predators and their prey, mainly at small scales in which data are easier to collect (Baumgartner et al. 2003, Benoit-Bird and Au 2003, Croll et al. 2005). Others found poor or highly variable correlations (Goss et al. 1997, Logerwell et al. 1998, Certain et al. 2011, Fauchald et al. 2011). According to Redfern et al. (2006), predictive models of cetacean distribution would be improved with the inclusion of direct data on prey distribution. However, prey distribution is not always the best predictor of predator spatial patterns. Torres et al. (2008) built fine-scale habitat models of bottlenose dolphins (*Tursiops truncatus*) in a coastal bay of Florida, but the spatial variability of prey patches precluded the success of predictive models. Ecosystem models, predicting the biomass of mid-trophic functional groups at large spatial scale (Lehodey et al. 2010), can overcome limitations related to the sampling of micronekton.

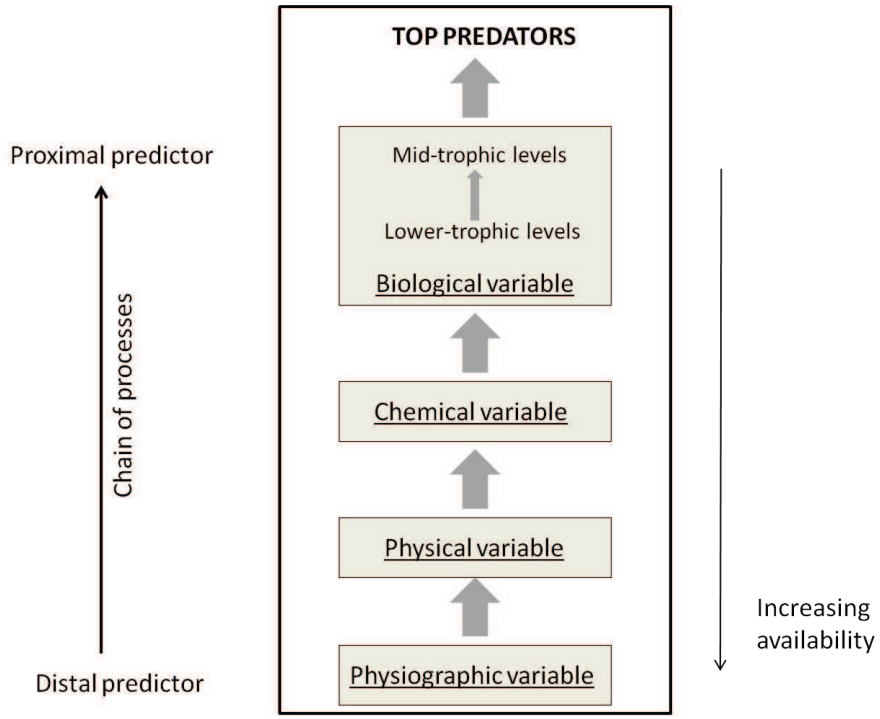


Figure III-2: Variable categories positioned according to their impact on top predators through the chain of processes.

2) Data model

Data used for species distribution modeling can be of three types (Anderson 2012):

Presence-only data which contain records of where a species has been observed but lack information about sites where it is absent.

Presence-absence data which contain records of where a species has been observed, as well as sites where it is absent (or assumed to be) despite sampling efforts.

Abundance data which also contain records of the species abundance at the sites where it has been observed.

Distribution maps of cetaceans and seabirds have been proposed based on presence-only data obtained at low costs from incidental sightings, strandings collected by networks of volunteers and the professional judgment of experts (*e.g.* MacLeod et al. 2005). Presence-only data have been used to infer broad species ranges using envelope models (Kaschner et al. 2006). In order to obtain higher quality data for more elaborated species distribution modeling, recording of effort, absences, group sizes, as well as factors influencing species

detection are required. I describe three methods for collecting data on spatial distributions of cetaceans and seabirds: non dedicated surveys, dedicated surveys and tagging studies. In each case, I point out the spatial and temporal scales (Figure III-3), the type of data collected and the inferences that can be made from these data (Figure III-4).

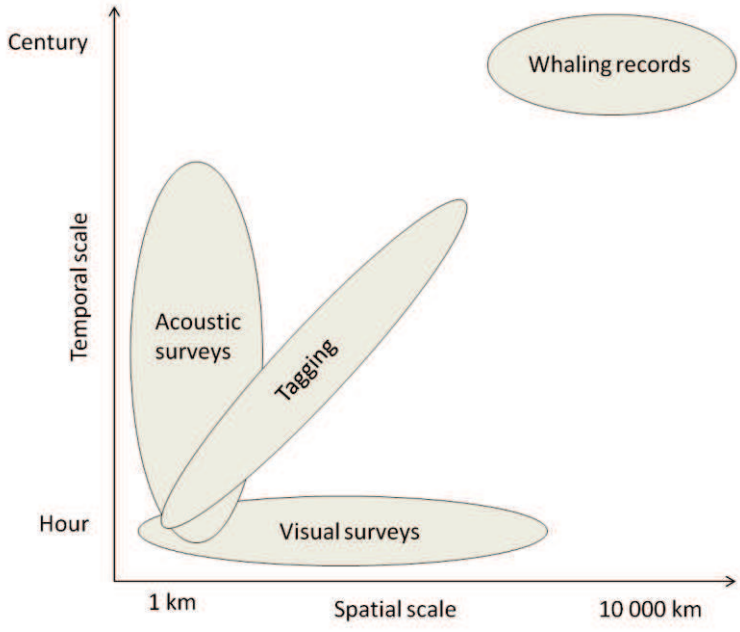


Figure III-3: Diagram showing the temporal and spatial scales for the collection of top predator data. Whaling records have broad spatial and temporal scales. Visual surveys can have a broad spatial extent but are often limited in their temporal extent. Acoustic surveys, although having a limited spatial extent, may encompass a long period of time. Tagging provides data on a range of temporal and spatial scales.

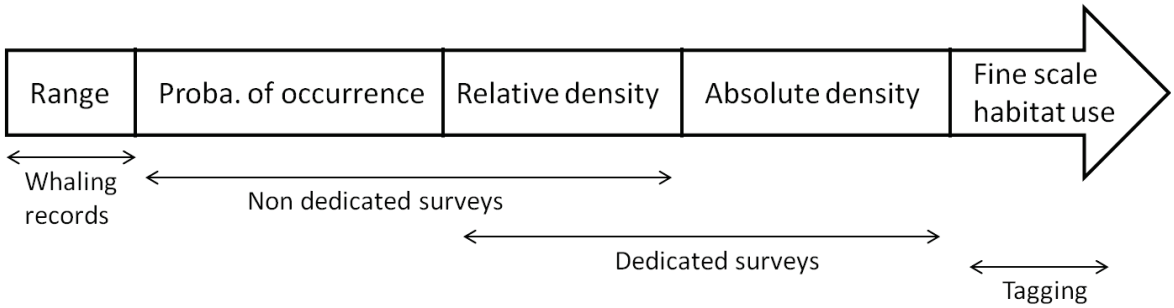


Figure III-4: Inferences that can be made from the different data collection methods. Cetacean ranges can be inferred from whaling records. Probability of occurrence is inferred from non dedicated surveys yielding presence-only data. Relative density is estimated from presence-absence data collected from dedicated and non dedicated surveys (when a standard protocol is applied). When the impact of both perception and availability bias on detection probability is known, absolute density can be inferred. Fine scale habitat use of individuals is estimated from tagging studies.

a) Non dedicated surveys

Surveys can be conducted from non dedicated platforms such as ferries, whale watching boats, fishing vessels, the so-called platforms of opportunity. For example, Cotté et al. (2010) took advantage of ferries routinely crossing the western Mediterranean Sea to collect cetacean data to build habitat models. Zador et al. (2008) used a database of albatross sightings collected by fishers, fisheries observers, biologists and birdwatchers, to determine their overlap with the Alaskan trawling fleet. Platforms of opportunity are a cost effective mean of collecting large amounts of data on top predator ecology (Redfern et al. 2006). The variable reliability of observations (for example expertise of observers regarding species identification (Moura et al. 2012) and the lack of control over the survey design are their main limitations (Evans and Hammond 2004, Redfern et al. 2006).

Platforms of opportunity provide presence-only data to infer probability of occurrence (Moura et al. 2012, Thorne et al. 2012). If rigorous survey protocols are applied by trained observers, including the record of survey effort, school sizes and meteorological factors potentially affecting detection conditions, presence-absence data are collected and relative density can be inferred (Zador et al. 2008, Cotté et al. 2010).

Commercial whaling records represent one of the largest opportunistic datasets for cetacean occurrence, spanning two centuries and approximating global coverage (Kaschner et al. 2006). Jaquet et al. (1996) used catch and sighting data from the US whaling industry to evaluate the historical distribution of sperm whales in the Pacific. However, whaling data often tells more about the distribution on whaling effort than about actual whale distribution. Whaling records have been used to make inferences on cetacean ranges (Jaquet et al. 1996).

b) Dedicated surveys

Visual surveys

Surveys are typically conducted from dedicated platforms. Cetaceans and seabirds are most commonly surveyed from vessels (Forney 2008, Tremblay et al. 2009). A variety of vessels may be used; small vessels are usually restricted to coastal areas. Moreover, *in situ* oceanographic data can be collected along with top predator data. High operating cost is often associated with these surveys. Behavioral responses of individuals to the vessel (avoidance/attraction) are another limitation for both cetaceans (Barlow et al. 2001) and

seabirds (Griffiths 1982). Aerial surveys have the ability to quickly cover extensive areas with a better cost effectiveness, making an efficient use of good weather windows. Aerial surveys have proven to be useful for rapid assessments of relative distribution and abundance of top predators in a study region (*e.g.* Leeney et al. 2012). Platform speed is sufficiently high for animal movement not to be considered. However, the high speed offers less time for detecting, estimating group sizes and identifying the species (Forney 2008).

Data can also be collected at relatively low cost from fixed observation points such as headlands, islands or oil rigs. In this case there are no complications arising from the movement of the observer. However coverage is limited to the immediate vicinity of the observation point and information that requires close proximity to animals is hard to collect (Evans and Hammond 2004).

When a platform is dedicated to a survey, a survey design can be implemented, in the limit of financial and logistical constraints. For this, the objectives of the study (estimation of abundance, comparison of densities, trend analysis) have to be clearly considered (Buckland et al. 2001). Surveys can be conducted according to a random (*e.g.* Vilchis et al. 2006) or systematic (*e.g.* Certain and Bretagnolle 2008, Gilles et al. 2011) survey design. In some cases, non systematic designs have been implemented to maximize encounters with cetaceans (Panigada et al. 2005). Systematic surveys, providing homogeneous coverage of the area (each point has an equal probability of being sampled) are necessary when the objective is abundance estimation (Evans and Hammond 2004). Systematic designs may include sets of equally spaced parallel lines (*e.g.* Gilles et al. 2011) or regular zigzag pattern lines (*e.g.* Williams and Thomas 2007). The later is often preferred as it allows continuous survey effort since no time is lost travelling between lines (Buckland et al. 2001, Strindberg and Buckland 2004). When previous knowledge of the area is available, a stratified survey design may be implemented (*e.g.* Williams and Thomas 2007). In this case, more effort should be allocated in areas where animal densities are expected to be higher to reduce variance of the overall estimate of abundance (Buckland et al. 2001). In practice, the actual survey design is a compromise between the theoretical sampling scheme and logistical considerations such as weather conditions, locations of ports and airports for refueling, or technical breakdowns (Redfern et al. 2006).

Cetaceans and seabirds are sampled at-sea following two methodologies:

Strip transect sampling

Observers travel along a line, recording all animals within a strip of known width. The critical assumption is that all animals within the strip are detected. Narrow strips may be necessary to ensure this holds to a good approximation (Tasker et al. 1984, Buckland et al. 2001). The strip transect methodology have been broadly used to census seabirds (Vilchis et al. 2006, Certain and Bretagnolle 2008, Sydeman et al. 2010).

Line transect sampling

Observers record animals while travelling along a line, as well as the distance from the line of all detected animals. Hence, all animals are recorded regardless of how far they are from the line. It relies on several assumptions: animals are distributed independently of lines, animals on the line are detected with certainty, they are detected at their initial locations and distances are measured accurately (Buckland et al. 2001). This methodology is more efficient than strip transect sampling for sparsely distributed objects since sample size is larger for the same amount of effort. Recording distances allows to model the decrease of detection probability with distance from the line and estimate abundance (distance sampling analysis) (Buckland et al. 2001). Line transect sampling has been used in most cetacean surveys (Ferguson et al. 2006a, Cañadas and Hammond 2008, Becker et al. 2010, Gilles et al. 2011).

Dedicated surveys typically provide presence-absence or abundance data and have been used to infer probability of occurrence (*e.g.* Panigada et al. 2008) or relative density (*e.g.* Certain et al. 2008). If the objective is to estimate absolute densities (*e.g.* Ferguson et al. 2006a, Redfern et al. 2008), it is critical to consider the impact of both perception and availability bias on detection probability. Failure of observers to detect animals that are available for detection generates perception biases (Pollock et al. 2006). They are affected by species-related factors (group size, behavior), survey conditions (Beaufort Sea state, glare, swell) and the observers themselves (Barlow et al. 2001). Perception biases also arise when multiple species are sampled together, cryptic species being underestimated compared to the more visible ones (Ballance 2008). Perception bias can be estimated using a tandem team of two observers on either side of the aircraft (Pollock et al. 2006). In contrast, availability bias arises when animals are submerged and thus unavailable for detection while the survey platform passes by Pollock et al. (2006). It is affected by the proportion of time spent at the

surface (Redfern et al. 2006). It can be estimated by using a double platform methodology (for example two aircrafts flying in tandem, (Hiby and Lovell 1998), by deploying time depth recorders on individuals (Pollock et al. 2006) or observing diving behavior (Laake et al. 1997).

Dedicated surveys aim at gathering rich datasets, including the record of effort, group size and detection conditions. However, they require substantial financial resources, which may constrain their spatial and temporal extent. Proper training of observers must also be considered with care in order to obtain accurate data (Evans and Hammond 2004).

Acoustic surveys

In addition to visual surveys, the presence of cetaceans may be also recorded indirectly from dedicated acoustic surveys. Acoustic surveys are increasingly being undertaken in conjunction with visual surveys, and the use of passive acoustics has been considered an important tool to increase datasets (Praca et al. 2009, Pirotta et al. 2011). Acoustic detections are less dependent of sea conditions than visual detection. In addition, data can be automatically collected and are less susceptible to variability in skills and experiences between operators. On the other hand, the non detection of silent animals (generating false absences), the unclear relationship between vocalization rates and cetacean densities, as well as the costs of equipments are disadvantages of acoustic surveys (Evans and Hammond 2004). However, autonomous instruments can continuously record acoustic data from vocalizing whales over long time periods (*e.g.* Wiggins 2003). They provide presence-only data over fairly large spatial and temporal scales (Redfern et al. 2006).

Tagging

Individual tagging studies yield data for species distribution modeling at a range of temporal and spatial scales (Hooker and Baird 2001). Contrary to at-sea surveys, providing information on top predators at the community level as the platform moves, electronic tags document top predators at the individual level as they move through space and time (Ballance 2008). In electronic based methodologies, tags are attached to the animal in order to calculate their locations. Satellite tracking using Argos transmitters is commonly used for both seabirds and cetaceans. Woodworth et al. (2012) instrumented melon-headed whales (*Peponocephala electra*) with Argos transmitters to investigate the influence of offshore eddies on their horizontal movements close to the Hawaiian Islands. Weimerskirch et al. (2004) also used

Argos transmitters to examine the foraging strategy of frigatebirds in the Mozambique Channel. For seabirds, the lighter Global Positioning Systems are commonly used, in particular for tracking small species (Pettex et al. 2012, Harding et al. 2013). In addition, the utilization of Global Location Sensors recording light levels has recently increased (Fort et al. 2012, Le Corre et al. 2012). The use of time-depth recorders permitted to investigate the diving behavior and time budgets of both cetaceans (Baumgartner and Mate 2003) and seabirds (Regular et al. 2013).

Tagging studies allow fine-scale data to be obtained on top predator individual locations, behavior, migration and habitat use. Density contour plots from kernel estimates are frequently computed to visualize densities of animal positions (Weimerskirch et al. 2004, Edren et al. 2010, Fort et al. 2012). However, tagging only provides data in the areas used by the animals, typically yielding presence-only data (Aarts et al. 2008). In addition, tags may have deleterious effects on individuals, including foraging behavior, time budgets or energetics (Vandenabeele et al. 2011). They sometime result in small sample sizes and may sample only a limited range of environmental variability, corresponding to conditions that facilitate tag deployment. Consequently, extrapolation of the results to populations and assessment of habitat preferences must be done with care (Redfern et al. 2006).

3) Statistical models for predicting cetacean and seabird distributions

The spatial distribution of animals results from different factors acting in parallel or interactive ways over different scales of space and time. It may result from both exogenous and endogenous ecological processes (Wagner and Fortin 2005). The response to spatially structured environmental factors generates exogenous spatial dependence in species distributions. Typically, physical processes such as climate create spatial structure in the environment, inducing deterministic structure in animal distributions. Thus, spatial distribution of species reflects their habitat preferences.

Endogenous ecological processes operating between neighboring individuals are inherently spatial and generate autocorrelation. For instance, social interactions between organisms, such as competition (Ballance et al. 1997) or local enhancement (Davoren et al.

2003a), yield patchiness in their distributions. In this respect, spatial distribution of animals also results from demography and population dynamics (Figure III-5).

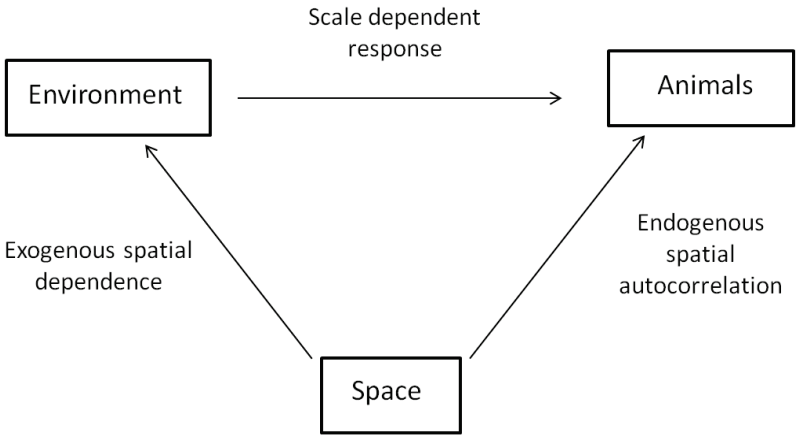


Figure III-5: Exogenous and endogenous ecological processes in species distribution, from Wagner and Fortin 2003.

Species distribution models (SDMs) relate species distribution data (occurrence or abundance at known locations) with information on environmental and/or spatial characteristics at these locations through statistical function, in order to map species distribution across a study region (Elith and Leathwick 2009). There are two kinds of SDMs. First, SDMs can be based exclusively on environmental predictors, modeling variation in occurrence or abundance of a species in an environmental space. We refer to environmental SDMs or habitat models (ecological niche factor analysis, maximum entropy modeling, generalized additive models…). Then, SDMs can be purely spatial, modeling species variation in occurrence or abundance in a two dimensional geographic space. In this case, we refer to spatial SDMs or spatially explicit models (kernel density estimators, geostatistical methods based on kriging…).

Variance in species distribution can be partitioned into several components (Wagner and Fortin 2005), as illustrated in Figure III-6: (1) purely environmental effects (explained, not spatially structured), (2) overlap of spatial and environmental effects (explained, spatially structured), (3) purely spatial effects (explained, spatially structured), (4) remaining variance (unexplained, not spatially structured). Environmental SDMs focus on components (1) and (2), whereas spatial SDMs focus on components (2) and (3). In practice, we want to increase the spatially structured component of variance and reduce its unexplained part.

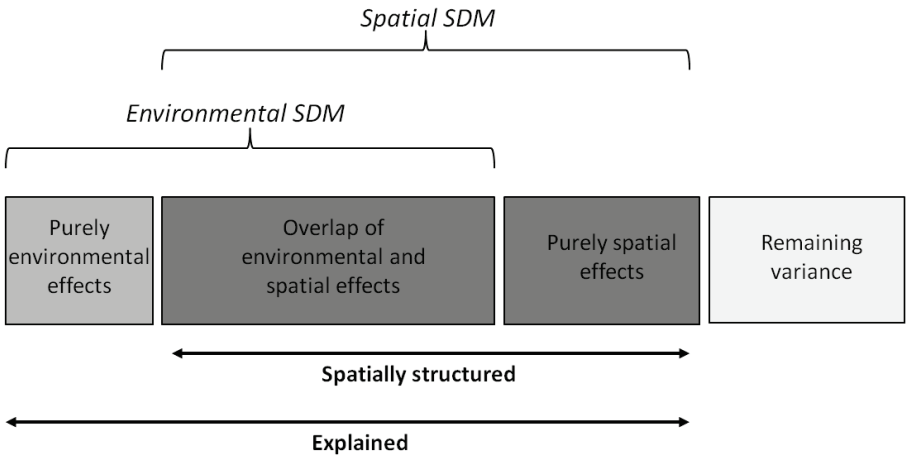


Figure III-6: Variance partitioning in species distribution models, from Wagner and Fortin 2005.

I present methods in environmental SDMs and spatial SDMs. Without making an exhaustive review, I introduce the objectives and assumptions of some methods classically employed to model cetacean and seabird distributions.

a) Habitat models

Habitat models assume environmental processes are dominant in species distributions (Elith and Leathwick 2009). It is believed that species aggregate as a result of exogenous environmental variables (Robinson et al. 2011). Since the spatial component is assumed to be included in environmental predictors, these models have been referred to as spatially invariant. Indeed, permuting the latitude/longitude coordinates will not change species- environment relationships (Guisan et al. 2006). The aim of habitat models is to model species-environment relationships in order to provide spatial predictions for a study area. Potential environmental predictors, sometimes known a priori, provide explanatory power. Modeling is done through the following steps: calibration, prediction, evaluation and quantification of uncertainty (Redfern et al. 2006). An important assumption is equilibrium (or at least pseudo-equilibrium) between species and their environment. This implies that species can potentially occur in all environmentally suitable locations (Barry and Elith 2006). Thus, the success of habitat models will depend on the degree to which history and disturbance are important in the system under study (Austin 2002). Habitat models differ by the quality of data needed for their calibration; they can be divided into presence-only and presence-absence methods.

Presence-only methods

Presence-only methods allow to use data when information on absences is unavailable or inadequate. Although they have several limitations, presence-only methods can be helpful for analyzing the distribution animals in the pelagic environment, where true absences can be difficult or impossible to obtain. Specifically, presence-only methods have proven to be useful for modeling species distribution when detectability is low (Praca et al. 2009). Basically, presence-only methods compare the environmental conditions of the sites where a species has been recorded with those of the study region.

Environmental envelope models

Envelope models generate predictive maps of species distribution based on the environmental characteristics of the sites where the species was recorded (*e.g.* DOMAIN, Carpenter et al. 1993). Species records are projected into a multidimensional space defined by a set of environmental variables (the environmental envelope), which is then projected into a two dimensional geographic space (*i.e.* a map). Fitted envelopes are generally multidimensional, ranging from simple rectilinear, trapezoidal, to more complex shapes (Farber and Kadmon 2003).

Kaschner et al. (2006) used envelope models to predict the average geographical ranges of 115 marine mammals. Species were assigned to broad scale niche categories based on a synthesis of available knowledge as well as expert knowledge. Potential relative environmental suitability was determined by relating broad scale niche categories to environmental conditions over the map. Envelope models are useful for investigating current knowledge about large scale distributions for a broad range of species, especially data poor species. The strengths of these models are their simple theoretical basis, their objectivity and generic applicability. However, due to their broad and static nature, they should only be applied to investigate large scale distributions (Redfern et al. 2006).

Ecological niche factor analysis

Ecological Niche Factor Analysis (ENFA) strongly relies on the concept of the ecological niche, defined as a hyper-volume in the multidimensional space of ecological variables within which the species can persist (Hutchinson 1957). ENFA computes habitat suitability maps by comparing the niche occupied by a species in the environmental space

with a reference set describing the whole study area (Hirzel et al. 2002). The multivariate niche is quantified by an index of marginality (referring to niche position) and an index of specialization (referring to niche width). ENFA extracts one axis for marginality and several axes for specialization. Outputs have intuitive ecological meaning, allowing direct comparisons between the niches of different species (Hirzel et al. 2002). However, when the species do not occupy all suitable habitats, ENFA tend to model many absences within the suitable habitat (Brotons et al. 2004).

Praca et al. (2009) modeled habitat suitability of three teuthophageous species in the northwestern Mediterranean Sea using ENFA. According to the authors, ENFA is very useful as a first attempt to estimate the suitability of an area from small datasets.

Maximum entropy modeling

The Maximum Entropy method (MaxEnt) is a machine learning method based on the concept of entropy, a measure of how much 'choice' is involved in the selection of an event (Phillips et al. 2006). A distribution with higher entropy involves more 'choices' and is thus less constrained. MaxEnt uses maximum likelihood to estimate a target probability distribution, by finding the probability distribution of maximum entropy according to a set of constraints. The probability distribution is defined over the pixels of the study area (background area) and over pixels of known presences (sample points). The constraints represent information on environmental variables at the presence sites. The expected value of each environmental variable should match its empirical average over the sample points. MaxEnt uses regularization techniques to prevent overfitting (Phillips et al. 2006). Elith et al. (2011) provided an accessible description of the MaxEnt algorithm. Advantages of MaxEnt include its ability to deal with a limited amount of information, to incorporate both continuous and categorical data and its efficient deterministic algorithms (Phillips et al. 2006). However, it is recommended to provide appropriate background samples, to deal with sample biases, and to carefully tune the model according to the data (Elith et al. 2011).

MaxEnt is increasingly being used to model habitat suitability of cetaceans (Edren et al. 2010, Moura et al. 2012, Thorne et al. 2012) and seabirds (Arcos et al. 2012) based on presence-only data (Figure III-7). Thorne et al. (2012) pointed out the utility of MaxEnt for predicting cetacean distribution in regions where sparse systematic surveys did not provide reliable effort and absence data, but where a quantitative analysis of the population is needed.

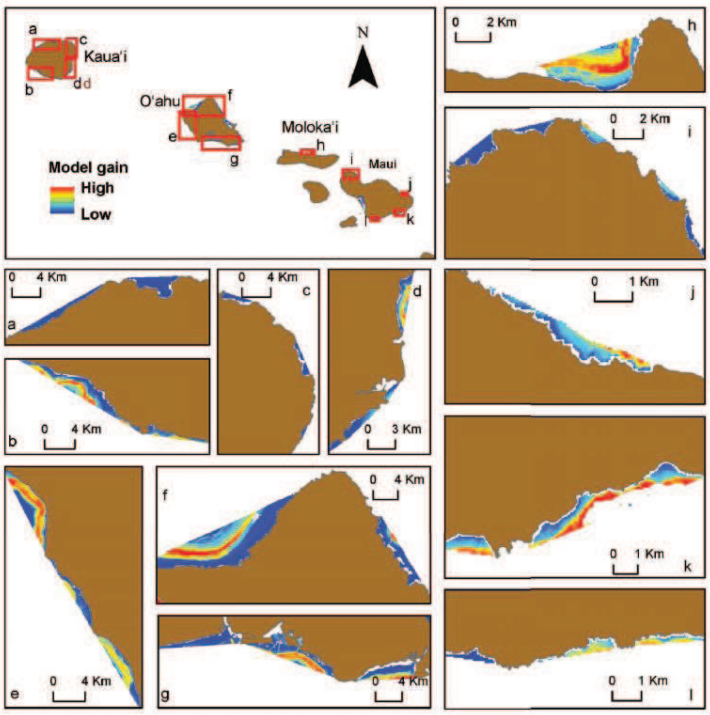


Figure III-7: Example of MaxEnt outputs showing spinner dolphin resting habitat in several bays of the Hawaiian Islands, from Thorne et al. 2012.

Presence-only data have several limitations. First, species prevalence (proportion of presences) cannot be determined from presence-only data. Sample selection bias (when some areas are more intensively sampled than others) is another serious limitation. It must generate a model that combines species distribution with the distribution of effort. In addition, the data do not describe the survey method (species records are not associated with information on search time or search area). This yields difficulties when defining the response variable (Elith et al. 2011). Consequently, if systematically collected presences and absences are available, it is always advised to use presence-absence methods (Brotons et al. 2004, Elith et al. 2011).

Presence-absence methods

Ordination techniques

Ordination techniques arrange species along environmental gradients. The ultimate aim is to summarize complex multivariate datasets into fewer dimensions. They have been widely used to explore relationships in community ecology (Dale 1975, Austin 1976). Canonical Correspondence Analysis (CCA) is an eigenvector ordination technique which relates community composition to variation in the environment. Species are ordinated along axes, constrained to be linear combinations of environmental variables. It assumes unimodal

and symmetrical responses of species. CCA seem relatively robust to violations of these assumptions (Ter Braak 1986). The outputs of CCA are given in biplots which permit direct interpretations of species-environment relationships between. Species are represented by points plotted at the centroids of the sampling sites; the further the points are from the origin, the more informative the ordination. Environmental variables are represented by arrows with lengths proportional to the importance of the variable in the community distribution (Ter Braak 1986). The major drawback of CCA is that the relevant environmental variables are assumed to be measured.

Although other ordination techniques exist (such as redundancy analysis), CCA has been the most commonly used to investigate cetacean and seabird community ecology. (Griffin and Griffin 2003) used CCA to partition habitat among Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Ballance et al. (2002) investigated temporal patterns in seabird habitat preferences in the eastern tropical Pacific using CCA. For some species the analysis explained a high proportion of variance and there were clear associations with water masses.

Regressions

Regressions relate a response variable to a single or a combination of environmental predictors. They encompass various techniques distinguished by their assumptions and the functional forms of the relationships (Table III-1). In classical linear regression, the regression is a linear function of the predictors. It assumes a Gaussian distribution for the response variable and a constant variance. Estimation is done using least square minimization (Guisan and Zimmermann 2000, Guisan et al. 2002).

Generalized Linear Models (GLMs) are mathematical extensions of linear models. They allow non Gaussian distributions for the response variable and non constant variances (*i.e.* overdispersion). When the response variable is binary (presence-absence), a Binomial distribution is used; when the response variable is a count, the Poisson distribution is used. A link function relates the linear predictor to the mean of the response variable. It allows transformation to linearity and constrains the response within the range of observed values. Estimation is often based on maximum likelihood. In case of a non linear response, parametric transformations of the predictor (*e.g.* polynomial) can be included in the model (Guisan and Zimmermann 2000, Guisan et al. 2002).

Table III-1: Overview of regression methods.

	Linear models	**Generalized linear models**	**Generalized additive models**
Distribution of the response variable	Gaussian	Gaussian, Binomial, Poisson, Gamma…	Gaussian, Binomial, Poisson, Gamma…
Relation between the response and the linear predictor (link function)	Identity	Identity, log, logit…	Identity, log, logit…
Formula	$Y_i = \alpha + \sum \beta_j X_{ij} + \varepsilon_i$ n observed values (i=1,…,n) k predictor variables (j=1,…,k) α: intercept ε_i: error term Y_i: response X_{ij}: predictor variables	$g(E(Y_i)) = \alpha + \sum \beta_j X_{ij} + \varepsilon_i$ n observed values (i=1,…,n) k predictor variables (j=1,…,k) α: intercept ε_i: error term Y_i: response X_{ij}: predictor variables $g()$: link function	$g(E(Y_i)) = \alpha + \sum \beta_j f_j(X_{ij}) + \varepsilon_i$ n observed values (i=1,…,n) k predictor variables (j=1,…,k) α: intercept ε_i: error term Y_i: response X_{ij}: predictor variables $g()$: link function $f_j()$: non parametric smoothing functions
Assumptions	- residuals independently and identically distributed - residuals follow a Gausian distribution - constant variance of the response variable - regression function linear in the predictors - independence among observations	- parametric relationships between the response and the predictors - independence among observations	- predictors are additive - non parametric relationships between the response and the predictors (smoothing functions) - independence among observations
Estimation technique	Least square minimization	Maximum likelihood	Penalized maximum likelihood

Generalized Additive Models (GAMs) are semi parametric extensions of GLMs. They rely on the specification of a link function and a distribution for the response variable but predictors are modeled non parametrically. In addition predictors are additive. The selection of an appropriate degree of smoothness for the predictors is critical. There must be a tradeoff between the number of observations and the number of degrees of freedom. GAMs have the ability to deal with non linear and non monotonic relationships between the response and the predictors; they are often referred to as data driven. They are prone to overfitting and outputs may sometimes be difficult to interpret ecologically (Guisan and Zimmermann 2000, Guisan et al. 2002). All regression techniques assume independence among observations; this is violated when spatial or temporal autocorrelation is present in the data.

Regressions have been commonly used to model cetacean distributions based on environmental variables to answer both fundamental and applied questions (Redfern et al. 2006). Becker et al. (2010) used GLMs and GAMs to predict cetacean densities off California and compared the performance of models built with remotely sensed and *in situ* data. Embling et al. (2010) used GAMs to predict relative densities of harbor porpoises (*Phocoena phocoena*) off Scotland (Figure III-8). High density areas, best explained by tidal currents, were proposed as suitable for Special Areas of Conservation. Panigada et al. (2008) modeled the presence-absence of fin whales in the Mediterranean using Binomial GAMs coupled with Generalized Estimating Equations to account for the temporal and spatial autocorrelation in their datasets.

Regressions have been a frequent tool to model seabird distributions (Tremblay et al. 2009). The habitats of six feeding guilds were modeled in the eastern tropical Pacific using Poisson GAMs (Vilchis et al. 2006). Weimerskirch et al. (2010) used binomial GAMs to explore functional relationships between environmental variables and foraging *vs* non foraging frigatebirds in the Indian Ocean. Their results indicated foraging hotspots at the edge of mesoscale eddies.

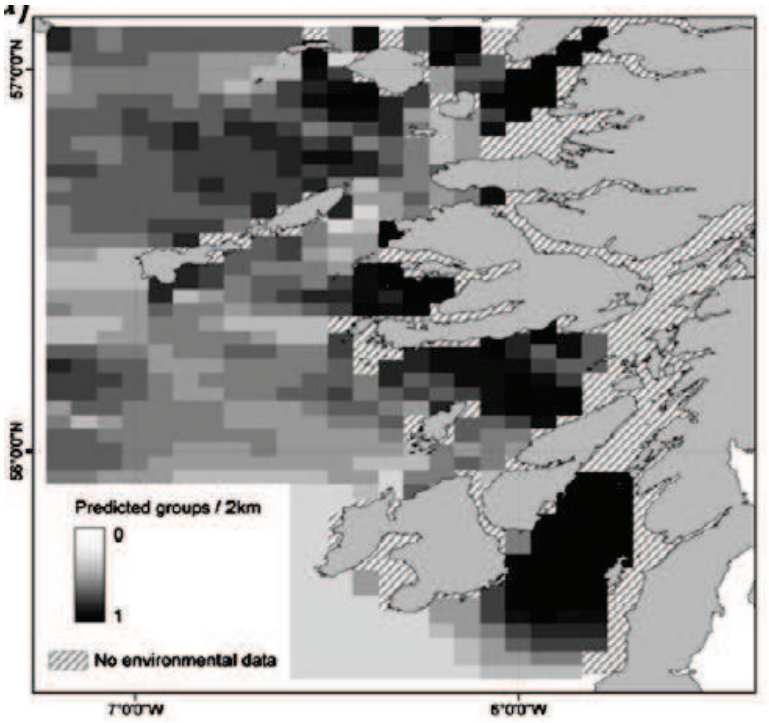


Figure III-8: Harbor porpoise densities predicted from GAMs in Southwest Scotland, from Embling et al. 2010.

Classification and regression trees

Tree models aim at explaining the variation of a response variable by repeatedly splitting the data into homogeneous groups, using combinations of categorical (classification trees) or numeric (regression trees) explanatory variables (De'ath and Fabricius 2000). Trees are fitted via binary recursive partitioning. A parent node is split into two child nodes and each child node becomes in turn a parent node (unless it is a terminal node). They can be used for interactive exploration and prediction of patterns and processes based on complex ecological data. They can handle a broad range of response types, accommodate missing data, fit complex nonlinear relationships and deal with interactions between predictors. They are easy to construct and interpret, representing an alternative to non parametric regression techniques (De'ath and Fabricius 2000). They constitute a heuristic technique and have more affinity with machine learning than with statistical analysis (Moore et al. 1991). Their relatively poor predictive performance is their principal drawback. This can be overcome by boosted regression trees, an adaptive method for assembling many simple trees to minimize misclassification errors and improve predictive performance (Elith et al. 2008).

Trees have been used less frequently than regression methods in cetacean and seabird distribution studies. Recently, Torres et al. (2013) used whaling data along with boosted regression trees to describe the offshore habitat of southern right whales (*Eubalaena australis*). Becker and Beissinger (2003) used classification tree models to examine scale-dependent habitat selection by marbled murrelets (*Brachyramphus marmoratus*) in an upwelling system.

Artificial neural networks

Artificial Neural Networks (ANNs) represent a complex non parametric process, often seen as a "black box approach". They are electronic networks of neurons that process and "learn" by comparing the classification of data records individually, functioning like an animal brain. They learn from experience and can rapidly solve hard computational problems. They are powerful tools for predictive modeling, especially when the underlying data relationships are unknown (Lek and Guégan 1999).

ANNs are a promising tool for predictive habitat distribution modeling (Guisan and Zimmermann 2000). They have rarely been applied to cetaceans and seabirds. Palialexis et al. (2011) predicted fish distributions from ANNs and noticed their ability to represent the original data. Yen et al. (2004b) used ANNs to predict distribution of marbled murrelets in British Columbia.

Comparing the performance of presence-only *vs* presence-absence methods (ENFA) for predicting bird habitats, Brotons et al. (2004) found that predictions from the later were more accurate. In addition, models for wide ranging species were more sensitive to absence data, highlighting the importance of using presence-absence methods when studying these organisms. Nevertheless, absence data encompass both true and false absences. True absences arise when habitat is unsuitable for the species, or when the species does not saturate its entire habitat by chance. False absences arise when species occurs at a site but is not present during the period of the survey, or when it is present but is undetected (Martin et al. 2005). True absences are not easy to collect for discrete and mobile species such as cetaceans and seabirds. Alternatively, pseudo-absences can be randomly generated (Zaniewski et al. 2002), although this practice has been recently questioned (Lobo et al. 2010).

b) Spatially explicit models

Spatial SDMs assume spatial processes are dominant in the distribution of species. It is believed that species aggregate through endogenous biological processes (Robinson et al. 2011). Spatial SDMs are sometimes used when there is a limited availability of environmental predictors and/or species data (Elith and Leathwick 2009). Spatial structure is not described by environmental predictors but is inherent in species distribution data. In contrast to habitat models, spatial SDMs do not aim at providing explanatory power.

Spatial methods are distinguished by the kind of data to which they are applied (Dale et al. 2002). If data are defined in a discrete space as randomly positioned points sampled around small spatial domains, this is the field of point pattern processes. If data are defined in a continuous space where sampling occurs at a finite number of sites, this is the field of geostatistics. Here I only describe geostatistics.

The purpose of geostatitics (Matheron 1971) is to model the spatial pattern of observations of a given variable as a function of distance in order to interpolate it between sampled sites with minimum error. Geostatistics are based on the autocorrelation concept, whereby values of samples that are close together have a tendency to be more similar (positive autocorrelation) (Dale et al. 2002). The main assumption underlying geostatitics is stationarity of the animal's distribution (*i.e.* processes that leads to the spatial distribution are independent of its localization or direction) (Wackernagel 2003). Basically, the geostatistical analysis is conducted in two stages. First, one has to model the spatial dependence in the data and estimate its parameters (variographic analysis). The second stage (spatial interpolation) consists in kriging the variable of interest over the study region in order to obtain a map that minimizes the interpolation error given the spatial dependence. As a consequence, covariance between two observations only depends on the distance between them.

Monestiez et al. (2006) conducted a geostatistical modeling of fin whales in the Mediterranean (Figure III-9). They associated geostatistics with the Poisson distribution to model both spatial variation and discrete observation process. This method was adapted to zero inflated count data and heterogeneous observation efforts arising from combining sparse observation data.

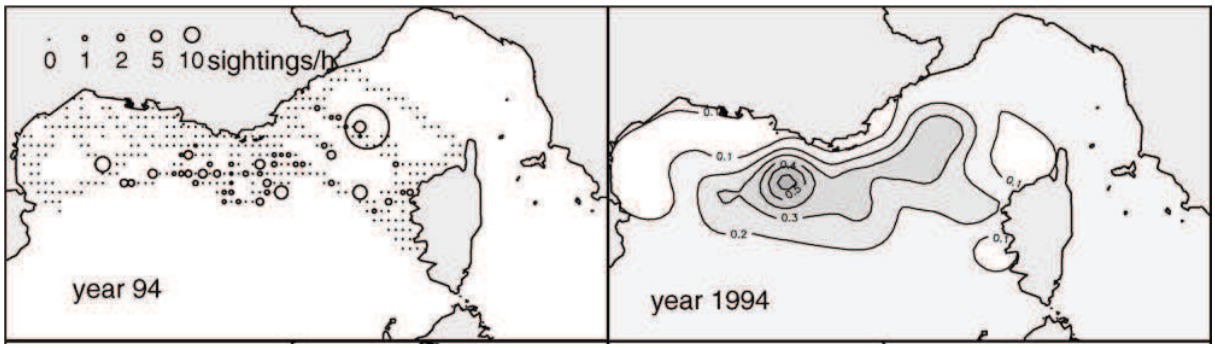


Figure III-9: Spatial SDMs outputs from Monestiez et al. 2006, showing fin whale sightings in the northwestern Mediterranean Sea (left) and the resulting kriging (right).

Kriging predicts species distribution by modeling spatial autocorrelation in the data. It might not be as powerful as habitat models which predict species distribution by using a large number of environmental variables biologically related to species distribution (Palialexis et al. 2011). Nevertheless, geostatistics are a robust tool for predicting species distribution and might provide more realistic predictions than habitat models.

Figure III-10 presents a synthetic view of spatial and habitat SDMs. Alternatively, spatial autocorrelation can be accounted for in the residuals of habitat models through autovariable regressions or generalized estimating equations (Dormann et al. 2007). When spatial patterns are considered in the modeling process, conclusions about environmental factors affecting species distribution can change greatly (Keitt et al. 2002).

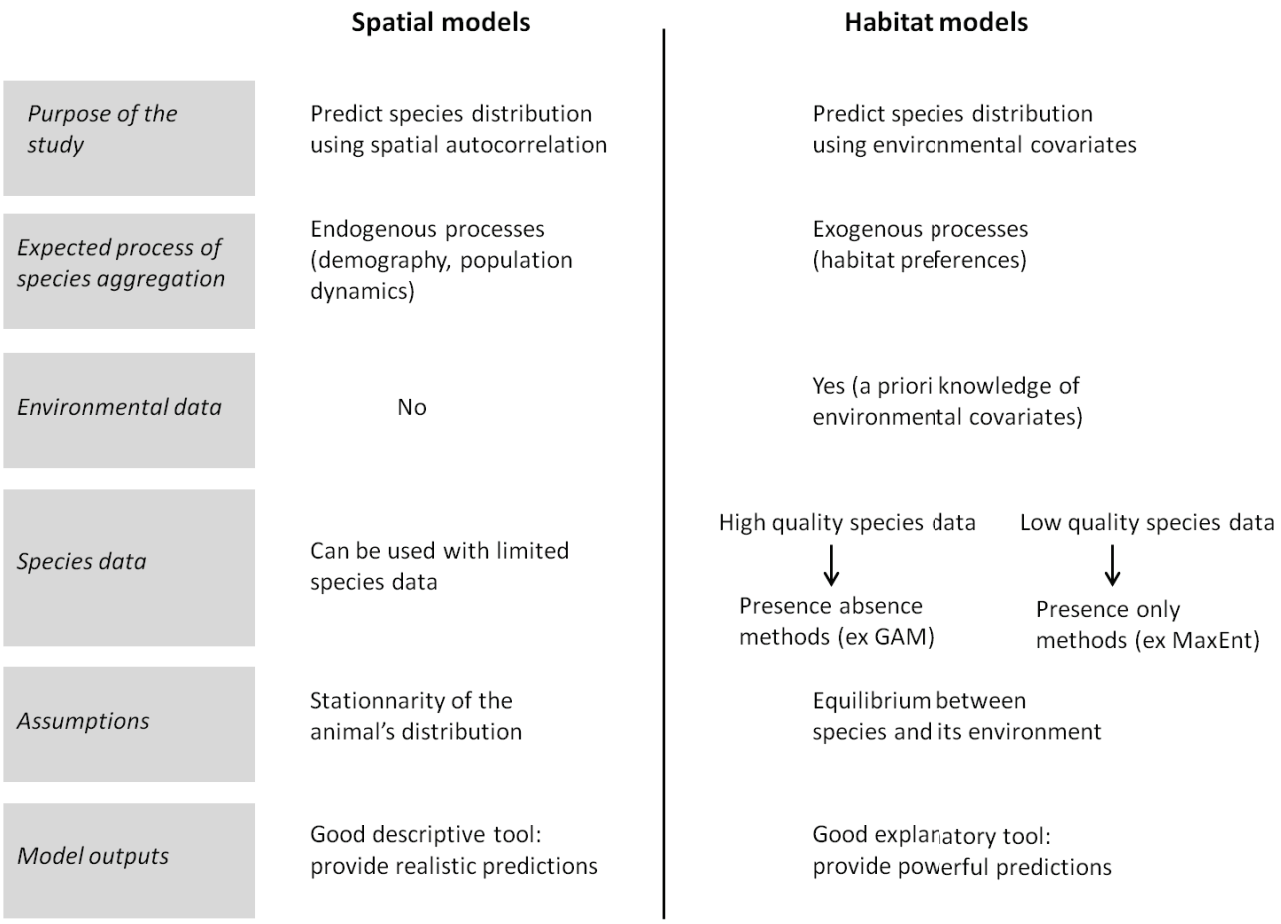


Figure III-10: Synthesis on the use of spatial and habitat models.

Chapter IV. Methodological choices

Photo credit: Observatoire PELAGIS / AAMP

1) Field methodology

a) Aerial protocol

Dedicated aerial surveys followed the general SCANS (Small Cetacean Abundance in the North Sea) methodology prepared for small cetaceans and adapted to aircrafts (Hammond et al. 2013). Transects were flown at a target altitude of 182 m (600 feet) and a ground speed of 167 km.h-1 (90 knots) with high-wing, double-engine aircrafts equipped with bubble windows (Figure IV-1). Survey crew consisted of two trained observers observing with naked eyes and a navigator in charge of data collection on a laptop computer (Figure IV-2). A fourth off-duty crew member was also present to enable rotation of crew members every 2 hours in an attempt to limit loss of vigilance due to tiredness in long flights. A GPS, logged to a computer equipped with 'VOR' software (designed for the aerial survey of the SCANS-II program, Hammond et al. 2013), collected positional information every 2 seconds. Beaufort Sea state, glare severity, turbidity, cloud coverage and an overall subjective assessment of detection conditions (good, moderate or poor as for small delphinids) were recorded at the beginning of each transect and whenever any of these values changed.

Figure IV-1: High wing aircraft (Britten Norman 2). Photo credit: Observatoire PELAGIS / AAMP.

Figure IV-2: Survey crew including two observers observing through bubble windows and a navigator in charge of data collection. Photo credits: Observatoire PELAGIS / AAMP.

For cetaceans, we collected data following a line transect methodology (Buckland et al. 2001) (Figure IV-3). Information recorded included identification to the lowest possible taxonomic level, group size and declination angle to the group when it passed at right angle to the aircraft (measured with a hand-held clinometer). Together with the altitude of the aircraft, angles provided perpendicular distances, which allowed distance sampling analyses to be conducted. For seabirds, we collected data using the strip transect methodology, with the assumption that all seabirds within the strip were detected (Tasker et al. 1984) (Figure IV-3). This methodology was used in an attempt to avoid disrupting the attention of the observers from cetaceans in areas of high seabird densities. The strip width was fixed at 200 m on both sides of the transect (Southwest Indian Ocean and French Polynesia). Identification was made to the lowest taxonomic level whenever possible, but groupings were inevitable for animals that could not be told apart from the air (e.g. the *Stenella* dolphins or the brown terns composed of the sooty *Onychoprion fuscatus* and the bridled tern *O. anaethaetus*).

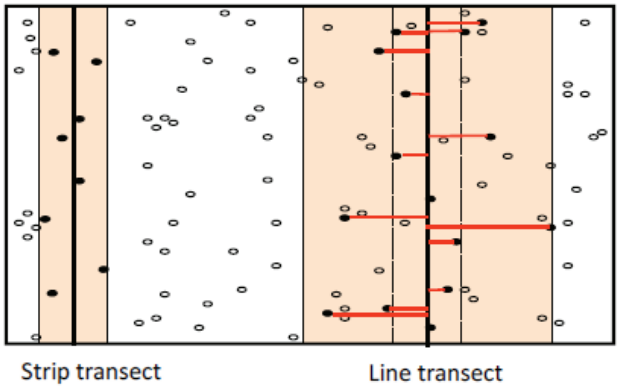


Figure IV-3: Strip transect sampling (left) in which all objects detected within the strip are recorded and line transect sampling (right) in which declination angles to detected objects are recorded.

b) General design of the surveys

The sampling design was organized at several spatial levels: regions (3 regions: western tropical Atlantic, Southwest Indian Ocean and French Polynesia), sectors (several sectors per region) and gross bathymetric strata (0-200 m: shelf, 200-2,000 m: slope, >2,000 m: oceanic). Zigzag transects were implemented to provide a good spatial coverage within strata and improved flight efficiency (maximizing flight time spent on effort) (Buckland et al. 2001). Transects were allocated among strata according to expected cetacean densities (chlorophyll-depleted oceanic waters received proportionately more effort). In each region, surveyed transects were split into legs of identical detection conditions, further divided into 10 km-long segments, so that variability in detection conditions and geographic location was small within segments. Aerial surveys were mainly conducted in the summer season (except in the Antilles) in order to avoid the trade wind season; doing this, we could not adequately survey large migratory whales.

2) Analytical methods

I first carried out regional modeling studies, separately analyzing the three regional datasets to answer specific ecological questions. In the western tropical Atlantic, the particularities of the dataset precluded the implementation of habitat SDMs. The limited survey effort resulted in a restricted range of sampled environmental variability and in rather low sighting numbers (in particular for cetaceans). In addition, the two sectors (the Antilles and Guiana) were surveyed at different seasons and had non overlapping environmental conditions. In each sector, I built spatial SDMs using geostatistics, to predict species distributions based on the endogenous spatial autocorrelation in the data. I also used distance sampling and geostatistics to provide relative abundance estimates for some megavertebrate taxa. I conducted a descriptive study to provide robust and realistic predictions in this comparatively data poor region (Figure IV-4).

In the Southwest Indian Ocean and French Polynesia, the larger extent of the surveys, implemented regionally, explored a wider range of environmental conditions and provided higher sighting numbers. I built habitat SDMs in both regions based on various environmental variables. I carried out an explanatory/predictive study to gain ecological

insights on cetacean and seabird distributions in relation to environmental factors, and to provide relative density predictions (Figure IV-4).

I then conducted a generic modeling study, jointly using the three regional datasets to search for emergent properties of cetacean distributions and to predict their relative density in a circumtropical belt. The pooling of regional datasets allowed to explore a wide range of environmental variability and to obtain numerous sighting numbers. I built habitat SDMs based on a set of environmental variables relevant at the ecosystem scale. I favored a predictive approach to provide the most generalizable predictions in a circumtropical envelope based on the surveyed regions (Figure IV-4).

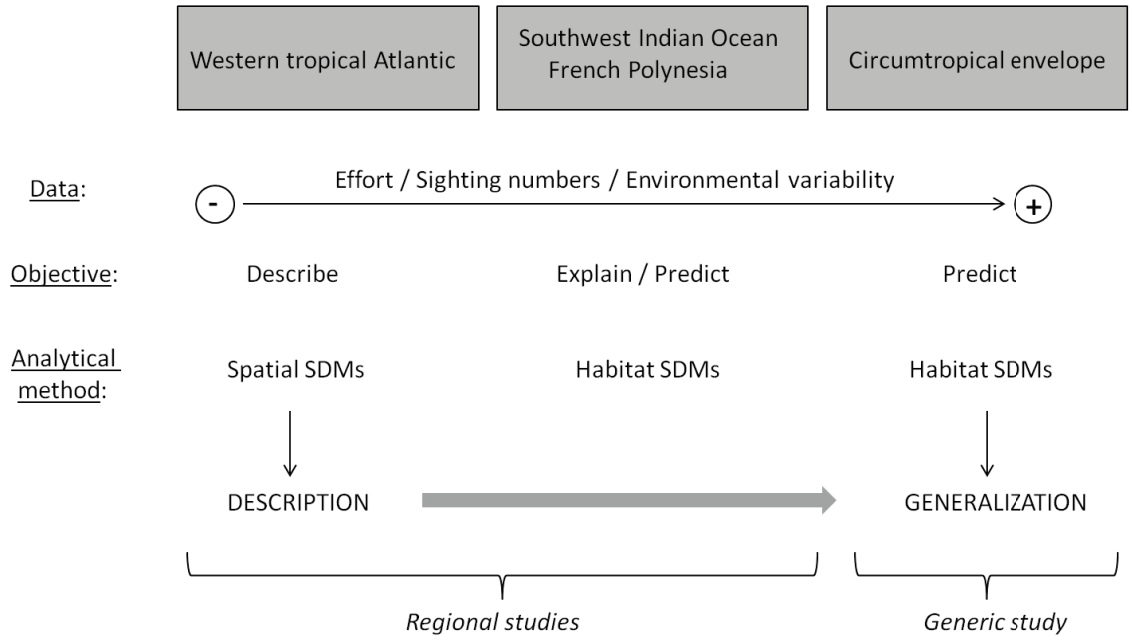


Figure IV-4: Regional and generic modeling approaches: coherence between the data, the objective and the analytical method.

a) Abundance estimation

Although abundance estimation was not the primary aim of this dissertation, I proposed relative abundance estimates in the western tropical Atlantic based on distance sampling (Buckland et al. 2001, Thomas et al. 2010). This method provides estimates of abundance and density in a study region with associated uncertainties. It relies on 2 stages (Figure IV-5).

First, one has to fit a detection function to perpendicular distances in order to estimate the proportion of missed animals in the covered region. In conventional distance sampling (Buckland et al. 2001), detection probability only depends on the distance from the transect. In multiple covariate distance sampling (Marques and Buckland 2004), detection probability can also be affected by detection variables. It is recommended to delete 5% of the sightings detected at the largest perpendicular distances. Detection models (uniform, hazard rate and half normal) are fitted to the distribution of perpendicular distances and the model that minimizes the Akaike Information Criterion (AIC) is selected. The effective strip width (ESW) is then estimated based on the selected detection model.

The second stage consists of extrapolating the number of animals seen in the covered region to the whole study region, the so-called design based estimate of abundance. For this, it is crucial that the transect lines be placed randomly with respect to the distribution of animals. Random line placement justifies the extrapolation of the sample statistics to the population, and ensures that the surveyed lines are representative of the study region. Additionally, three assumptions are critical: (1) the probability of detecting an animal on the transect is certain, referred as the g(0)=1 assumption, (2) no responsive movement occurred prior to detection and (3) distances are measured accurately. The density of sightings is estimated by dividing the number of sightings by the covered surface area (calculated as two times the ESW multiplied by total transect length). The density of individuals is obtained by multiplying this estimate by the expected group size. Abundance is estimated by multiplying the density of individuals by the surface area of the study region. Uncertainty has an encounter rate, a detection function and a group size component (Buckland et al. 2001).

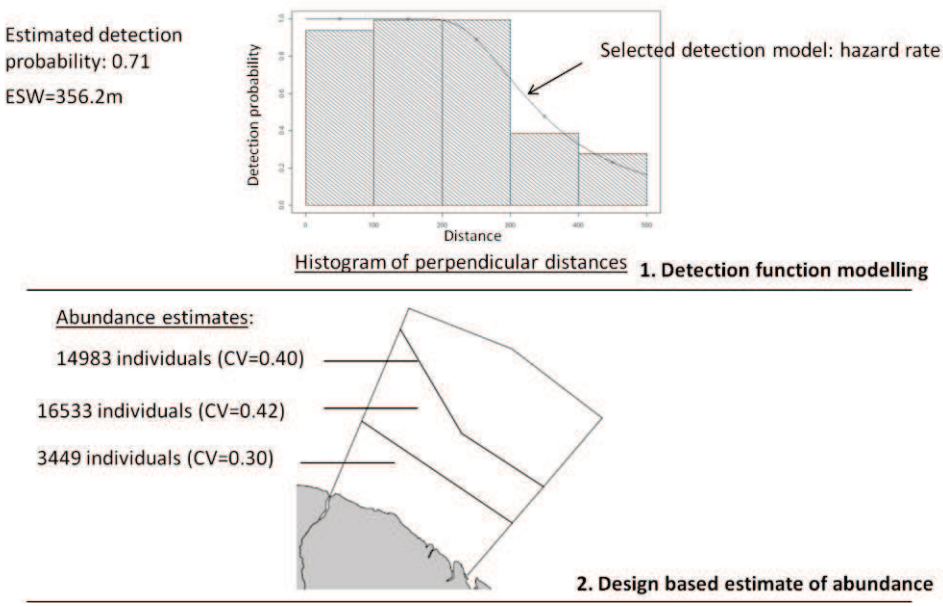


Figure IV-5: The two stages of abundance estimation (example of bottlenose dolphins in Guiana).

b) Geostatistical modeling

A geostatistical approach (Monestiez et al. 2006, Bellier et al. 2011) was implemented in the western tropical Atlantic for two reasons. First, zigzag designs produced a non homogeneous distribution of transects in the sampled sectors (Strindberg and Buckland 2004), and the distribution of animals may not be independent of the positions of transects. Yet, geostatistics take into account the spatial autocorrelation between transects and observations in density and abundance estimations (Van der Meer and Leopold 1995). Second, geostatistics allowed mapping the local density of sightings. I used the modified kriging described by Monestiez et al. (2006), that includes a Poisson modeling of the observation process, to map the local density of sightings. The approach has two stages (Figure IV-6).

First, one has to model the spatial dependence in the data and estimate its parameters (variographic analysis). The choice of the spatial dependence model is a crucial stage. The second stage consists in kriging the density of sightings over the study region to obtain a map of local density of sightings that minimizes the interpolation error given the spatial dependence. Multiplying this local density of sightings by mean group size and integrating it over the study region provides an abundance estimation. The underlying hypothesis is stationarity of the animal's distribution (*i.e.* processes that leads to the spatial distribution are independent of its localization or direction) (Wackernagel 2003). Consequently, covariance

between two observations only depends on the distance between them. Since detection probability was not directly accessible from this methodology, it necessarily relies on the fitted detection function to estimate the proportion of missed animals in the covered region.

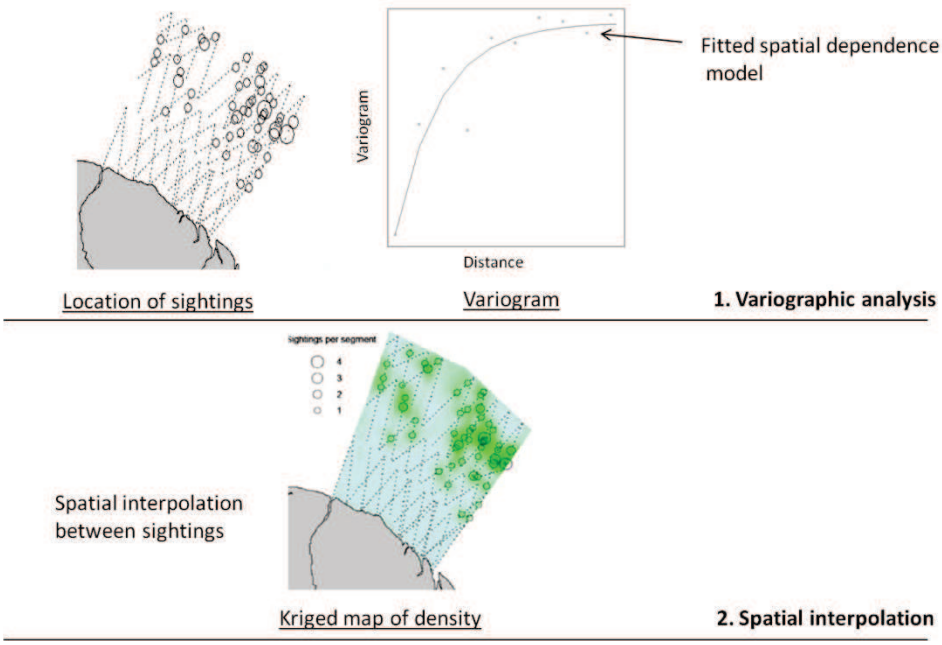


Figure IV-6: The two stages of geostatistical modeling (example of brown terns in Guiana).

c) Habitat modeling

I modeled the habitats of cetacean and seabird guilds at the regional scale in the Southwest Indian Ocean and French Polynesia, and at the circumtropical scale, in an envelope defined by the range of environmental conditions sampled in the three tropical regions. The aerial surveys provided presences and group sizes of cetaceans and seabirds. Assuming the reliability of absences, I used a presence-absence habitat modeling method. I relied on GAMs adapted to count data for their ability to model non parametric relationships between species and their environment.

In the regional studies, I built habitat models based on static and oceanographic variables (Chapters VI and VII), as well as on mid-trophic levels exclusively (Chapter VIII). These environmental variables (data sources, resolutions) are presented in the related articles (ANNEXES 2 to 4). In the generic study (Chapter IX), I relied on a variety of physiographic, physical, chemical and biological variables, representative of oceanographic processes at the ecosystem scale. They are presented in Chapter IX.

Habitat modeling was done through the following stages: model building, model selection, prediction and uncertainty estimation (Figure IV-7).

In GAMs, the link function $g()$ relates the mean of the response variable given the variables $\mu=E(Y|X_1,...,X_p)$ to the additive predictor $\alpha + \sum f_i(X_i)$:

$$g(\mu) = \alpha + \sum f_i(X_i)$$

The components $f_i(X_i)$ of the additive predictor include non parametric smooth functions (splines) of the variables (Wood and Augustin 2002). The response variable was the number of individuals. As count data are often characterized by heavy tailed distributions, I used an overdispersed Poisson distribution with variance proportional to the mean and a logarithmic link function. I limited the amount of smoothing for each spline to model non linear trends but to avoid overfitting that would have no ecological meaning (Forney 2000). I accounted for non constant effort by using an offset in the model. The offset was calculated by multiplying the effort by twice the ESW. The ESW was estimated prior to habitat modeling using multiple covariate distance sampling (Marques and Buckland 2004).

I fitted the models containing all possible combinations of four non collinear environmental variables (as indicated by Spearman correlation coefficients). Four variables were retained in the model to avoid excessive complexity while providing a reasonable explanatory power. I retained the model which had the lowest Generalized Cross Validation (GCV) score. I used explained deviance to evaluate each model's fit to the data.

I generated a grid of environmental variables within which I predicted the habitats of cetacean and seabird guilds. I provided extrapolations to unsurveyed areas while staying within the range of environments sampled by the training data, and within the same general time frame (Elith and Leathwick 2009).

As uncertainty is an inherent component of spatial prediction, I mapped the coefficient of variation associated with the prediction.

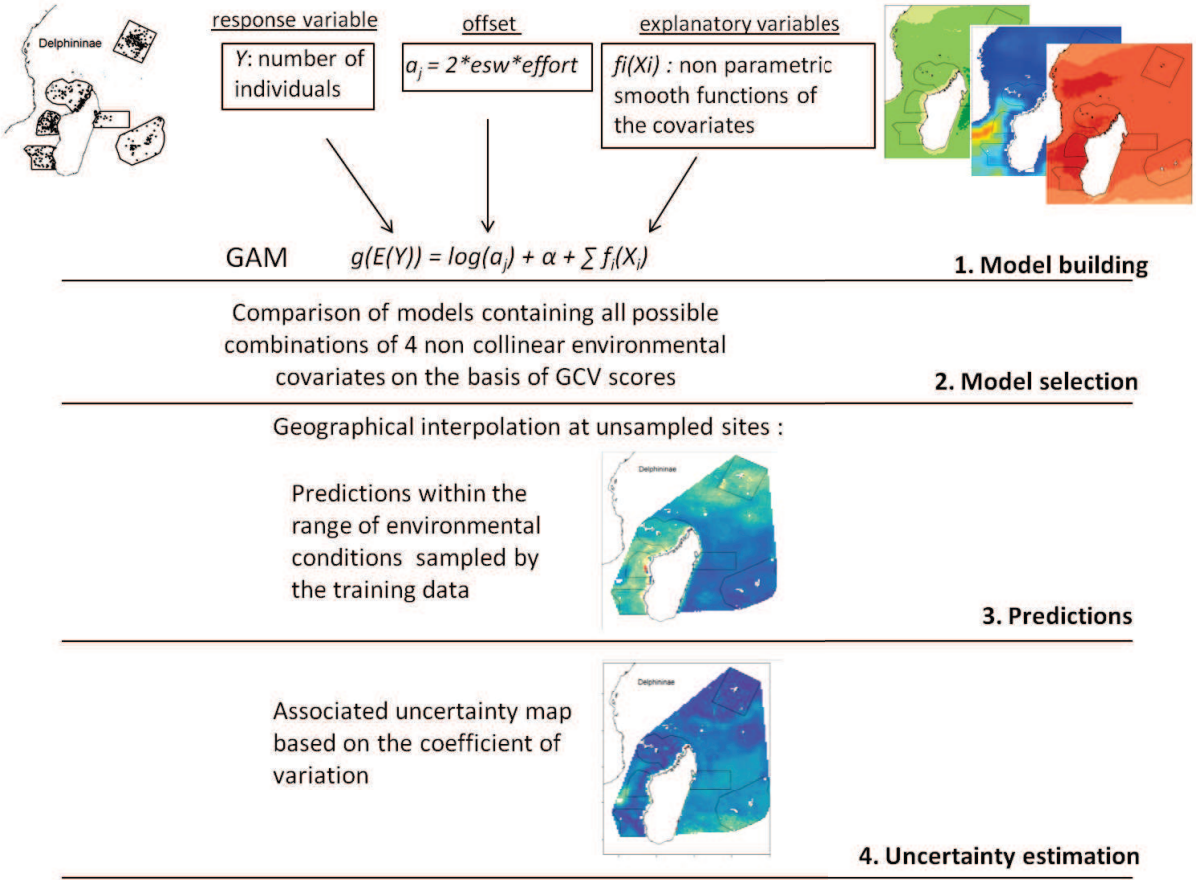


Figure IV-7: Stages of habitat modeling (example of Delphininae in the Southwest Indian Ocean).

Chapter V. Cetacean and seabird communities from two contrasting ecosystems in the western tropical Atlantic

Photo credit: Observatoire PELAGIS / AAMP

This chapter is a synthesis of an article published in *Journal of Marine Systems*, presented in ANNEX 1:

Mannocci, L, Monestiez, P, Bolaños-Jiménez, J, Dorémus, G, Jeremie, S, Laran, S, Rinaldi, R, Van Canneyt, O, Ridoux, V, 2013. Megavertebrate communities from two contrasted ecosystems in the western tropical Atlantic. *Journal of Marine Systems* 111-112: 208-222.

1) Objective

Dedicated aerial surveys were conducted across the EEZs of the Antilles and Guiana, in the western tropical Atlantic (WTA), to establish a baseline knowledge of large marine vertebrates in these tropical waters. The Antilles and Guiana belong to two connected biogeographic provinces, respectively the "Caribbean Province", including the Gulf of Mexico and the Northern Caribbean Sea, and the "Guianas coastal province", running from Northern Brazil to Trinidad. Although they are geographically close to each other, the Antilles and Guiana are characterized by contrasting oceanographic conditions and productivity levels, chlorophyll concentration being on average 10 times higher in Guiana. We expected cetaceans and seabirds with high costs of living to be constrained to the highly productive Guiana waters and cetaceans and seabirds with more economical life styles to cope with the less productive waters of the Antilles.

The objective was to compare cetacean and seabird communities between these contrasting ecosystems in terms of encounter rates, species composition, relative abundance and spatial distribution. This study yielded new insights about cetaceans and seabirds which are poorly documented in this tropical region. Indeed, apart from the Gulf of Mexico, where large scale surveys resulted in a basic understanding of their distributions, abundances and habitats (*e.g.* Baumgartner et al. 2001, Davis et al. 2002, Fulling et al. 2003), little information is available in the WTA. In addition, this study gave the opportunity to investigate differences in communities between these ecosystems of contrasting productivity and to discuss the ecological mechanisms responsible for the observed patterns.

2) Material and methods

a) Study areas

The oceanographic characteristics of the Antilles and Guiana are described in Chapter II.

b) Survey period and survey design

Aerial surveys were conducted from the 4 February to the 5 March 2008 across the French EEZ of the Antilles (123,000 km²), and from the 29 September to the 10 October 2008

off Guiana (138,000 km²). In the Antilles sector, the survey was stratified according to the windward / leeward side of the islands and depth, including three strata: inshore Caribbean, inshore Atlantic and offshore Atlantic (Figure V-1). In the Guiana sector, a stratified survey design was implemented according to approximate depth categories, including three strata: neritic (0-200 m), slope (200-2,000 m) and oceanic (>2,000 m) (Figure V-1).

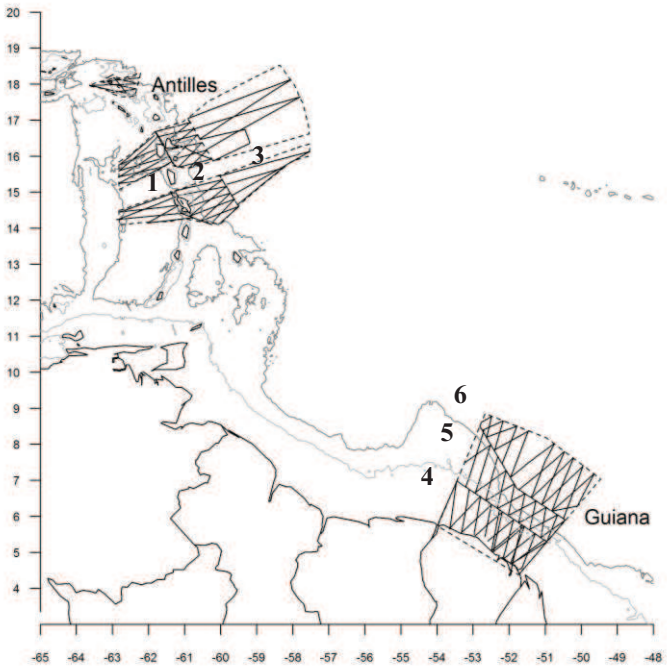


Figure V-1: Map of the surveyed sectors (Antilles and Guiana) in the western tropical Atlantic. Strata are shown in the Antilles (1: inshore Caribbean, including the Caribbean side of Martinique and Guadeloupe; 2: inshore Atlantic, including the Atlantic side of Martinique and Guadeloupe and St Bartélémy and St Martin islands and 3: offshore Atlantic) and in Guiana (4: neritic, 5: slope and 6: oceanic). The 200 m (light grey) and 2,000 m (dark grey) isobaths are provided.

c) Field methodology

The aerial survey followed the general methodology described in Chapter IV, except that, for the collection of seabird data, strip width was 500 m on both sides of the transect line in the Antilles and 150 m in Guiana. In both sectors, the high-wing double-engine aircraft was a Partenavia P68.

d) Analytical methods

We used both distance sampling (Buckland et al. 2001, Thomas et al. 2010) and geostatistics (Monestiez et al. 2006, Bellier et al. 2011), relying on different assumptions, to

estimate relative densities and abundances of several cetacean and seabird taxa in the Antilles and Guiana. In addition, geostatistics allowed the local density of sightings to be mapped. The analyses were conducted for taxa with at least 20 sightings. The detailed implementation of these methods is presented in ANNEX 1. We also provided descriptive statistics of depth and distance from the coast associated with the sightings and for the whole sector.

3) Results

a) General description

Details on survey effort, survey conditions and cetacean and seabird sightings are presented in ANNEX 1 (Tables 1, 2 and 3).

b) Encounter rates

In Guiana, the encounter rate of cetaceans was 3 times greater (1.76 sightings / 100 km) than in the Antilles (0.58 sightings / 100 km); this difference was even more pronounced in terms of individuals (respectively 22.59 and 4.23 individuals / 100 km). In the Antilles, 0.12 sightings of mysticetes and 0.44 sightings of odontocetes were made per 100 km of effort. In Guiana, 0.04 sightings of mysticetes and 1.70 sightings of odontocetes were made per 100 km of effort. Overall, the encounter rate of sperm and beaked whales was higher in the Antilles (0.18 sightings / 100 km) compared to Guiana (0.13). The encounter rate of large delphinids was higher in Guiana (0.17 sightings / 100 km) compared to the Antilles (0.11). The encounter rate of small delphinds was almost 10 times higher in Guiana (1.40 sightings / 100 km, compared to 0.15 in the Antilles).

The encounter rate of seabirds was slightly greater in the Antilles (4.70 sightings / 100 km, 12.54 individuals / 100 km) compared to Guiana (3.64 sightings / 100 km, 17.12 individuals / 100 km). Procellariiformes were rarely encountered in both sectors. Charadriiformes were more frequently encountered in Guiana (2.82 sightings / 100 km) compared to the Antilles (1.56). The encounter rate of Pelecaniformes was 4 times higher in the Antilles (2.92 sightings / 100 km) compared to Guiana (0.81).

c) Composition of odontocete and seabird communities

In the Antilles, odontocete sightings were almost equally partitioned between small delphinids, large delphinids and sperm and beaked whales, the later being slightly more frequently recorded (40.5% of the sightings) (Figure V-2a). However, in terms of individuals, small delphinids dominated (representing 71.9% of the individuals). In Guiana, the composition of the odontocete community was different. Small delphinids (mostly represented by bottlenose dolphins) dominated in terms of sightings (82.6%) and individuals (86.6%) (Figure V-2b). Subsequently, sightings were almost equally partitioned between large delphinids and sperm and beaked whales.

In the Antilles, Pelecaniformes dominated in terms of sightings (61.9%) and were represented by 7.7% of frigatebirds, 69.2% of tropicbirds and 23.1% of boobies (Figure V-3a). Charadriiformes totalized 34.6% of the sightings and were mainly represented by terns. In terms of individuals, Charadriiformes dominated. In Guiana, the seabird community was strongly dominated by Charadriiformes (76.3% of the sightings and 89.4% of the individuals), within which, as in the Antilles, terns accounted for more than 95% (Figure V-3b). Pelecaniformes totalized 22.3% of the sightings and were almost exclusively represented by frigatebirds.

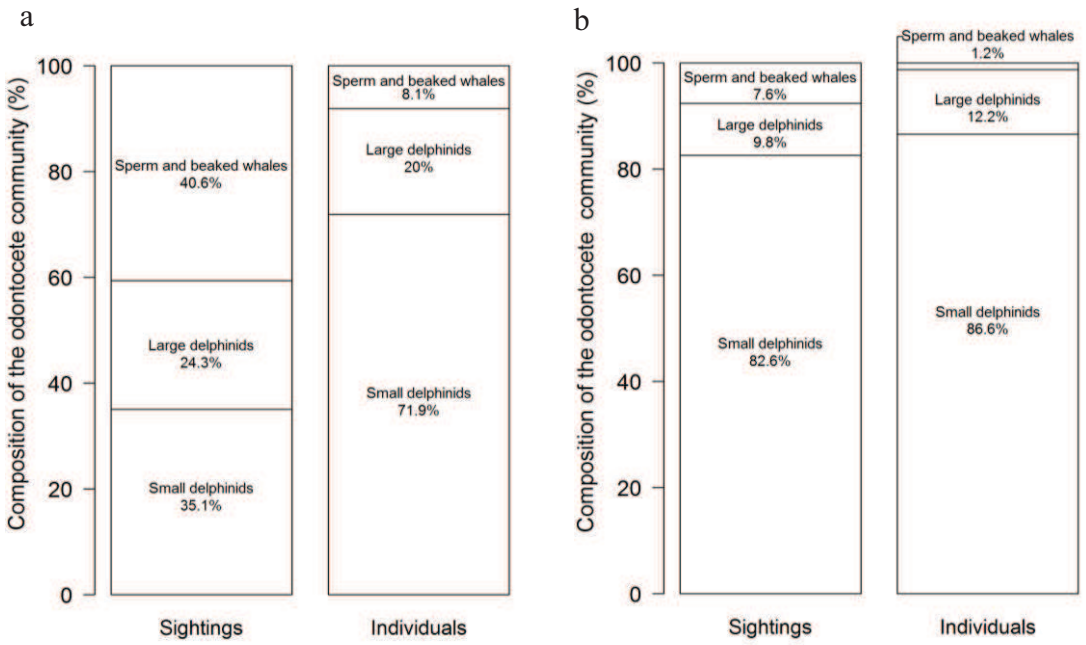


Figure V-2: Composition of the odontocete community in the Antilles (a) and in Guiana (b).

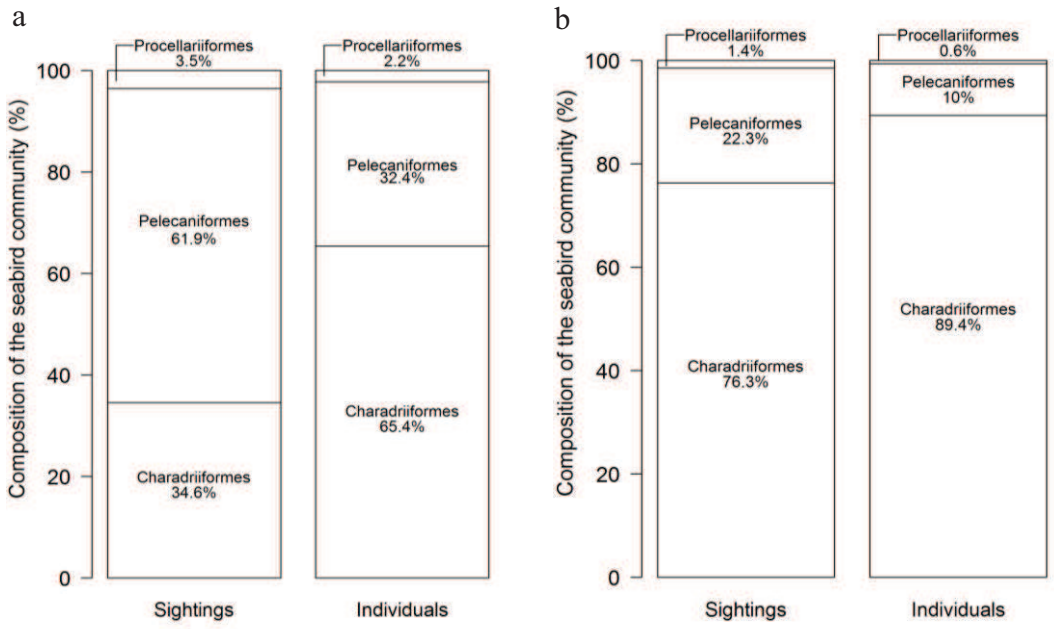


Figure V-3: Composition of the seabird community in the Antilles (a) and in Guiana (b).

d) Relative abundances

Overall, distance sampling and geostatistics provided similar estimates of abundance for the analyzed taxa in the Antilles and Guiana (ANNEX 1, Tables 4 and 5). For magnificent frigatebird in Guiana, the overall geostatistical estimate was lower. When there was no sighting in a stratum, distance sampling estimated an abundance of 0 and a CV of 0, whereas geostatistics estimated a non zero abundance and a relatively high CV *(*for example for Guiana dolphin). We only present distance sampling estimates in the text.

In the Antilles, cetacean sightings were too low to fit detection functions and provide species-specific estimates of abundance. In Guiana, sighting numbers were appropriate for bottlenose dolphin (*Tursiops truncatus*) and Guiana dolphin (*Sotalia guianensis*). Bottlenose dolphin was the most abundant cetacean, with an estimate of 34,965 individuals (CV=0.28). For Guiana dolphin, the overall estimate was of 2,076 individuals (CV=0.44), all located in the neritic stratum.

We estimated abundances for several seabird taxa. In the Antilles, we estimated an abundance of 7,870 brown terns (CV=0.23) and 1,693 brown boobies (CV=0.23). For both taxa, abundance was lower in the offshore Atlantic stratum. The estimate for tropicbirds was of 2,647 individuals (CV=0.11). We also estimated an abundance of 349 magnificent frigatebirds (*Fregata magnificens*) (CV=0.30). In Guiana, sooty terns appeared to be the most

abundant species (40,996 individuals (CV=0.27)), and their abundance was greater in the oceanic stratum. In contrast, magnificent frigatebirds and grey terns were only abundant in the neritic stratum (respectively 5,389 individuals (CV=0.52) and 16,999 individuals (CV=0.34)).

e) Spatial distribution

In the Antilles, cetaceans were mainly encountered over the inshore Atlantic and Caribbean strata, with more numerous sightings around the slope, especially in the Atlantic. In Guiana, cetacean sightings were fairly evenly distributed across all strata, albeit sightings were more numerous in the neritic stratum (ANNEX 1, Appendix A). We implemented the geostatistical analysis for bottlenose dolphins and Guiana dolphins. Bottlenose dolphins were widely sighted and their distribution appeared to be random (as shown by the pure nugget effect in the variogram, ANNEX 1, Appendix C). Geostatistics estimated a constant density (1.27 sightings / 100 km²) across all strata; as a result we obtained a flat map (Figure V-4a). Bottlenose dolphins showed no preference for the analyzed physiographic features but were not observed closer than 14 km from the coast. In contrast, Guiana dolphins had a very coastal distribution (Figure V-4b) and most sightings were within the first 10 km. Mean depth used by Guiana dolphins was 7.5 m (sd=11.2 m) (ANNEX 1, Table 6).

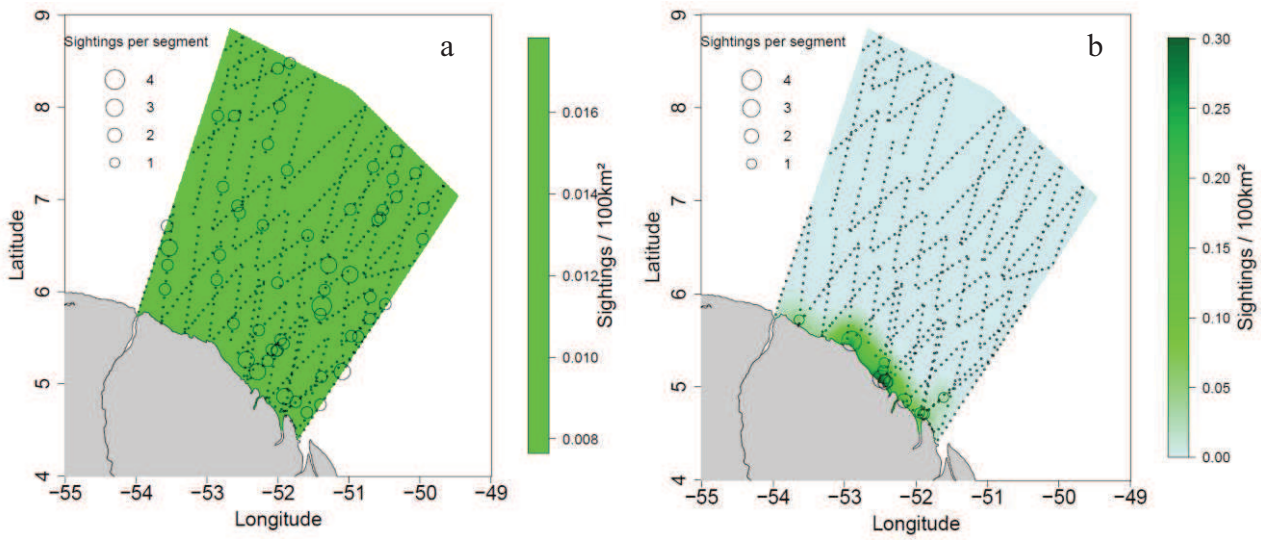


Figure V-4: Density of sightings in Guiana for bottlenose dolphin (a) and Guiana dolphin (b).

In the Antilles, seabirds were more frequently encountered in the inshore Atlantic and Caribbean strata (ANNEX 1, Appendix A). Tropicbirds were mainly aggregated around the islands, with a lower density of sightings offshore (Figure V-5a). Brown boobies were sighted in both inshore Atlantic and Caribbean strata, but density of sightings was higher in

the latter. They were aggregated around the islands (East of Martinique, West of Guadeloupe) (Figure V-5b). Brown terns were recorded in all strata with noticeable aggregations in the south. Density of sightings was the highest in the inshore Atlantic stratum and the lowest in the offshore Atlantic stratum (Figure V-5c). In Guiana, seabirds were mainly distributed along the coast and in the oceanic stratum; the deeper part of the continental shelf and the inner slope were poorly frequented (ANNEX 1, Appendix A). Sooty terns were mostly distributed in the slope and oceanic strata, with a higher density of sightings in oceanic waters (Figure V-6a). They mainly used the offshore waters (mean=260.1 km, sd=66.6 km) (ANNEX 1, Table 6). In contrast, magnificent frigatebirds and grey terns used inshore waters (means of 21.46 km and 63.55 km respectively) (ANNEX 1, Table 6). Density of magnificent frigatebirds was high between the Approuage and Oyapock rivers and around *Grand Connétable* Island (Figure V-6b). The density of grey terns was the highest along the coast (Figure V-6c).

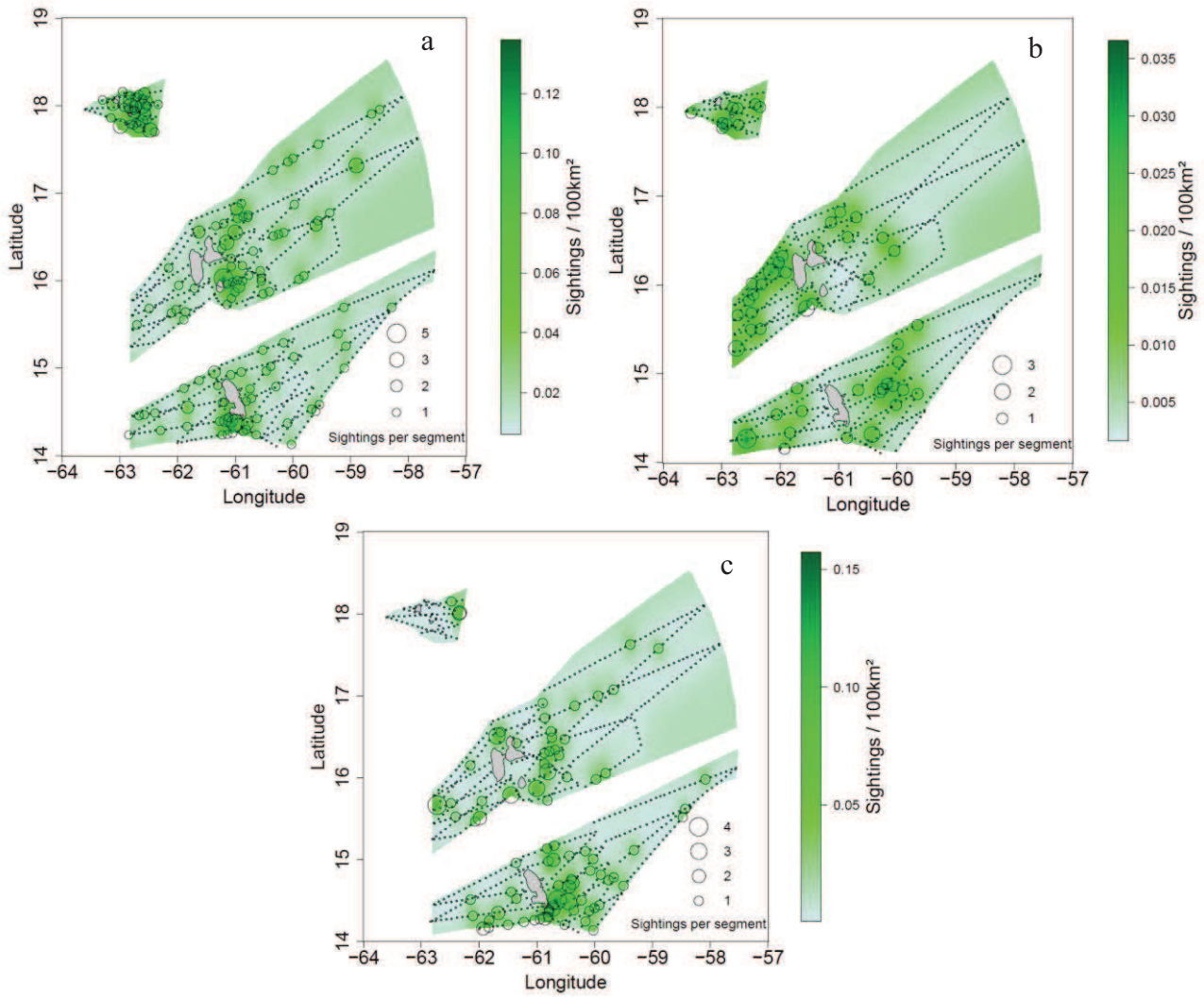


Figure V-5: Density of sightings in the Antilles for tropicbirds (a), brown boobies (b) and brown terns (c).

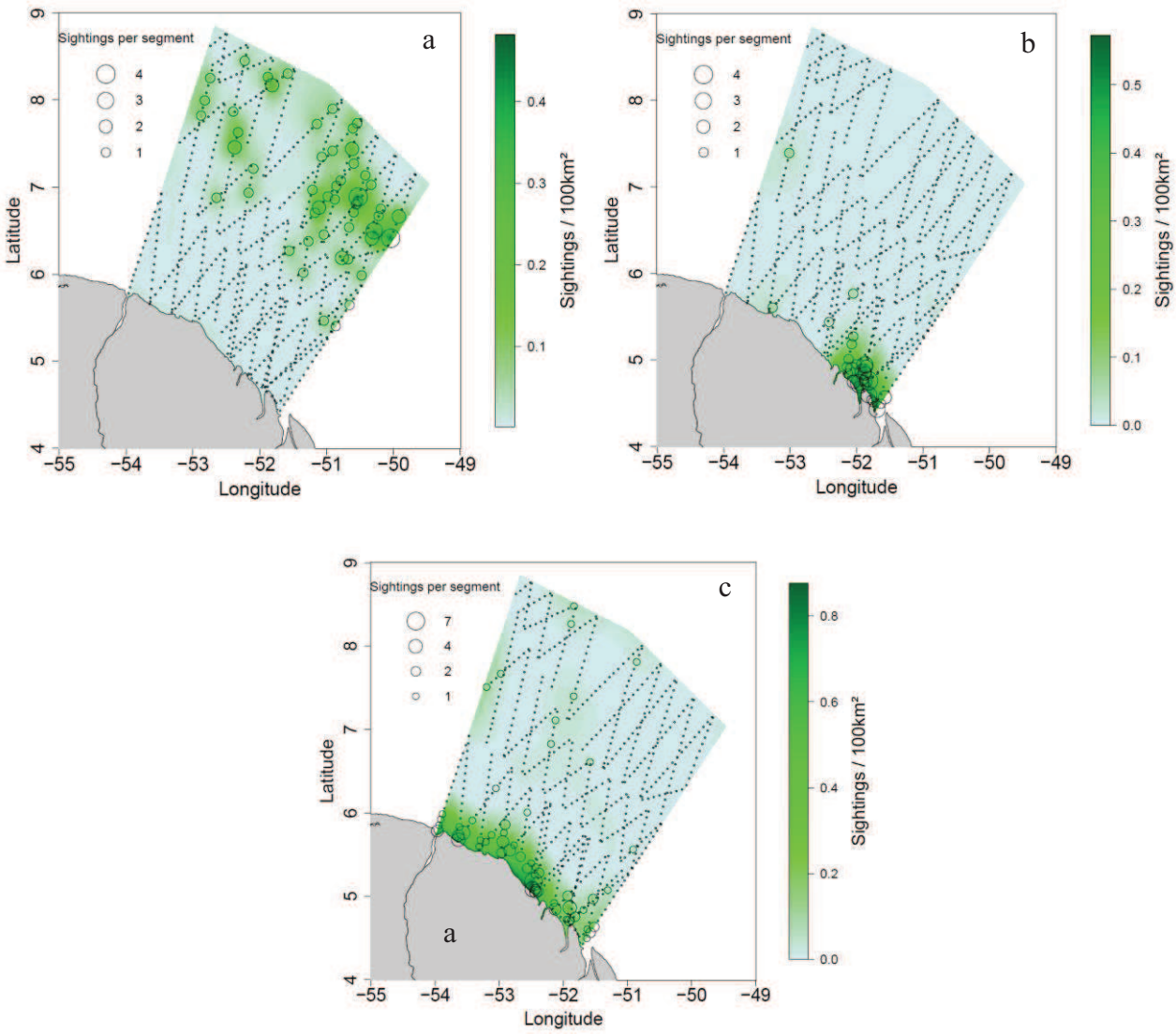


Figure V-6: Density of sightings in Guiana for sooty tern (a), magnificent frigatebird (b) and grey terns (c).

4) Discussion

a) Methodological considerations

Survey methods

The combination of detection bias (animals missed while they are present at the surface, often as the result of bad survey conditions) and availability bias (animals not available at the surface) (Pollock et al. 2006) makes the present abundances likely underestimated. However, our objective was more to investigate differences in cetacean and seabird communities between the Antilles and Guiana than to conduct a thorough quantitative

analysis of abundance. In addition, survey conditions were not homogeneous between both sectors. In Guiana, the high turbidity of the very coastal waters prevented the detection of animals swimming under the surface. In the Antilles, sea state was suboptimal and animals swimming at or under the surface may have been missed, resulting in an underestimation of their abundances. Hence, sea state may also have contributed to the observed differences in communities between both sectors.

For seabirds, sometimes encountered in high densities and strongly aggregated, the strip transect methodology has proven to be adapted and useful for monitoring populations at large spatial scales (Certain and Bretagnolle 2008). An underestimation of seabird abundance may have occurred, notably in coastal waters. The strip width was reduced from 500 m in the Antilles to 150 m in Guiana. Certain and Bretagnolle (2008) showed that variation of detection probability in aerial surveys of pelagic seabirds did not occur in a strip of 150 m and that the effect up to 230 m was very weak. Seabird abundance may have been underestimated in the Antilles, albeit this is probably less the case for large and easily detectable species such as frigatebirds or boobies, frequent in this sector.

The aerial surveys were carried out in two different seasons. In the Antilles, it coincided with the migration of humpback whales (Clapham 2002), leading to a higher encounter rate of mysticetes compared to Guiana. However, for our community composition analysis we were mainly interested in odontocetes, which probably reside year-round in the region. In addition, the dependence of seabirds to colonies may have caused a "colony effect" if surveys occurred during the breeding period (Hyrenbach et al. 2007). Our surveys provided a real-time picture of cetacean and seabird communities, but only reflected a given situation of the environment. For this reason, the present results should be related to the sampled periods.

Analytical methods

We used both distance sampling and geostatistics to estimate relative densities and abundances of several taxa. When sightings were not uniformly distributed and their distribution was not independent from the distribution of transects, geostatistics corrected the estimate (*e.g.* for magnificent frigatebirds in Guiana). When there were no sightings in a stratum, distance sampling estimated an abundance of 0 and a CV of 0, whereas geostatisics estimated a non zero abundance and a very high CV (*e.g.* for Guiana dolphins). The zero

abundance estimate of distance sampling is still included in the confidence interval of geostatistics, but the latter probably gives a more realistic result. Nevertheless, due to low sighting numbers, we were close to the limit of utilization of both approaches. As they rely directly on the effective strip width estimated from detection function fitting, geostatistics cannot be used independently from distance sampling. Since they allow mapping local the density of sightings, providing information on an animal's distribution in a study region, geostatistics are a good complement to distance sampling (Bellier and Monestiez 2008).

Despite these methodological considerations, it is clear that these multispecific aerial surveys added new knowledge on large marine vertebrates in this poorly documented region. We provided for the first time an integrated and large-scale vision of the diversity and distribution of cetaceans and seabirds inhabiting the French EEZ of the Antilles and Guiana. We derived estimates of abundance for two cetacean species in Guiana and for several seabird taxa in both sectors. This provided a useful baseline, in particular for cetaceans, for which few estimates of abundance exist in the WTA.

b) Comparison with previous studies

Cetaceans

Dedicated effort has been limited in the WTA and quantitative information is rare, except in the Gulf of Mexico (*e.g.* Davis et al. 2002). According to strandings (Cardona-Maldonado and Mignucci-Giannoni 1999), and sightings (Swartz et al. 2003, Gero et al. 2007, Yoshida et al. 2010), the Antilles and Guiana appear to be inhabited by a diverse cetacean fauna. All cetacean species identified during the surveys were previously reported in the Wider Caribbean (Ward et al. 2001). We focus on the most commonly encountered species.

Guiana dolphin is continuously distributed from southern Brazil to Honduras (Flores and DaSilva 2008). Its ecological niche is defined as a narrow strip of coastal waters (Wedekin et al. 2010). This is consistent with our sightings in Guiana where they were restricted to coastal and shallow waters, and aggregated close to river mouths and estuaries (Edwards and Schnell 2001, Rossi-Santos et al. 2006). Our minimum estimate of abundance was of 2,076 individuals (CV=44.32). The only published estimates of abundance for this species are from studies of portions of Brazilian coastal waters (Torres and Beasley 2003, Cantor et al. 2012). Bottlenose dolphins were widely distributed in Guiana and showed no preferences for specific physiographic features. The same pattern was observed in Abrolhos

Bank (Brazil), where they were widespread and used various depth, whereas Guiana dolphins were the only species inhabiting waters within 10 km from the coast (Rossi-Santos et al. 2006). Although bottlenose dolphins are widely distributed in the WTA, there is very little information on their abundance. Our minimum estimate of abundance (34,965 individuals (CV=0.28)) is the first for Guiana.

The only published line transect survey carried out in the Lesser Antilles (Yoshida et al. 2010) suggested low cetacean densities in offshore waters beyond the insular shelf. During our survey, cetacean sightings were the most frequent in slope habitats. Humpback whales and sperm whales were the most commonly sighted cetaceans. Humpback whales migrate to the eastern Caribbean for mating and calving in the winter season (Clapham 2002) with a peak in February and March (Mignucci-Giannoni 1998). Breeding areas occur on offshore banks and off insular coasts of the Atlantic margins of the Antilles (Winn et al. 1975, Whitehead and Moore 1982). They were almost exclusively seen in inshore waters on the Atlantic side of the Antilles. Sperm whales were sighted on 7 occasions, notably around Guadeloupe. The Lesser Antilles population of sperm whales was estimated at 145 individuals (95% CI 94-219), known to undertake inter-island movements (Gero et al. 2007).

Seabirds

Since there had been no at-sea surveys for seabirds in the Lesser Antilles and Guiana, we will compare our abundance estimates with censuses at breeding colonies (*e.g.* Boyé et al. 2009). Such a comparison has successfully been done using demographic parameters to subtract the non breeding component of the at-sea population (Van der Meer and Leopold 1995, Clarke et al. 2003). Our at-sea abundance estimates include immatures, breeding and non breeding adults, as we could not differentiate them from the air. Feeding communities represent the at-sea component of seabird community ecology and often comprise individuals that come from scattered or distant breeding colonies, potentially including extensive portions of populations that breed in other regions (Ballance 2008).

Grand Connétable Island is the only seabird breeding site between the Amazon and the Orinoco. It hosts large colonies during the breeding season (between April and September), including 1,500 pairs of royal terns (*Sterna maxima*), 8,000 pairs of Sandwich terns (*S. sandvicensis)* and several hundreds of pairs of sooty terns (Bird Life International 2012). Hence, royal terns and Sandwich terns may represent a significant amount of our grey

tern category. Additionally, approximately 650 pairs of magnificent frigatebirds nest there year-round (Weimerskirch et al. 2006, Bird Life International 2012). Overall, our at-sea abundance estimates were in the order of magnitude of breeding pairs, considering that the survey was conducted at the end of the breeding season, when adults as well as dispersing youngs may be present. Sooty terns are completely pelagic and highly gregarious (Hertel and Ballance 1999, Surman and Wooller 2003). This is well reflected in our map of local density. However, our estimate of abundance was high compared to breeding numbers, suggesting that non breeders from other regions represented a significant amount of the at-sea population. For grey terns, our abundance estimate was in concordance with the number of breeding pairs. Their density was high along the coast, where roosting sites are probably numerous. Magnificent frigatebirds were aggregated around *Grand Connétable* Island; hence, a significant amount of the population was probably breeding during the survey.

In the Antilles, seabird densities were higher close to the islands, and probably related to the proximity of colonies. Depending on survey synchrony with the breeding season, the location of colonies was shown to have a strong influence on seabird at-sea distribution (Ballance et al. 1997, Smith and Hyrenbach 2003, Ford et al. 2004, Jaquemet et al. 2005). Offshore aggregations can be related to feeding opportunities. For example, there was a high density of brown terns south of Martinique where there are important colonies (*Ilets et falaises de St Anne* and *Rocher du Diamant*) hosting 3,500 to 12,000 pairs of sooty terns (Lemoine and Dubief 2008). The aggregation of tropicbirds observed around *Marie Galante* can be related to a known colony hosting 200 to 450 pairs of red-billed tropicbirds (*Phaethon aethereus*) (Levesque and Mathurin 2008). Similarly, the high density of brown boobies (*Sula leucogaster)* east of Guadeloupe might be related to the vicinity of a colony (Levesque and Mathurin 2008). The distribution of brown terns and tropicbirds was much more pelagic compared to brown boobies, which are mainly inshore feeders (Harrison 1991).

c) Contrasting cetacean and seabird communities in the Antilles and Guiana

Our study revealed differences in cetacean and seabird communities between the Antilles and Guiana, two sectors of contrasted oceanography and productivity levels.

Seabird encounter rate was similar in both sectors. Charadriiformes were frequently encountered and dominated by terns in both sectors. Procellariiformes were rare in the Antilles and in Guiana. Pelecaniformes were more frequently encountered in the Antilles and

represented by frigatebirds, boobies and tropicbirds, while they were mainly represented by frigatebirds in Guiana.

Previous studies have shown that productivity affected seabird community structure at the macro scale (Ballance et al. 1997, Smith and Hyrenbach 2003, Hyrenbach et al. 2007, Schick et al. 2011). In the ETP, sooty terns foraged in waters of low productivity and red footed boobies (*Sula sula*) and masked boobies (*S. dactylatra*) in waters of higher productivity, in accordance with their costs of flight (Ballance et al. 1997). Conversely, in our study, sooty terns were abundant in both high productivity and low productivity sectors, and boobies were only abundant in the low productivity sector. Nevertheless, the high proportion of tropicbirds within the Antillean community appeared in accordance with the study of Vilchis et al. (2006) who noted their associations with low surface chlorophyll waters.

Since seabirds are constrained to breed on land, the availability of substrate and the size of colonies may also be strong determinants of at-sea communities during the breeding season (Hertel and Ballance 1999). Notably, the limited space available to breeding seabirds in Guiana may have promoted competition for nest sites. Hence, the low abundance of boobies and tropicbirds in Guiana may be related to the absence of appropriate breeding sites.

The encounter rate of odontocetes was 3 times higher in Guiana compared to the Antilles (5 times higher in terms of individuals). In Guiana, small delphinids strongly dominated the odontocete community and bottlenose dolphins were particularly abundant. In the Antilles, the community was more equally partitioned between small delphinids, large delphinids and sperm and beaked whales. Nevertheless, the different physiographic habitats in both sectors (the narrow insular shelf around the Antilles *versus* the wide continental shelf in Guiana) may have influenced these community compositions.

Many studies have shown that highly productive areas are associated with high densities of cetaceans (*e.g.* Ballance et al. 2006, Cañadas et al. 2005, Jaquet and Whitehead 1996, Tynan et al. 2005). Conversely, oligotrophic areas are often characterized by low cetacean densities (*e.g.* in the Bahamas, MacLeod et al. 2004). Therefore, the much higher encounter rate of cetaceans in Guiana may be related to the higher productivity in that sector.

The structure of cetacean communities may change according to productivity. Schick et al. (2011) studied cetacean communities from Nova Scotia to the Gulf of Mexico and described two groups of cetaceans separated along a surface chlorophyll gradient. Piscivorous

species were found in the cooler, more productive waters of the continental shelf and teuthophagous species in offshore, warmer and less productive waters at the shelf break. In Guiana, the dominance of small delphinids, which are limited by their physiology to shallow diving (Williams et al. 1993) and are mainly piscivorous (Pauly et al. 1998), may be related to the more abundant food resources in the epipelagic layer. The dominance of bottlenose dolphins within small delphinids in Guiana may result from a competitive exclusion of similar species, as seen in the Bahamas (MacLeod et al. 2004). In contrast, in the Antilles, sperm and beaked whales accounted for a greater proportion of the odontocete community. Sperm whales, which feed on deep-sea squids, have been shown to be positively correlated with the intensity and thickness of middle and deep scattering layers (Jaquet and Whitehead 1996). Despite the oligotrophy of the epipelagic waters in the Caribbean province (Longhurst 2007), the secondary production may be greater in deeper layers, promoting feeding opportunities for these deep diving teuthophagous. Therefore, the observed differences between odontocete communities in both sectors may be the result of a differential location of food resources (in the epipelagic layer in Guiana *versus* in deeper layers in the Antilles).

5) Conclusion

This study provided valuable information on cetaceans and seabirds in the Antilles and Guiana. It highlighted differences in cetacean and seabird communities between these geographically close sectors characterized by contrasting productivity levels. In particular, small delphinids appeared to respond to productivity, with a high abundance of bottlenose dolphins in Guiana. In order to obtain a more complete picture of cetacean and seabird communities along a continuous productivity gradient, it would be useful to implement the aerial survey regionally, from Guiana to the whole Antillean Arc.

Chapter VI. Predicting cetacean and seabird habitats in the Southwest Indian Ocean

Photo credit: Observatoire PELAGIS / AAMP

This chapter is a synthesis of an article published in *Ecography*, presented in ANNEX 2:

Mannocci, L, Laran, S, Monestiez, P, Dorémus, G, Van Canneyt, O, Watremez, P, Ridoux, V, 2013. Predicting top predator habitats in the Southwest Indian Ocean. *Ecography* 36: 001-018.

1) Objective

The optimization of foraging success represents a strong selection pressure on top predators. At the individual scale, energetic constraints were shown to govern top predator strategies of resources utilization; energetically costly cetaceans selecting the highest quality prey (Spitz et al. 2012). We hypothesized that, at the ecosystem scale, energetic constraints also govern top predator strategies of habitat utilization. Predators with energetically costly life styles may be constrained to select the highest quality habitats to meet their high energetic needs, whereas less active predators may be able to satisfy their needs by exploiting either high or low quality habitats.

We collected cetacean and seabird sighting data during a multispecific aerial survey in the Southwest Indian Ocean (SWIO). This region encompasses three biogeographic provinces characterized by heterogeneous oceanographic conditions (Longhurst 2007). The Mozambique Channel is characterized by very dynamic mesoscale eddies (De Ruijter et al. 2004) generating productivity enhancements (TewKai and Marsac 2009). In the rest of the region, surface productivity is contrasted, with oligotrophic waters in the South (oceanic waters to the east of Madagascar and around the Mascarene Islands) and richer waters to the North (around the Seychelles plateau) (New et al. 2005).

We used GAMs along with time-averaged oceanographic variables and static variables to predict cetacean and seabird habitats at the regional scale in the SWIO. The first objective was to investigate cetacean and seabird responses to the spatial heterogeneity in habitat quality and relate these distributional properties to their energetic constraints. The second objective was to evaluate cetacean and seabird responses to different levels of temporal integration in habitat quality, more precisely to contemporaneous *versus* time-averaged habitat quality.

2) Material and methods

a) Study region

The oceanographic characteristics of the SWIO are described in Chapter II.

b) Energetic guilds

The classification of cetaceans and seabirds into energetic guilds is detailed in Chapter II. Twenty-two species of seabirds and seventeen species of cetaceans are represented in the energetic guilds considered in this study (ANNEX 2, Table 1).

c) Survey period and survey design

The aerial survey was conducted from December 2009 to April 2010. The study region was stratified into six geographic sectors: Northern Mozambique Channel (NMC, including Comoro and Glorioso Islands), Central Mozambique Channel (CMC, including Juan de Nova), Southern Mozambique Channel (SMC, including Europa and Bassas da India), Seychelles (SE), Tromelin - Madagascar (TM) and Reunion - Mauritius (RM) (Figure VI-1). Each sector was subdivided into bathymetric strata corresponding roughly to shelf (0-200 m), slope (200-2,000 m) and oceanic domains (>2,000 m).

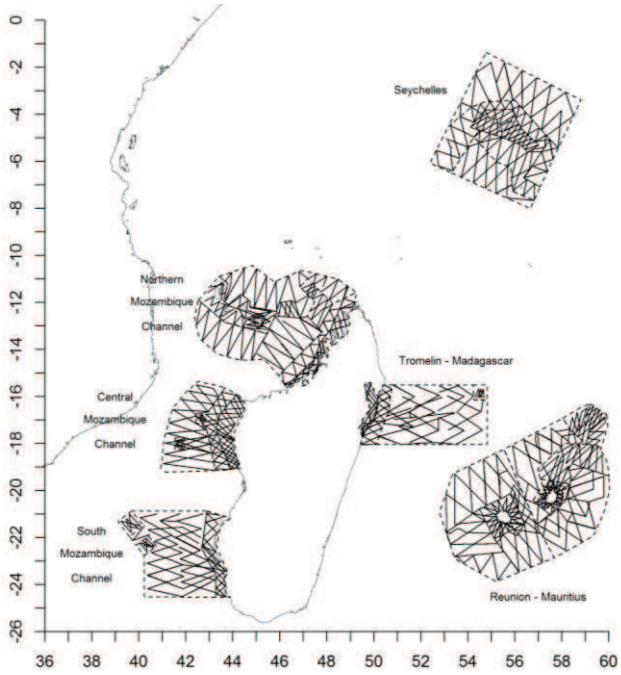


Figure VI-1: Map of the study region in the SWIO. Transects were conducted within six geographic sectors.

d) Aerial survey methods

The aerial survey followed the general methodology described in Chapter IV. Survey platforms were two Britten Norman 2.

e) Analytical methods

We used multiple covariate distance sampling (Marques and Buckland 2004) to model the effect of sea state, glare severity and subjective conditions on cetacean detection probability, in addition to distance (Chapter IV). We used GAMs to relate the number of cetaceans and seabirds per 10 km-segment to environmental variables. The general habitat modeling framework is presented in Chapter IV; its specific implementation in the SWIO is detailed in ANNEX 2.

We relied on remotely sensed oceanographic and static variables to model cetacean and seabird habitats (ANNEX 2, Table 2 and Figure 2). Data sources and resolutions are detailed in ANNEX 2. Oceanographic variables were chlorophyll-a concentration (CHL), sea surface temperature (SST), net primary production (NPP) and the standard error of sea level anomaly (SLA). We considered oceanographic variables at three temporal resolutions: (1) a short-term or contemporaneous resolution, corresponding to a weekly time period, (2) a medium-term or seasonal resolution (abbreviated as 'seas'), corresponding to oceanographic conditions averaged over the season of the survey (December 2009 - April 2010) and (3) a long-term or climatological resolution (abbreviated as 'clim'), corresponding to oceanographic conditions averaged over the same season (December to April) from 2003 to 2010. We used slope and distance to the nearest colony (D_{colony}) as static variables (the latter only for seabirds).

If predators responded better to time-averaged habitat quality, replacing time-averaged oceanographic variables in the selected models by their instantaneous equivalents would yield lower explained deviances. If predators responded better to contemporaneous habitat quality, this would yield higher explained deviances.

3) Results

a) General description

Details on survey effort, survey conditions and cetacean and seabird sightings can be found in ANNEX 2 (Table 3 and Figure 3).

b) Detection function modeling

Best fitting detection models were half normal for Delphininae and Globicephalinae and hazard rate for sperm and beaked whales (ANNEX 2, Table 4). Glare severity significantly affected the detection of Delphininae. No detection variable had a significant effect on Globicephalinae. Sea state significantly affected the detection of sperm and beaked whales. There were no detection functions for seabirds, as implied by the strip transect methodology.

c) Habitat modeling

Selected models

Explained deviances for cetaceans were comprised between 10.7% and 4% (Figure VI-2). For Delphininae, the selected model included NPP_{clim}, SST_{seas} and SLA_{seas}. For Globicephaline, CHL was preferred over NPP. For sperm and beaked whales, only climatological variables were selected (NPP_{clim}, SST_{clim} and SLA_{clim}). There was a higher NPP optimum for Delphininae (2.7 in log scale) compared to sperm and beaked whales (2.4). Overall, cetacean densities increased with SST. The densities of sperm and beaked whales increased in areas of higher standard error of sea level anomaly, suggesting an affinity for higher mesoscale activity. There was a weak effect of slope on Delphininae. Densities of Globicephalinae decreased with slopes greater than 4%. There was a positive linear relationship between slope and sperm and beaked whales.

For seabirds, explained deviances were higher and ranged from 19.6% (boobies) to 39.7% (grey terns) (Figure VI-2). Distance to the nearest colony was an important predictor, explaining between 6.6% (boobies) and 32.1% (petrels and shearwaters) of deviance. Based on the interpretation of curves, we can notice a colony effect up to about 200 km for tropicbirds and frigatebirds and 500 km for petrels and shearwaters and brown terns. Either seasonal or climatological variables were selected depending on the guild. Many seabirds showed unimodal relationships with CHL. Densities of brown terns and grey terns increased with SST. Noddies, boobies and petrels and shearwaters showed increasing relationships with the standard error of sea level anomaly, whereas tropicbirds and grey terns showed decreasing relationships. Slope was selected only for brown terns, with a decreasing relationship with higher slope values

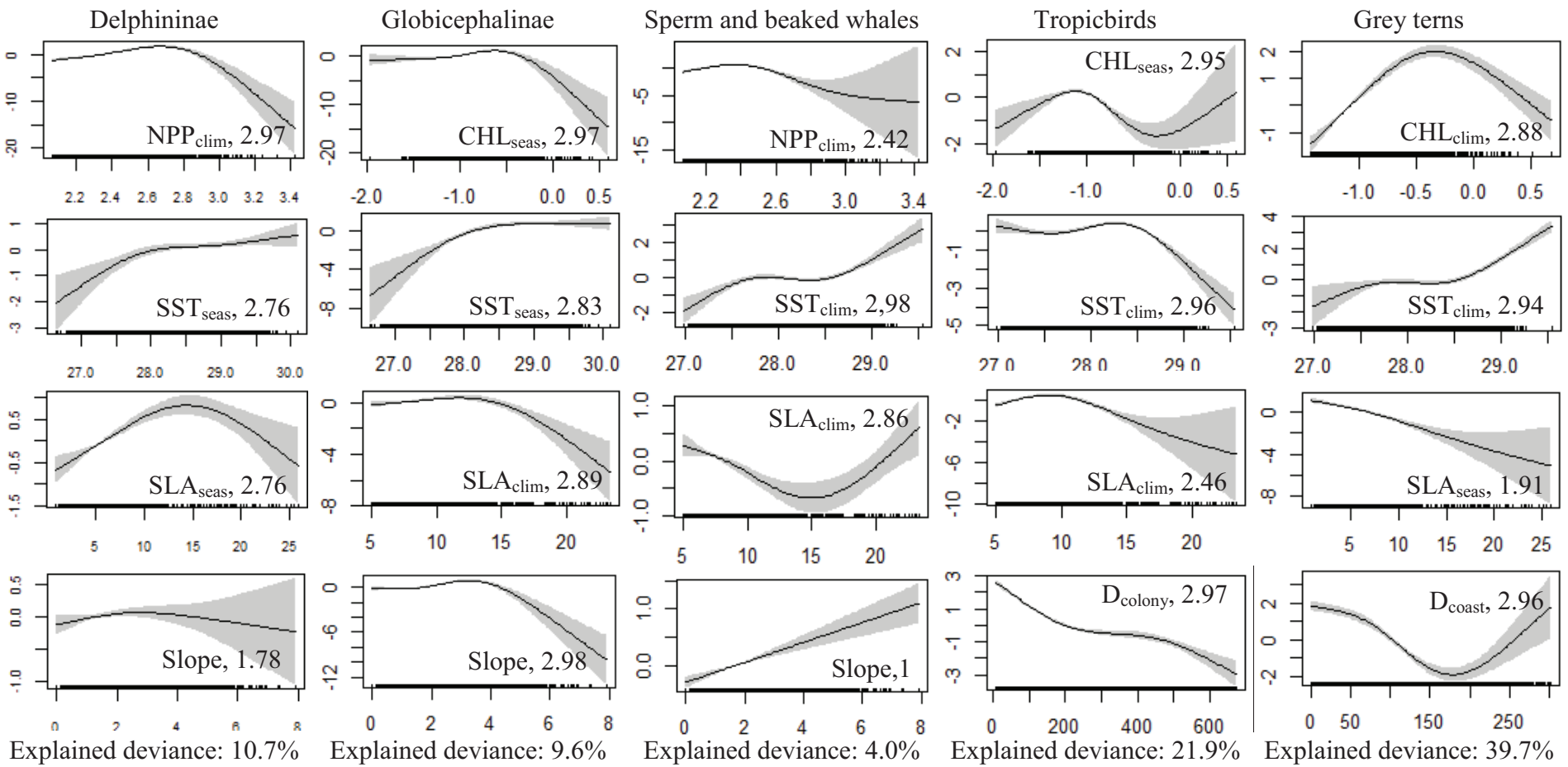


Figure VI-2: Forms of smooth functions for the selected variables for each guild. CHL and NPP were log-transformed, slope was square-root-transformed. Estimated degrees of freedom are provided for each smoother. The solid line in each plot is the smooth function estimate and shaded regions represent approximate 95% confidence intervals. Zero on the y axis indicates no effect of the variable (given that the other variables are included in the model).

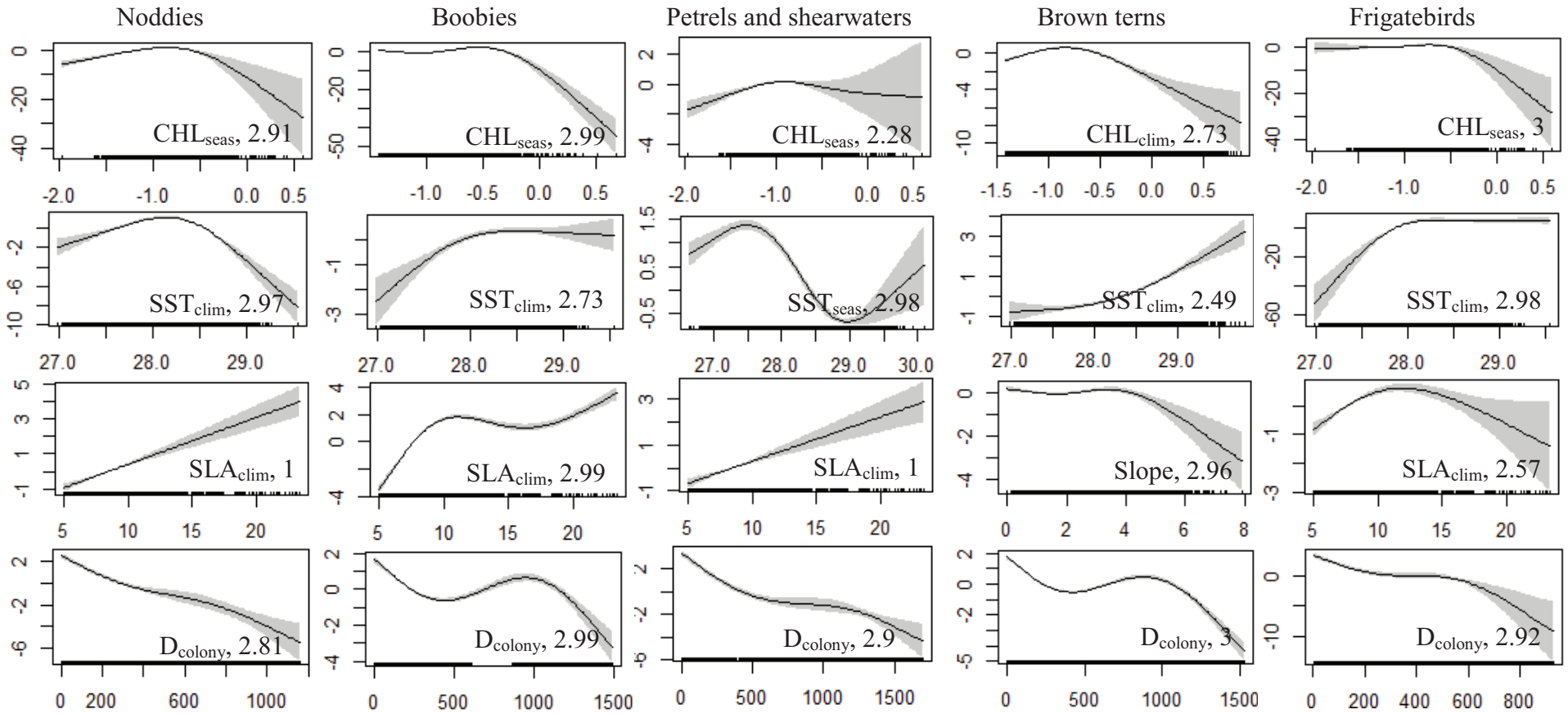


Figure VI-2 (continued).

Predictions

Prediction maps differed for the three cetacean guilds (Figure VI-3). Areas with the highest predicted densities of Delphininae were the Mozambique Channel, especially its center and south and the Seychelles. In contrast, low densities of Delphininae were predicted around the Mascarenes (including TM and RM sectors). For Globicephalinae, maximum densities were predicted in the Mozambique Channel, particularly in the slope strata, as well as around the Seychelles and predicted densities were lower in the Mascarenes. For sperm and beaked whales, predicted densities were less contrasted between these three areas. They were the highest in the high mesoscale activity area in the center of the Mozambique Channel. As for Delphininae and Globicephalinae, predicted densities were lower around the Mascarenes but to a lesser extent. Indeed, the ratios of predicted densities in the six sectors differed for the three guilds. For Delphininae, predicted densities showed a 1-to-13 ratio between the highest (CMC) and lowest density sectors (RM) (Figure VI-4a). For Globicephalinae, there was a 1-to-7 ratio (Figure VI-4b) and for sperm and beaked whales, only a 1-to-3 ratio (Figure VI-4c). Predicted densities (standardized for each guild by its mean density) showed a positive relationship with the climatology of net primary production (NPP_{clim}). For the three cetacean guilds, density increased with increasing primary production. However, the slope of the regression line was the highest for Delphininae, intermediate for Globicephalinae and the lowest for sperm and beaked whales, indicating that Delphininae responded more strongly to primary production compared to Globicephalinae and sperm and beaked whales (Figure VI-4d).

For seabirds, prediction maps mainly reflected colony locations (Figure VI-3). Tropicbird predicted densities were high around Reunion, Mauritius, the Seychelles, Europa, Nosy Vé, Cape Amber, as well as outside the sampled sectors, notably around Aldabra and Cosmoledo. There were high predicted densities of grey terns along Madagascar coastlines. Noddy densities were predicted to be the highest around the Seychelles, Glorieuses and Saint Brandon. For boobies, densities were the highest around Tromelin and Europa, as well as in the high mesoscale activity area. For petrels and shearwaters, densities were the highest around Reunion and Mauritius. High densities of brown terns were predicted in the Mozambique Channel with particularly high densities around Juan de Nova Island. Intermediate densities were also predicted in offshore waters, comprising the whole Mozambique Channel and the northeast of Madagascar. Frigatebird densities were the highest around Europa, the Seychelles (including Amirantes) and Comoros.

Predictions appeared in accordance with the observed distributions of cetacean and seabird guilds (ANNEX 2, Figure 3). Uncertainty maps (ANNEX 2, Appendix 4) showed that, overall, high predicted densities were associated with a low uncertainty, whereas low predicted densities were associated with a higher uncertainty. Uncertainty in seabird predicted densities increased with distance from the colony, as illustrated for tropicbirds and noddies.

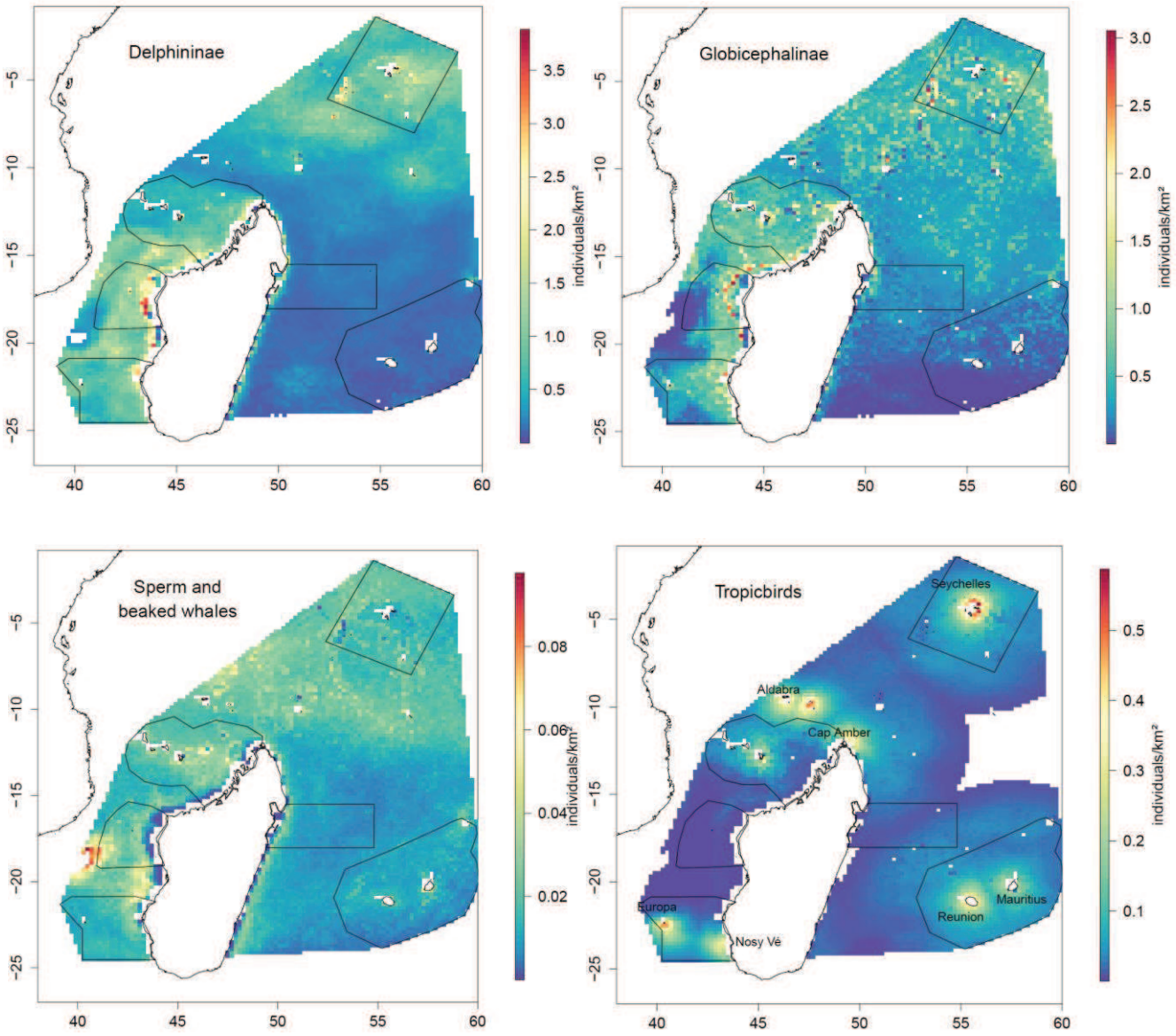


Figure VI-3: Predicted relative density (individuals / km²) for each guild in the Southwest Indian Ocean. Predictions are in a convex hull encompassing the surveyed sectors. The absence of predictions beyond the range of variables used in model fitting resulted in white areas on certain maps. For grey terns, the prediction map was truncated to the North as white terns (*Gygis alba*) were not differentiated from grey terns in the Seychelles.

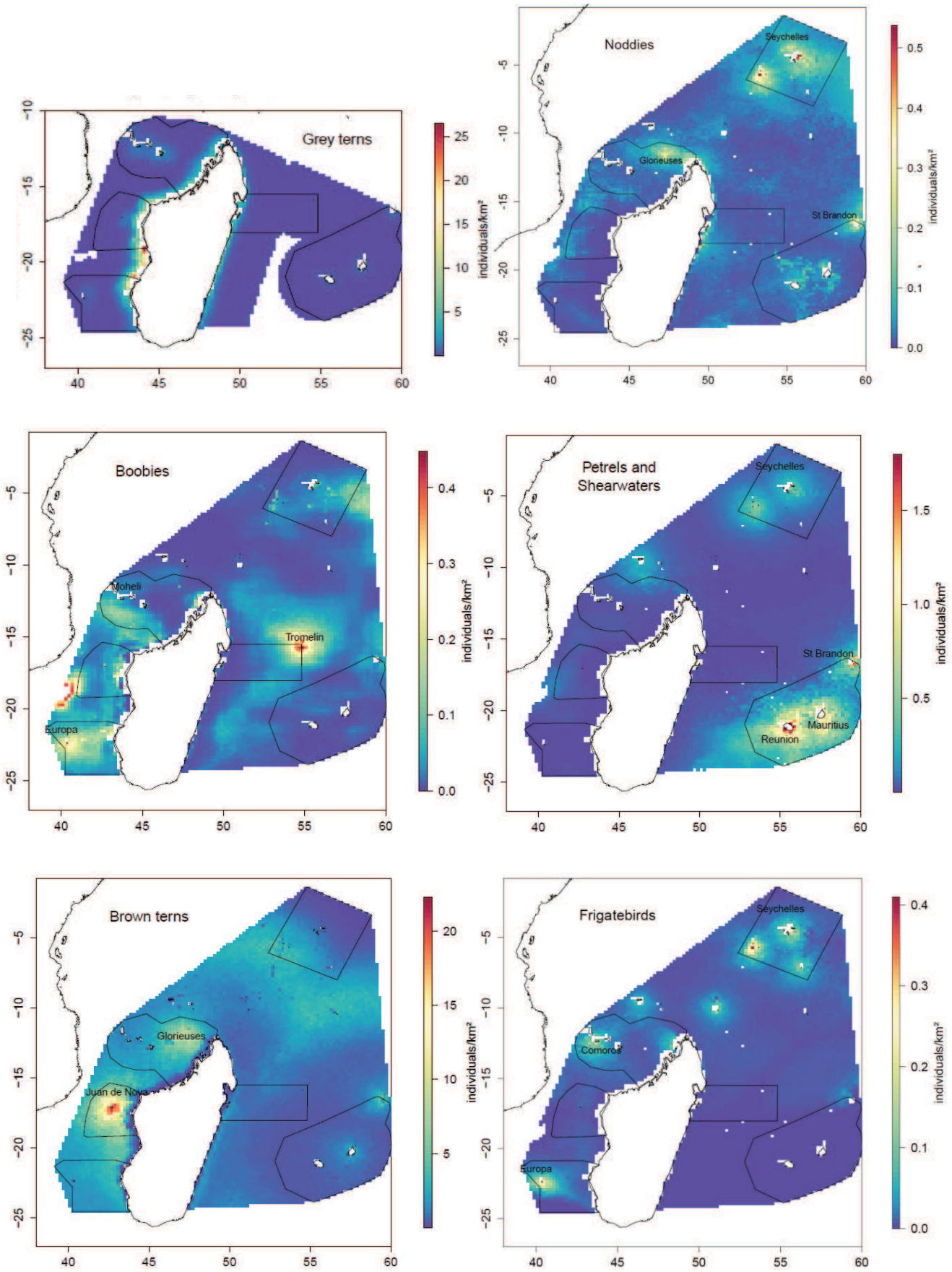


Figure VI-3 (continued).

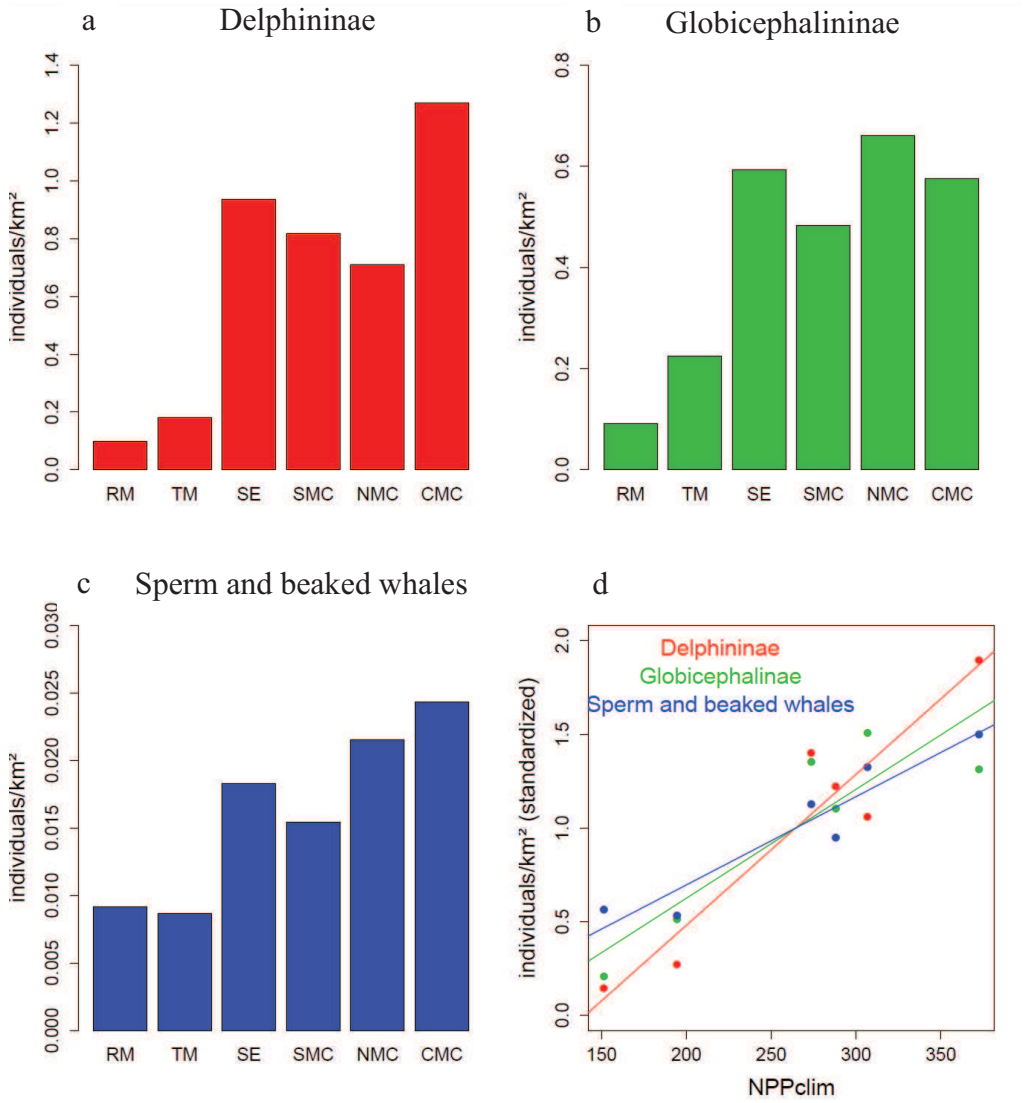


Figure VI-4: Predicted relative densities in the six geographic sectors for Delphininae (a), Globicephalinae (b) and sperm and beaked whales (c), and plotted against the climatology of primary production, after standardization for each guild by the mean density (d). Regression lines are overlaid to materialize each guild relationship to primary production.

d) Response to contemporaneous *versus* averaged oceanographic conditions

Replacing time-averaged variables in the selected models by their contemporaneous equivalents always negatively altered model deviances. For all guilds, deviance was always higher for models built with time-averaged variables (Figure VI-5). This indicates that top predators may not primarily react to short-term variations of their environment but may respond better to averaged oceanographic conditions.

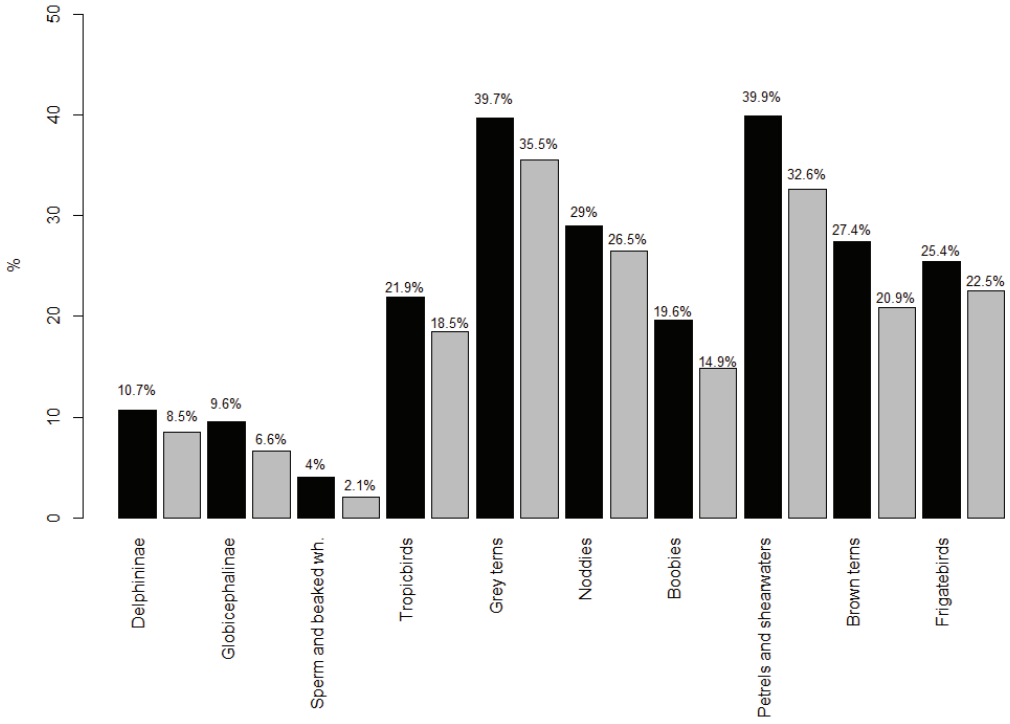


Figure VI-5: Explained deviances of models built with time-averaged (black) and contemporaneous (grey) oceanographic variables for each guild.

4) Discussion

a) Methodological considerations

Survey conditions can affect the detection of cetaceans and generate perception bias (Pollock et al. 2006). We found a significant effect of sea state on sperm and beaked whale detection. Their characteristic resting dives just below the surface (*e.g.* for sperm whales, Miller et al. 2008) may explain this negative effect of deteriorated sea state. Sea state did not have a significant effect on the detection of Delphininae and Globicephalinae. Nevertheless, it may have biased the estimated numbers of individuals. For cetaceans, the estimation of condition-specific ESWs, allowed to incorporate the non homogeneous spatial distribution of survey conditions in habitat modeling (notably the comparatively higher sea state in the Mascarenes). For seabirds, we assumed that all individuals within the strip were detected (Tasker et al. 1984), but some seabirds were undoubtedly missed within the strip.

b) Acquisition of new data in the SWIO

This multispecific aerial survey allowed to cover for the first time extensive pelagic waters in the SWIO, encompassing contrasting oceanographic conditions. It provided valuable information on cetacean and seabird distributions in the austral summer.

Most previous seabird studies in the SWIO relied on telemetry and focused on the breeding component of populations. Telemetry studies, in which each tracked individual is known (sex, status, breeding colony), provided information about seabird movements, activity patterns (Weimerskirch et al. 2004, Catry et al. 2009a) and feeding ecology (Jaquemet et al. 2008, Catry et al. 2009b). In addition, seabird-habitat relationships were previously demonstrated from telemetry studies. For example, Weimerskirch et al. (2010) highlighted a positive effect of cyclonic eddies on the foraging of frigatebirds. Le Corre et al. (2012) combined tracking data for seven pelagic seabirds to identify foraging hotspots in the western Indian Ocean. They highlighted three breeding areas: the Seychelles, the southern Mozambique Channel and the Mascarene archipelago. Boobies and frigatebirds were generally distributed close to their breeding colonies, whereas Procellaridae and tropicbirds had wider distributions and utilised different habitats when breeding or dispersing. These three places also appeared as high density areas in our prediction maps but our aerial survey did not allow differentiating breeding from dispersing seabirds. Nonetheless, the two approaches appear complementary: telemetry surveys give a real-time picture of an individual while it moves in its environment, and aerial or boat-based surveys provide a real-time picture of seabird at-sea populations while the platform moves (Ballance 2008).

Previous cetacean studies in the SWIO mainly relied on boat-based surveys in inshore areas. Although effort was limited in comparison to our aerial survey, they provided useful information on cetacean communities and species diversity around some islands (*e.g.* Mayotte, Kiszka et al. 2011). The most extensive previous survey in terms of effort (9,784 km, mostly located in the Arabian Sea), characterized twelve widespread species and proposed relative abundances for several cetaceans; the spinner dolphin dominated in terms of encountered individuals and the sperm whale, in terms of groups (Ballance and Pitman 1998). Although this survey covered offshore waters, it was based on a ship of opportunity and resulted in a non standard design and a non homogeneous coverage and may not be fully comparable with our dedicated aerial survey.

c) Contrasting cetacean distributions in the SWIO

The SWIO encompasses a range of oceanographic conditions. The Mozambique Channel is characterized by very dynamic mesoscale eddies, the Seychelles are influenced by the monsoon and have productive surface waters, while the Mascarenes remain oligotrophic year-round (Longhurst 2007). Cetacean predicted distributions were contrasting across these three areas: densities were the highest in the Mozambique Channel and the Seychelles and the lowest around the Mascarenes. Thus, cetaceans quite logically appeared more abundant in productive regions. This is also true for other top predators, such as tunas, as reflected in fisheries data. Indeed, catches of bigeye tuna *Thunnus obesus* (longline fisheries) and yellowfin tuna *Thunnus albacares* (purse seine fisheries) are mostly distributed in the equatorial area to the north of Madagascar and in the Mozambique Channel, but not in the Mascarenes (Ménard et al. 2007).

Our models predicted high densities of cetaceans in the Mozambique Channel. In particular, Delphininae densities were the highest in the center and southern Mozambique Channel, where mesoscale activity is the most dynamic. Top predators, including tunas (Tew Kai and Marsac 2010) and frigatebirds (TewKai and Marsac 2009, Weimerskirch et al. 2010) are known to associate with mesoscale eddies in the Mozambique Channel. According to Sabarros et al. (2009), advection of coastal nutrient-rich waters and eddy-eddy interactions enhance biological production, which sustains the stocks of micronekton through bottom-up processes and in turn shapes the distribution of top predators.

d) Responses to the spatial heterogeneity in habitat quality in accordance with costs of living

In this study, energetically costly Delphininae appeared to be more dependent on productivity than the other cetacean guilds. High Delphininae densities were predicted in the most productive habitats (Mozambique Channel and the Seychelles) and conversely, low densities (as much as 13 times lower) were predicted around the Mascarenes. In contrast, the less active sperm and beaked whales were present in both high and low productivity habitats and seemed less dependent on habitat quality (they showed only a 1-to-3 ratio between the highest and lowest density sectors). Globicephalinae, with a 1-to-7 ratio, appeared intermediate. Therefore, at the ecosystem scale, cetacean distributions appeared to concord with their costs of living.

Sooty terns, characterized by a low cost of flight (Flint and Nagy 1984), were observed in all sectors and occupied all habitats. As for sperm and beaked whales, they may not heavily depend on productivity. However, this pattern was not strongly reflected in our prediction map, showing a very high density area around the Juan de Nova colony. Indeed, distance to the nearest colony explained a significant amount of deviance for some seabirds and prediction maps mainly reflected colony locations. Seabird at-sea distributions strongly depend on where they breed (Le Corre et al. 2012) and the colony effect (Hyrenbach et al. 2007) was a predominant pattern in our predictions. Differences in seabird energetic costs were partly reflected in this colony effect. Tropicbirds, which have high energetic costs, were tightly related to their colonies (influence of the colony up to 200 km). Conversely, sooty terns and petrels and shearwaters showed a broader colony effect (up to 500 km). This illustrates that energetically costly seabirds are constrained to forage closer to their colonies.

e) Responses to persistent oceanographic features

Following the present results, top predators appeared to be distributed according to averaged oceanographic features, and did not seem to react to short-term oceanographic variability. Either seasonal or climatological variables were selected in the models depending on guilds, indicating no strong preferences for the medium or long-term resolutions. Indeed, oceanographic conditions during the survey period did not differ much from the climatology, and both resolutions yielded similar information. When relying on large-scale surveys, evaluating top predator responses to time-averaged environmental parameters has proven useful to build habitat models (Kaschner et al. 2006). A technical advantage is that averaged remote sensing products (composites) are less affected by cloud coverage. On the other hand, responses to instantaneous environmental conditions can be more appropriately evaluated by telemetry studies (Baumgartner and Mate 2003, Weimerskirch et al. 2010).

This study showed that cetaceans and seabirds responded better to persistent (highly predictable) compared to ephemeral (less predictable) environmental situations. This is consistent with memory-based foraging strategy (Davoren et al. 2003a, b). Especially in tropical oceans where resources are dispersed, top predators may have learned to exploit oceanographic features that determine recurrent access to food resources.

5) Conclusion

In this study, we used cetacean and seabird sighting data collected from a dedicated aerial survey in the SWIO along with GAMs to highlight their responses to time-averaged oceanographic conditions and propose regional habitat predictions. For cetaceans, predictions stressed different responses to habitat quality and the dependence of the energetically costly Delphininae to primary production. For seabirds, predictions primarily reflected colony locations, although the colony effect was stronger for energetically costly seabirds. Strategies of habitat utilization at the ecosystem scale appeared in accordance with top predator energetic costs. This study emphasized the importance of predictable oceanographic features for cetaceans and seabirds, although further research is needed to support this finding.

Chapter VII. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre

Photo credit: Pamela Carzon

This chapter is the synthesis of an article in revision in *Progress in Oceanography*, presented in ANNEX 3:

Mannocci, L, Catalogna, M, Dorémus, G, Laran, S, Lehodey, P, Massart, W, Monestiez, P, Van Canneyt, O, Watremez, P, Ridoux, V. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre.

1) Objective

Top predators have adapted their foraging strategies to exploit the extremely scarce resources of oligotrophic oceanic provinces. However, they may respond differently to the productivity of their habitats owing to their energetic constraints. We expected predators with energetically costly life styles to be constrained to select the most productive habitats to match their high energetic requirements, and less active predators to satisfy their needs by exploiting either high or low productivity habitats.

We collected cetacean and seabird sighting data from an aerial survey in the EEZ of French Polynesia (FP), in the core of the South Pacific oligotrophic gyre. FP is characterized by a productivity gradient, with nutrient-depleted waters in the south, around the Australs archipelago and more productive waters to the north, near the Marquesas, where an island mass enhances productivity (Signorini et al. 1999).

This study is a 'sister study' of Chapter VI in another large tropical region; the objectives are the same and the approach is globally similar. We used GAMs along with static and oceanographic covariates to predict the habitats of contrasting cetacean and seabird guilds across FP. The first objective was to investigate top predator responses to the productivity gradient in relation to their energetic costs. Our aerial survey provided a snapshot of top predator distributions in FP in the austral summer 2011, which was concurrent with a moderate La Niña episode (Climate Prediction Center 2011). Therefore, the second objective was to evaluate the capacity of cetaceans and seabirds to respond to the contemporaneous (reflected by the seasonal situation of this survey) *versus* the averaged (or climatological) oceanographic situation.

2) Materials and methods

a) Study region

The oceanographic characteristics in FP are described in Chapter II.

b) Energetic guilds

The classification of cetaceans and seabirds into energetic guilds is explained in Chapter II. Thirty-two species of seabirds and sisteen species of cetaceans are represented in the energetic guilds considered in this study (ANNEX 3, Table 1).

c) Survey period and survey design

The dedicated aerial survey was conducted from January to early May 2011. The study region was divided into six geographic sectors: Society, Australs, North Tuamotu, South Tuamotu, Gambier and Marquesas. Most of the effort was deployed in the oceanic stratum (depth ≥ 2,000 m). Around North Tuamotu and the elevated islands of the Society, Australs, Gambier and Marquesas, a slope stratum was also defined (depth < 2,000 m) (Figure VII-1).

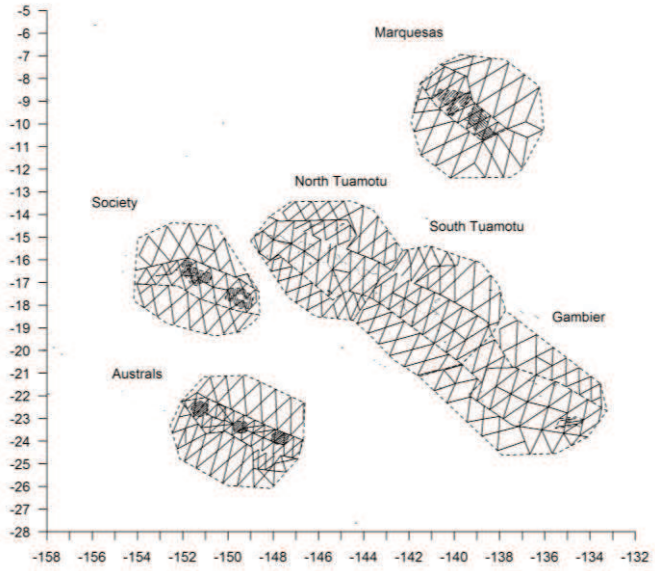


Figure VII-1: Map of the study region in FP. Transects were implemented within six geographic sectors.

d) Aerial survey methods

The aerial survey followed the general methodology described in Chapter IV. Survey platforms were three Britten Norman 2.

e) Analytical methods

We used multiple covariate distance sampling (Marques and Buckland 2004) to model the effect of sea state, glare severity and subjective conditions on cetacean detection probability, in addition to distance (Chapter IV). We used GAMs to relate the number of cetaceans and seabirds per 10 km-segment to environmental variables. The general habitat modeling framework is presented in Chapter IV; its specific implementation in FP is detailed in ANNEX 3.

We relied on remotely sensed oceanographic and static variables to model cetacean and seabird habitats (ANNEX 3, Table 2 and Appendix A). Oceanographic variables were chlorophyll-a concentration (CHL), sea surface temperature (SST), net primary production (NPP) and the standard error of sea level anomaly (SLA). Data sources and resolutions are detailed in ANNEX 3. We considered oceanographic variables at two temporal resolutions: (1) the seasonal resolution (abbreviated as 'seas'), corresponding to contemporaneous oceanographic conditions averaged over the duration of the survey (January–May 2011) and (2) the climatological resolution (abbreviated as 'clim'), corresponding to oceanographic conditions averaged over the same season (January–May) from 2003 to 2011. In this study, the seasonal resolution was the most instantaneous resolution (cloud coverage precluded the consideration of the weekly resolution). We also considered static covariates: slope and depth for cetaceans, and slope and either distance to the nearest colony (D_{colony}) or to the nearest coast (D_{coast}) for seabirds.

If top predators responded to the contemporaneous situation of the survey, we expected seasonal rather than climatological oceanographic covariates to be selected in the final models. Alternatively, if top predators responded better to the average oceanographic situation, climatological oceanographic covariates should be preferred.

3) Results

a) General description

Details on survey effort, survey conditions and cetacean and seabird sightings can be found in ANNEX 3 (Table 3, Figure 2a and Figure 3a).

b) Detection function modeling

Best-fitting detection models were half normal for the three cetacean guilds (ANNEX 3, Table 4 and Appendix D). Turbidity significantly affected the detection of Delphininae. No detection covariate had a significant effect on Globicephalinae. Sea state significantly affected the detection of sperm and beaked whales.

c) Habitat modeling

Selected models

For cetaceans, explained deviances varied between 4.9% for sperm and beaked whales and 29.9% for Globicephalinae. Either climatological or seasonal covariates were selected in the best models (Figure VII-2). Sperm and beaked whales showed an increasing relationship with NPP. For Delphininae and Globicephalinae, smooth functions increased in the core of sampled NPP values (indicated by the 10^{th} and 90^{th} quantiles). Delphininae and sperm and beaked whales showed unimodal relationships with SST, although uncertainty was higher in cooler waters, as expressed by the large confidence intervals. For Globicephalinae, the smooth function indicated an optimum SST within the 10^{th} and 90^{th} quantiles. Densities of Delphininae decreased for higher standard errors of sea level anomaly, whereas densities of sperm and beaked whales increased, indicating an affinity for areas of higher mesoscale activity. Globicephalinae densities increased with higher slope values. Delphininae densities decreased with depth.

For seabirds, explained deviances ranged from 13.9% for petrels and shearwaters to 29.4% for frigatebirds. Climatological covariates were primarily selected in the best models (Figure VII-2). For noddies, white terns, sooty terns and frigatebirds, only climatological oceanographic covariates were selected. The guild of petrels and shearwaters was the only one for which only seasonal covariates were selected. Distance to the nearest coast or colony explained between less than 2% of the deviance, for petrels and shearwaters and sooty terns, and 13.6% for boobies, indicating contrasting dependences to colonies or roosting sites. Seabird densities decreased with distance to the coast or to the colony, except for sooty terns, for which densities were maximum at about 200 km from the coast. Many seabirds showed monotonically increasing relationships with NPP or CHL. Smooth functions suggested optimum SSTs for grey terns, white terns, frigatebirds, boobies and petrels and shearwaters,

although for the latter two, confidence intervals were large in cooler waters. Densities of sooty terns increased with SST. Densities of frigatebirds and boobies decreased with the standard error of SLA, whereas they increased for tropicbirds and sooty terns. Slope was selected for tropicbirds, grey terns, noddies and boobies, with either increasing or decreasing relationships. In general, smooth functions were the least reliable at the extremes of the sampled data (where they were often associated with large confidence intervals) due to the limited amount of data at the edges of covariate ranges.

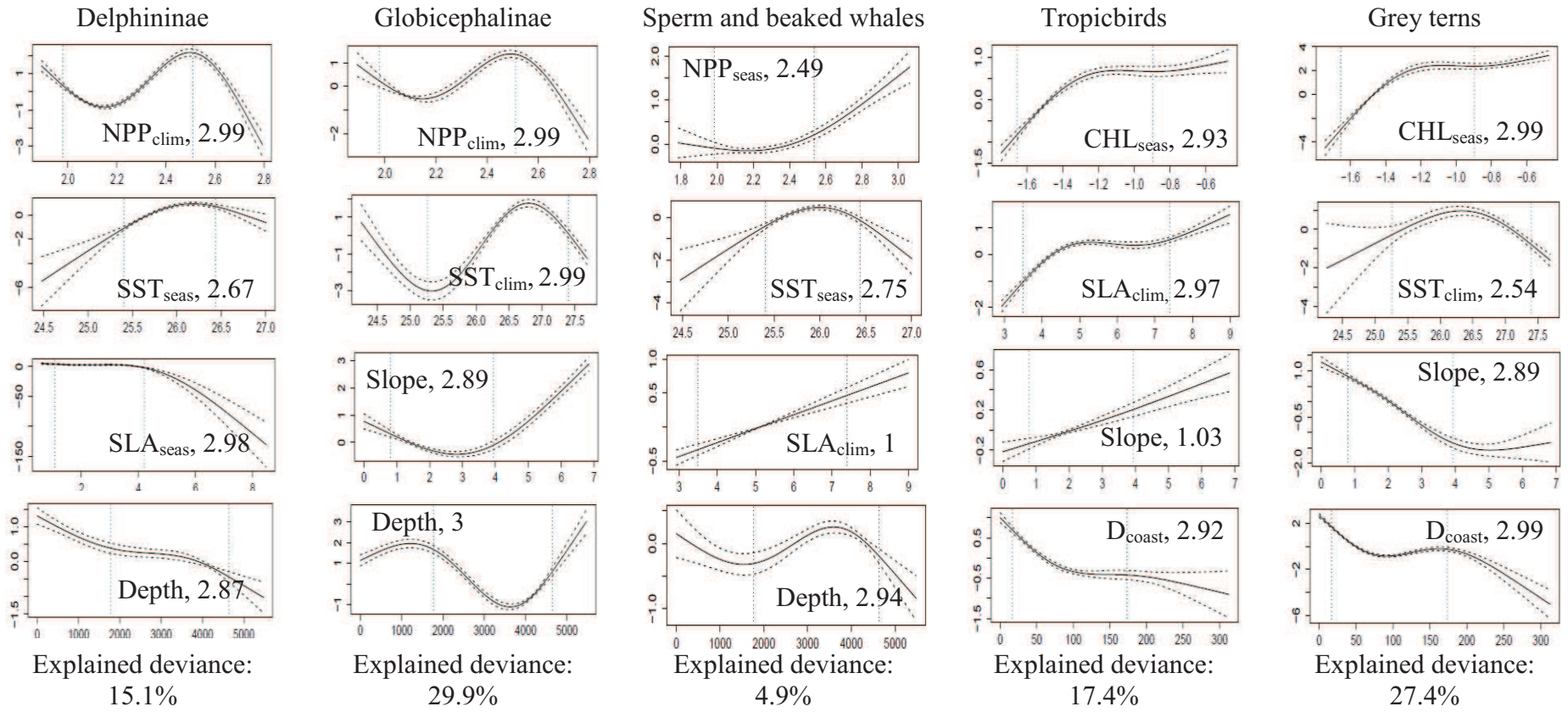


Figure VII-2: Forms of smooth functions for the selected covariates for each guild. CHL and NPP were log transformed, slope was square root transformed. Estimated degrees of freedom are provided for each smoother. The solid line in each plot is the smooth function estimate, dashed lines represent approximate 95% confidence intervals. Zero on the y axis indicates no effect of the predictor (given that the other predictors are included in the model). The tenth and nineteenth quantiles of data are provided as vertical dotted lines for each plot.

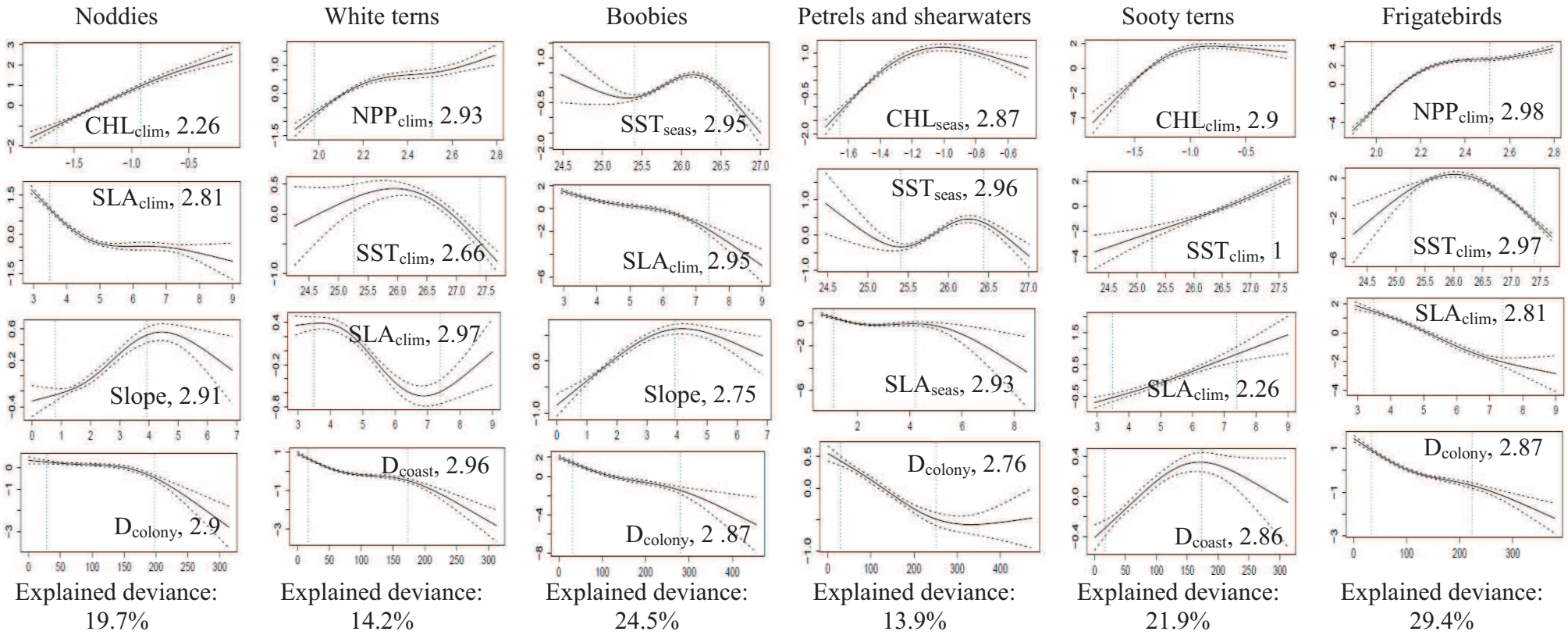


Figure VII-2 (continued).

Predictions

Predicted distributions differed for the three cetacean guilds (Figure VII-3). A latitudinal gradient was apparent for Delphininae, with the highest densities in the Marquesas, intermediate in the Society and Tuamotu and the lowest in the Australs. Mean predicted densities showed a 1-to-26 ratio between the Australs and the Marquesas (Figure VII-4). A latitudinal gradient was also apparent in the predicted distribution of Globicephalinae. Predicted densities were the highest around the Marquesas, intermediate around Tuamotu and the Society and the lowest in the Australs. Mean predicted densities showed a 1-to-31 ratio between the Australs and the Marquesas (Figure VII-4). For sperm and beaked whales, predicted densities were high around the Marquesas (notably to the west), low in a latitudinal band situated between 14 and 22°S, before increasing again south of 22°S, around the Australs. In contrast to Delphininae and Globicephalinae, mean predicted densities showed only a 1-to-3.5 ratio between the lowest (Society) and highest (Marquesas) density sectors (Figure VII-4).

Seabird predicted distributions also revealed a latitudinal gradient, with the lowest predicted densities around Gambier or the Australs (Figure VII-3, Figure VII-4). Tropicbirds had an inshore distribution, with higher predicted densities around the Marquesas and the Society. For grey terns, higher densities were predicted inshore, notably around the Marquesas and Tuamotu and very low densities were predicted in southern FP. For noddies, the highest densities were predicted in North Tuamotu, followed by the Marquesas, and very low densities were predicted south of 20°S. For white terns, the predicted map showed a wide distribution extending to offshore waters (although densities were maximum around the islands), with only a 1-to-4 ratio in predicted densities (Figure VII-4). Boobies had an inshore distribution, with the highest densities predicted in Tuamotu and the lowest in the Australs. Petrels and shearwaters were mainly distributed north of 20°S, with the highest densities predicted in North Tuamotu and the Society. Sooty terns were principally distributed north of 14°S, with maximum densities offshore, at the limit of the surveyed sectors. The highest densities of sooty terns were predicted around the Marquesas. Frigatebirds had an inshore distribution around Tuamotu and Marquesas, with the highest densities predicted around the latter.

Overall, habitat predictions were in accordance with the observed distributions (ANNEX 3, Figures 2a and 3a). Uncertainty maps showed that high predicted densities were

associated with low uncertainty, whereas low predicted densities were associated with higher uncertainty (ANNEX 3, Appendix F). Uncertainty in predicted seabird densities increased with distance from the islands. Typically, two roughly triangular areas located west and southeast of the Marquesas, further offshore from any island than the maximum distance flown by survey aircrafts, corresponded to poor predictions for most seabird guilds (except for petrels and shearwaters).

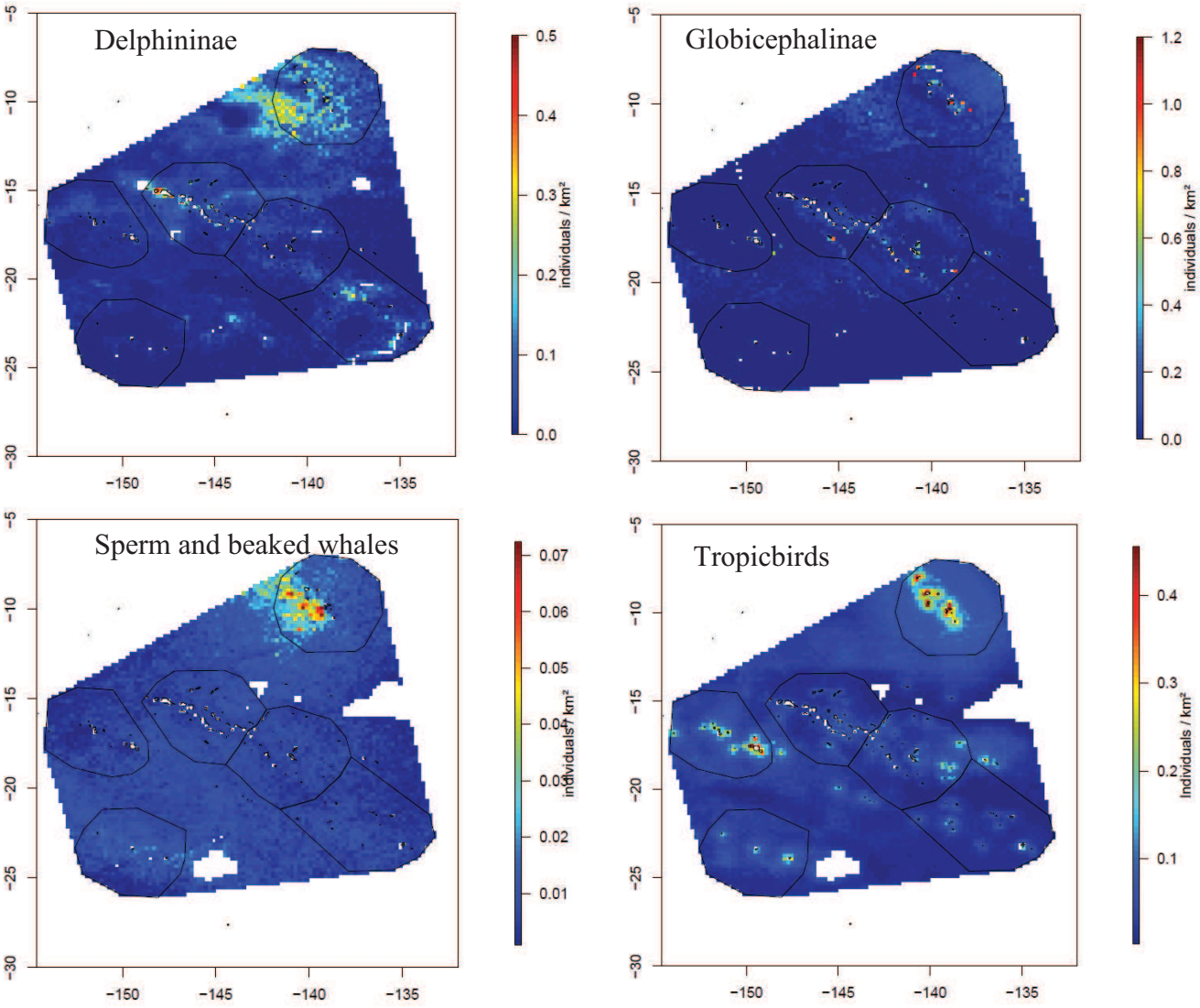


Figure VII-3: Predicted relative densities (individuals / km²) for each guild in French Polynesia. Predictions are in a convex hull encompassing the surveyed sectors. White areas in predicted maps indicate the absence of predictions beyond the range of environmental covariates used in model fitting.

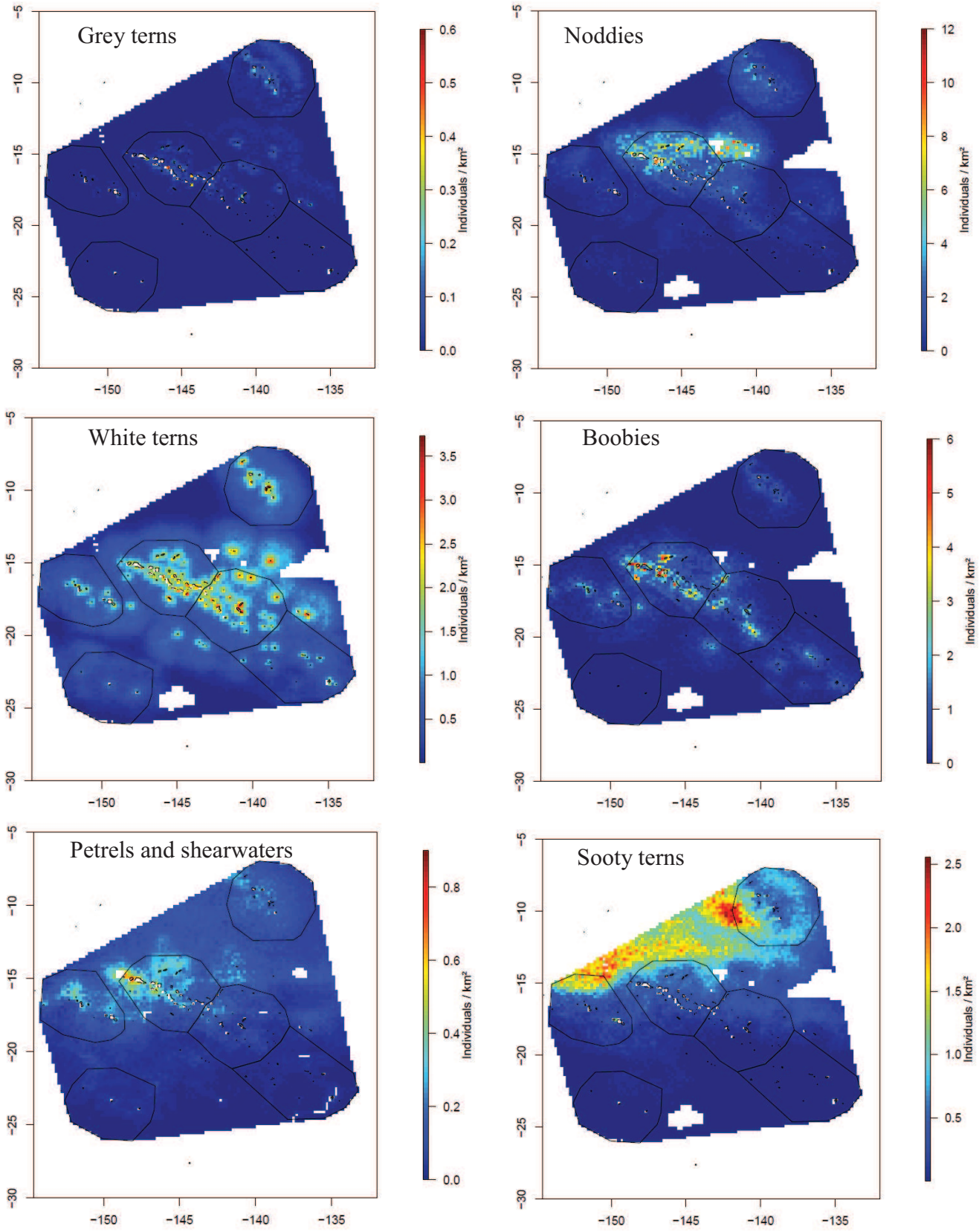


Figure VII-3 (continued).

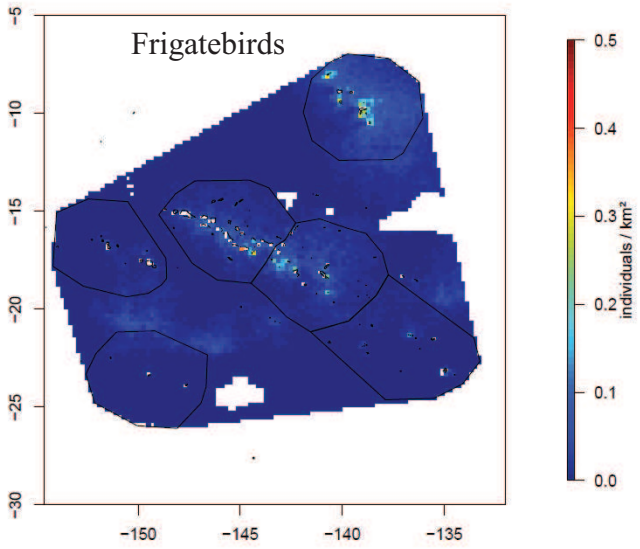


Figure VII-3 (continued).

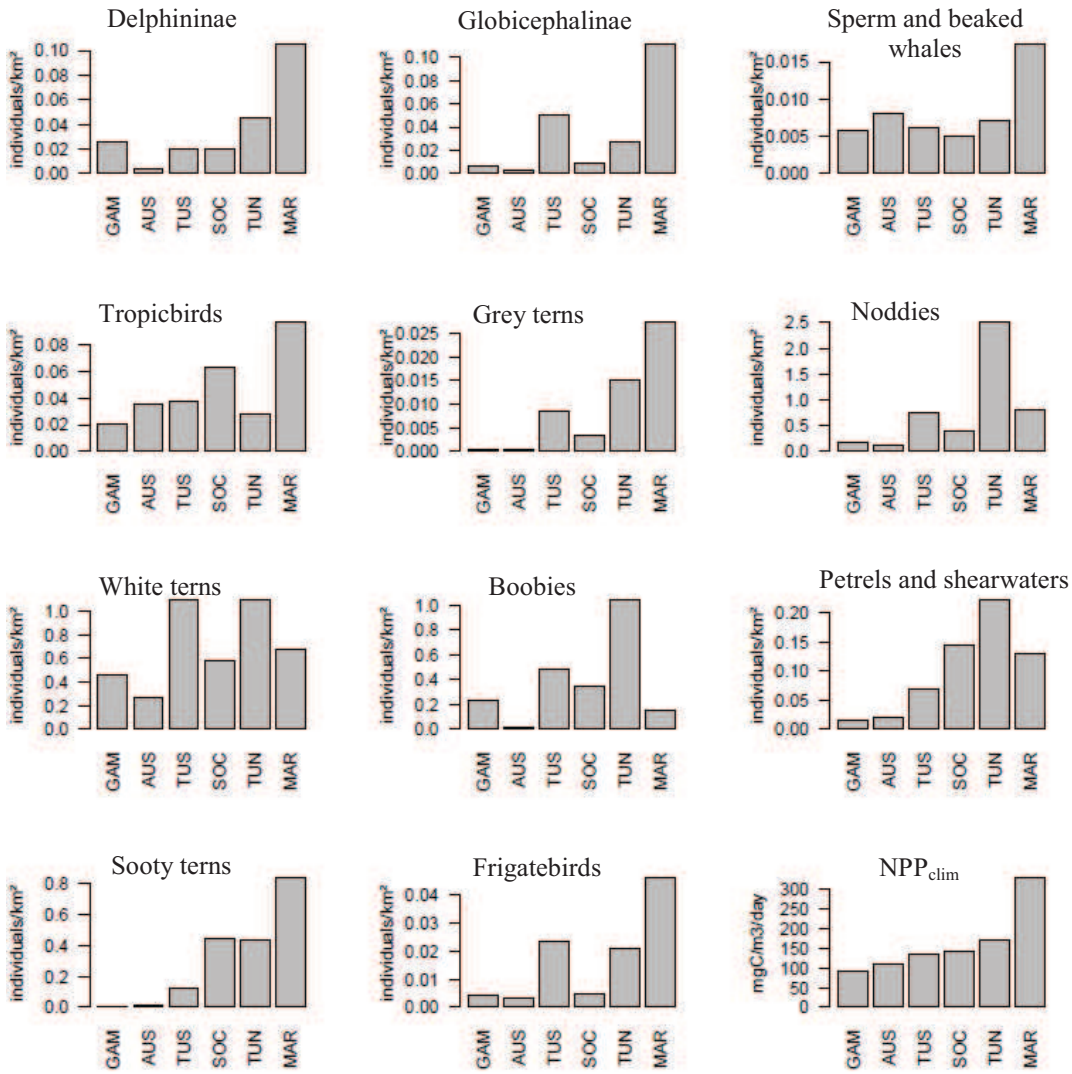


Figure VII-4: Mean predicted relative densities (individuals / km²) for each guild in the six geographic sectors (from the least productive to the left to the most productive to the right). GAM: Gambier, AUS: Australs, STU: South Tuamotu, SOC: Society, NTU: North Tuamotu, MAR: Marquesas.

4) Discussion

a) Methodological considerations

We tested and modeled the effect of survey conditions on the detection of cetaceans, before incorporating it in habitat modeling. Sea state, which was more deteriorated around the Marquesas, significantly affected the detection of sperm and beaked whales. Accounting for this effect in habitat modeling strengthened the initial perception, based on uncorrected encounter rates, that the Marquesas were the sector of highest cetacean densities. Similar corrections could not be performed for seabirds, which were sampled with a strip transect methodology, implying equal detection probabilities across the survey band width. Therefore, possible seabird detection biases related to a deteriorated sea state around the Marquesas could not be accounted for.

Model predictors identified in this study, either oceanographic or static, were previously found to be relevant for cetaceans and seabirds in the northeast and tropical Pacific where environmental data were collected simultaneously with sightings (Becker et al. 2010, 2012, Ferguson et al. 2006a, Redfern et al. 2008, Vilchis et al. 2006, Yen et al. 2004a). However, for a given predictor, the forms of the relationships differed between FP and other regions of the Pacific. This probably resulted from the contrasting ranges of oceanographic variables between these regions, suggesting a limited model transferability (Elith and Leathwick 2009). In addition, logistical constraints inherent to aerial surveys (including the obligate presence of an airport with adequate aircraft maintenance) prevented us from sampling the whole range of environmental conditions present in FP. As a result, waters situated north of the Marquesas and around Rapa in the southeastern Australs, as well as some areas located between the main archipelagos could not be surveyed. These poorly sampled areas corresponded fairly well to the more uncertain predictions (ANNEX 3, Appendix F).

b) Responses to the spatial variability of oceanographic features

Our survey provided for the first time insights into the distribution of cetaceans and seabirds in one of the most oligotrophic regions of the tropical Pacific, which had remained poorly studied to date. The understanding of cetacean and seabird habitats in Pacific waters has primarily focused on eutrophic systems, such as the California Current (Ainley et al. 1995, Ford et al. 2004, Becker et al. 2010) or the Humboldt Current (Anderson, 1989,

Weichler et al., 2004) and mesotrophic systems, such as the ETP (Ballance et al. 2006, Ferguson et al. 2006a).

We investigated cetacean and seabird responses to the spatial variability of oceanographic features in FP. Our prediction maps highlighted the three principal oceanographic domains in the region: (1) the north (between 7 and 14°S), with high surface productivity, (2) the center (between 14 and 22°S), with low eddy activity and low surface productivity and (3) the south (between 22 and 26°S), with strong eddy activity but low productivity.

In the north, densities were comparatively high for the three cetacean guilds and several seabird guilds (*e.g.* sooty terns). Gannier (2009) previously noted the high relative abundance of odontocetes around the Marquesas compared to the Society Islands. The north is characterized by an enhancement of phytoplankton production, occurring to the west of the Marquesas (Signorini et al. 1999). Bertrand et al. (1999) highlighted three micronekton zones from acoustic echo-sounding and found a maximum abundance south of the Marquesas, between 7 and 13°S. The highest tuna catches per unit effort were also reported in this area (Bertrand et al. 2002). Thus, the high densities of top predators are probably related to the abundant food resources.

Conversely, in the center, densities of all cetaceans were low, probably as a consequence of the low abundance of micronekton (Bertrand et al. 1999). In the southern part of the region, densities of cetaceans (except sperm and beaked whales) and seabirds were very low. This area is defined by a strong eddy activity (Martinez et al. 2009) but low surface productivity, unlike what is often observed elsewhere (*e.g.* in the Mozambique Channel Channel, TewKai and Marsac 2009). Mesoscale eddies induce a productivity enhancement in the euphotic zone if (1) nutrients are available in sufficient quantities in the water column and (2) eddy energy is strong enough to drive nutrients to the surface (Uz et al. 2001). This is clearly not the case around the Australs, in the core of the oligotrophic gyre, as illustrated by the very low nitrate concentrations at 200 m (CSIRO Atlas of regional seas, 2009). Sperm and beaked whales were the only cetaceans present at comparatively intermediate densities around the Australs. With their long and deep dives (Watkins et al. 1993, Tyack et al. 2006) and less active lifestyles, they may be able to forage on more dispersed resources than cetaceans with more costly lifestyles. Alternatively, their presence may be related to more abundant deep resources, not accessible to other cetaceans. Thus, oceanographic data describing surface

productivity might be partly irrelevant to predict the distribution of deep divers, unlike suggested in previous studies at very large spatial scales (Jaquet and Whitehead 1996).

Barlow (2006) conducted an extended cetacean line transect survey in the EEZ of the Hawaiian Islands, characterized by low surface productivity and situated at a similar latitudinal range as FP in the northern hemisphere. Low densities of cetaceans, especially delphinids, were reported compared to the more productive waters of the ETP. However, densities of deep divers, including sperm whales and beaked whales, were similar or even higher than in the ETP. This appeared consistent with our results in FP, where deep divers were present with fairly similar densities in both high and low productivity habitats, whereas the costly delphinids appeared constrained to exploit more productive habitats.

c) Strategies of habitat utilization in relation with costs of living

We provided the ratios of predicted densities across surveyed sectors for each guild to assess its dependence on habitat productivity. Cetaceans responded to the productivity gradient. However, the energetically costly small and large delphinids depended more strongly on productivity, showing a 1-to-26 and a 1-to-31 ratio respectively between the lowest and highest density sectors, compared to the less active sperm and beaked whales which only showed a 1-to-3.5 ratio.

Overall, seabirds responded to the productivity gradient, although less clearly than cetaceans did and apparently irrespective of their energetic costs, as illustrated by two guilds of terns. White terns, despite their supposedly intermediate costs of flight, were widely distributed and only showed a 1-to-4 ratio in their predicted densities. Unexpectedly, sooty terns, characterized by low costs of flight (Flint and Nagy 1984), were concentrated in the most productive waters to the leeward side of the Marquesas and between 12 and 15°S to the north of the Society and Tuamotu archipelagos. Sooty terns are mostly winter breeders in the Marquesas (Thibault and Bretagnolle 2007); thus, they were probably not bound to colonies during the survey, as suggested by the maximum densities predicted 200 km offshore. This also disagrees with the study of Ballance et al. (1997), in which sooty terns were abundant in the low productivity waters of the ETP. Nevertheless, productivity around the Marquesas is probably not greater than productivity in the least productive waters of the ETP.

The availability of appropriate sites for nesting and roosting may be crucial determinants for seabirds. White terns usually lay one egg on a bare branch in a tree and form

loose colonies, making their exhaustive census difficult. About 60 000 pairs of white terns are reported in FP, with a majority of small colonies (Thibault and Bretagnolle 2007). These comparatively modest breeding numbers contrast with their at-sea dominance and may be due to a large underestimation of colonies and/or a large proportion of dispersing individuals not bound to colonies. Conversely, sooty terns, which nest on the ground and form very dense colonies, may find the most appropriate nesting habitats in the Marquesas (hundreds of thousand pairs reported by Thibault and Bretagnolle (2007). Sooty terns also breed on seven of the Line Islands, with 1 million pairs reported on Caroline atoll (Kepler et al., 1992), 3 million on Starbuck and up to 15 million on Christmas, the largest population in the Pacific (Perry 1980). Interestingly, when extending the predictions to the west, our model suggested high densities of sooty terns in offshore waters around Caroline atoll (9.937°S, 150.211°W).

Furthermore, the current locations of nesting sites may be heavily influenced by historical (concurrent with the arrival of the first Polynesians) and current anthropogenic pressures, including habitat destruction, direct exploitation and introduced predators (Steadman 1995). For example, the absence of sooty tern colonies in southern FP may be the consequence of extirpations, notably in the Australs, where historical colonies are documented but none remains today (Thibault and Bretagnolle 2007). As a ground-nesting species, the sooty tern is highly vulnerable to predation and direct exploitation. Consequently, the current distribution of some seabirds in FP may better reflect past and present pressures on colonies than energetic constraints.

d) Responses to contemporaneous *versus* averaged oceanographic conditions

Our survey in FP occurred during a moderate La Niña episode (Climate Prediction Center 2011), characterized by slightly lower sea surface temperatures and eddy activity and higher productivity compared to the 10-year average (ANNEX 3, Appendix A). This 'experimental situation' gave us the opportunity to evaluate the capacity of cetaceans and seabirds to respond to the seasonal *versus* the climatological oceanographic situation.

For cetaceans, there was no clear pattern towards the selection of seasonal or climatological covariates in the best models. They did not appear to respond strongly to the conditions of the survey; however, sighting numbers were generally low and possibly impaired our capacity to highlight responses to rather subtle changes in oceanographic conditions. For most seabirds (all guilds but petrels and shearwaters), the climatological

covariates were primarily selected. Hence, these guilds did not respond to the atypical situation observed during the survey but appeared to follow the climatological situation and continued to exploit areas that are on average more favorable to them. Furthermore, locations of the main colonies are generally not flexible between years. Breeders engaged in reproduction and individuals of species dependent on roosting sites do not have the capacity to fully adapt their large-scale distributions to yearly variations in oceanography. Rather, they may express this anomalous situation by an impaired breeding success or body condition (*e.g.* Anderson, 1989). Petrels and shearwaters were an exception, as only seasonal covariates were retained in the best model. There may be a large proportion of non-breeding procellariforms migrating through FP (Vanderwerf et al. 2006). They may be less constrained to the vicinity of colonies and more mobile than other primarily resident seabirds and are probably more responsive to short-term oceanographic variations. This was previously noted for the sooty shearwater *Puffinus griseus* in the California Current (Oedekoven et al. 2001).

Our results in FP are different from findings in the California and Humboldt Current upwelling systems, where top predators responded to El Niño Southern Oscillation episodes by distribution shifts (Oedekoven et al. 2001, Benson et al. 2002), changes in body condition (Boersma 1998), alteration of reproductive success (Ainley et al., 1995, Anderson, 1989), switching of prey (Oedekoven et al. 2001) or even mortality (Trillmich and Limberger 1985). Upwellings are highly productive systems where anomalous climatic situations propagate through the food chain from lower to higher-trophic levels (Barber and Chavez 1983, Chavez et al. 2003). In contrast, FP is situated in one of the least productive regions of the Pacific and this La Niña episode was probably not sufficient to enhance productivity.

5) Conclusion

We used habitat models to relate cetacean and seabird sightings to oceanographic and static predictors and proposed regional predictions. Cetaceans responded positively to the productivity gradient characterizing FP. However, the energetically costly delphinids showed stronger responses than sperm and beaked whales. Cetacean strategies of habitat utilization appeared in agreement with their energetic constraints. For seabirds, the availability of colonies and roosting sites appeared the most crucial determinants of their at-sea distributions. Our preliminary results suggest that cetaceans and seabirds did not respond strongly to the situation of the survey, but seemed to exploit areas recurrently favorable to them.

Chapter VIII. Predicting cetacean habitats from the distribution of their prey in two contrasted tropical regions

Photo credit: Jeremy Kiszka

This chapter is a synthesis of an article to be submitted to *Marine Ecology Progress Series*, presented in ANNEX 4:

Lambert, C, Mannocci, L, Lehodey, P, Ridoux, V. Predicting cetacean habitats from their energetic needs and the distributions of their prey in two contrasted tropical regions.

1) Objective

So far, the majority of cetacean habitat modeling studies relied on static and oceanographic predictors (Baumgartner and Mate 2003, Cañadas et al. 2005, Ferguson et al. 2006a). Very few studies related cetacean distributions to the distribution of their prey (the micronekton), often as a result of the unavailability of such information.

We implemented cetacean habitat models based on the same sightings as in Chapters VI and VII in the Southwest Indian Ocean (SWIO) and French Polynesia (FP), but we relied on direct predictors, *i.e.* prey distribution. In absence of synoptic datasets of micronekton at such large spatial scale, we turned to numerical models. These models represent useful surrogates, even though their outputs and design require continuous evaluation and improvement. One original modeling approach of micronekton has been developed as a component of the Spatial Ecosystem And Population Dynamics Model (SEAPODYM) driven by key variables (temperature, currents, primary production and euphotic depth), provided by ocean models or obtained directly or indirectly from remote sensing (Lehodey et al. 2010).

In the present study, we hypothesized that cetacean strategies of habitats utilization were in accordance with their energetic needs, and that they should distribute among habitats with respect to their quality. Contrary to Chapters VI and VII, here, we characterized habitat quality by the distribution of their prey, using micronekton outputs from SEAPODYM. The objectives were (1) to model cetacean habitats using simulated micronekton distributions in the SWIO and FP and (2) to compare their habitats between both regions. We expected energetically costly cetaceans to preferentially forage in habitats of high abundance of micronekton to meet their high energetic requirements and less active cetaceans to meet their needs by foraging in habitats characterized by either high or low abundance of micronekton.

1) Material and methods

a) Study regions

The oceanographic characteristics of the SWIO and FP are described in Chapter II.

b) Cetacean guilds

Three guilds with decreasing costs of living where studied: Delphininae, Globicephalinae and sperm and beaked whales (same species composition as in Chapters VI and VII).

c) Survey period and survey design

We relied on the aerial surveys conducted in the SWIO and FP (see Chapters VI and VII).

d) Aerial survey methods

Aerial surveys followed the general methodology described in Chapter IV. Survey platforms were two Britten Norman 2 in the SWIO and three Britten Norman 2 in FP.

e) SEAPODYM outputs

The SEAPODYM model (Lehodey et al. 2010), was initially developed to predict the distribution of tuna populations in pelagic ecosystems (Lehodey et al. 2008). It relies on physical and biogeochemical models to simulate two sub-models describing the prey populations (micronekton) and the predator populations. In the present study, we only used the model simulating prey populations. Micronekton encompasses actively swimming organisms, ranging from plankton (< 2 cm) to larger nekton (> 20 cm), which includes cephalopods, crustaceans, fishes and jellyfishes. These mid-trophic levels represent a crucial link between oceanographic and biogeochemical processes of the global ocean and predator distributions. The ultimate aim of SEAPODYM is to provide a realistic model of the complex pelagic marine ecosystems, including interactions between all species composing trophic webs, with both bottom-up and top-down controls.

SEAPODYM uses allometric relationships (linking size/weight to species abundance) to model several functional groups of micronekton. Each functional group is modeled as a single multi-species population, with continuous mortality rates and recruitment. The model is based on the concept that primary production is transferred to upper-trophic levels through an energy efficiency coefficient. This energy feeds the eggs/larvae pool, inducing their development and recruitment into the upper size-window. Organisms are

recruited in the forage population when they reach the minimal size and disappear from it when they either die or exceed the maximum size. Production is then defined as the amount of energy transferred through the size-window. This parameterization of the model is based on biochemical and energetic principles, such as metabolism at the cellular level, allowing the model to predict the development time at a given temperature. This is a crucial element as it determines the time of growth and recruitment of organisms.

Micronekton is characterized by vertical migrations induced by daylight variations. Such behavior is thought to be mainly a predator avoidance strategy: micronekton sinks to deeper layers during daytime where predation pressure is lower (Brodeur et al. 2005). SEAPODYM includes six functional groups defined by their migration patterns: epipelagic, non-migrant mesopelagic, migrant mesopelagic, non-migrant bathypelagic, migrant bathypelagic and highly migrant bathypelagic (Lehodey et al. 2010). Migrant mesopelagic and highly migrant bathypelagic organisms spend the night in the epipelagic layer, moving back to their respective layers during the day. Migrant bathypelagic organisms also perform a migration, but only between the mesopelagic and bathypelagic layers.

The three layers are defined relative to the euphotic depth (ANNEX 4, Appendix 2). The boundary between the epipelagic and the mesopelagic layer is at 1.5 times the euphotic depth, whereas the limit between the mesopelagic and the bathypelagic layer is at 5.5 times the euphotic depth and the lower boundary of the bathypelagic layer is at 10.5 times the euphotic depth. SEAPODYM outputs were provided at a 0.25° × week resolution.

f) Analytical methods

We used GAMs to relate the number of cetaceans per 0.25° pixel to SEAPODYM outputs. In addition to the six functional groups of micronekton, both in terms of biomass and production, the euphotic depth was included to consider the changing accessibility of micronekton to cetaceans between the different geographic sectors. The general habitat modeling framework is presented in Chapter IV; its specific implementation in this study is detailed in ANNEX 4.

For model fitting we averaged SEAPODYM outputs over the survey period in each sector (between 2 to 7 weeks), in order to obtain a close temporal match with the response variable. We produced prediction maps based on the selected models and SEAPODYM outputs averaged over the period of each survey (3-4 months) in both regions.

2) Results

a) Micronekton simulated distributions

Micronekton distributions provided by SEAPODYM were composed of 12 covariates for each region (6 micronekton functional groups, both in biomass and in production) (ANNEX 4, Appendices 3 and 4). For both regions, biomasses and productions were higher for the non-migrant bathypelagic, migrant bathypelagic and highly migrant bathypelagic groups compared to the other micronekton groups, except for the epipelagic production in the SWIO, which showed higher maximum values than non-migrant bathypelagic production.

In the SWIO, the distributions of epipelagic and mesopelagic functional groups were quite contrasted, with high biomass and production in the Mozambique Channel, off Kenya and around the Seychelles, as opposed to the less contrasted distribution of bathypelagic micronekton (ANNEX 4, Appendix 3). In FP, all functional groups reflected the latitudinal gradient characterizing the region (ANNEX 4, Appendix 4). Higher biomass and production were found for all micronekton groups in the north of the region, although the productions of the non-migrant bathypelagic and migrant bathypelagic functional groups were less variable than the others. Epipelagic, non-migrant mesopelagic and migrant mesopelagic functional groups were also characterized by fairly high biomass at the extreme south of FP.

b) Selected models

Delphininae

In the SWIO, the distribution of Delphininae was best predicted by a model containing, in order of decreasing contributions, euphotic depth (40%), non-migrant mesopelagic micronekton (biomass; 27%), epipelagic micronekton (biomass; 21%) and migrant bathypelagic micronekton (production; 12%) (Figure VIII-1a). This model explained 21.7% of the deviance. In the 5%-95% quantiles interval (corresponding to the core data), the relationships were negative with the euphotic depth, positive with the non-migrant mesopelagic micronekton and unimodal with the last two micronekton groups.

In FP, the selected model (19% of explained deviance) also contained euphotic depth, but as the least contributing variable (11%) (Figure VIII-1b). The other selected variables were different from the SWIO model: non-migrant bathypelagic micronekton (both biomass and production; contribution of 42% and 18%) and epipelagic micronekton (production; 29%). In the 5%-95% quantiles interval, relationships were positive with non-migrant bathypelagic (biomass) and epipelagic micronekton, but negative with non-migrant bathypelagic micronekton (production) and euphotic depth.

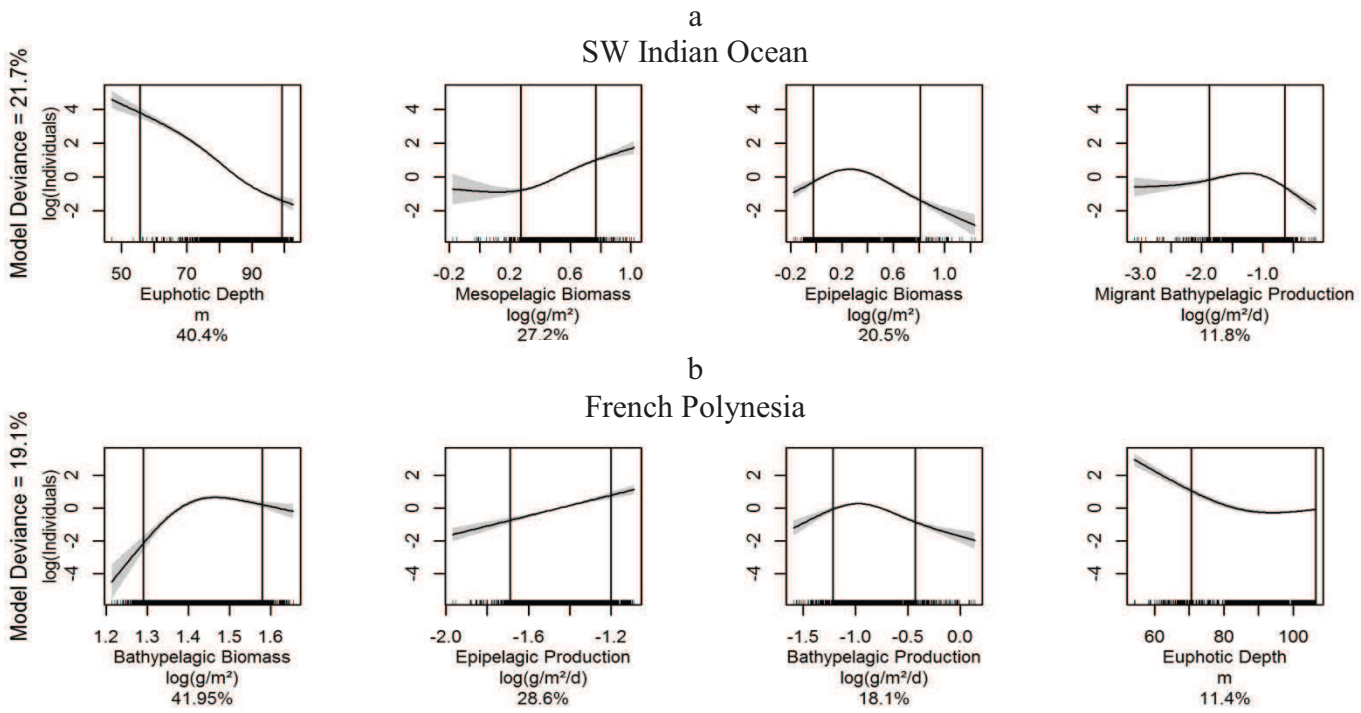


Figure VIII-1: Smoothed functions for the selected variables for Delphininae in the Southwest Indian Ocean (a) and French Polynesia (b). The solid line is the smooth function; shaded regions represent the 95% confidence intervals. The percentage indicated below each graph is the contribution of each covariate in the linear predictor. The 5-95% quantiles interval is provided for each predictor.

Globicephalinae

For this guild in the SWIO, the selected model explained 18% of the deviance and contained, in order of decreasing contributions, epipelagic micronekton (production; 30%), euphotic depth (28%), highly migrant bathypelagic micronekton (production; 22%) and non-migrant mesopelagic micronekton (biomass; 21%) (Figure VIII-2a). In the 5-95% quantiles interval, relationships were negative (and linear) with euphotic depth and non-migrant

mesopelagic micronekton, positive with highly migrant bathypelagic micronekton and unimodal for epipelagic micronekton.

In FP, the euphotic depth was not selected in the model and the model explained 47% of the deviance. The selected model contained non-migrant bathypelagic micronekton (biomass; contribution of 60%), non-migrant mesopelagic micronekton (both biomass and production; contribution of 11% and 19% respectively) and migrant bathypelagic micronekton (production; 10%) (Figure VIII-2b). In the 5-95% quantiles interval, the relationship was positive with non-migrant bathypelagic micronekton, but for the other three groups, predicted density remained very close to zero, indicating a weak effect of these variables.

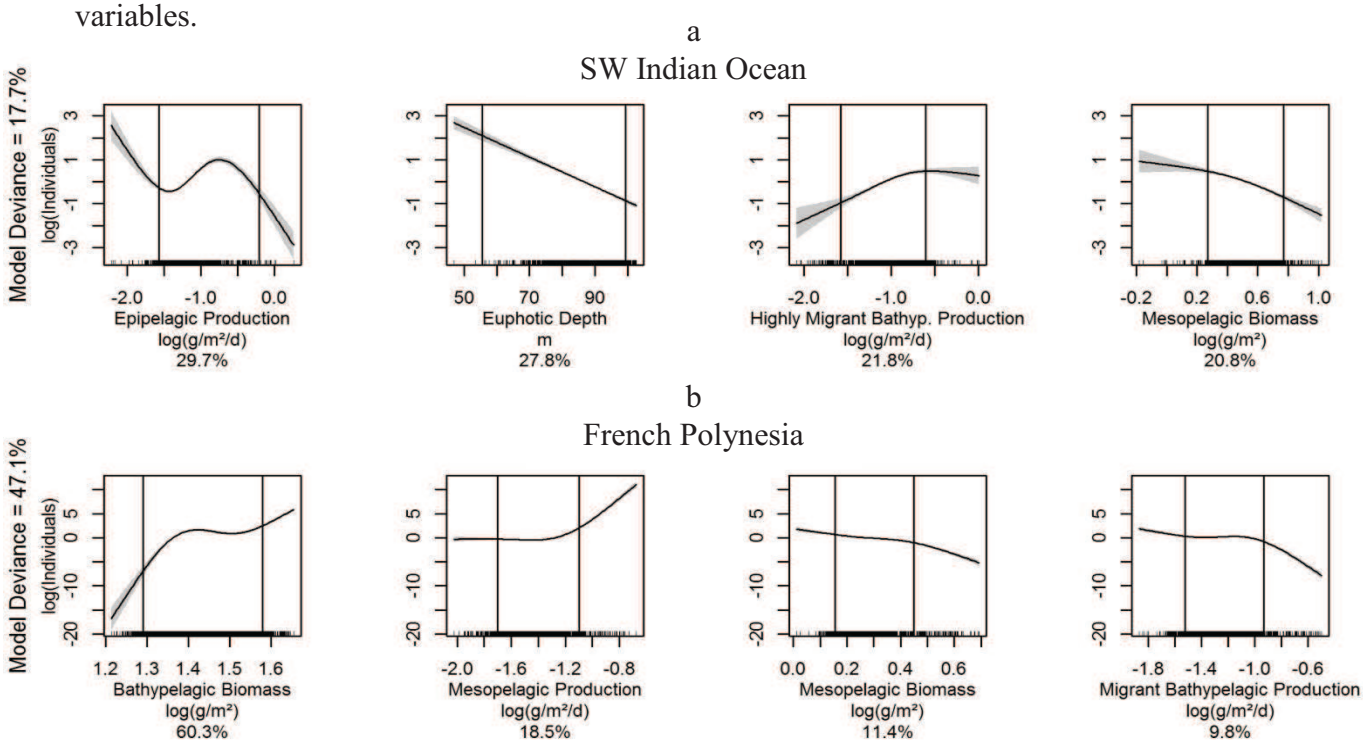


Figure VIII-2: Smoothed functions for the selected variables for Globicephalinae in the Southwest Indian Ocean (a) and French Polynesia (b).

Sperm and beaked whales

The model for sperm and beaked whales had the lowest explained deviances, both in the SWIO and in Polynesia, with 9% and 13% respectively. In the SWIO, their distribution was best predicted by highly migrant bathypelagic micronekton (production; contribution of 36%), euphotic depth (25%), migrant bathypelagic micronekton (production; 24%) and

epipelagic micronekton (production; 16%) (Figure VIII-3a). Relationships were globally negative for three of the variables in the 5-95% quantiles intervals (euphotic depth, migrant bathypelagic micronekton, epipelagic micronekton) but positive with the highly migrant bathypelagic micronekton).

In FP, the selected model included migrant mesopelagic micronekton (biomass; contribution of 38%), migrant bathypelagic micronekton (biomass and production; 24% and 21% respectively) and euphotic depth (18%) (Figure VIII-3b). Relationships were complex in the 5-95% quantiles intervals, with unimodal relationships for the last three variables and a positive relationship with the migrant mesopelagic micronekton.

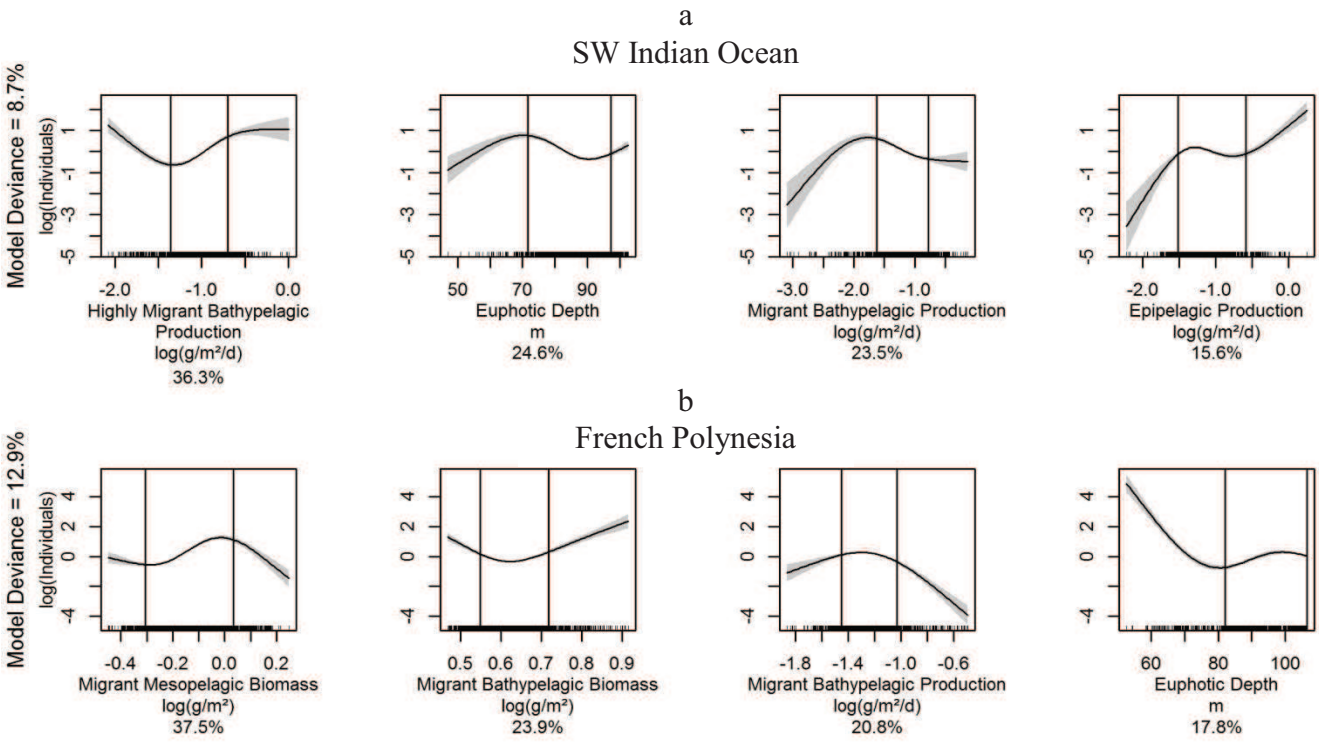


Figure VIII-3: Smoothed functions for the selected variables for sperm and beaked whales in the Southwest Indian Ocean (a) and French Polynesia (b).

c) Predictions

Delphininae

In the SWIO, high densities of Delphininae were predicted in the north of the region (especially off Kenya and southeast of the Seychelles), in the Mozambique Channel and south of Madagascar (Figure VIII-4a). Lowest predicted densities were around the Mascarenes (Tromelin-Madagascar and Reunion-Mauritius). The mean predicted density was of 2.7 individuals per km² over the whole region (Table VIII-1). Overall, uncertainty was the lowest where predicted density was the highest (Figure VIII-5a). Mean predicted densities showed a 1-to-16 ratio between the highest and the lowest density sectors.

In FP, the model predicted much lower densities, with a mean predicted density over the region of only 0.1 individuals per km² (Table VIII-1). Predicted densities were the highest in the southwest of the Marquesas and the lowest in the south of the region (south 20°S, Figure VIII-5b). Uncertainty was the lowest where predicted density was the highest (same range as in the SWIO, Figure VIII-5b). Mean predicted densities showed a 1-to-19.5 ratio between the highest and the lowest density sectors.

Table VIII-1: Statistics of the predictions for Delphininae: mean predicted densities (individuals / km²) and mean CV (%) for each sector and for the whole regions. NMC: northern Mozambique Channel, CMC: central Mozambique Channel, SMC: southern Mozambique Channel, RM: Reunion-Mauritius, SE: Seychelles, TM: Tromelin-Madagascar, MAR: Marquesas, NTU: North Tuamotu, STU: South Tuamotu, GAM: Gambier, SOC: Society, AUS: Australs.

Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	2.80 ± 1.32	14.8 ± 8.30	MAR	0.39 ± 0.31	17.9 ± 5.7
SMC	2.42 ± 0.95	14.2 ± 4.95	NTU	0.13 ± 0.05	15.9 ± 6.2
CMC	4.37 ± 1.29	12.0 ± 3.12	STU	0.09 ± 0.03	15.2 ± 3.5
RM	0.27 ± 0.16	22.2 ± 6.97	GAM	0.04 ± 0.03	24.6 ± 14.0
SE	4.81 ± 3.11	12.7 ± 2.33	SOC	0.08 ± 0.03	14.6 ± 3.6
TM	0.24 ± 0.08	27.3 ± 3.16	AUS	0.02 ± 0.01	31.4 ± 11.4
Whole region	2.66 ± 4.13	17.8 ± 7.40	Whole region	0.10 ± 0.12	20.4 ± 9.6
Between-sector ratio	16.2		Between-sector ratio	19.5	

Globicephalinae

In the SWIO, the predicted distribution of Globicephalinae was similar with that of Delphininae. The highest densities were predicted off Kenya, south of Madagascar (close to

the shelf) and in the Mozambique Channel (Figure VIII-4a). The mean predicted density was of 1.3 individuals per km² for the whole region (Table VIII-2). The lowest predicted densities were east of Madagascar and east of the Mascarenes. Uncertainty was low over the whole region, except close to the shelf in the north of Madagascar and the Mascarenes (Figure VIII-5a). Mean predicted densities showed a 1-to-9 ratio between the highest and the lowest density sectors.

In FP, the mean predicted density over the region was low (0.1 individuals per km², Table VIII-2). The predictions were quite homogeneous (Figure VIII-4b), especially in the north. Predicted densities were the highest densities west of the Marquesas and the lowest south of 20°S. Overall, a low uncertainty was associated with high predicted densities. It reached high values in the south, where predicted densities were the lowest (Figure VIII-5b). Mean predicted densities showed a 1-to-25.5 ratio between the highest and the lowest density sectors, the highest ratio among the three guilds.

Table VIII-2: Statistics of the predictions for Globicephalinae: mean predicted densities (individuals / km²) and mean CV (%) for each sector and for the whole regions. Sector abbreviations as in Table VIII-1.

Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	2.85 ± 1.68	14.70 ± 9.4	MAR	0.28 ± 0.50	18.1 ± 3.8
SMC	1.92 ± 1.21	13.13 ± 4.3	NTU	0.14 ± 0.34	15.52 ± 5.0
CMC	2.91 ± 1.11	13.46 ± 5.4	STU	0.09 ± 0.12	14.12 ± 2.6
RM	0.44 ± 0.16	15.54 ± 4.7	GAM	0.04 ± 0.04	48.1 ± 41.1
SE	1.53 ± 0.99	12.63 ± 3.2	SOC	0.07 ± 0.03	16.3 ± 5.9
TM	0.31 ± 0.24	15.63 ± 1.7	AUS	0.01 ± 0.02	71.84 ± 33.7
Whole region	1.29 ± 1.83	14.01 ± 4.1	Whole region	0.07 ± 0.2	34.6 ± 29.5
Between-sector ratio	9.4		Between-sector ratio	25.5	

Sperm and beaked whales

The predicted distribution of sperm and beaked whales in the SWIO differed from the other two guilds, with a much lower mean predicted density over the whole region (0.04 individuals per km², Table VIII-3). The highest densities were predicted close to the slopes of Madagascar (in the Mozambique Channel and to the south), the Seychelles and off Kenya. The predicted distribution was more homogenous than for Delphininae and Globicephalinae, with intermediate densities both in oligotrophic and productive waters (Figure VIII-4a). The

between-sector ratio was low compared to the other two guilds, with only a 1-to-2.2 ratio between the highest and the lowest density sector. An overall low uncertainty was associated with both high and low predicted densities (Figure VIII-5a).

In FP, the mean predicted density over the whole region was of 0.04 individuals per km², the same as in the SWIO, (Figure VIII-4b, Table VIII-3). Sperm and beaked whales were homogenously distributed compared to the other two guilds, with the highest predicted densities in the north and south of FP, and the lowest in its central part. Nevertheless, given the high densities predicted in the Marquesas compared to the other sectors, the between-sector ratio was of 1-to-11. Uncertainty showed a different pattern compared to the other two guilds: low uncertainties were associated with both low and intermediate predictions (Figure VIII-5b). An area of high uncertainty was found at the north-east corner of the region.

Table VIII-3: Statistics of the predictions for sperm and beaked whales: mean predicted densities (individuals / km²) and mean CV (%) for each sector and for the whole regions. Sector abbreviations as in Table VIII-1.

Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	0.06 ± 0.04	15.84 ± 5.2	MAR	0.11 ± 0.20	22.20 ± 5.0
SMC	0.06 ± 0.02	12.99 ± 2.8	NTU	0.02 ± 0.02	19.05 ± 7.9
CMC	0.06 ± 0.05	16.48 ± 2.6	STU	0.01 ± 0.01	16.60 ± 4.9
RM	0.03 ± 0.01	14.82 ± 3.8	GAM	0.02 ± 0.01	12.40 ± 3.0
SE	0.07 ± 0.03	13.90 ± 3.5	SOC	0.02 ± 0.01	17.76 ± 4.7
TM	0.03 ± 0.01	16.30 ± 2.2	AUS	0.02 ± 0.01	11.90 ± 1.5
Whole region	0.04 ± 0.02	14.90 ± 3.9	Whole region	0.04 ± 0.05	18.40 ± 6.5
Between-sector ratio	2.2		Between-sector ratio	11	

The predictions appeared consistent with the observed cetacean distributions (ANNEX 4, Appendix 1). In the SWIO, Delphininae were mainly distributed in the central and northern Mozambique Channel and around the Seychelles, where our model predicted high densities. In FP, the sightings of Delphininae showed a latitudinal gradient, in accordance with the predictions. Observations and predictions were also consistent for Globicephalinae, with high observed and predicted densities in the Mozambique Channel in the SWIO and around the Marquesas in FP. Sperm and beaked whales showed fairly uniform observed distributions both in the SWIO and in FP, a pattern also predicted by the models.

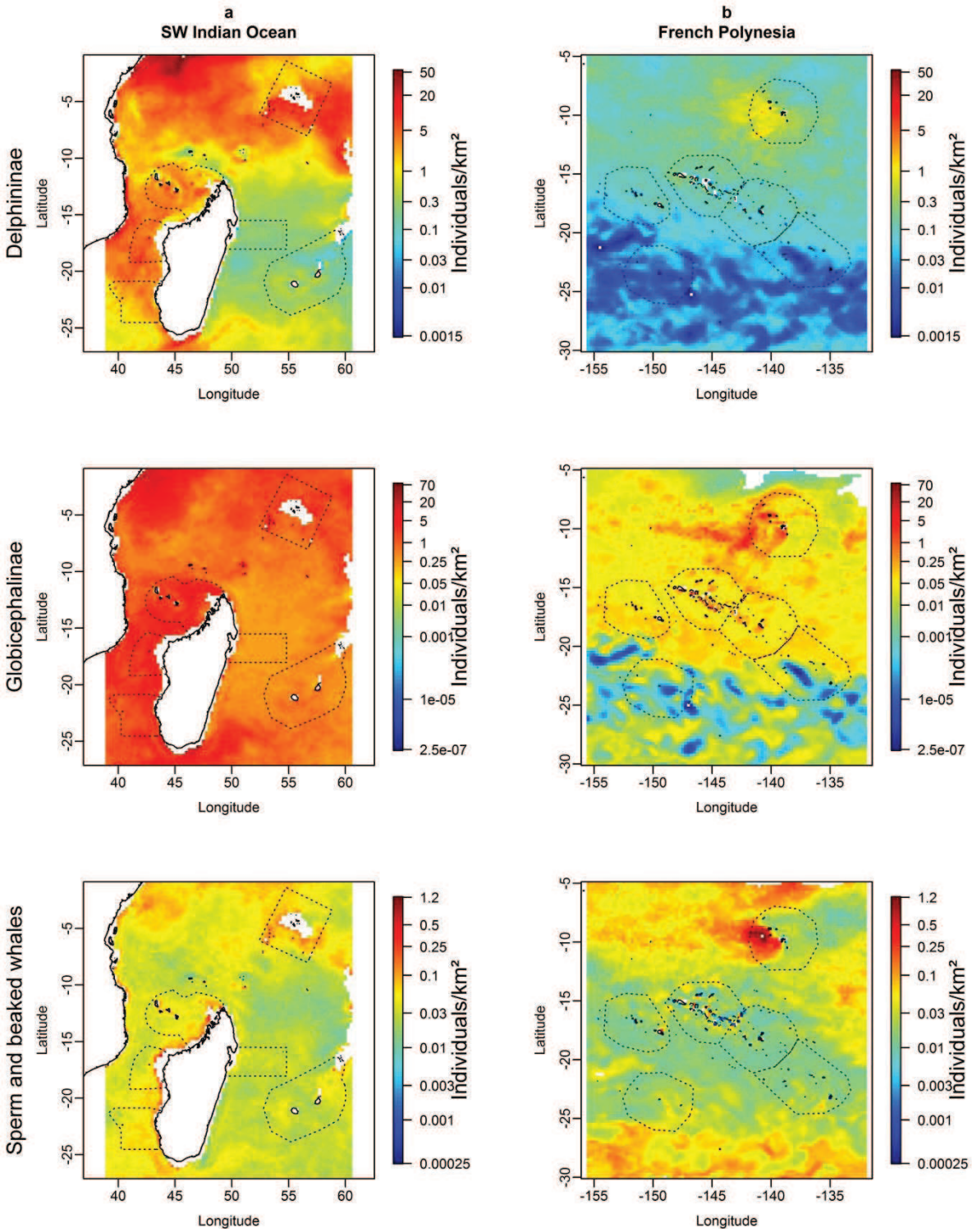


Figure VIII-4: Predicted relative densities (individuals / km²) for the three cetacean guilds in the SWIO (a) and FP (b). The limitation of predictions inside the range of sampled covariates values resulted in empty pixels in FP. In the SWIO, empty pixels were due to the absence of SEAPODYM outputs for the deeper micronekton groups in the neritic strata (depth < 200m). Colours are log-scaled. In order to enhance the contrasts, we used the same colour scale for each guild in both regions, but the colour scale is not comparable between the different guilds.

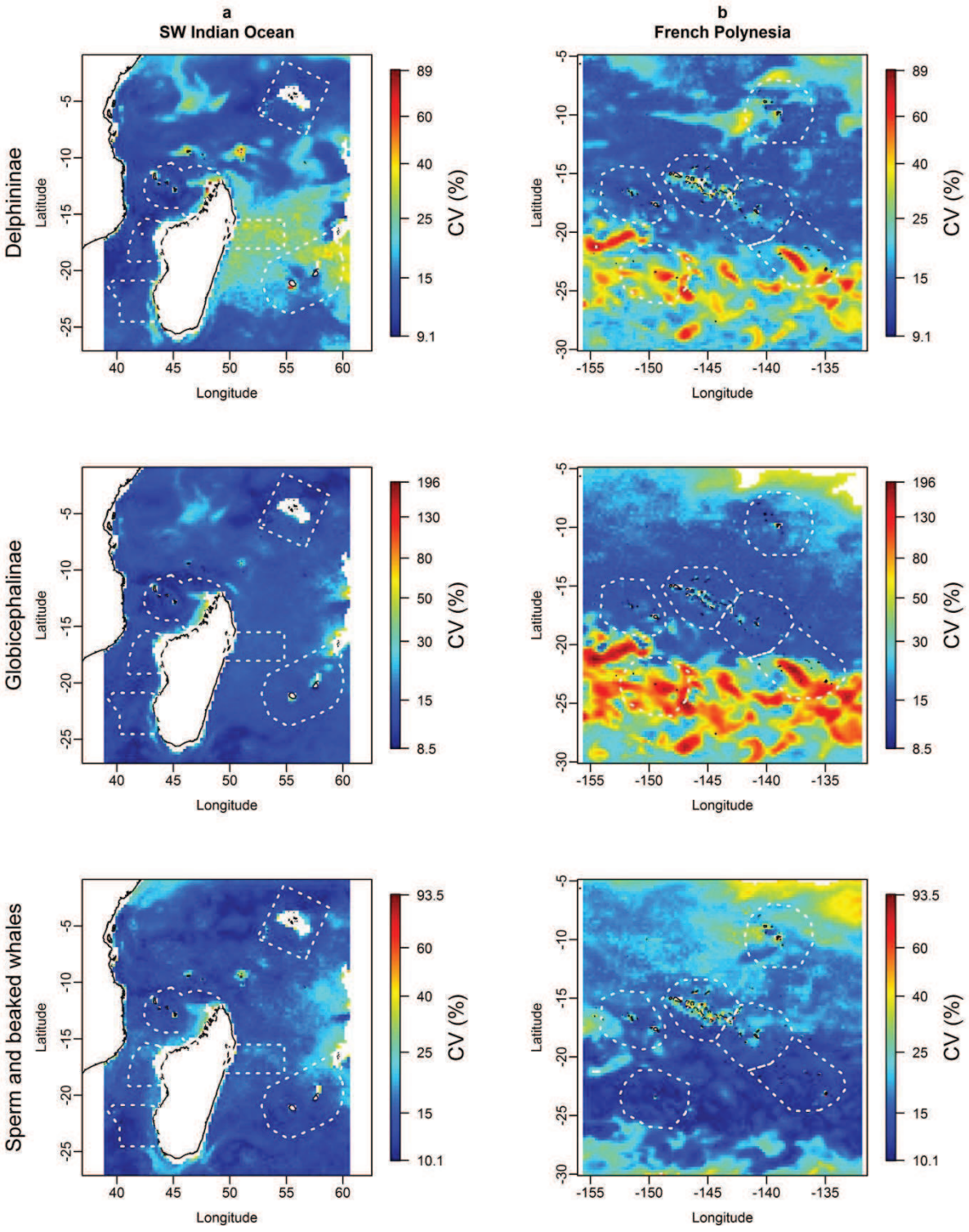


Figure VIII-5: Uncertainty maps (CV, %) associated with the predictions for the three cetacean guilds in the SWIO (a) and FP (b). The limitation of predictions inside the range of sampled covariates values resulted in empty pixels in FP. In the SWIO, empty pixels were due to the absence of SEAPODYM outputs for the deeper micronekton categories in the neritic strata (depth < 200m). In order to enhance the contrasts, we used the same colour scale (in log) for each guild in both regions, but the colour scale is not comparable between the different guilds.

3) Discussion

a) Comparison with previous studies

In this study, we relied on the same sightings and modeling procedure as in Chapters VI and VII, but we used micronekton simulated distributions as direct predictors of cetacean habitats. The deviances of the models built in Chapters VI and VII with more distal predictors were between 9.6% and 29.9% for Delphininae and Globicephalinae and were around 5% for sperm and beaked whales. By comparison, in this study, models had higher explained deviances, ranging from 18% to 47% for Delphininae and Globicephalinae, and from 9% to 13% for sperm and beaked whales. Nonetheless, the results of both types of studies can only be partially compared, because modeling was done using a larger sampling unit (the pixel in this study compared to the 10 km-segment in Chapters VI and VII). In spite of this difference, it is interesting to notice that models built with micronekton distributions provided higher explained deviances.

The two types of studies yielded similar prediction maps overall, although in Chapters VI and VII predictions were provided in a smaller region defined by a minimal convex polygon. In spite of the log-scaled colors, the prediction maps were similar for Delphininae in both the SWIO and FP, with highest predicted densities in the Mozambique Channel and the Seychelles in the SWIO, and around the Marquesas in FP. Both modeling studies predicted very low densities of sperm and beaked whales in the SWIO and FP as compared to the other two guilds, with the highest densities on the slope of Madagascar in the SWIO and around the Marquesas in FP. Globicephalinae is the guild for which the results differed the most. In Chapters VI and VII, we predicted intermediate densities of Globicephalinae to the east of Madagascar, while in the present study lower densities were predicted in this area, as compared to the Mozambique Channel.

To date, no study has been performed using SEAPODYM micronekton variables to predict cetacean habitats. Apart from the SEAPODYM model developed to predict tuna populations dynamics (Lehodey et al. 2008), it has been successfully used to analyze tuna catch data (Briand et al. 2011), to simulate the habitats of sea turtles (Abecassis et al. 2013) and to predict large-scale population dynamics of several tuna species based on hindcast simulation from coupled physical-biogeochemical models (Lehodey et al. 2008, 2010, Senina

et al. 2008, Sibert et al. 2012). This study stands out by using micronekton distributions as predictors of cetacean habitats. Such direct predictors provide additional insights into cetacean habitats, through the integration of the food web, as micronekton is two trophic levels closer to cetaceans than primary production. In addition, as depth is a key factor in cetacean foraging strategies, the consideration of the vertical dimension should improve habitat models.

However, it must be kept in mind that SEAPODYM outputs are simulated data, thus including some uncertainty. Since uncertainty on model parameters was overall low (CVs ranged from 14% to 35%) and predictions were similar with static and oceanographic variables, we reasonably think that SEAPODYM is accurate enough to ensure robust predictions at large spatial scales. Further, it must be noticed that in areas where SEAPODYM micronekton groups are not modeled (*i.e.* in the neritic strata), we were not able to provide predictions of cetacean densities. This may be of importance in the case of Delphininae, given that this guild contains several species with extensive coastal populations (Bearzi 2005, Torres and Read 2009).

Predator-prey associations have previously been studied at a smaller scale, namely the prey patch level. Torres et al. (2008) demonstrated that dolphin habitat models performed better with environmental variables than with prey distribution. This was probably explained by habitat heterogeneity at the fine scale, in accordance with the patchiness of prey distribution. Benoit-Bird et al. (2013) also studied the spatial associations between predators and they prey in two seabird species and 1 seal species. They demonstrated the importance of prey patch characteristics but found no direct association. These studies indicate that, at the small scale, prey patch characteristics (notably the physical habitat inducing prey aggregation) are more important for predator distributions than the overall distribution of prey biomass. However, processes highlighted at such small spatial scales are probably not relevant at the broader scale studied here.

b) Costs of living induce habitat selection

Delphininae are the most energetically costly of our guilds. The most abundant observed genera (*Stenella spp* and *Tursiops spp*) are known to largely forage at night, from the surface to 200 m, following both vertical and horizontal migration of mesopelagic micronekton (Benoit-Bird and Au 2003, Klatsky et al. 2007). They also perform regular or

more occasional excursions down to 400-500 m, depending on species (Dolar et al. 2003, Klatsky et al. 2007).

In the SWIO, mean predicted densities showed a 1-to-16.2 ratio between sectors, with high predicted densities in high quality habitats. Delphininae showed a negative relationship with euphotic depth and a positive relationship with the biomass of mesopelagic micronekton, indicating a preference for areas where biomass was the highest and the most accessible. Delphininae appeared to select areas where they can forage at lower cost. In areas of high predicted densities, the mean euphotic depth was of 80 m, thus placing the boundary between the epipelagic and the mesopelagic layers at 120 m and the boundary between the mesopelagic and the bathypelagic layers at 360 m. Their diving abilities should allow Delphininae to reach the areas of high mesopelagic biomass to forage. In contrast, in oligotrophic areas (Mascarenes and east of Madagascar), the euphotic depth was deeper (on average 100 m). Therefore, the boundary between the epipelagic and the mesopelagic layers was at 150 m and the boundary between the mesopelagic and the bathypelagic layers was at 450 m. Given these boundaries and the low productions and biomasses in epipelagic and mesopelagic layers, Delphininae may have to forage on the bathypelagic layer to meet their energetic needs. This may induce high costs of foraging if they dive at their maximum abilities. Therefore, it seems that in the SWIO, Delphininae selected areas where they can reach high biomasses of mesopelagic micronekton with the lowest effort (where euphotic depth is shallow), in order to optimize their foraging success.

In FP, epipelagic and mesopelagic productions and biomasses were far lower than in the SWIO, while productions and biomasses of the bathypelagic layer were equivalent in both regions. This may explain the importance of the bathypelagic micronekton in the selected model. In such an oligotrophic region, Delphininae may not be able to fulfill their needs by foraging in the epipelagic and mesopelagic layers and therefore had to dive deeper to reach the bathypelagic layer. They remained in the north of the region where the bathypelagic layer was shallower (about 360 m) and thus more accessible. Delphininae were nevertheless positively related to the epipelagic micronekton production and were concentrated around the Marquesas, the only sector where both surface and deep productivity were high.

Globicephalinae had similar patterns as Delphininae, but appeared to select habitats on a different basis. In the SWIO, high densities of Globicephalinae were found in areas with intermediate epipelagic micronekton production and low euphotic depth. They seemed to

select areas where high surface production was the easiest to reach. In FP, the bathypelagic biomass was an important predictor, with a similar relationship as for Delphininae, while the other three variables had low contributions and apparently no effects on density. Therefore, Globicephalinae also seemed to select this deep layer, where they can sustain their energetic needs. However, in contrast to Delphininae, this layer was probably more accessible for Globicephalinae which can dive deeper: up to 1,019 m for *Globicephala macrorhynchus* (Aguilar de Soto et al. 2008), up to 1,500 m for *Peponocephala electra* according to its diet (Jefferson and Barros 1997) and up to 700 m for *Pseudorca crassidens* (Oleson et al. 2010). Contrary to Delphininae, Globicephalinae did not only forage on the highest bathypelagic biomasses, but also on intermediate biomasses. This may be due to their lower energetic costs, allowing them to forage deeper and not only in the highest quality habitats.

On the one hand, we expected costly predators to preferentially forage in high quality habitats within each region. Our results highlighted similar distribution patterns for Delphininae and Globicephalinae, with a sharp preference for habitats of high micronekton production and/or biomass, in accordance with our hypothesis and previous studies based on primary production (Chapters VI and VII). On the other hand, we expected to find important differences between our study regions. For Delphininae and Globicephalinae, predicted densities were indeed much higher in the productive SWIO than in the oligotrophic FP.

Patterns differed for sperm and beaked whales characterized by the lowest cost of living. In the SWIO, they showed slight preferences for areas of high production. Sperm and beaked whales had similar density irrespective of habitat quality, as shown by the low ratio of mean predicted densities between sectors (1-to-2.2). They may accommodate to both productive and oligotrophic areas. In FP, this ratio was higher (1-to-11) because densities were higher around the Marquesas compared to the other sectors. However, in FP, mean predicted densities were the same as in the SWIO (0.04 individuals per km²). This similarity between a productive but contrasted region and an oligotrophic region indicates that sperm and beaked whales may sustain their low energetic needs in both high and low quality habitats.

Beaked whales are known to forage between 460 and 1,890 m (Baird et al. 2006, Tyack et al. 2006), while sperm whales forage between 400 and 1,300 m (Watkins et al. 1993, Amano and Yoshioka 2003) and Kogidae potentially forage to 1,500 m, as inferred from their diets (Willis and Baird 1998). These foraging ranges include the three layers defined by

SEAPODYM; hence the selected variables seemed consistent with their diving abilities. Nonetheless, sperm whales are known to perform both deep and shallow foraging dives (less than 200m; Watkins et al. 1993). As they were a commonly observed species in the SWIO, this diving pattern may explain the presence of the epipelagic production as a predictor in the model in this region (although as the least contributory).

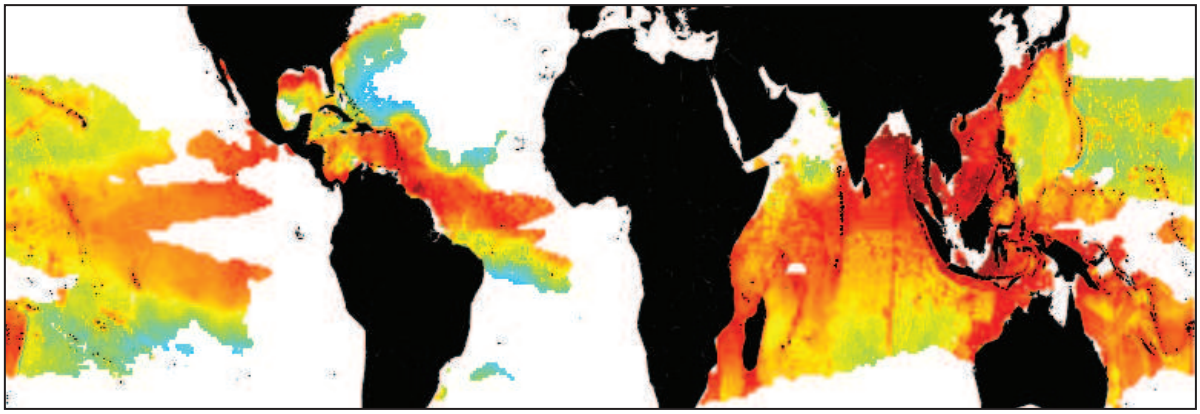
Our results seemed to agree with our expectation that sperm and beaked whales were less dependent on habitat quality since predicted densities were less contrasted both within and between regions. The mean predicted densities were similar in the SWIO and in FP and the between-sector ratios were low in both regions (although higher in FP).

4) Conclusion

The use of micronekton simulated distributions as direct predictors of cetacean habitats provided fairly good results to consider SEAPODYM as a useful tool in habitat modeling studies. The higher deviances, the overall low uncertainty and the consistency between the predictions presented here and the predictions obtained in previous studies (Chapters VI and VII) indicate that these results are robust.

This study confirms the results obtained in Chapters VI and VII about strategies of habitat utilization and costs of living of cetaceans. Delphininae and Globicephalinae showed a strong dependency to habitat quality. In the productive but contrasted SWIO, they optimized their foraging strategy by selecting areas where they can reach the highest biomass and/or production of micronekton with the lowest efforts. In the oligotrophic FP, they had to select the bathypelagic layer to sustain their energetic needs, which may induce greater foraging costs. Conversely, for sperm and beaked whales, the models did not highlight any strong differences within and between regions, indicating they can accommodate to both productive and oligotrophic areas to fulfill their energetic requirements. It would be useful to confront these results with future surveys in the study regions to evaluate the performance of our models.

Chapter IX. Generic relationships of cetaceans with the quality of their habitats in tropical oceans



This chapter corresponds to an article in preparation that is given here *in extenso* as in its current development prior to submission:

Mannocci, L, Monestiez, P, Spitz, J, Ridoux, V. Generic relationships of cetaceans with the quality of their habitats in tropical oceans.

1) Introduction

The aim of macroecology is to understand patterns and determinants of species broad-scale distributions (Brown 1995, Blackburn and Gaston 2003). Beyond describing and explaining these patterns, macroecology seeks to reveal general laws and emerging properties which support the nature, structure and function of ecosystems (Kent 2005). To date, the vast majority of macroecological studies has been conducted on terrestrial ecosystems (Lumaret and Jay-Robert 2002, Gaston and Blackburn 2003a, Blackburn et al. 2004). Macroecological patterns have been less explored in the pelagic marine realm, perhaps owing to the great logistical constraints associated with sampling these distant and extensive waters (Richardson and Poloczanska 2008).

Conversely to terrestrial ecosystems where species diversity peaks around the equator (Hillebrand 2004), high diversity at mid latitudes appears to be the general emerging pattern in the oceans (Tittensor et al. 2010). Top predators, like other taxa of various trophic levels, concentrate in subtropical hotspots, showing predictable patterns related to specific oceanographic features (Worm et al. 2003, 2005). For example, warm waters, sufficient dissolved oxygen concentrations and mesoscale oceanic gradients at the origin of fronts and eddies, characterize the optimal habitat of tunas and billfishes (Worm et al. 2005). Although the diversity of cetaceans seems to be well predicted by sea surface temperature (Whitehead et al. 2008), which generic oceanographic properties govern their habitats at the macro-scale is poorly known.

The ability of the environment to provide suitable conditions for the survival, reproduction and persistence of a population has been referred to as habitat quality (Block and Brennan 1993). In the oceans, habitat quality can be described by the quantity and the nature of primary production, or by different indicators of these variables. Chlorophyll concentration and net primary production inform the quantity of primary production (respectively reflecting the biomass of primary producers and the rate at which they fix the carbon). The quantity of primary production is influenced by physiographic features, such as bottom slope, and dynamic physical features, such as mesoscale eddies or upwellings, which contribute to fueling nutrients in the euphotic layer (Springer et al. 1996, Oschlies and Garçon 1998, Vaillancourt et al. 2003). In addition, dominant phytoplankton groups (Alvain et al. 2008) inform the nature of primary production, at the origin of two broad categories of food chains.

Food chains based on small phytoplankton (*e.g.* flagellated algae) lead to jellyfishes and other gelatinous species, while food chains based on large phytoplankton (*e.g.* diatoms) lead to the production of fishes (Parsons and Lalli 2002). The latter typically support top predators like cetaceans. The nature of primary production is influenced by the silicate:nitrate ratio (Redfield 1958), a chemical variable. Since diatoms require dissolved silicate to form their external shell, their growth is limited when the silicate:nitrate ratio falls under 1:1. In this situation, smaller phytoplankton dominates the community and the first category of food chains dominates (Turner et al. 1998).

In previous studies, we showed that the energetic constraints of cetaceans governed the quality of their habitats in three regions of the tropical Atlantic, Indian and Pacific Oceans (Mannocci et al. 2013a, b, Mannocci et al. in revision). Using three guilds characterized by increasing costs of living (sperm and beaked whales, Globicephalinae and Delphininae), we showed that energetically costly cetaceans were constrained to select the highest quality habitats to meet their high energetic requirements, whereas less active cetaceans satisfied their needs by exploiting either high or low quality habitats. In the present study, we propose to identify generic properties of cetacean distributions in tropical waters using the same guilds.

Knowledge of generic properties governing species distributions is important for the theoretical understanding of broad-scale patterns, but it is also of relevance to conservation. Yet, since maintenance of the integrity of ecosystems and preservation of biodiversity are best founded on a mechanistic understanding, macroecology and conservation biology are intimately linked (Gaston and Blackburn 2003b). Cetaceans face a suite of anthropogenic pressures posed by *inter alia* fisheries (Read 2008), collisions (Laist et al. 2001), anthropogenic noise (Weilgart 2007), pollution (Aguilar et al. 2002) and global warming (Alter et al. 2010). These pressures generate additional mortality, alter the survival and fecundity or disrupt the vital behaviors of cetaceans, characterized by a limited resilience capacity. Additionally, as charismatic large vertebrates, they also constitute flagship species (Simberloff 1998) for the conservation of pelagic ecosystems. Owing to their wide ranges, their effective conservation is considered beneficial to the larger system (umbrella species) (Simberloff 1998, Caro and O'Doherty 1999). In addition, they reflect the underlying state of pelagic ecosystems as a result of both anthropogenic and ecological factors (sentinel species) (Moore 2008). In this respect, understanding the macroecological patterns of cetaceans can give insights into the conservation of these organisms and of their underlying ecosystems.

This study aimed at revealing generic properties of cetacean distributions in tropical oceans and at predicting their densities at the circumtropical scale. To reach these goals, we built species density models for Delphininae, Globicephalinae and sperm and beaked whales, based on a range of habitat quality descriptors. Although they represent 50% of the ocean surface, few data are available on cetaceans in tropical oceans (Kaschner et al. 2012). Statistical models based on high quality sighting data collected in a few representative tropical regions along with relevant environmental predictors represent valuable tools to fill these geographical gaps. In addition, model predictions can inform about the state of tropical ecosystems by using cetaceans as sentinels of the pelagic environment, a concept that is often referred to by scientists and managers but has rarely been demonstrated.

2) Material and methods

a) Cetacean data

Cetacean data were obtained from aerial surveys in the Exclusive Economic Zone of three tropical regions: the western tropical Atlantic (132,000 km²) (Mannocci et al. 2013a), the Southwest Indian Ocean (SWIO) (1.4 million km²) (Mannocci et al. 2013b) and the central South Pacific (CSP) (1.75 million km²) (Mannocci et al. in revision) (Figure IX-1). Aerial surveys were conducted in the summer in order to avoid the trade wind season and hence to benefit from the best sighting conditions. Surveys covered 7,149 km in Guiana, 83,737 km in the Southwest Indian Ocean and 97,277 km in the central South Pacific. Delphininae were the most frequently seen guild (839 sightings, 12,137 individuals), followed by Globicephalinae (219 sightings, 8,835 individuals) and sperm and beaked whales (252 sightings, 490 individuals).

The aerial protocol was consistent across the three tropical regions. It followed the general SCANS (Small Cetacean Abundance in the North Sea) methodology developed for small cetaceans and adapted for aircraft (Hammond et al. 2013). Cetacean data were collected following a line transect methodology (Buckland et al. 2001). Information recorded included identification to the lowest possible taxonomic level, group size and declination angle to the group when it passed at right angle to the aircraft. Together with the altitude of the aircraft, angles provided perpendicular distances, which allowed distance sampling analyses to be conducted (Buckland et al. 2001). Beaufort Sea state, glare severity, turbidity,

cloud coverage and an overall subjective assessment of detection conditions (good, moderate or poor as for small delphinids) were recorded as detection covariates. The aerial protocol is detailed in the regional publications.

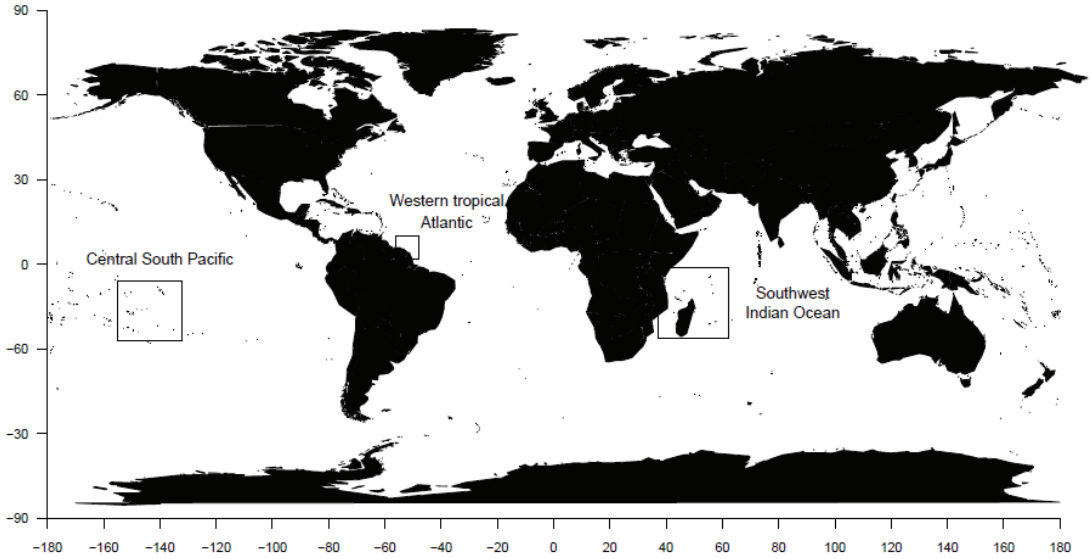


Figure IX-1: Location of the three surveyed tropical regions. Western tropical Atlantic (Mannocci et al. 2013), Southwest Indian Ocean (Mannocci et al. 2013), central South Pacific (Mannocci et al. in revision).

b) Environmental data

We created a comprehensive database of 14 key environmental variables. The temporal resolution was the climatology of the survey periods since it was previously shown that climatological variables yielded better explained deviances than the same variables contemporaneous to the surveys (Mannocci et al. 2013b). The variables comprised physiographic, physical, chemical and biological parameters, to examine their relationships with cetacean densities (Table IX-1).

Depth and slope were the two physiographic variables. We obtained bathymetric data from the General Physiographic Chart of the Ocean (GEBCO, http://www.gebco.net/) which provided a one minute global bathymetric surface. Slope was derived from GEBCO using the raster package in R (Hijmans and van Etten 2012)

We used a range of physical variables. We obtained monthly wind speed and wind stress curl at a 0.25° resolution from the Scatterometer Climatology of Ocean Winds, averaged over 8 years (1999-2007) of QuikSCAT observations (Risien and Chelton 2008). We considered the standard error of sea level anomaly (sdSLA) as an indicator of mesoscale

activity (see Mannocci et al. 2013b). Standard errors of SLAs were calculated for the 2002-2012 period based on weekly SLAs at a 0.25° resolution from Aviso (http://www.aviso.oceanobs.com/duacs/). We extracted temperature, salinity and mixed layer depth from CSIRO Atlas of Regional Seas (CARS) 2009 at a 0.5° resolution (Condie and Dunn 2006). CARS is derived from historical archives of sub-surface ocean property measurements (primarily research vessel instrument profiles and autonomous profiling buoys). It is created by interpolating available oceanographic profile data, most of which collected in the last 50 years. We averaged temperature in the euphotic layer (taking 100 m as an approximation for euphotic depth). We considered salinity at the surface. We used the mixed layer depth calculated from salinity and temperature values, as reported in Condie and Dunn (2006).

Chemical variables (dissolved oxygen, silicate and nitrate concentrations) were retrieved from CARS. We computed the depth of the minimum dissolved oxygen concentration. We calculated the silicate:nitrate ratio (referred to as Redfield ratio, Redfield 1958) in (1) the euphotic layer (0-100 m) and (2) a deeper layer (100-400 m), approximating the layer where nutrients are potentially uplift to the surface by mesoscale eddies (Menkes et al. 2002) (thereafter named the eddy layer).

Three biological variables were also considered. Remotely sensed chlorophyll-a concentration (CHL) was obtained at a 9 km and monthly resolution from MODIS sensor (available at http://oceancolor.gsfc.nasa.gov/) for the 2002-2012 period. Monthly net primary production (NPP) was based on the Vertically Generalized Production Model (Behrenfeld and Falkowski 1997) for 2002-2012. It was retrieved at a 9 km resolution from Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/). In addition, we used the monthly climatology of dominant phytoplankton groups derived from the PHYSAT model at a 9 km resolution. This algorithm identified 5 phytoplankton groups (nanoeucaryotes, *Prochlorococcus*, *Synechococcus*, diatoms, Coccolithophores and *Phaeocystis*-like) from the spectral shape of the water leaving radiance measured by satellites between 1998 and 2006 (Alvain et al. 2008).

All variables were continuous except dominant phytoplankton group which constituted a categorical variable. Rasters of all environmental variables were aggregated to match a grid of 0.5° Latitude x 0.5° Longitude using the SDMTools (VanDerWal et al. 2012) and raster packages in R.

Table IX-1: Environmental variables classified into four categories, underlying oceanographic processes and relationships with habitat quality (↗: Habitat quality increases with the variable, ↘: habitat quality decreases with the variable, ∩ : habitat quality is related to an optimum of the variable. Data sources: (1) General Bathymetric Chart of the Oceans (http://www.gebco.net/) (2) Scatterometer Climatology of Ocean Winds (Risien and Chelton 2008) (3) AVISO (http://www.aviso.oceanobs.com/duacs/) (4) CSIRO Atlas of Regional Seas (Condie and Dunn 2006) (5) Ocean Color (http://oceancolor.gsfc.nasa.gov/ (6) Ocean productivity (http://www.science.oregonstate.edu/ocean.productivity/) (7) PHYSAT model (Alvain et al. 2008)

Environnemental variable	Unit	Data source	Underlying oceanographic process	Relationship with habitat quality
Physiographic				
Depth (DEP)	m	(1)	Low DEP is associated with high primary production	↘
Slope (SLO)	°	(1)	Elevated SLO is associated with high primary production and prey aggregation	↗
Physical				
Wind speed (WSP)	m/s	(2)	High WSP influences surface circulation and increases the depth of the mixed layer	↗
Wind stress curl (WSC)	N m^{-2} 10^4 km	(2)	Positive WSC lift the thermocline inducing high primary production	↗
Standard error of sea level anomaly (sdSLA)	m	(3)	High sdSLA indicates high mesoscale activity potentially linked to high primary production and prey aggregation	↗
Temperature from 0 to 100 m (TEM)	°C	(4)	TEM has a physiological effects on prey and influences the structure of the upper water column	∩
Surface salinity (SAL)	PSU	(4)	Low SAL indicates the proximity of a large river associated with nutrient discharges and high primary production	↘
Mixed layer depth (MLD)	m	(4)	Deep MLD is associated with increased nutrient inputs from deeper layers and high primary production	↗
Chemical				
Depth of the minimum dissolved oxygen concentration (DEPOX)	m	(4)	Shallow DEPOX reflects the decomposition following high productivity events, DEPOX has a physiological effect on prey	↘ ∩
Silicate:nitrate ratio from 0 to 100 m (SIL:NIT1)	-	(4)	SIL:NIT ratios greater than 1:1 favor the growth of diatoms and food chains leading to top predators	↗
Silicate:nitrate ratio from 100 to 400 m (SIL:NIT2)	-	(4)	SIL:NIT ratios greater than 1:1 favor the growth of diatoms and food chains leading to top predators	↗
Biological				
Chlorophyll concentration (CHL)	mg / m^3	(5)	High CHL indicates a high biomass of primary producers	↗
Net primary production (NPP)	mg C/ m^3 / d	(6)	High NPP reflects a high rate of primary production	↗
Dominant phytoplankton group (PHY)	-	(7)	Large phytoplankton are at the origin of food chains leading to top predators	Large phytoplankton

c) Detection function modeling

We used multiple covariate distance sampling (Marques and Buckland 2004) to model the effect of detection covariates on cetacean detection probability, in addition to distance. If the covariate provided a significantly smaller AIC, we estimated an effective strip width (ESW) for each of the covariate levels; alternatively, we estimated a unique ESW for use under all detection conditions (see Mannocci et al. 2013b). The ESW was subsequently used in species density modeling.

d) Data processing

We aggregated cetacean sightings and survey effort into grid cells at the spatial resolution of environmental variables using ArcGIS 10 (Environmental Systems Research Institute 2010). Numbers of individuals of the three guilds and survey effort were summed in each grid cell. Mean ESWs in each grid cell were calculated for the three guilds.

e) Species density modeling

We used generalized additive models (GAMs) to relate numbers of cetaceans per grid cell to environmental variables. GAMs are flexible regression techniques which can fit non linear relationships and improve model performance (Barry and Elith 2006). In GAMs, the link function $g()$ relates the mean of the response variable given the covariates $\mu=E(Y|X_1,...,X_p)$ to the additive predictor $\alpha + \sum f_i(X_i)$:

$$g(\mu) = \alpha + \sum f_i(X_i)$$

The components $f_i(X_i)$ of the additive predictor include non parametric smooth functions (splines) of the covariates (Wood and Augustin 2002).

Our response variable Y was the number of individuals. As count data are often characterized by heavy tailed distributions, we used an overdispersed Poisson distribution with variance proportional to the mean and a logarithmic link function. Accounting for non constant effort, we used the logarithm of sampled area (survey effort multiplied by twice the ESW) in each grid cell as an offset. GAMs were fitted in R using the mgcv package in which degrees of freedom for each smooth function are determined internally in model fitting and thin plate regression splines are the default (Wood 2006). Nevertheless, we limited the

maximum amount of smoothing to 4 degrees of freedom for each spline to model non linear trends but to avoid overfitting that would have no ecological meaning (Forney 2000).

For each cetacean guild, we fitted the models containing all possible combinations of four environmental variables, excluding combinations of collinear variables (*i.e.* with pair-wise Spearman rank correlation coefficients < 0.6 or > -0.6). Four predictors were considered in the model to avoid an excessive complexity while providing a reasonable explanatory power. We retained the model with the lowest Generalized Cross Validation (GCV) score. We used explained deviance to evaluate each model's fit to the data.

The selected models were used to predict relative densities of the three guilds in each grid cell, based on the climatology of the summer of each hemisphere. We limited the predictions to a circumtropical envelope encompassing the environmental conditions sampled in the three surveyed regions (model-based interpolation, Elith and Leathwick, 2009). Prediction envelopes were first constrained by the range of sampled temperatures and then by the range of the other environmental variables selected in the models.

We standardized predicted densities between guilds based on their availability at the surface. According to the literature, sperm and beaked whales spend on average 13% of the time at the surface (Papastavrou et al. 1989, Barlow et al. 1997, Jaquet et al. 2000, Hooker et al. 2012), Globicephalinae, 70% (Barlow et al. 1997, Hooker et al. 2012, Minamikawa et al. 2013) and Delphininae, 74% (Baird et al. 2001, Corkeron and Martin 2004, Forcada et al. 2004, Gomez de Segura et al. 2006).

We provided uncertainty maps associated with the predictions, as measured by the coefficient of variation (CV). Uncertainty estimations were derived from the Bayesian covariance matrix of the model coefficients within the mgcv package (Wood 2006).

In order to evaluate the predictive performance of our models, we conducted a block cross-validation by fitting the models leaving out one geographic sector in turn. The cross-validation was not applied to sectors with extreme environmental conditions because leaving out these sectors would limit the range of environmental variables, thereby restricting the prediction envelope. Predictions were confronted to observations using the concordance index (C-index) estimated in R with the Hmisc package (Harrell 2010). The C-index is a generalization of the area under the Receiver Operating Characteristic (ROC) curve; it measures how well a model discriminates between different responses. If C=0.5, predictive

ability is no better than random, if C>0.5, there is a predictive ability, if C=1, there is a perfect fit between observations and predictions (Swets 1988).

3) Results

a) Detection functions

Best fitting detection models were half normal for the three cetacean guilds (Table IX-2, Supplementary material IX-1). Cloud coverage significantly affected the detection of Delphininae. No detection covariate had a significant effect on Globicephalinae. Sea state significantly affected the detection of sperm and beaked whales.

Table IX-2: Detection models and effective strip widths (ESWs) estimated for the three cetacean guilds.

Cetacean guild	Truncation distance	Detection model	Effect of covariate on detection	
			Detection covariate	ESW
Delphininae	500 m	Half normal	Cloud coverage	Low: 246 m Medium: 228 m High: 211 m
Globicephalinae	500 m	Half normal	No significant detection covariate	254 m
Sperm and beaked whales	500 m	Half normal	Sea state	0-1-2: 279 m 3: 226 m 4-5: 202 m

b) Generic relationships of cetaceans with the quality of their habitats

The modeling approach highlighted generic properties of cetacean distributions with habitat quality in tropical oceans, as represented by the selected environmental variables. Explained deviances ranged between 18% for sperm and beaked whales and 46% for Delphininae, with an intermediate value for Globicephalinae (37%) (Figure IX-2). Delphininae showed unimodal relationships with CHL (optimum around 0.5 mg/m^3) and depth (optimum around -1,500 m) and a decreasing relationship with salinity. Densities of Delphininae were the highest when nanoeucaryotes were the dominant phytoplankton group, followed by cyanobacteria (*Prochlorococcus* and *Synechococcus*) and diatoms (but with a large confidence interval). Globicephalinae showed unimodal relationships with CHL (optimum around 0.6 mg/m^3), the silicate:nitrate ratio in the eddy layer (optimum just over

1:1) and depth (optimum around -1,500 m). Densities of Globicephalinae also increased with temperature. Sperm and beaked whales showed an increasing relationship with NPP (up to 15 mgC/m^3/d), followed by a strong decrease with a large confidence interval. Their densities showed strong increasing relationships with depth of the minimum oxygen and slope. Their relationship with depth was bimodal, with optima around -1,500 m and -4,000 m.

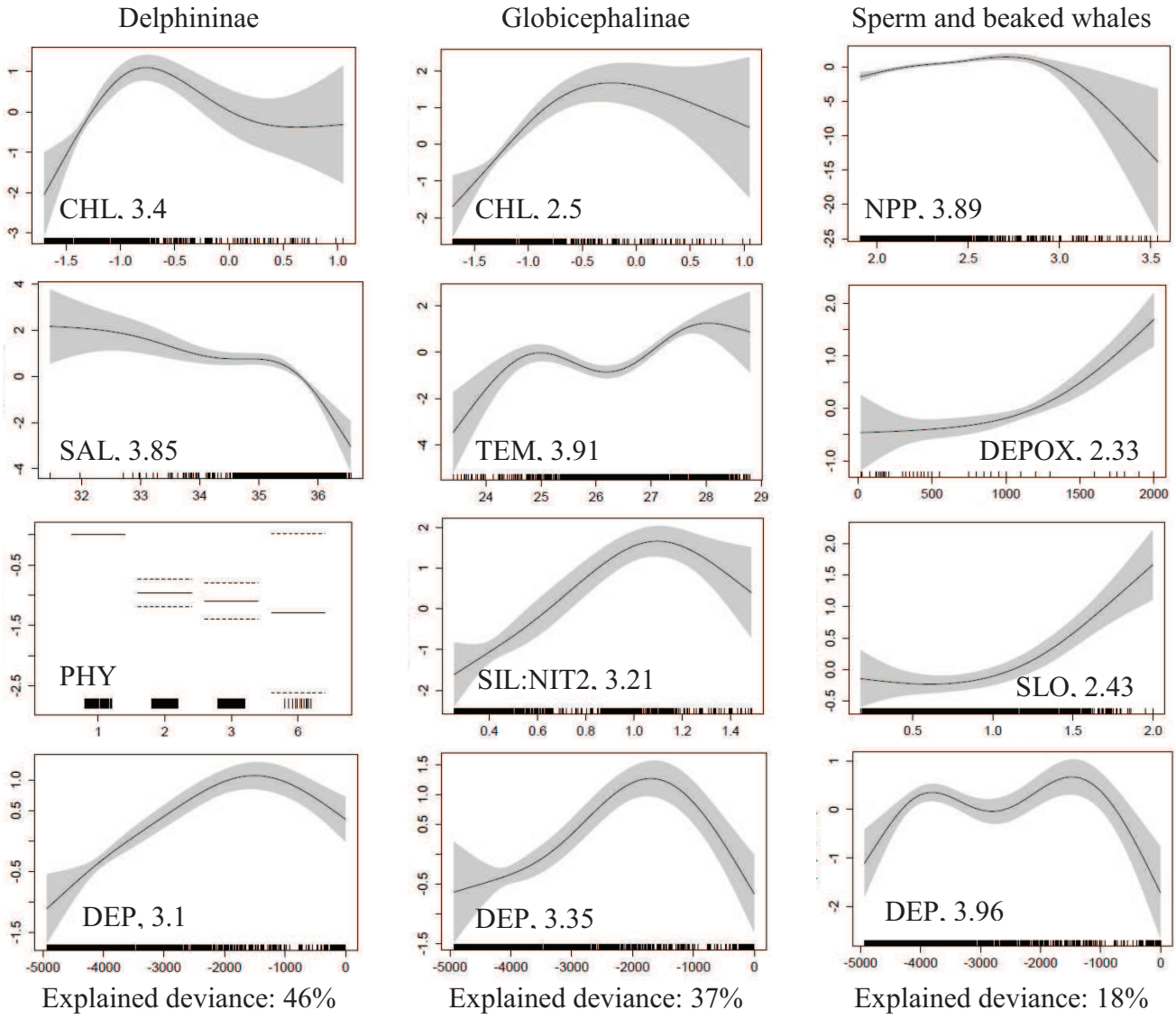


Figure IX-2: Forms of smooth functions for the selected covariates for each cetacean guild, representing the generic properties of cetacean distributions. CHL and NPP were log-transformed, slope was square-root-transformed. All variables were continuous except dominant phytoplankton group (1: nanoeucaryotes, 2: *Prochlorococcus*, 3: *Synechococcus*, 4: diatoms) which was categorical (no smooth function). Estimated degrees of freedom are provided for each smoother. The solid line is the smooth function estimate and shaded regions represent approximate 95% confidence intervals. Zero on the y axis indicates no effect of the covariate (given that the other covariates are included in the model).

c) Circumtropical patterns of cetacean distributions

The prediction envelope was delimited by the range of temperatures sampled in the surveyed regions (from 22.8 to 28.8°C). It therefore excluded the Pacific warm pool and the cool upwelling regions (the eastern margins of South America and Africa and the equatorial Pacific). Subsequently, for each cetacean guild, the extent of the prediction envelope corresponded to the minimum envelope among the four selected environmental variables (Supplementary material IX-2). For Delphininae, the prediction envelope excluded the central North Atlantic and the Arabian Sea, where salinity was higher than the maximum sampled values. For Globicephalinae, it excluded the East and South China Seas, where the silicate:nitrate ratio exceeded the sampled values. For sperm and beaked whales, it was influenced by missing values in the depth of the minimum oxygen concentration.

Prediction maps were quite different between the three guilds. After correction for surface availability, predicted densities were much lower for sperm and beaked whales compared to Delphininae and Globicephalinae (predicted densities of the same order of magnitude). Predicted densities of Delphininae were contrasted between ocean basins (Figure IX-3a). They peaked in the western Pacific, notably in the South China Sea, and in the northeastern Indian Ocean, in particular in the Bay of Bengal and Andaman Sea. Predicted densities were intermediate to high in the Indian Ocean, the equatorial Atlantic, the Caribbean Sea and the northern Gulf of Mexico, as well as in the eastern and southwestern Pacific. Conversely, predicted densities were depressed in the central Atlantic and in the South Pacific subtropical gyre. Predicted densities of Globicephalinae showed marked differences between ocean basins (Figure IX-3b). They were very low in the Atlantic compared to the Indian Ocean. Predicted densities were the highest in the northern Indian Ocean, Philippine Sea, Mozambique Channel and equatorial Pacific. They were the lowest in the central North and South Atlantic and in the South Pacific subtropical gyre. For sperm and beaked whales, predicted densities appeared less contrasted both between and within ocean basins and the prediction map was much more homogeneous (Figure IX-3c). Densities were predicted to be the highest in the southwestern Pacific, notably in the Coral Sea. Overall, predictions for the three cetacean guilds were in agreement with observed distributions in the three surveyed regions (Mannocci et al. 2013a, b, Mannocci et al. in revision).

a Delphininae

b Globicephalinae

c Sperm and beaked whales

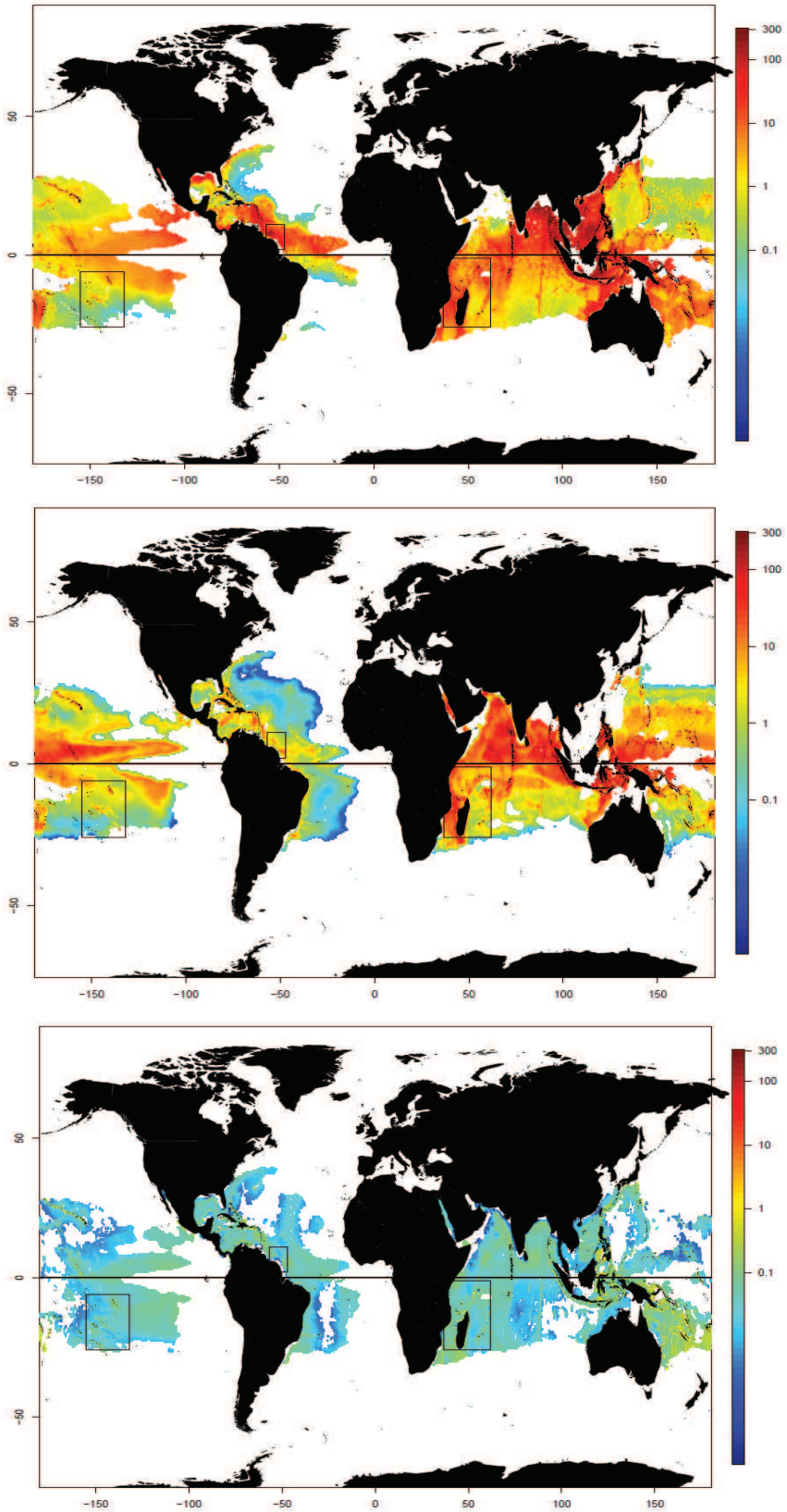


Figure IX-3: Predicted relative densities (individuals/km²) of cetacean guilds: Delphininae (a), Globicephalinae (b) and sperm and beaked whales (c). Environmental variables were gridded on a 0.5°x0.5° grid. We standardized predicted densities between guilds based on their availability at the surface. Study regions are shown in the rectangles.

d) Associated uncertainty

In general, higher CVs were associated with areas of lower predicted densities. For Delphininae, CVs were highest in the central North Pacific (Figure IX-4a). CVs were also high in low salinity regions (Guiana, Bay of Bengal) as a result of the large confidence interval of the relationship with salinity. For Globicephalinae, there was a fairly high uncertainty over the map compared to the other two guilds. In addition, CVs were high on the contour of the prediction envelope where temperature was the lowest (Figure IX-4b). For sperm and beaked whales, CVs peaked in the coastal parts of the Arabian Sea, the Bay of Bengal and along northern South America (Figure IX-4c).

a Delphininae

b Globicephalinae

c Sperm and beaked whales

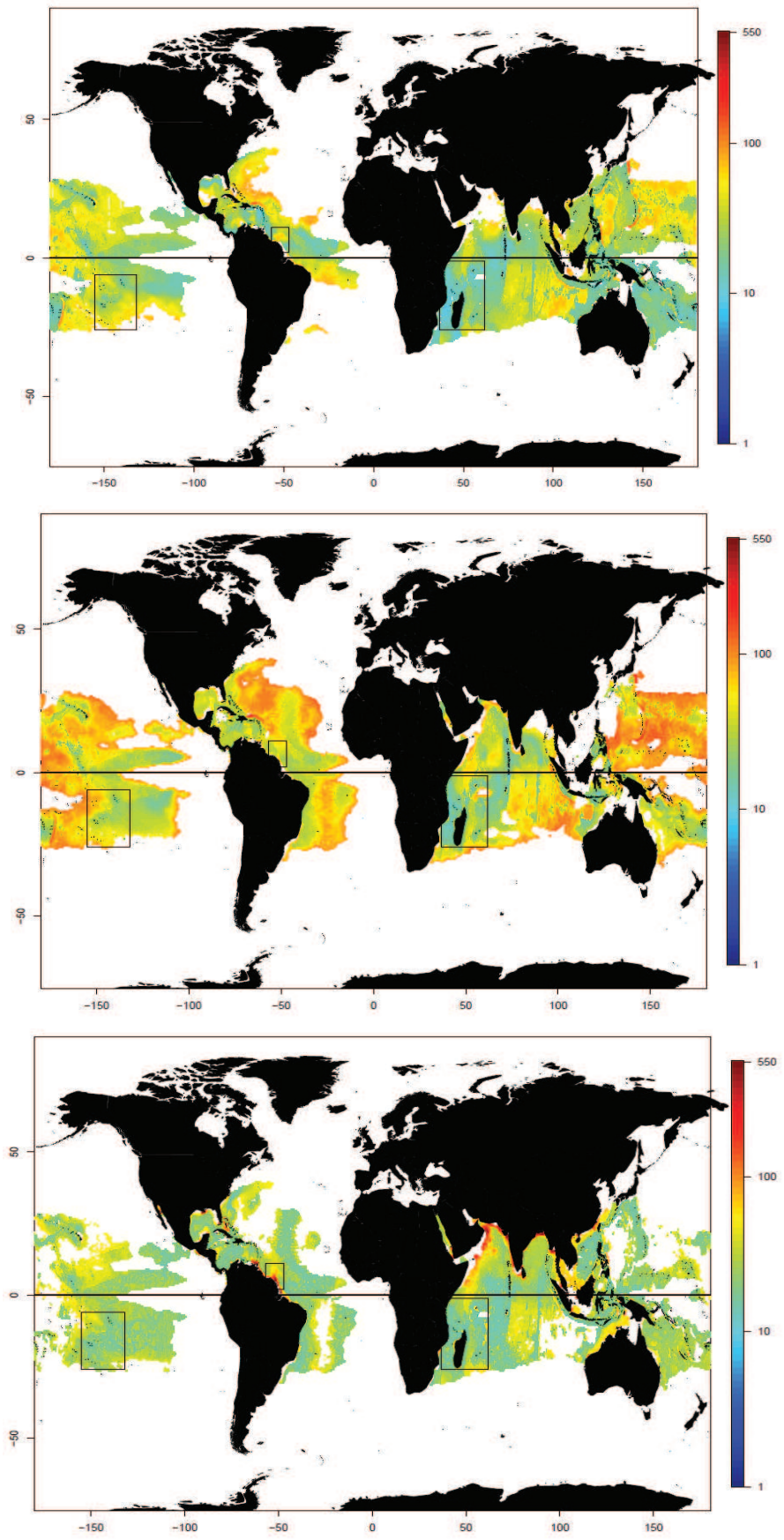


Figure IX-4: Uncertainty associated with predicted densities of cetacean guilds: for Delphininae (a), Globicephalinae (b) and sperm and beaked whales (c). Study regions are shown in the rectangles.

e) Model performances

Models had fair performances although there were differences between sectors (Table IX-3). Predictive ability was the highest for Delphininae, with an average C-index of 0.663. Although predictive ability was the lowest in North Tuamotu, the C-index exceeded 0.7 in five sectors. For Globicephalinae, the average C-index was of 0.571. Predictive ability was rather low in some sectors of the central South Pacific, but the C-index was higher than 0.6 in the Southwest Indian Ocean. For sperm and beaked whales, the average C-index was of 0.596; it was the lowest in North Tuamotu and the highest in Reunion-Mauritius.

Table IX-3: Concordance index (C-index) calculated in the surveyed sectors. The cross-validation procedure was not applied to sectors with extreme environmental conditions. As a consequence, the C-index was not available for Delphininae in Guiana (low SAL) and in the Northern Mozambique Channel (high CHL), for Globicephalinae in the Northern Mozambique Channel (high CHL), North Tuamotu (low SIL:NIT2) and the Australs (low TEM) and for sperm and beaked whales in Guiana (high NPP), the Australs (high DEPOX) and Gambier (low NPP).

Surveyed sector	Delphininae	Globicephalinae	Sperm and beaked whales
Guiana	-	0.528	-
Northern Mozambique Channel	-	-	0.618
Central Mozambique Channel	0.528	0.625	0.629
Southern Mozambique Channel	0.635	0.605	0.588
Seychelles	0.670	0.618	-
Tromelin-Madagascar	0.791	0.698	0.683
Reunion-Mauritius	0.741	0.595	0.709
Society	0.886	0.530	0.643
Australs	0.888	-	-
North Tuamotu	0.385	-	0.536
South Tuamotu	0.521	0.493	0.440
Gambier	0.715	0.354	-
Marquesas	0.546	0.710	0.527
Average C-index	**0.663**	**0.571**	**0.596**

4) Discussion

In this study, we used a modeling approach to highlight generic properties of cetacean distributions in tropical waters and to predict their densities in a circumtropical belt. This modeling exercise stands out from other studies that predicted marine predator

distributions at the mega scale. First, while most studies focused on species (*e.g.* Kaschner et al. 2006), we modeled cetacean guilds characterized by contrasted energetic requirements. Second, we used a variety of environmental predictors to describe habitat quality, whereas most studies involved only a few standard predictors (Worm et al. 2005, Davies et al. 2010). Third, we predicted for the first time their relative densities at the circumtropical scale. Presence-only distribution models have used expert knowledge to assign cetacean species to broad niche categories; this yielded global range maps (Kaschner et al. 2006, Ready et al. 2010). Although these maps are informative, they ignore the relative importance of different areas within the predicted ranges.

a) Methodological considerations

The aerial surveys sampled a wide spectrum of oceanographic conditions in diverse biogeochemical provinces. Guiana waters are under the influence of major river discharge and have a high productivity. The SWIO region lays at the intersection of the Eastern Africa coastal province, characterized by a high mesoscale activity and enhanced productivity, the Indian monsoon gyre and the Indian South Subtropical gyre, where productivity is much lower. The central South Pacific is entirely located within the oligotrophic subtropical gyre, although a latitudinal productivity gradient is present (Longhurst 2007). The surveyed region was comparatively small in the western tropical Atlantic. Therefore, the oceanographic characteristics of this basin are likely under-represented in our generic models. We used the environmental conditions sampled in the three oceans to define a circumtropical prediction envelope for each cetacean guild. Doing this, we provided extrapolations to unsurveyed areas while staying within the range of environments sampled by the training data and within the same general time frame (summer season) (Elith and Leathwick 2009). Although our surveys allowed to sample wide regions, they still represent a small surface within the total extent of the circumtropical prediction envelope and it would be useful to incorporate data from other tropical regions in the modeling process.

We described habitat quality using a combination of satellite and *in situ* measurements of surface, water column and sea floor properties. Although ocean color measurements are influenced by suspended sediments and dissolved organic matter, they are the best available proxy for the quantity of primary production. CSIRO Atlas of regional seas documents a variety of surface and sub-surface properties using interpolation from point data (Condie and Dunn 2006). Errors may arise from both the interpolation method and the quality

of the original data (Barry and Elith 2006). Nevertheless, it provides comprehensive three dimensional fields and complements satellite data. We also used the PHYSAT model (Alvain et al. 2008) which relies on ocean color to detect major phytoplankton groups. These products have been previously validated using *in situ* pigment data from a wide range of oceanographic conditions.

The explained deviances of our circumtropical models were higher than those of regional models, classically varying between 10% and 20% (Ferguson et al. 2006a, Becker et al. 2010, Forney et al. 2012, Mannocci et al. 2013b). Explained deviance was the lowest for sperm and beaked whales. Several factors may have contributed to this. Since sperm and beaked whales spend an important amount of time submerged, they can remain undetected by observers (Pollock et al. 2006). This may have lead to a significant proportion of false absences in the data (Martin et al. 2005) for this particular guild compared to the other two. This guild is also probably the most heterogeneous, encompassing species with different habitat preferences (as illustrated by the two depth optima). These factors could blur the signal in the data; hence, more noise may be left unexplained by the model. Alternatively, even if we made every effort to incorporate parameters describing the ocean in its three dimensions, the variables considered here may be inappropriate for explaining the distribution of these deep divers which likely depend on deep oceanographic features that are yet poorly documented.

b) Generic relationships of cetaceans with the quality of their habitats

In order to emphasize relationships that would be stable across the three oceans, we focused on key linkages of cetaceans with physiographic, physical, chemical and biological features characterizing the quality of their habitats. They represent indirect predictors since they are correlated with a series of intermediate variables (Vaughan and Ormerod 2003) rather than having direct relationships with cetaceans. Indirect predictors can provide robust predictions at large spatial scales (*e.g.* Pearson and Dawson 2003) and result in more parsimonious models as they encompass a wide range of correlated variables (Vaughan and Ormerod 2003).

Our modeling approach revealed generic properties of cetacean distributions in tropical oceans. Cetaceans responded to depth and the quantity of primary production in the three tropical oceans. Delphininae and Globicephalinae also responded to the nature of

primary production, in addition to its quantity. Sperm and beaked whales responded to slope, Globicephalinae, to temperature and Delphininae, to salinity. Multiple authors have previously noted cetacean relationships with depth and primary production at the regional scale (Yen et al. 2004a, Ferguson et al. 2006a, b, Becker et al. 2010). The association of sperm and beaked whales with slope was documented at multiple occasions (Gregr and Trites 2001, Waring et al. 2001, Cañadas et al. 2005). Delphininae were shown to be associated with low salinity waters in the eastern tropical Pacific (Ferguson et al. 2006a). The present study indicates that these commonly found relationships can be considered as generic since they hold in the three tropical oceans.

In previous studies at the regional scale, we showed that the energetically costly Delphininae and Globicephalinae occupied the highest quality habitats (defined in terms of primary production; Mannocci et al. b, Mannocci et al. in revision) to meet their high energetic requirements, whereas the less active sperm and beaked whales occupied either high or low quality habitats, as a result of their lower energetic needs. Cetacean dependences on the quality of their habitats with respect to their costs of living appeared consistent at the circumtropical scale. Yet, the circumtropical patterns of sperm and beaked whales were much more homogeneous compared to the other two guilds, indicating that they may be less sensible to habitat quality. However, although all guilds showed generic relationships with depth and primary production, a high quality habitat for a guild did not necessarily represent a high quality habitat for the other guilds. Furthermore, historical and present anthropogenic pressures on populations, competitive interactions, as well as constraints linked to reproduction, may affect the quality of their habitats and their resulting density patterns.

c) Validation of predictions

For prediction purposes, it is important to assess model's predictive power (Schröder 2008). We used a block cross-validation to evaluate the genericity of our models within the surveyed regions (internal validation). We obtained a fair predictive ability on average, although there were variations between sectors. In order to evaluate the full genericity of a model, it is recommended to perform external validation by using independent data collected in distinct regions (Fielding and Bell 1997). Our aerial surveys are the only dedicated large-scale surveys in tropical waters, apart from the comprehensive line transects conducted in the Gulf of Mexico (GOM), southeast United States (SE) and eastern tropical Pacific (ETP), which extents fall only marginally in our circumtropical envelopes. This severely

limited the potential for real external validation. Nevertheless, we can visually compare our results with modeling outputs available in these regions.

We predicted high densities of Delphininae on the continental shelf and shelf edge of GOM. This corresponds fairly well to high suitability areas for *Stenella sp* and *Tursiops sp* (Best et al. 2012), the main genera composing this guild. We also predicted intermediate densities of Delphininae on the continental shelf of SE where coastal waters have a high suitability for *Tursiops sp* (Best et al. 2012). We predicted intermediate densities of Globicephalinae in the shelf edge of SE, in accordance with high suitability areas for pilot whales. In addition, oceanic waters of the GOM represented a high suitability area for beaked whales, sperm whales and *Kogia sp* (Best et al. 2012). This appears in accordance with our predictions for sperm and beaked whales.

Our prediction envelopes in the ETP encompassed the eastern Pacific warm pool and the countercurrent thermocline ridge, but excluded the Costa Rica dome and the equatorial front, two areas of enhanced productivity important to many cetaceans (Ballance et al. 2006). The countercurrent appeared as a high density area for spotted dolphins (*Stenella attenuata*) and spinner dolphins (*S. longirostris*), like the eastern warm pool for spinner dolphins and rough-toothed dolphins (*Steno bredanensis*) (Redfern et al. 2008, Forney et al. 2012). This seems consistent with our predictions for Delphininae. However, densities of short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*) were the highest (Forney et al. 2012) outside our prediction envelope. Forney et al. (2012) predicted high densities of dwarf sperm whales (*Kogia sima*) and Cuvier's beaked whales (*Ziphius cavirostris*) in the eastern warm pool and *Mesoplodon sp* in the countercurrent. Furthermore, catch data in the Pacific indicated that sperm whales were abundant in equatorial waters (Jaquet et al. 1996). This appears consistent with our predictions for sperm and beaked whales.

d) Management implications

The application of macroecological concepts can help to manage species and their supporting ecosystems (Brown 1995). Through spatial predictions based on generic properties of cetacean distributions, we provide managers with valuable tools for decision making.

Tropical oceans are bordered by emerging countries that may not have the resources to support marine research. This modeling approach will (1) provide prompt spatial

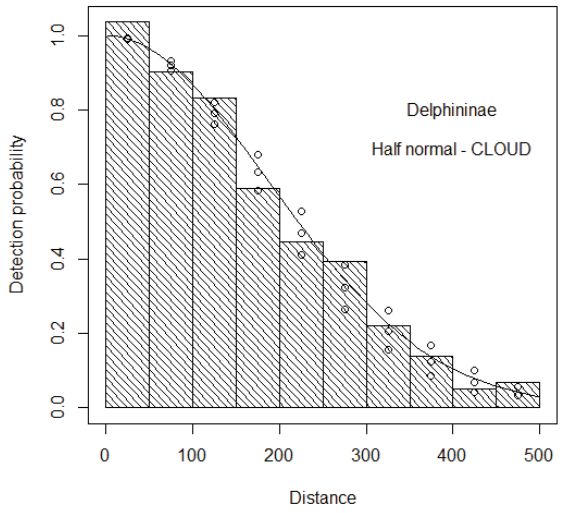
predictions of cetacean densities in these waters where data are very scarce or inexistent and (2) inform about the state of ecosystems by using cetaceans as sentinels of the marine environment. Recent economical growth has lead to cumulative impacts in coastal and offshore waters of emerging countries (including fishing, shipping and climate change) (Halpern et al. 2008). Such pressures can severely impact the quality of pelagic habitats. Owing to their position at the top of the food chains and their life history characteristics which make them vulnerable to human-induced alterations of their ecosystems, cetaceans constitute valuable sentinels of the marine environment (Moore 2008). They integrate the impact of natural and anthropogenic factors over space and time (Fossi et al. 2012) and they have a key role in maintaining the structure and functions of pelagic ecosystems (Bowen 1997, Fossi et al. 2012). In this respect, healthy cetacean communities may reflect healthy pelagic ecosystems.

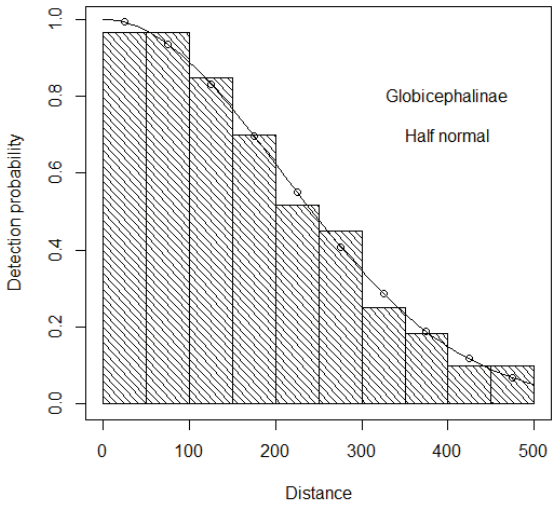
e) Recommendations for future surveys

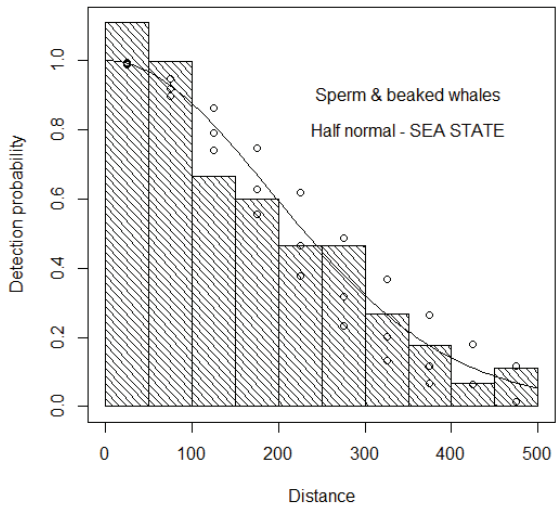
The outputs of this study can be used to make recommendations on priorities for data collection. First, it would be very valuable to obtain more data in areas where predictions are the most uncertain. The use of shipping lines as trans-oceanic platforms of opportunity would allow the acquisition of new data at low cost in remote oceanic regions. This would help to reduce the uncertainty of Delphininae and Globicephalinae predictions in the central North and South Atlantic and similarly in the northern Indian Ocean, as well as in the South China Sea. Furthermore, if we refer to Longhurst's partitioning of the oceans (Longhurst 2007), some relevant biogeochemical provinces were not considered in this modeling exercise. Notably, it would be extremely worthwhile to include tropical upwelling systems in the modeling exercise, such as the Pacific Equatorial divergence province and the Humboldt Current. The results of this study can be used to determine a minimum set of regions to sample for a representative coverage of oceanographic conditions in the tropics. This would constitute a cost effective way of acquiring new data in order to provide predictions within a full circumtropical envelope with a reduced uncertainty.

Supplementary material IX-1: Detection models for the three cetacean guilds according to multiple covariate distance sampling

A half normal detection model was selected for the three cetacean guilds. Cloud coverage significantly affected the detection of Delphininae; sea state significantly affected the detection of sperm and beaked whales (fitted detection models for each level of the covariate are shown). No covariate significantly affected the detection of Globicephalinae (the fitted detection model is shown).



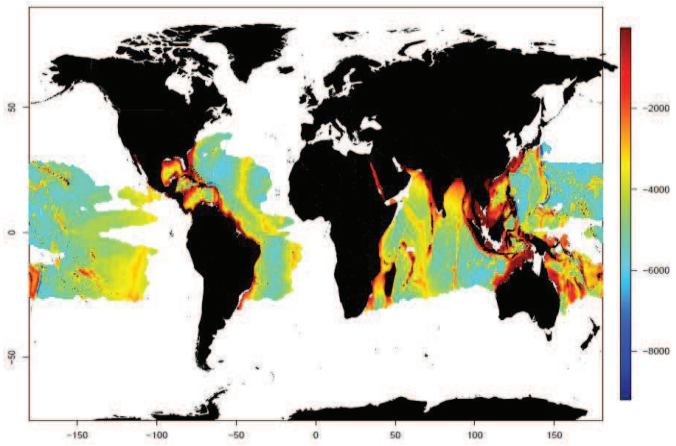




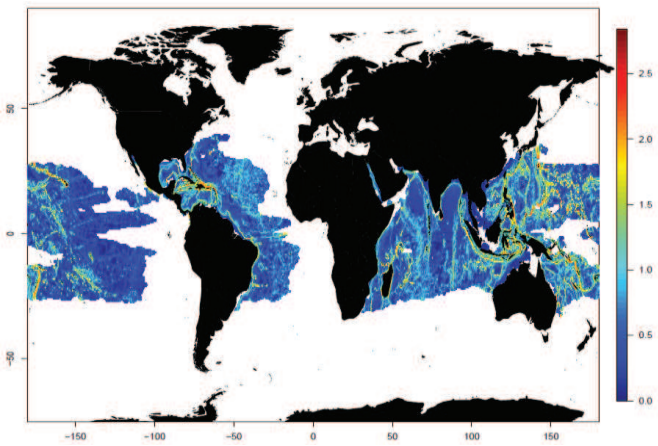
Supplementary material IX-2: Envelopes for environmental variables

For each environmental variable, the extent of the envelope was first delimited by the range of sampled temperatures in the surveyed regions and then by its own sampled range. For each guild the prediction envelope corresponded to the minimum envelope among the four selected variables.

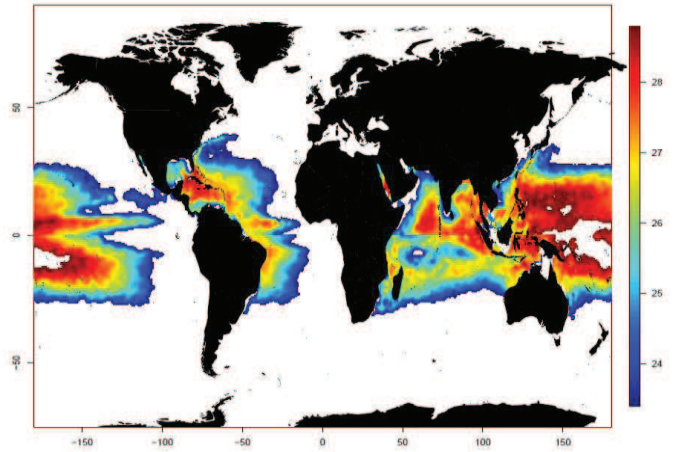
Depth (m)



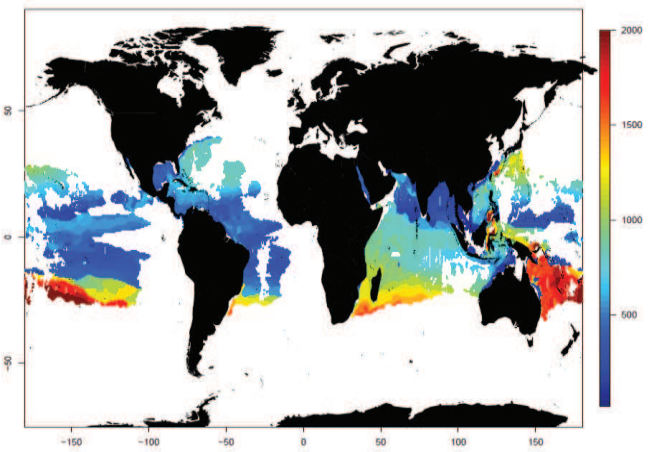
Slope (°) (square-root transformation)



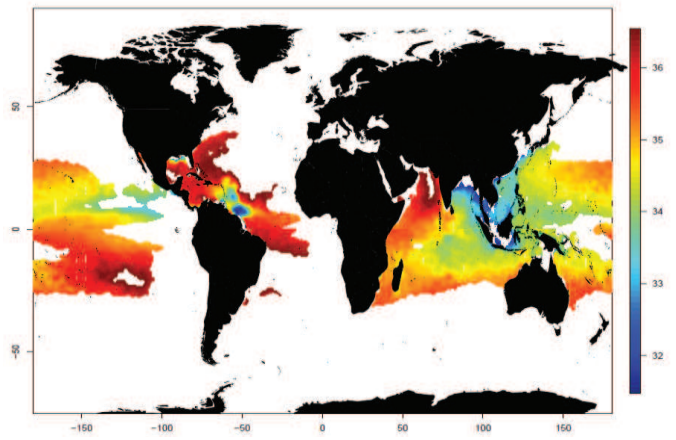
Temperature in the euphotic layer (°C)



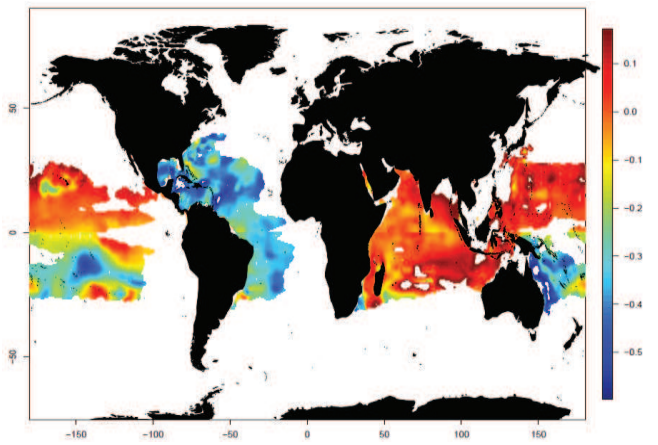
Depth of the minimum dissolved oxygen concentration (m)



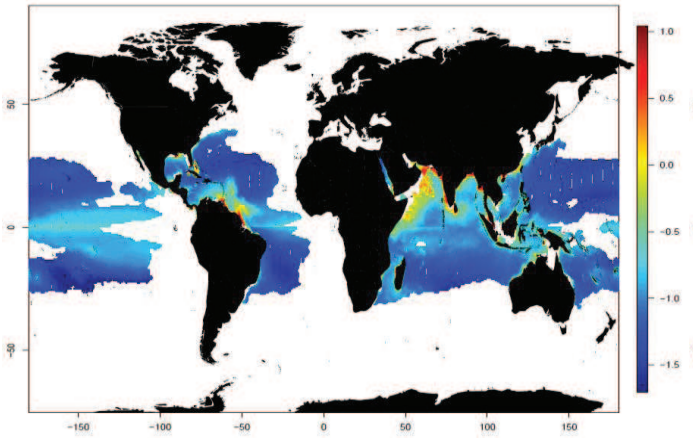
Surface salinity (PSU)



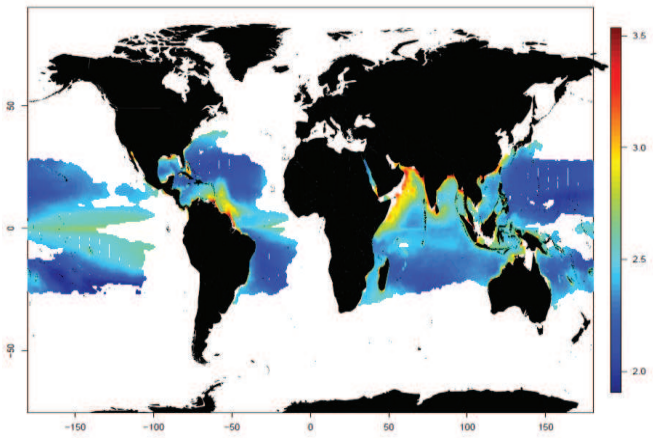
Silicate:nitrate ratio in the eddy layer



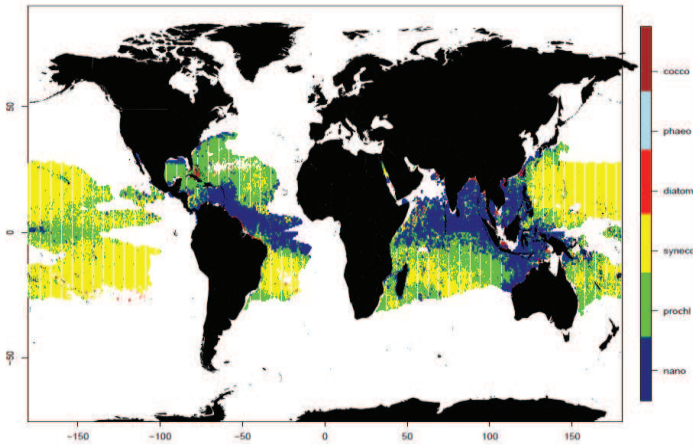
Chlorophyll concentration (mg/m^3) (log)



Net primary production (mgC/m^3/d) (log)



Dominant phytoplankton group



Chapter X. General discussion

Photo credit: Pamela Carzon

1) General outcomes of the dissertation

In this dissertation, I studied cetacean and seabird strategies of habitat utilization at the regional and the circumtropical scale. The three objectives were (1) to evaluate their responses to the spatial heterogeneity of habitat quality, (2) to evaluate their responses to contemporaneous *versus* averaged habitat quality and (3) to highlight generic properties of cetacean distributions in tropical oceans. To fulfill these objectives, I modeled the habitats of cetacean and seabird guilds, defined according to their likely costs of living, using sightings collected from dedicated aerial surveys in three tropical regions and a variety of environmental parameters describing the quality of pelagic habitats. The most noteworthy outcomes of this dissertation are summarized below.

Relevant data on cetacean and seabird distributions in poorly studied tropical waters

The knowledge of cetacean and seabird distributions is very heterogeneous across the oceans. Less than 25% of the world's ocean surface has been surveyed and large gaps in survey coverage are found in tropical latitudes (Kaschner et al. 2012). While some tropical regions have been intensively surveyed in space and time (for example the ETP, where the need to monitor the impact of dolphin incidental mortality in the tuna purse-seine fishery resulted in three decades of research), nearly nothing is known in other tropical regions. Our dedicated aerial surveys permitted to sample for the first time three extensive tropical regions (the western tropical Atlantic (WTA), the Southwest Indian Ocean (SWIO) and French Polynesia (FP)), and thus yielded extremely relevant data on cetaceans and seabirds in these tropical waters.

Predictions of cetacean and seabird distributions in unsurveyed areas

I used high quality sighting data to successively predict the relative densities of cetaceans and seabirds at the scale of the sector, the region and the circumtropical belt (see Figure I-5). I predicted cetacean and seabird habitats in two sectors of the WTA (Chapter V) and at the regional scale in the SWIO and FP (Chapters VI to VIII). Then, I predicted cetacean habitats in a circumtropical belt including most tropical waters (Chapter IX). These spatial predictions are very valuable since they cover unsurveyed areas both within the study regions and within the circumtropical belt.

New insights on cetacean and seabird strategies of habitat utilization

Some authors previously noticed the relationship between top predator habitats and their energetic costs of foraging, mostly for seabirds (Ballance et al. 1997, Hyrenbach et al. 2007). In this dissertation, I explicitly tested the hypothesis of habitats selection on the basis of energetic costs. I found that the energetic costs of cetaceans and seabirds governed their strategies of habitats utilization and that they distributed among habitats with respect to their quality. This finding emerged from modeling studies in three contrasting tropical regions in which habitat quality was described by various environmental parameters, including primary production (Chapters VI and VII) and the distribution of micronekton (Chapter VIII). The present study also suggests that cetacean and seabirds better respond to averaged habitat quality, as described by recurrent oceanographic features, than to contemporaneous habitat quality.

Emerging properties of cetacean distributions in tropical waters

I combined sighting data from three tropical regions with relevant environmental parameters to build circumtropical habitat models of cetaceans. This is the first time cetacean habitat models are built using multi-ocean sighting datasets to reveal emerging properties of their distributions.

The results of this dissertation have implications for both fundamental (sections X-3) through X-5)) and applied marine research (section X-6)).

2) Methodological considerations and limitations

a) Aerial methodology

Aerial surveys offer a number of advantages over ship-based surveys. The aerial methodology allowed to quickly cover the three tropical regions with lower costs and better flexibility relative to weather conditions compared to dedicated ship surveys, hence resulting in a higher rate of platform usage in optimal detection conditions. Aerial surveys also yield more accurate distance measurements and group size estimates compared to ship-based surveys and responsive movement is generally not a problem (Evans and Hammond 2004).

Perception and availability bias affect the detection of animals (Pollock et al. 2006). The availability bias can be estimated from two aircrafts flying in tandem or circle backs performed by a single aircraft (Hiby and Lovell 1998). Since animals are encountered at different phases of their dive cycles, the proportion of missed individuals can be estimated. The general aim of our aerial surveys was to provide a first assessment of the diversity and distribution of top predators in poorly documented waters rather than providing absolute abundance estimates; hence, we did not implement such survey methodologies. The availability bias was the highest for sperm and beaked whales which spend a significant proportion of their time submerged and are more likely to remain undetected. Since the species composing this guild are the same in the three regions and their diving behaviour should not differ much between regions, I can reasonably assume that the availability bias is constant among regions. Testing the spatial variation of the availability bias would require deploying time depth recorders to obtain dive profiles (Pollock et al. 2006) of cetaceans accross the three regions. Provided the availabily bias remains effectively constant, considering it would have resulted in multiplying predicted densities by a given factor for each cetacean guild (as done for the circumtropical predictions in Chapter IX). In this dissertation, I was mainly interested in the spatial distribution of predicted densities and their ratios between the surveyed sectors for each energetic guild independently; these core results should be unaffected by the availability bias.

In cetacean habitat models, I considered the perception bias induced by survey conditions by using multiple covariate distance sampling (Marques and Buckland 2004) to estimate condition-specific ESWs. For seabirds, the strip transect methodology (Tasker et al. 1984) assumed that all individuals were detected within the strip, so I used a fixed ESW in habitat models. Some seabirds, notably of the smallest and the most cryptic species, were probably missed within the strip, for example as a result of sun glare and sea state. Nevertheless, according to Certain and Bretagnolle (2008), perception bias has a minor effect on most seabird species observed from large-scale aerial surveys.

Although a proper training of observers occurred before the surveys, perception bias may arise from the simultaneous search of cetaceans and seabirds. We can expect a selective decrease of the observer's vigilance if the visual search focuses on the most frequent and visible species (seabirds) to the detriment of rarer and more discrete species (cetaceans) (Desimone and Duncan 1995). However, no significant negative effect of the multi-species protocol was found on the detection of small delphinids (Amandine Ricart, MSc Thesis 2013).

We followed a standard aerial protocol derived from the SCANS methodology adapted to aircrafts (Hammond et al. 2013) to sample cetaceans and seabirds in the study regions. There were slight variations of the survey methodology in the WTA. First, the survey was not implemented regionally, as done in the SWIO where the covered area included the EEZs of France and adjacent countries. This resulted in a limited survey effort, a restricted range of sampled environmental variability and low sighting numbers. In addition, the two sectors (the Antilles and Guiana) were surveyed at different seasons and had non overlapping environmental conditions. This precluded the implementation of regional habitat models in the WTA.

b) Modeling framework

To model the habitats of cetaceans and seabirds, I relied on GAMs which are broadly used statistical methods. Their main advantage is their flexibility for fitting the complex and non linear relationships characterizing species distributions. For this reason, they often result in improved model performances (Barry and Elith 2006). However, GAMs are prone to overfitting (in the most extreme case the number of predictors equals the number of observations). According to Vaughan and Ormerod (2003), the ratio of sample sites to environmental variables should exceed 10:1 to avoid excessive parameterization and improve the reliability of the subsequent modeling. In order to avoid overfitting, I restricted the number of candidate explanatory variables to four, so the ratio was largely above this threshold.

Uncertainty in habitat models stems from both error in model specification and in data collection (Barry and Elith 2006). Error in model specification comes from the fact that, by essence, models summarize complex distributional patterns with a reduced set of predictors. The complexity of ecological systems is thus an inherent limitation to our ability to model species distributions. However, simple models are usually preferred over more complex ones for the sake of generality (Dambach and Rödder 2011). In addition, error in the data generates noise which smoothes out ecological relationships. Error arises from the limited information available for model parameterization, difficulties in surveying rare or cryptic species and inaccurately described or undescribed environmental variables (Barry and Elith 2006). The question is not to eliminate these sources of error (which is merely impossible), but to quantify uncertainty and incorporate it into model predictions (Miller et al. 2004). In this respect, I always provided uncertainty maps associated with the predictions.

Shmueli (2010) distinguishes between explanatory modeling, which aims at testing causal explanations, and predictive modeling, which aims at providing predictions in new situations (either in space or time). These two kinds of modeling differ in their requirements. For example, while correlation between variables is a problem in explanatory modeling, it does not impact the predictive ability of a model. The goal of this study was more to highlight cetacean and seabird associations with their environment in order to provide spatial predictions, than to elucidate causal drivers of their distributions. Ecological understanding is still critical, particularly for the selection of candidate variables and interpretation of the results. Models for prediction need to reflect the balance between specific fit to the training data and generality, allowing reliable predictions in new situations (Elith and Leathwick 2009). This can be achieved by information criteria such as the AIC, which balances explained variation against model complexity, or cross-validation criteria such as the GCV used in this study, which tests model performance by leaving out every data in turn (Wood 2006).

Direct (or causal) variables are often considered as the best predictors of species distributions (Guisan and Zimmermann 2000, Elith and Leathwick 2009). Since the use of such predictors is often limited by their restricted availability, indirect proxies of species distributions that are much easier to collect are typically used. In this dissertation, I used a range of ecologically relevant predictors, from the most direct (micronekton) to the most indirect (depth or slope). For widely distributed species in environments characterized by few fine-scale variations, such as top predators in pelagic ecosystems, indirect predictors can provide robust predictions at coarse spatial scales (Robinson et al. 2011).

There was a significant proportion of signal unexplained by the models, as indicated by the low to medium deviances. Such values are nonetheless typical of cetacean and seabird GAMs (Ferguson et al. 2006a, Vilchis et al. 2006, Becker et al. 2010, Forney et al. 2012). The deviances of the regional models were higher for seabirds (ranging between 14% and 40%) compared to cetaceans (ranging between 4% and 30%, with static and oceanographic predictors) (Chapters VI and VII). This was due to the importance of distance to the colony in the model for breeding seabirds, reflecting their central place foraging mode of life. Deviances of models built with micronekton (ranging between 9% and 47%) (Chapter VIII) were higher than deviances for the same cetacean guilds with the less direct predictors. Incorporating simulated prey distribution resulted in an increased explanatory power, although models were based on a different modeling unit (the 0.25° x 0.25° Seapodym pixel).

Furthermore, deviances of the circumtropical models were higher than those of the regional models (but the difference was not large with regional models built with micronekton). This may be due to the larger sample sizes, the inclusion of a variety of environmental predictors, as well as the fewer false absences since circumtropical models were based on a larger modeling unit (a 0.5° x 0.5° pixel).

Among cetaceans, deviances were always the lowest for sperm and beaked whales. This may be due to the combination of (1) the highest proportion of false absences as a result of their long dives which limit their availability at the surface, (2) their less marked habitat preferences in accordance with their lowest costs of living, (3) inappropriate environmental variables to describe their deep pelagic habitats and (4) the heterogeneity in the species composing this guild. It would be useful to quantify the contribution of each of these factors in the explained deviance.

Evaluation should be an integral part of the modeling process (Guisan and Zimmermann 2000). Two main approaches exist for evaluating the predictive power of a model. The first approach is to use a single dataset to calibrate the model and evaluate it, typically by using cross-validation (this is named internal validation). In the generic modeling study, sample size was sufficient to perform a block cross-validation to evaluate the generality of the models (Chapter IX). The second and more robust approach is to use an independent dataset (named external validation) (Guisan and Zimmermann 2000, Robinson et al. 2011). According to Vaughan and Ormerod (2003), the success of internal validation has little value and the only valid test is to rely on independent data collected in a discrete geographical region. In some cases, evaluation with field data is impossible. This is the case in this dissertation. The aerial surveys collected large-scale data for the first time in these regions and were implemented only once. This precluded the evaluation of the predictive power of the models based on independent datasets. The resulting prediction maps should not be viewed as end points, but rather as possible images of the reality which could be validated with future surveys. Nonetheless, obtaining data from areas situated far from continent or any large island is challenging.

c) Spatial extrapolation

Spatial extrapolation is a major topic in applied ecology. While ecological data are typically collected over small areas and short temporal durations, phenomena such as global

warming or biodiversity loss operate over very large areas and/or over extended periods of time (Miller et al. 2004). In this study, I extrapolated cetacean distributions from the individual transect to the sector, from the sector to the region and from the region to the circumtropical belt. Along this process, I provided predictions to new and unsurveyed areas while staying within the range of environmental variables used in model fitting (this is geographical extrapolation rather than environmental extrapolation) (Elith and Leathwick 2009). Extrapolation to new environments is extremely risky since uncertainty increases exponentially the further we leave the observed data range (Dormann et al. 2007). Geographical extrapolation should be reliable provided the data and model are reasonable and correlations between predictor variables are stable across the geographical domain of the prediction (Elith and Leathwick 2009). Since I stayed within the same range of environmental variables, the uncertainty associated with the spatial extrapolation should not be larger than the uncertainty related to the training data.

d) The energetic guild approach

In this study, I used direct metabolic measurements (for seabirds) or indicators of costs of living (for cetaceans) to categorize them as having high, medium or low costs of living and examine their habitats in relation to their general energetic requirements. This classification is a simplified image of the reality and there may be differences within guilds. For example, the extensive use of wind and gliding behavior of red footed boobies (Weimerskirch et al. 2005) may induce lower costs of flight for this species compared to other boobies. Similarly, there are some differences within Delphininae, as illustrated by the common dolphin (*Delphinus delphis*) and striped dolphin (*Stenella coeruleaolalba*) in the Bay of Biscay, characterized by different costs of living in spite of having very similar body shapes (Spitz et al. 2012).

Grouping cetaceans and seabirds into guilds raised some methodological issues. In particular, cetacean guilds might contain species with various body sizes and group sizes; hence, species within a guild might exhibit different detectabilities, as illustrated by the sperm and beaked whale guild, which includes sperm whales, *Kogia spp* and beaked whales. This affected the offsets used in the GAMs but probably did not impact cetacean-habitat relationships. Guilds might also contain species with different habitat preferences; this might have contributed to the low explained deviances. For example, in the SWIO, the deviance of the habitat model for the sperm and beaked whale guild was three times lower compared to the deviance for Cuvier's beaked whales only (ANNEX 2, Appendix 5). Nonetheless, these

guilds have a clear heuristic value for the exploration of cetacean and seabird habitats utilization in relation to their energetic costs. Furthermore, this approach allowed the full exploitation of aerial survey data in which identification to the species level is not always possible.

3) Response to the spatial heterogeneity of habitat quality

a) A "spatial version" of the optimal foraging theory

The optimal foraging theory (OFT) states that a predator must balance energy gained from prey acquisition with energy spent searching for prey in order to minimize its net energy gain (MacArthur and Pianka 1966, Pyke et al. 1977). The OFT underlies strategies of resource selection (Boyce and McDonald 1999). In particular, energetic costs of living in cetaceans were shown to govern the quality of their diets (Spitz et al 2012). In this dissertation, I show that the OFT may also underlie top predator strategies of habitats utilization. I propose that the energetic costs of top predators govern the quality of their prefered habitats: energetically costly predators would be constrained to select the highest quality habitats to meet their high energetic requirements, whereas less active predators could satisfy their needs by exploiting either high or low quality habitats. I show that the OFT, initially developed at the scale of the individual to understand resource selection, can be extended to the spatial scale to give insights into strategies of habitats utilization.

Ballance et al. (1997) found that seabird communities were structured by costs of flight along a productivity gradient in the ETP. Only seabirds with economical flight were able to exploit the dispersed prey patches of low productivity waters. Recently, Wilson et al. (2012) found that cormorants were distributed into the marine environment in accordance with the OFT. They equipped birds with GPS and accelerometers and showed that they preferentially used areas and depths which resulted in minimized foraging costs. They provided simultaneous measurements of energy expenditure (from accelerometers) and successfully validated the hypothesis of habitat utilization governed by foraging costs. This seems is accordance with the results of this dissertation.

b) Description of the quality of pelagic habitats

Various descriptors of the pelagic environment have been used in cetacean and seabird habitat models (state-of-the-art in Chapter IV), but, to my knowledge, the notion of quality of pelagic habitats was introduced here for the first time. The quality of benthic habitats was previously documented in both freshwater and marine ecosystems, essentially from the characteristics of the physical substrate (Diaz et al. 2004). For example, it was shown that complex substrate provided the highest quality habitats for fishes owing to their refuge effect (Rodwell et al. 2003). In Chapters VI and VII, I characterized high quality habitats by a high primary production or by indirect indicators of primary production (mesoscale activity, depth, slope). In Chapter VIII, high quality habitats were defined by high biomass and/or production of micronekton. In Chapter IX, habitat quality was described by the quantity and the nature of primary production, or by more or less direct indicators of these parameters (physiographic, physical, chemical and biological variables).

c) Energetic constraints govern cetacean and seabird strategies of habitats utilization

Strategies of habitats utilization were in general agreement with the energetic costs of cetaceans in the three tropical regions. In the WTA, there was a much higher proportion of small delphinids within the odontocete community, with a great abundance of bottlenose dolphins in the most productive Guiana sector compared to the oligotrophic lesser Antilles. In the SWIO and FP, ratios between the lowest and the highest predicted density sectors for the three guilds gave more quantitative insights. In both regions, Delphininae and Globicephalinae showed a greater ratio of densities between low and high quality habitats, indicating a greater dependence on habitat quality than in sperm and beaked whales. This was emphasized by studies relying on both indicators of primary production and micronekton. In FP, the ratios for Delphininae and Globicephalinae were higher compared to the SWIO, probably as the result of the greater contrast between the Marquesas and the other sectors of FP. For sperm and beaked whales, these same ratios were similar in both regions, strengthening the fact that they are probably not very sensitive to habitat quality. The much more homogeneous circumtropical patterns of sperm and beaked whales also argued in favors of their lower sensitivity to habitat quality.

For seabirds, the dependence on habitat quality appeared hidden by their various breeding strategies and levels of dependence on colonies or roost sites. As central place foragers, seabirds are constrained to colonies during the breeding season, and their at-sea distributions primarily reflect colony locations (Jaquemet et al. 2004, Hyrenbach et al. 2007, Le Corre et al. 2012). Nonetheless, oceanographic parameters affect patterns of colony sizes and locations since recurrently high productivity within species-specific foraging ranges to some islands is necessary for the settlement of large colonies (Ballance et al 1997). I included distance to the nearest colony as a predictor in habitat models in order to consider seabird dependence on colonies. The case of sooty terns illustrates the complexity of seabird responses to habitat quality for different periods of their life or annual cycle. In the SWIO, they occupied all sectors irrespective of their productivity, in accordance with their economical lifestyles, but there was a very high density area around the Juan de Nova colony (hosting 2 million pairs, Jaquemet et al. 2008) where reproduction occurred during the survey (Chapter VI). Conversely, in FP, sooty terns were only present around the productive Marquesas and did not appear to be breeding during the survey (as suggested by maximum densities predicted 200 km offshore) (Chapter VII). Nevertheless, in both regions, differences in energetic costs were partly reflected in the colony effect; costly seabirds were more tightly related to their colonies, as shown by smaller radius halos of high densities.

d) Additional factors influencing habitat quality

The environmental variables considered in this study are not the only factors influencing habitat quality and the optimization of foraging success may not be the only determinant of strategies of habitats utilization. I present other factors which can influence habitat quality (the first two are specific to seabirds).

The quality of nesting sites

Seabirds rely on two very different habitat types: ocean for food and land for reproduction. While the quality of pelagic habitats is important for foraging seabirds, the availability and appropriateness of nesting sites is crucial for breeding seabirds. High-quality nesting sites are different between seabird species and are often defined by the required substrate. For example, petrels and shearwaters nest in burrows and crevices, white terns nest in trees, boobies nest on a variety of habitats including ground, slope and trees, and

frigatebirds usually nest on the bare ground (Hoyo 1996). In the absence of terrestrial predators and disturbance, nesting sites should be of higher quality for many seabirds.

The presence of sub-surface predators

In addition to oceanographic parameters, the presence of sub-surface predators may be a strong determinant of habitat quality for seabirds. Most tropical seabirds are restricted to the water surface for foraging; seabirds that lack waterproof plumage cannot even sit on water (*e.g.* frigatebirds) (Hoyo 1996). Tropical seabirds depend on sub-surface predators, including predatory fishes and marine mammals that drive prey to the surface; hence, they can only exploit the vertical habitat through their associations with sub-surface predators (Ballance et al. 1997). In the ETP, the presence of yellowfin tunas and spotted and spinner dolphins is important for feeding seabirds (Au and Pitman 1986, Ballance et al. 1997, Ballance 2008). Spear et al. (2007) found that, among the 30 most abundant seabird species, 78% of prey species were obtained when feeding in association with sub-surface predators. Some seabirds are even known to be near-obligate commensals of tunas (Au and Pitman 1986).

Avoidance of super predators

For seabirds, at-sea predation is rare, although white sharks can occasionally take individuals that alight on water (Johnson et al. 2006). The most significant predation pressure may occur at breeding colonies. The minimization of predation risk can be a significant selection pressure for some cetaceans. Killer whale is the most important marine predator of cetaceans. Large sharks also occasionally forage on small dolphins or on the weaker individuals and calves of large cetaceans (Ballance 2009). Pitman et al. (2001) suggested killer whale predation on sperm whales as a potentially important selective pressure in the evolution of sperm whale ecology, possibly at the origin of their complex social behavior and at-sea distribution patterns. In Shark bay (Australia), the patterns of habitat use of bottlenose dolphins appeared to be shaped by both prey availability and predation risk (Heithaus and Dill 2006). When shark abundance was low, dolphins used deep and shallow habitats and were distributed within patches proportionally to prey density. When shark abundance was high, dolphins greatly reduced their use of the productive shallow patches in favor to deep patches where predation was lower. However, this situation appears quite particular to such shallow bays, and other mechanisms may be in place in the pelagic open waters that constitute most of our surveyed sectors.

Anthropogenic pressures

Anthropogenic pressures can strongly affect habitat quality. Cetacean and seabird densities may be lower than expected from the quality of pelagic habitats as a result of past and present anthropogenic pressures. For example, in the ETP, the incidental kill of more than four million dolphins in the tuna purse seine fisheries in the 1960s and 1970s (Wade 1995) caused the depletion of some stocks with little evidence of recovery since then (Gerrodette and Forcada 2005). Dolphin densities may be lower than expected owing to the quality of pelagic habitats, as a result of these past human pressures. The same may apply to various seabird species that have been exploited for their eggs by Polynesians, leading for instance to the extirpation of sooty terns from the Australs (Thibault and Bretagnolle 2007). Furthermore, it is interesting to note that the overexploitation of large predatory fishes may relax their foraging pressure on mid-trophic levels, therefore potentially improving the quality of pelagic habitats for other top predators such as cetaceans and seabirds.

Interspecific competition

The presence of competitors can influence the quality of habitats of both cetaceans and seabirds. For instance, in the Bahamas, MacLeod et al. (2004) proposed that permanent cetaceans competitively excluded ecologically similar cetaceans which only entered the area during high productivity events, when the competitive exclusion relaxed. Owing to their larger size and their plunge diving abilities, masked boobies competitively excluded other species of feeding flocks in the most productive waters of the ETP (Ballance et al. 1997).

4) Response to recurrent oceanographic features

a) Different predictabilities of oceanographic features

Pelagic habitats are characterized by different predictability in time and persistent features can be distinguished from ephemeral features (Hyrenbach et al. 2007). Persistent features are areas of predictable high primary production and prey aggregation, such as oceanic fronts or water mass boundaries. Ephemeral features are short-lived gradients in water properties, created by a variety of physical mechanisms and associated biological enhancement, for example, ephemeral fronts that occur along the edges of eddies. Shelf breaks, submarine canyons and seamounts (static features) represent an additional category of features, associated with predictable high primary production and prey aggregation.

In order to reduce the time spent searching for prey, top predators should target features associated with recurrently high productivity. Within these features, more numerous foraging opportunities should lead on average to increased foraging success. Hence, to forage optimally, top predators may respond to persistent rather than ephemeral oceanographic features. I investigated the responses of cetaceans and seabirds to different levels of temporal integration in oceanographic features in the SWIO and FP (Chapters VI and VII).

b) Cetaceans and seabirds responded to persistent oceanographic features

In the SWIO, I evaluated cetacean and seabird responses to short-term oceanographic features, described by the weekly resolution, *versus* medium and long-term features, respectively described by the seasonal and climatological resolutions. This was done by replacing time-averaged variables in the selected models by their short-term equivalents. For all guilds, explained deviances were always less, suggesting that they may respond better to persistent oceanographic features. Since oceanographic conditions during the survey did not differ much from that of the 10 year-climatology, cetaceans and seabirds did not show strong preferences for medium or long-term features.

FP is characterized by a greater inter-annual variability than the SWIO and the survey period was concurrent with a moderate La Niña episode. This 'experimental situation' gave the opportunity to evaluate cetacean and seabird responses to the medium-term (or seasonal) *versus* the long-term (or climatological) situation. Since cloud coverage precluded the consideration of a more instantaneous resolution, the seasonal resolution was the finest resolution considered in this region. I tested all combinations of variables at both resolutions in the model selection procedure. For cetaceans, either seasonal or climatological variables were retained in the best models, suggesting that they may not respond strongly to the fairly atypical situation observed during the survey. For all seabirds but petrels and shearwaters, only climatological variables were selected, suggesting that they did not respond strongly to the situation of the survey, but exploited areas that are on average favorable to them year after year.

Ideally, to assess the responses of cetaceans and seabirds to medium *versus* long-term oceanographic features in FP, the survey should be repeated during a normal and an El Niño year. Comparing predictions of models fitted at the temporal scale of each survey would show

whether their distributions differed among these contrasted situations. Ballance et al. (2002) found that seabird habitat associations remained consistent over time in the ETP. Oceanography and geography (latitude and longitude) explained most of the variance in seabird distributions and adding year as a temporal variable only marginally increased the explained variances. This seems to indicate that seabirds did not change their distributions from one year to another, in accordance with our findings.

Colony locations explained an important amount of seabird distributions in both regions. Since colony locations are static and breeding at a colony can only carry on if food resources are sufficient and recurring year after year around this colony, seabirds may respond to persistent oceanographic features. Conversely, cetaceans are not constrained to colonies but, owing to their foraging mode, they likely respond better to persistent features. Indeed, compared to seabirds, which locate prey by observing the activity of sub-surface predators (Ballance et al. 1997, Jaquemet et al. 2004), or congeners, resulting in a network foraging (Wittenberger and Hunt 1985), cetaceans forage by visual or acoustic detection within a smaller radius than seabirds can do when foraging in network. Therefore, cetaceans may be able to perceive a smaller area of their ecosystem and thus probably take better advantage of persistent or recurring oceanographic situations for foraging.

c) Consistence with memory-based foraging strategies

These results suggest that top predators may have learned to exploit oceanographic features that determine recurrent access to food resources and are consistent with memory-based foraging strategies (Davoren et al. 2003a). It was shown from computer simulations that a predator exhibiting memory-based foraging strategy could harvest about 1.6 times more prey items than if it did not rely on memory (Benhamou 1994). In long-lived animals such as top predators, foraging probably relies on experience acquired after years or even generations, if foraging culture can be transmitted as is the case in some, if not most, cetaceans (Rendell and Whitehead 2001). For seabirds which forage from a central place, the use of past experience or memory permits a more rapid location and exploitation of food patches (Davoren et al. 2003b). In particular, for immature individuals, the period of pre-breeding colony attendance may provide an important opportunity to learn where prey can be harvested profitably (Hunt et al. 1999).

Although the interpretation of these results appears meaningful in an ecological sense, the lesser variability characterizing variables at time-averaged resolutions may also have contributed to the higher explained deviances of the habitat models in the SWIO and FP. Therefore, additional research is obviously needed to further support these interpretations.

5) Generic properties of cetacean distributions

a) From ecological to macroecological insights

In the first part of this dissertation (Chapters V through VIII), I was interested in ecological questions at the scale of three separate tropical regions: (1) I described where cetaceans and seabirds occurred, (2) I proposed ecological interpretations for the observed distributions and (3) I predicted their habitats at the regional scale. In the WTA, I mainly focused on points (1) and (2), whereas in the SWIO and FP I also dealt with point (3). I then shifted to a macroecological approach in order to highlight generic properties of cetacean distributions at the circumtropical scale (Chapter IX). Macroecology is a big-picture statistical approach to ecology (Smith et al. 2008). It tries to infer general laws from statistical manifestations expressed across broad spatial scales (Brown 1999). Macroecological studies have included the elucidation of patterns of species richness, abundance, body size, range size and were primarily directed toward terrestrial ecosystems (Blackburn and Gaston 2003).

b) Oceanographic processes influence cetacean macroecological patterns

The interest in quantifying and understanding large-scale ecological patterns in marine ecosystems has recently increased, along with the increasing availability of large-scale environmental and biological data (Witman and Roy 2009). The marine environment is characterized by a close match between the physical environment and its biological components. Oceanographic processes acting across a range of spatial and temporal scales are the basis of the environmental structure that influences a suite of biological processes which in turn influences the formation of macroecological patterns. As vectors of food and organisms, oceanographic processes are fundamental to marine macroecological patterns (Leichter and Witman 2009). They drive the macroecological patterns of organisms at low trophic levels. For example, climate and oceanography provided a framework for explaining the latitudinal variation in copepod diversity (Rombouts et al. 2009).

In this dissertation, I showed that oceanographic processes also influence the macroecological patterns of organisms at higher-trophic levels. I highlighted generic relationships between the distribution of three cetacean guilds and the spatial patterns of a range of environmental variables reflecting oceanographic processes at the ecosystem scale. Cetaceans responded to depth and the quantity of primary production in the three tropical oceans. Delphininae and Globicephalinae responded to the nature of primary production in addition to its quantity. Sperm and beaked whales responded to slope, Globicephalinae, to temperature and Delphininae to salinity.

c) How generic are the models ?

If the circumtropical models are generic enough, I can expect similar results with the regional models. It is not easy to compare the circumtropical and the regional models since only a limited number of environmental variables were used at the regional scale and they exhibited a much wider variability at the circumtropical scale. Nevertheless, chlorophyll concentration, net primary production, depth and slope had significant relationships with cetacean densities at both the regional and the circumtropical scale. In addition, overall, the circumtropical predictions were in accordance with the regional predictions. Notably, the latitudinal density gradient was apparent in FP and the Mozambique Channel appeared as a high density area in the SWIO for both Delphininae and Globicephalinae.

The genericity of a model is enhanced if (1) it is built on a large dataset with intrinsic variability, (2) predictor variables have direct ecological significance, or alternatively (3) the associations between indirect and direct variables are consistent between regions (Graf et al. 2006, Strauss and Biedermann, 2007). The habitat models were based on pooled regional datasets with contrasted environmental conditions with sometimes only limited overlaps. This resulted in a large dataset characterized by high intrinsic variability. For example, average sea surface temperature was 27.4°C in Guiana; in the SWIO it was between 27.8 (Reunion-Mauritius) and 29.2°C (Central Mozambique Channel); in FP it ranged between 25.3 (Australs) and 27.3°C (Society). Average net primary production was 1,172 mgC/m^2/day in Guiana; in the SWIO it ranged between 150 (Reunion-Mauritius) and 370 mgC/m^2/day (Juan de Nova-Madagascar); in FP it ranged between 93 (Gambier) and 330 mgC/m^2/day (Marquesas). In addition, although the predictors of the generic models had indirect relationships with cetaceans, their relationships with more direct variables should be

consistent in the three oceans (for example, the associations between bottom slope and productivity and prey aggregation should be similar in the three ocean basins).

6) Management implications

a) Useful substitutes of information on top predators in tropical oceans

Habitat models are increasingly used for the management and conservation of species and ecosystems. Their potential applications include forecasting species occurrence in poorly documented regions (Fleishman et al. 2001, Lumaret and Jay-Robert 2002), defining adequate areas for species protection (Cañadas et al. 2005, Louzao et al. 2006), or predicting species responses to environmental change (Pearson and Dawson 2003, Cheung et al. 2009). First of all, our habitat models provide predictions of cetacean and seabird distributions in many extended unsurveyed areas in a timely maner. Considering that the implementation of dedicated surveys in these areas would be expensive, logistically challenging and time consuming, and that our models rely on environmental variables than can be easily quantified over large spatial scales, these predictions represent useful substitutes of information in tropical areas where data are scarce or absent (Kaschner et al. 2012).

b) Relevance for the designation of marine protected areas

The importance of marine protected areas (MPAs) in ocean conservation strategies and policies has been increasing in the last decades. However, a combination of criticisms over their feasibility and utility has limited their setting up in pelagic areas. They include the dynamic character of physical processes in the pelagic realm, both in space and time and the difficulty of implementing MPAs beyond national jurisdictions (Game et al. 2009).

The present habitat modeling studies showed that cetacean and seabird distributions were largely affected by oceanographic processes conditioning primary production and prey aggregation. The degree to which these features reoccur, the amount of time they persist and how much their location vary in time and space determines the feasibility of MPAs (Game et al. 2009). In addition, owing to their cheap and easy accessibility and their extensive spatial coverage, remote sensing data can be useful for identifying potential MPAs (Game et al. 2009). I demonstrated the responses of cetaceans and seabirds to persistent oceanographic features characterized by remote sensing and produced prediction maps according to the forms of these responses. I believe this approach could help in implementing pelagic MPAs.

As suggested by Hyrenbach et al. (2000), temporally persistent hydrodynamic features could be used to delineate core areas defined by average habitat extents and buffers could be defined according to the variability around these average conditions.

As highly mobile pelagic vertebrates, the home ranges of cetaceans and seabirds obviously exceed the frontiers of national EEZs. Therefore, meaningful conservation efforts can only be achieved through the support of regional and international consensus. The aerial survey data are currently used to inform the conservation of cetaceans as part of regional initiatives, such as the Agoa sanctuary recently implemented in the EEZ of the French Antilles and deemed to merge with similar effort by neighboring countries in the whole Antillean Arc.

c) Consideration of uncertainty

There is an increasing recognition of the importance of uncertainty for management and conservation applications (Elith and Leathwick 2009). Rather than viewing it as an obstacle that needs to be reduced or removed, uncertainty should be viewed as a fact of life, a phenomenon that needs to be characterized if the ultimate aim is decision-making (Barry and Elith 2006). A spatially explicit display of the uncertainty associated with predictions is particularly useful to highlight areas in which there is a high confidence in the results and areas where future efforts should be directed (Miller et al. 2004). The uncertainty maps associated with the regional and the circumtropical predictions are particularly relevant in this respect.

d) Benefits of the macroecological approach for conservation

The most severe anthropogenic pressures in the marine environment occur at regional to global scales (Halpern et al. 2008). Addressing these issues and the related decreasing biological diversity requires a macroecological approach in order to seek robust solutions to large-scale problems (Brown 1995). For instance, Jennings et al. (2008) showed that emerging ecological theory can be synthesized to address applied problems on a global scale. They provided baselines for assessing the relative impacts of humans and predicting the global contribution of marine animals to biogeochemical processes. In this dissertation, I highlighted emergent properties of cetacean distributions in tropical waters. These properties

can be useful to conservation practitioners who seek general guidelines that could be applied over multiple regions for decision making (McAlpine et al. 2008).

7) Conclusions and perspectives

The first objective of this dissertation was to evaluate the response of cetaceans and seabirds with contrasting energetic costs of living to the spatial heterogeneity of habitat quality. I implemented regional modeling studies in two extensive tropical regions and characterized habitat quality by primary production and the distribution of micronekton. Energetically costly cetaceans occupied high quality habitats whereas less active cetaceans occupied with habitats of lesser quality. Seabird dependence on habitat quality was less clear owing to the colony effect and to other factors influencing the quality of their habitats. The second objective was to evaluate cetacean and seabird responses to contemporaneous *versus* averaged habitat quality. I considered environmental variables at different temporal resolutions and found that time-averaged variables provided higher explained deviances. Cetaceans and seabirds appeared to respond to persistent oceanographic features in accordance with memory-based foraging strategies. Nevertheless, further research is needed to support these findings. The third objective was to highlight generic properties of cetacean distributions in tropical waters. I conducted a macroecological study to provide circumtropical predictions. All cetacean guilds responded to depth and the quantity of primary production in the three tropical oceans. These circumtropical predictions should be validated with independent data.

Below are several perspectives of this dissertation, either regarding methodological prospects or possible ecological applications.

To decompose the variation in cetacean and seabird densities into environmental and spatial components

We could incorporate environmental and spatial variables in the models to consider both exogenous and endogenous ecological processes influencing predator distributions (Wagner and Fortin 2005). The explicit consideration of the neighbouring spatial context would allow examining interactions between species. This would be particularly meaningful for seabirds which depend on the presence of sub-surface predators for foraging. Subsequently, we could decompose the variation in predator densities into environmental (as described by physiographic, oceanographic, biological variables) and spatial components

(Figure X-1). This could be achieved by implementing partial regression analysis (Legendre and Legendre 2012) using the percentage of total explained deviance as the measure of explained variation (e.g. Lumaret and Jay-Robert 2002). This would help to clarify the influence of the different variables and determine the most influential ones for predators.

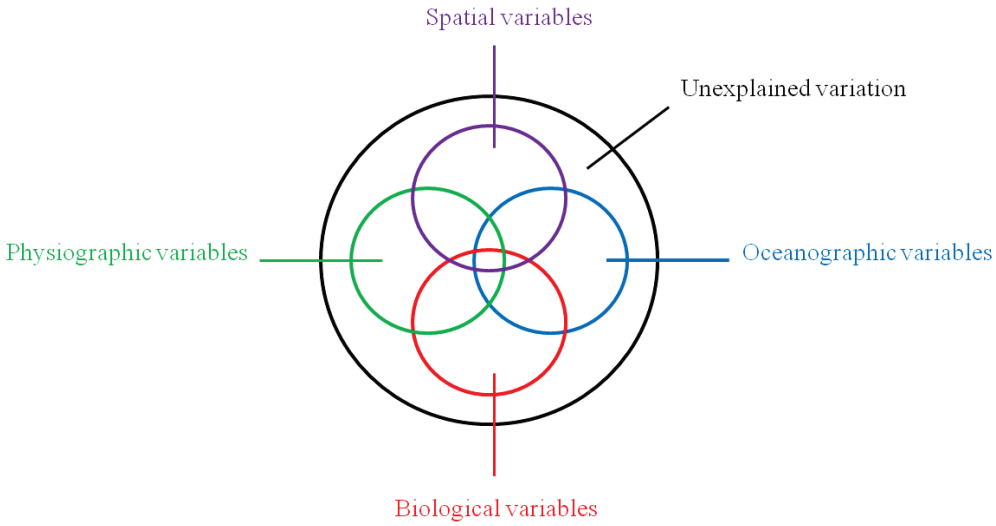


Figure X-1: Diagram illustrating the decomposition of the variation in the response variable into four categories of variables. The overlap of the circles represents the joint effect of the different variables.

To confront predictions based on different categories of environmental variables

We could build habitat models using different categories of environmental variables (physiographic, oceanographic, biological) separately based on the same statistical unit (*e.g.* a pixel of 0.5° x 0.5°) to allow a full comparison. We could confront predictions for each guild and elucidate which variable category provides the best predictive power. Ultimately, this would indicate the most powerful category of environmental variables for large-scale habitat modeling of cetaceans and seabirds.

To extend the circumtropical predictions to other tropical waters and to other guilds

It would be worthwhile to include other tropical regions in the circumtropical predictions. In particular, it would be worthwhile to incorporate the US surveys implemented by NOAA Fisheries Services in the Gulf of Mexico (65,000 km of effort) (Best et al. 2012) and the ETP (including over 17,000 sightings of cetaceans and 400,000 km of effort) (Barlow et al. 2009). This would allow to rely on a larger statistical sample and to extend the prediction envelopes. In addition, we could implement the same generic modeling approach

for seabird guilds (this would necessitate an exhaustive inventory of breeding colonies), as well as for other megavertebrates (large predatory fishes, elasmobranchs, sea turtles).

To reveal anthropogenic pressures in some regions

Habitat models assume an equilibrium between the environment and observed species distributions (Guisan and Zimmermann 2000). Due to multiple anthropogenic pressures, some cetacean and seabird populations might not be in equilibrium with their environment. During our aerial surveys, the collection of data on human activities (fishing vessels, merchant ships, marine debris) along with top predator sightings highlighted contrasts in human pressures between regions. We could use these data and the global cumulative index of Halpern et al. (2008) to categorize tropical regions as having low, moderate or high human impacts. We could build habitat models using cetacean and seabird sightings collected in low impact regions to forecast predictions in the whole circumtropical belt. The difference between predictions and observations would reveal the effect of anthropogenic pressures on top predators. Notably, it would be useful to build dolphin habitat models using sightings collected in regions of low anthropogenic impact and project them into the ETP where dolphins have been heavily impacted by bycatch. If predicted densities are significantly higher than observed densities, this would reveal a non recovery of dolphin populations.

Toward a long-term monitoring of top predators in French overseas territories

The ultimate aim of French aerial surveys is to build a long-term monitoring strategy of top predators. Systematic monitoring of top predator distribution and abundance is essential to inform their conservation status (Donovan 2005), as well as the environmental status of their underlying ecosystems (Moore 2008). Information on the spatial distribution of top predators, as provided in this dissertation, along with its temporal variation are essential to determine predictable areas and times of aggregations on which conservation measures could be focused (Evans and Hammond 2004). Repeating the aerial surveys at different time intervals would allow the distribution of top predators to be followed in both space and time. An aerial survey is planned in New Caledonia and Wallis and Futuna in austral summer 2014-2015. In addition, an aerial survey is programmed at the regional scale in the western tropical Atlantic in 2016. This would yield independent data to test the validity of the circumtropical predictions. In addition, this would provide a basis for a monitoring strategy of top predators in French overseas territories.

References

Photo credit: Olivier Van Canneyt

Aarts, G. et al. 2008. Estimating space-use and habitat preference from wildlife telemetry data. - Ecography 31: 140–160.

Abecassis, M. et al. 2013. A Model of Loggerhead Sea Turtle (*Caretta caretta*) Habitat and Movement in the Oceanic North Pacific. - PLoS ONE 8: e73274.

Aguilar, A. et al. 2002. Geographical and temporal variation in levels of organochlorine contaminants in marine mammals. - Mar. Environ. Res. 53: 425–452.

Aguilar de Soto, N. et al. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). - J. Anim. Ecol. 77: 936–947.

Ainley, D. G. 1977. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. - Adapt. Antarct. Ecosyst. Proc. Third SCAR Symp. Antarct. Biol. Smithson. Inst. Wash. DC USA: 669–685.

Ainley, D. G. et al. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. - Mar. Ecol. Prog. Ser. 118: 69–79.

Alter, E. S. et al. 2010. Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. - Mar. Policy 34: 943–954.

Alvain, S. et al. 2008. Seasonal distribution and succession of dominant phytoplankton groups in the global ocean: A satellite view. - Glob. Biogeochem. Cycles 22, GB3001, doi:10.1029/2007GB003154.

Amano, M. and Yoshioka, M. 2003. Sperm whale diving behavior monitored using a suction-cup-attached TDR tag. - Mar. Ecol. Prog. Ser. 258: 291–295.

Andersen, V. et al. 1997. Macroplankton and micronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments. - Deep Sea Res. Part Ocean. Res. Pap. 44: 193–222.

Anderson, D. J. 1989. Differential responses of boobies and other seabirds in the Galápagos to the 1986-87 El Niño-Southern Oscillation event. - Mar. Ecol. Prog. Ser. 52: 209–216.

Anderson, R. P. 2012. Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. - Ann. N. Y. Acad. Sci. 1260: 66–80.

Arcos, J. M. et al. 2012. Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine important bird areas (IBAs) in Spain. - Biol. Conserv. 156: 30.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. - Avian Biol. 1: 223–286.

Ashok, K. and Yamagata, T. 2009. Climate change: The El Niño with a difference. - Nature 461: 481–484.

Au, W. 2009. Echolocation. - In: Encyclopedia of marine mammals 2nd Edition. Academic Press. Perrin, W.F., Wursig, B. and Thewissen, J.G.M.

Au, D. W. K. and Pitman, R. L. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. - Condor: 304–317.

Austin, M. 1976. On non-linear species response models in ordination. - Vegetatio 33: 33–41.

Austin, M. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. - Ecol. Model. 157: 101–118.

Baird, R. W. et al. 2001. Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. - Can. J. Zool. 79: 988–996.

Baird, R. W. et al. 2006. Studies of beaked whale diving behavior and odontocete stock structure in Hawai in March /April 2006. Report prepared under Contract No. AB133F-06-CN-0053 to Cascadia Research Collective, Olympia, WA from the Southwest Fisheries Science Center, National Marine Fisheries Service.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. California Sea Grant College System, National Oceanic and Atmospheric Administration, in cooperation with Centro de Investigaciones Biológicas del Noroeste. Mexico.

Ballance, L. T. 2008. Understanding seabirds at sea: why and how. - Mar. Ornithol. 35: 127–135.

Ballance, L. T. 2009. Cetacean ecology. - In: Encyclopedia of marine mammals 2nd Edition. Academic Press. Perrin, W.F., Wursig, B. and Thewissen, J.G.M, pp. 196–206.

Ballance, L. T. and Pitman, R. L. 1998. Cetaceans of the western tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. - Mar. Mammal Sci. 14: 429–459.

Ballance, L. T. and Pitman, R. L. 1999. Foraging ecology of tropical seabirds. - Proc 22 Int Ornithol Congr: 2057–2071.

Ballance, L. T. et al. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. - Ecology 78: 1502–1518.

Ballance, L. T. et al. 2002. Investigations into temporal patterns in distroibution, abundance and habitat relationships within seabird communities of the eastern tropical Pacific NOAA-SWFC Administrative report LJ-02-17.

Ballance, L. T. et al. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. - Prog. Ocean. 69: 360–390.

Barber, R. T. and Chavez, F. P. 1983. Biological consequences of El Ninio. - Science222: 1203–1210.

Barham, E. G. 1966. Deep scattering layer migration and composition: observations from a diving saucer. - Science 151: 1399–1403.

Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. - Mar. Mammal Sci. 22: 446–464.

Barlow, J. et al. 1997. A report of cetacean acoustic detection and dive interval studies (caddis) conducted in the Southern Gulf of California, 1995. NOAA Technical Memorandum NMFS NOAA-TM-NMFS-SWFSC-25.

Barlow, J. et al. 2001. Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. - J. Cetacean Res. Manag. 3: 201–212.

Barlow, J. et al. 2008. Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem. - Mar. Ecol. Prog. Ser. 371: 285–295.

Barlow, J. et al. 2009. Predictive modeling of cetacean densities in the eastern Pacific Ocean.

Barry, S. and Elith, J. 2006. Error and uncertainty in habitat models. - J. Appl. Ecol. 43: 413–423.

Baumgartner, M. F. and Mate, B. R. 2003. Summertime foraging ecology of North Atlantic right whales. - Mar. Ecol. Prog. Ser. 264: 123–135.

Baumgartner, M. F. et al. 2001. Cetacean habitats in the northern Gulf of Mexico. - Fish. Bull.-NOAA 99: 219–239.

Baumgartner, M. F. et al. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. - Mar. Ecol. Prog. Ser. 264: 66.

Bearzi, M. 2005. Dolphin sympatric ecology. - Mar. Biol. Res. 1: 165–175.

Becker, B. H. and Beissinger, S. R. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. - Mar. Ecol. Prog. Ser. 256: 243–255.

Becker, E. A. et al. 2010. A comparison of California current cetacean habitat models developped using in situ and remotely sensed sea surface temperature data. - Mar. Ecol. Prog. Ser. 413: 163–183.

Becker, E. A. et al. 2012. Forecasting cetacean abundance patterns to enhance management decisions. - Endanger. Species Res. 16: 97–112.

Begon, M. et al. 2006. Ecology: From Individuals to Ecosystems. - Wiley-Blackwell.

Behrenfeld, M. J. and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. - Limnol. Ocean. 42: 1–20.

Bellier, E. and Monestiez, P. 2008. Model based block kriging to estimate spatial abundance of wildlife populations from count data. - In: Proceedings of the Eighth International Geostatistics Congress. Julian Ortiz & Xavier Emery, pp. 119–128.

Bellier, E. et al. 2011. Decomposing the heterogeneity of species distributions into multiple scales: a hierarchical framework for large- scale count surveys. - Ecography 35: 001–016, 2012

Benhamou, S. 1994. Spatial memory and searching efficiency. - Anim. Behav. 47: 1423–1433.

Benoit-Bird, K. 2004. Prey caloric value and predator energy needs: foraging predictions for wild spinner dolphins. - Mar. Biol. 145: 435–444.

Benoit-Bird, K. J. and Au, W. W. L. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. - Behav. Ecol. Sociobiol. 53: 364–373.

Benoit-Bird, K. J. and Au, W. W. L. 2009. Cooperative prey herding by the pelagic dolphin, Stenella longirostris. - J. Acoust. Soc. Am. 125: 125–137.

Benoit-Bird, K. J. et al. 2013. Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. - PloS One 8: e53348.

Benson, S. R. et al. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. - Prog. Ocean. 54: 279–291.

Berta, A. et al. 2006. Marine mammals: evolutionary biology. - Elsevier/Academic Press.

Bertrand, A. et al. 1999. Acoustic characterisation of micronekton distribution in French Polynesia. - Mar. Ecol. Prog. Ser. 191: 127–140.

Bertrand, A. et al. 2002. Tuna food habits related to the micronekton distribution in French Polynesia. - Mar. Biol. 140: 1023–1037.

Best, B. D. et al. 2012. Online cetacean habitat modeling system for the US east coast and Gulf of Mexico. - Endanger. Species Res. 18: 1–15.

Biggs, D. C. 1992. Nutrients, plankton, and productivity in a warm-core ring in the western Gulf of Mexico. - J. Geophys. Res. Oceans 97: 2143–2154.

Bird Life International 2012. Important Bird Areas factsheet: Connétable Downloaded from http://www.birdlife.org.

Blackburn, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. - Fish Bull US 67: 71–115.

Blackburn, T. M. and Gaston, K. J. 2003. Macroecology: Concepts and Consequences: 43rd Symposium of the British Ecological Society. - Cambridge University Press.

Blackburn, T. M. et al. 2004. The influence of spatial resolution on macroecological patterns of range size variation: a case study using parrots (Aves: Psittaciformes) of the world. - J. Biogeogr. 31: 285–293.

Block, W. M. and Brennan, L. A. 1993. The habitat concept in ornithology. - Curr. Ornithol. 11: 35–91.

Boersma, P. D. 1998. Population trends of the Galápagos penguin: impacts of El Niño and La Niña. - Condor 100: 245–253.

Bonadonna, F. et al. 2001. Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal Arctocephalus gazella. - Mar. Ecol. Prog. Ser. 223: 287–297.

Borstad, G. 1982. The influence of the meandering Guiana Current and Amazon River discharge on surface salinity near Barbados. - J. Mar. Res. 40: 421–433.

Bowen, W. 1997. Role of marine mammals in aquatic ecosystems. - Mar. Ecol. Prog. Ser. 158: 267–274.

Boyce, M. S. and McDonald, L. L. 1999. Relating populations to habitats using resource selection functions. - Trends Ecol. Evol. 14: 268–272.

Boyd, I. 1997. The behavioural and physiological ecology of diving. - Trends Ecol. Evol. 12: 213–217.

Boyé, A. et al. 2009. Important Bird Areas- French Overseas Départements and Territories Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/AmCntryPDFs/French_Guiana.pdf.

Briand, K. et al. 2011. A study on the variability of albacore (*Thunnus alalunga*) longline catch rates in the southwest Pacific Ocean. - Fish. Ocean. 20: 517–529.

Brodeur, R. D. et al. 2005. Micronekton–What are they and why are they important. - Pac Mar Sci Org Pices Press 13: 7–11.

Brotons, L. et al. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. - Ecography 27: 437–448.

Brown, J. H. 1995. Macroecology. - University of Chicago Press.

Brown, J. H. 1999. Macroecology: progress and prospect. - Oikos: 3–14.

Buckland, S. T. et al. 2001. Introduction to distance sampling: Estimating abundance of biological populations. - Oxford University Press.

Burger, J. and Gochfeld, M. 2004. Marine birds as sentinels of environmental pollution. - EcoHealth 1: 263–274.

Cañadas, A. and Hammond, P. S. 2008. Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean: implications for conservation. - Endanger. Species Res. 4: 309.

Cañadas, A. et al. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. - Deep-Sea Res. 49: 2053–2073.

Cañadas, A. et al. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. - Aquat. Conserv. Mar. Freshw. Ecosyst. 15: 495–521.

Cantor, M. et al. 2012. Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study. - Mar. Mammal Sci. 28: 63–83.

Cardona-Maldonado, M. A. and Mignucci-Giannoni, A. A. 1999. Pygmy and Dwarf Sperm Whales in Puerto Rico and the Virgin Islands, with a Review of Kogia in the Caribbean. - Caribb. J. Sci. 35: 29–37.

Caro, T. M. and O'Doherty, G. 1999. On the use of surrogate species in conservation biology. - Conserv. Biol. 13: 805–814.

Carpenter, G. et al. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. - Biodivers. Conserv. 2: 667–680.

Catry, T. et al. 2009a. Movements, at-sea distribution and behaviour of a tropical pelagic seabird : the wedge-tailed shearwater in the western Indian Ocean. - Mar. Ecol. Prog. Ser. 391: 231–242.

Catry, T. et al. 2009b. Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. - Mar. Ecol. Prog. Ser. 374: 259–272.

Certain, G. and Bretagnolle, V. 2008. Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys. - Remote Sens. Environ. 112: 3314–3322.

Certain, G. et al. 2008. Delphinid spatial distribution and abundance estimates over the shelf of the Bay of Biscay. - ICES J. Mar. Sci. 65: 656–666.

Certain, G. et al. 2011. Investigating the coupling between small pelagic fish and marine top predators using data collected from ecosystem-based surveys. - Mar. Ecol. Prog. Ser. 422: 23–39.

Chassot, E. et al. 2011. Satellite remote sensing for an ecosystem approach to fisheries management. - ICES J. Mar. Sci. J. Cons. 68: 651–666.

Chavez, F. P. et al. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. - Science 299: 217–221.

Cheung, W. W. et al. 2009. Projecting global marine biodiversity impacts under climate change scenarios. - Fish Fish. 10: 235–251.

Clapham 2002. Humpback whale. - In: Encyclopedia of marine mammals. Academic Press. Perrin, W.F., Wursig, B. and Thewissen, J.G.M, pp. 589–592.

Clarke, E. et al. 2003. Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. - J. Appl. Ecol. 40: 278–292.

Climate Prediction Center 2011. El nino Souther Oscillation (ENSO) diagnostic discussion issued by Climate Prediction Center/NCEP/NWS.

Condie, S. A. and Dunn, J. R. 2006. Seasonal characteristics of the surface mixed layer in the Australasian region: implications for primary production regimes and biogeography. - Mar. Freshw. Res. 57: 569–590.

Corkeron, P. J. and Martin, A. R. 2004. Ranging and diving behaviour of two "offshore"bottlenose dolphins, *Tursiops sp.*, off eastern Australia. - J. Mar. Biol. Assoc. UK 84: 465–468.

Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. 66: 293–314.

Cotté, C. et al. 2010. Habitat use and abundance of striped dolphins in the western Mediterranean Sea prior to the morbillivirus epizootic resurgence. - Endanger. Species Res. 12: 203–214.

Cotté, C. F. d'Ovidio et al. 2011. Scale-dependent interactions of Mediterranean whales with marine dynamics. - Limnol. Ocean. 56: 219.

Croll, D. A. et al. 2005. From wind to whales: trophic links in a coastal upwelling system. - Mar. Ecol. Prog. Ser. 289: 30.

Croxall, J. P. et al. 2012. Seabird conservation status, threats and priority actions: a global assessment. - Bird Conserv. Int 22:1–34.

Cury, P. M. et al. 2008. Ecosystem oceanography for global change in fisheries. - Trends Ecol. Evol. 23: 338–346.

Dale, M. B. 1975. On objectives of methods of ordination. - Vegetatio 30: 15–32.

Dale, M. R. et al. 2002. Conceptual and mathematical relationships among methods for spatial analysis. - Ecography 25: 558–577.

Dambach, J. and Rödder, D. 2011. Applications and future challenges in marine species distribution modeling. - Aquat. Conserv. Mar. Freshw. Ecosyst. 21: 92–100.

Davies, R. G. et al. 2010. Ambient, productive and wind energy, and ocean extent predict global species richness of procellariiform seabirds. - Glob. Ecol. Biogeogr. 19: 98–110.

Davis, R. W. et al. 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. - Deep Sea Res. Part 49: 121–142.

Davoren, G. K. et al. 2003a. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. - Ecol. Monogr. 73: 463–481.

Davoren, G. K. et al. 2003b. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. - Mar. Ecol. Prog. Ser. 256: 229–242.

De Ruijter, W. P. M. et al. 2004. Eddies and dipoles around South Madagascar: formation, pathways and large-scale impact. - Deep-Sea Res.: 383–400.

De'ath, G. and Fabricius, K. E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. - Ecology 81: 3178–3192.

Desimone, R. and Duncan, J. 1995. Neural mechanisms of selective visual attention. - Annu. Rev. Neurosci. 18: 193–222.

Diaz, R. J. et al. 2004. A review of approaches for classifying benthic habitats and evaluating habitat quality. - J. Environ. Manage. 73: 165–181.

Dolar, M. et al. 2003. Comparative feeding ecology of spinner dolphins (Stenella longirostris) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. - Mar. Mammal Sci. 19: 1–19.

Donovan, G. P. 2005. Cetaceans: can we manage to conserve them? The role of long-term monitoring. - In: Long-term Monitoring - why, what,where, when and how. Solbé, J. pp. 161–174.

Dormann, C. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. - Ecography 30: 609–628.

Edren, S. et al. 2010. Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. - Ecography 33: 698–708.

Edwards, H. H. and Schnell, G. D. 2001. Status and ecology of *Sotalia fluviatilis* in the Cayos Miskito Reserve, Nicaragua. - Mar. Mammal Sci. 17: 445–472.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. - Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Elith, J. et al. 2008. A working guide to boosted regression trees. - J. Anim. Ecol. 77: 802–813.

Elith, J. et al. 2011. A statistical explanation of MaxEnt for ecologists. - Divers. Distrib. 17: 43–57.

Ellis, H. I. and Gabrielsen, G. W. 2002. Energetics of free-ranging seabirds. - In: Biology of marine birds. CRC Marine Biology Series. Schreiber, E.A. and Burger, J..

Embling, C. B. et al. 2010. Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). - Biol. Conserv. 143: 267–279.

Environmental Systems Research Institute 2010. ArcGIS Desktop: release 10.

Estes, J. et al. 2001. Predators, ecological role of. - In: Encyclopedia of biodiversity. Academic Press. pp. 857–878.

Etnoyer, P. et al. 2004. Persistent pelagic habitats in the Baja California to Bering Sea (B2B) ecoregion. - Ocean.-Wash. DC-Ocean. Soc.- 17: 90–101.

Evans, G. T. and Taylor, F. J. R. 1980. Phytoplankton accumulation in Langmuir cells. - Limnol Ocean. 25: 840–845.

Evans, P. G. and Hammond, P. S. 2004. Monitoring cetaceans in European waters. - Mammal Rev. 34: 131–156.

Graf, R. et al. 2006. On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. - Ecography 29: 319–328.

Farber, O. and Kadmon, R. 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. - Ecol. Model. 160: 115–130.

Fauchald, P. 1999. Foraging in a hierarchical patch system. - Am. Nat. 153: 603–613.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. - Mar. Ecol. Prog. Ser. 391: 139–151.

Fauchald, P. and Tveraa, T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. - Ecology 84: 282–288.

Fauchald, P. and Tveraa, T. 2006. Hierarchical patch dynamics and animal movement pattern. - Oecologia 149: 383–395.

Fauchald, P. et al. 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. - Ecology 81: 773–783.

Fauchald, P. et al. 2011. Scale-dependent response diversity of seabirds to prey in the North Sea. - Ecology 92: 228–239.

Ferguson, M. C. et al. 2006a. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. - Ecol. Model. 193: 645–662.

Ferguson, M. C. et al. 2006b. Predicting Cuvier's (*Ziphius cavirostris*) and Mesoplodon beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean. - J. Cetacean Res. Manag. 7: 287–299.

Fiedler, P. C. and Reilly, S. B. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. II: Effects on abundances estimated from tuna vessel sightings, 1975-1990. - Fish. Bull.-Natl. Ocean. ATMOSPHERIC Adm. 92: 451–451.

Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. - Environ. Conserv. 24: 38–49.

Fleishman, E. et al. 2001. Modeling and Predicting Species Occurrence Using Broad-Scale Environmental Variables: an Example with Butterflies of the Great Basin. - Conserv. Biol. 15: 1674–1685.

Flint, E. N. and Nagy, K. A. 1984. Flight energetics of free-living sooty terns. - The Auk 101: 288–294.

Flores, P. A. C. and DaSilva, V. M. F. 2008. Tucuxi and Guiana dolphin. - In: Encyclopedia of marine mammals 2nd Edition. Academic Press. Perrin, W.F., Wursig, B. and Thewissen, J.G.M, pp. 1188–1192.

Forcada, J. et al. 2004. Bottlenose dolphin abundance in the NW Mediterranean: addressing heterogeneity in distribution. - Mar. Ecol. Prog. Ser. 275: 275–287.

Ford, R. G. et al. 2004. The biogeographic patterns of seabirds in the central portion of the California Current. - Mar. Ornithol. 32: 77–96.

Forney, K. A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. - Conserv. Biol. 14: 1271–1286.

Forney, K. A. 2008. Surveys. - In: Encyclopedia of marine mammals. Academic Press. Perrin, W.F., Wursig, B. and Thewissen, J.G.M, pp. 1129–1131.

Forney, K. A. et al. 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. - Endanger. Species Res. 16: 113–133.

Fort, J. et al. 2012. Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*). - Front. Ecol. Environ. 10: 237–242.

Fossi, M. C. et al. 2012. The role of large marine vertebrates in the assessment of the quality of pelagic marine ecosystems. - Mar. Environ. Res. 77: 156–158.

Frederiksen, M. et al. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. - J. Anim. Ecol. 75: 1259–1268.

Fritz, H. et al. 2003. Scale–dependent hierarchical adjustments of movement patterns in a long–range foraging seabird. - Proc. R. Soc. Lond. B Biol. Sci. 270: 1143–1148.

Froidefond, J. et al. 1988. Migration of mud banks and changing coastline in French Guiana. - Mar. Geol. 84: 19–30.

Fulling, G. L. et al. 2003. Abundance and distribution of cetaceans in outer continental shelf waters of the US Gulf of Mexico. - Fish. Bull. 101: 923–932.

Furness, R. W. and Tasker, M. L. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. - Mar. Ecol. Prog. Ser. 202: 253–264.

Game, E. T. et al. 2009. Pelagic protected areas: the missing dimension in ocean conservation. - Trends Ecol. Evol. 24: 360–369.

Ganachaud, A. et al. 2010. Observed and expected changes to the tropical Pacific Ocean. - In: Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Secretariat of the Pacific Community. Secretariat of the Pacific Community. JD Bell, JE Johnson and AJ Hobday.

Gannier, A. 2009. Comparison of odontocete populations of the Marquesas and Society Islands (French Polynesia). - J. Mar. Biol. Assoc. United Kingd. 89: 931–941.

Gaston, K. J. and Blackburn, T. M. 2003a. Dispersal and the interspecific abundance-occupancy relationship in British birds. - Glob. Ecol. Biogeogr. 12: 373–379.

Gaston, K. J. and Blackburn, T. M. 2003b. Macroecology and conservation biology. - Macroecology Concepts Consequences Oxf. Blackwell Sci.: 345–67.

Gero, S. et al. 2007. Population estimate and inter-island movement of sperm whales, Physeter macrocephalus, in the Eastern Carribbean Sea. - J. Cetacean Res. Manag. 9: 143–150.

Gerrodette, T. and Forcada, J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. - Mar. Ecol. Prog. Ser. 291: 1–21.

Gibbs, R. J. 1980. Wind-controlled coastal upwelling in the western equatorial Atlantic. - Deep Sea Res. Part 27: 857–866.

Gilles, A. et al. 2011. Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management. - Endanger. Species Res. 14: 157–169.

Gomez de Segura, A. et al. 2006. Abundance of small cetaceans in waters of the central Spanish Mediterranean. - Mar. Biol. 150: 149–160.

Goss, C. et al. 1997. Small-scale interactions between prions Pachyptila spp. and their zooplankton prey at an inshore site near Bird Island, South Georgia. - Mar. Ecol. Prog. Ser. 154: 41–51.

Gregr, E. J. and Trites, A. W. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. - Can. J. Fish. Aquat. Sci. 58: 1265–1285.

Griffin, R. B. and Griffin, N. J. 2003. Distribution, habitat partitioning, and abundance of Atlantic spotted dolphins, bottlenose dolphins, and loggerhead sea turtles on the eastern Gulf of Mexico continental shelf. - Gulf Mex. Sci. 21: 23–34.

Griffiths, A. M. 1982. Reactions of some seabirds to a ship in the Southern Ocean. - Ostrich 53: 228–235.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - Ecol. Model. 135: 147–186.

Guisan, A. et al. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. - Ecol. Model. 157: 89–100.

Guisan, A. et al. 2006. Making better biogeographical predictions of species' distributions. - J. Appl. Ecol. 43: 386–392.

Halpern, B. S. et al. 2008. A global map of human impact on marine ecosystems. - Science 319: 948–952.

Hammond, P. S. et al. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. - Biol. Conserv. 164: 107–122.

Haney, J. C. et al. 1995. Sea-bird aggregation at a deep North Pacific seamount. - Mar. Biol. 123: 1–9.

Harding, A. et al. 2013. Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. - Deep Sea Res. Part II Top. Stud. Ocean. in press.

Harrell, F. E. 2010. Package "Hmisc."

Harrison, P. 1991. Seabirds: An Identification Guide. - Houghton Mifflin Company.

Harrison, C. S. et al. 1983. Hawaiian seabird feeding ecology. - Wildl. Monogr.: 3–71.

Hazen, E. L. and Johnston, D. W. 2010. Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. - Fish. Ocean. 19: 427–433.

Heithaus, M. R. and Dill, L. M. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? - Oikos 114: 257–264.

Heithaus, M. R. et al. 2008. Predicting ecological consequences of marine top predator declines. - Trends Ecol. Evol. 23: 202–210.

Hertel, F. and Ballance, L. T. 1999. Wing ecomorphology of seabirds from Johnston Atoll. - Condor 101: 549–556.

Hiby, L. and Lovell, P. 1998. Using aircraft in tandem formation to estimate abundance of harbour porpoise. - Biometrics 54: 1280–1289.

Hidaka, K. et al. 2003. Biomass and taxonomic composition of micronekton in the western tropical–subtropical Pacific. - Fish. Ocean. 12: 112–125.

Hijmans, R. and van Etten, J. 2012. Package "raster."

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. - Am. Nat. 163: 192–211.

Hirzel, A. H. et al. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? - Ecology 83: 2027–2036.

Hooker, S. K. and Baird, R. W. 2001. Diving and ranging behaviour of odontocetes: a methodological review and critique. - Mammal Rev. 31: 81–105.

Hooker, S. K. et al. 2012. Deadly diving? Physiological and behavioural management of decompression stress in diving mammals. - Proc. R. Soc. B Biol. Sci. 279: 1041–1050.

Hoyo, J. D. 1996. Handbook of the Birds of the World, Volume 3 (JD Hoyo, A Elliott, and J Sargatal, Eds.). - Lynx Edicions.

Hu, C. et al. 2004. The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: Observation from space and S-PALACE floats. - Deep Sea Res. Part II 51: 1151–1171.

Huettmann, F. and Diamond, A. W. 2001. Seabird colony locations and environmental determination of seabird distribution: a spatially explicit breeding seabird model for the Northwest Atlantic. - Ecol. Model. 141: 261–298.

Hunt, G. and Schneider, D. 1987. Scale-dependent processes in the physical and biological environment of marine birds. - In: Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge University Press. Croxall JP, pp. 7–42.

Hunt, G. L. et al. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. - Proc. Int. Ornithol. Congr. 22: 2040–2056.

Hutchinson, G. E. 1957. Concluding Remarks. - Cold Spring Harb. Symp. Quant. Biol. 22: 415–427.

Hyrenbach, K. D. et al. 2000. Marine protected areas and ocean basin management. - Aquat. Conserv. Mar. Freshw. Ecosyst. 10: 437–458.

Hyrenbach, K. D. et al. 2007. Community structure across a large-scale ocean productivity gradient: Marine bird assemblages of the Southern Indian Ocean. - Deep Sea Res. Part 54: 1129–1145.

Jaquemet, S. et al. 2004. Seabird community structure in a coastal tropical environment: importance of associations with sub-surface predators and of Fish Aggregating Devices (FADs). - Mar. Ecol. Prog. Ser. 268: 281–292.

Jaquemet, S. et al. 2005. Foraging habitats of the seabird community of Europa Island (Mozambique Channel). - Mar. Biol. 147: 573–582.

Jaquemet, S. et al. 2008. Comparative foraging ecology and ecological niche of a superabundant tropical seabird : the scooty tern Sterna fuscata in the southwest Indian Ocean. - Mar. Biol.: 505–520.

Jaquet, N. and Whitehead, H. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. - Mar. Ecol. Prog. Ser. 135: 1–9.

Jaquet, N. et al. 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. - Mar. Ecol. Prog. Ser. 145: 1–10.

Jaquet, N. et al. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. - Can. J. Zool. 78: 407–419.

Jefferson, T. and Barros, N. 1997. Peponocephala electra. - Mammalian Species: 1–6.

Jefferson, T. A. et al. 1991. A review of Killer Whale interactions with other marine mammals: predation to co-existence. - Mammal Rev. 21: 151–180.

Jennings, S. et al. 2008. Global-scale predictions of community and ecosystem properties from simple ecological theory. - Proc. R. Soc. B Biol. Sci. 275: 1375–1383.

Johns, W. et al. 1998. Annual cycle and variability of the North Brazil Current. - J. Phys. Ocean. 28: 103–128.

Johnson, R. L. et al. 2006. Seabird predation by white shark and Cape fur seal at Dyer Island. - South Afr. J. Wildl. Res. 36: 00–00.

Johnston, D. W. et al. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. - Mar. Ecol. Prog. Ser. 295: 279–293.

Karl, D. M. 2002. Nutrient dynamics in the deep blue sea. - TRENDS Microbiol. 10: 410–418.

Karl, D. et al. 2002. Dinitrogen fixation in the world's oceans. - Springer.

Kaschner, K. et al. 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. - Mar. Ecol. Prog. Ser. 316: 285–310.

Kaschner, K. et al. 2012. Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. - PloS One 7: e44075.

Kearney, M. 2006. Habitat, environment and niche: what are we modelling? - Oikos 115: 186–191.

Keitt, T. H. et al. 2002. Accounting for spatial pattern when modeling organism-environment interactions. - Ecography 25: 616–625.

Kenney, R. D. et al. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. - J. Cetacean Res. Manag. 2: 251–260.

Kent, M. 2005. Biogeography and macroecology. - Prog. Phys. Geogr. 29: 256–264.

Kepler, C. B. et al. 1992. Ecological Studies on Caroline Atoll, Republic of Kiribati, South-central Pacific Ocean Part 2. Seabirds, Other Terrestrial Animals, and Conservation. - In: Results of the first Joint US-USSR Central Pacific Expedition (BERPAC) : Autumn 1988. Washington, DC : U.S. Fish and Wildlife Service, pp. 139–164.

Kiszka, J. et al. 2011. Ecological niche segregation within a community of sympatric dolphins around a tropical island. - Mar. Ecol. Prog. Ser. 433: 273–288.

Klatsky, L. J. et al. 2007. Offshore bottlenose dolphins (*Tursiops truncatus*): Movement and dive behavior near the Bermuda Pedestal. - J. Mammal. 88: 59–66.

Laake, J. et al. 1997. Probability of Detecting Harbor Porpoise from Aerial Surveys: Estimating g(0). - J. Wildl. Manag. 61: 63–75.

Ladd, C. et al. 2005. Hydrographic features and seabird foraging in Aleutian Passes. - Fish. Ocean. 14: 178–195.

Laist, D. W. et al. 2001. Collisions between ships and whales. - Mar. Mammal Sci. 17: 35–75.

Le Borgne, R. et al. 2010. Variability of open ocean food webs in the tropical Pacific to climate change. - In: Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Secretariat of the Pacific Community. Secretariat of the Pacific Community. JD Bell, JE Johnson and AJ Hobday, pp. 189–250.

Le Corre, M. et al. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. - Biol. Conserv. 156: 83–93.

Leeney, R. H. et al. 2012. Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. - J. Mar. Biol. Assoc. United Kingd. 92: 1823–1833.

Legand, M. et al. 1972. Relations trophiques et distributions verticales en milieu pélagique dans l'Océan Pacifique intertropical. - Cah. ORSTOMSérie Océanographie 10: 303–393.

Legendre, L. and Le Fèvre, J. 1995. Microbial food webs and the export of biogenic carbon in oceans. - Aquat. Microb. Ecol. 9: 69–77.

Legendre, P. and Legendre, L. 2012. Numerical ecology. - Elsevier.

Lehodey, P. et al. 2003. Modelling climate-related variability of tuna populations from a coupled ocean–biogeochemical-populations dynamics model. - Fish. Ocean. 12: 483–494.

Lehodey, P. et al. 2008. A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. - Prog. Ocean. 78: 304–318.

Lehodey, P. et al. 2010. Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups. - Prog. Ocean. 84: 69–84.

Leichter, J. J. and Witman, J. D. 2009. Basin-scale oceanographic influences on marine macroecological patterns. - In: Marine Macroecology. University of Chicago Press. J D Witman and K Roy, pp. 205–226.

Lek, S. and Guégan, J.-F. 1999. Artificial neural networks as a tool in ecological modelling, an introduction. - Ecol. Model. 120: 65–73.

Lemoine, V. and Dubief, L. 2008. Important Bird Areas in the Caribbean - Martinique Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/CaribCntryPDFs/martinique_%28to_france%29.pdf.

Levesque, A. and Mathurin, A. 2008. Important Bird Areas in the Caribbean - Guadeloupe Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/CaribCntryPDFs/guadeloupe_%28to_france%29.pdf.

Lewison, R. L. et al. 2004. Understanding impacts of fisheries bycatch on marine megafauna. - Trends Ecol. Evol. 19: 598–604.

Libralato, S. et al. 2006. A method for identifying keystone species in food web models. - Ecol. Model. 195: 153–171.

Lifson, N. and McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. - J. Theor. Biol. 12: 46–74.

Lobo, J. M. et al. 2010. The uncertain nature of absences and their importance in species distribution modelling. - Ecography 33: 103–114.

Logerwell, E. A. et al. 1998. Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. - Ecography 21: 212–223.

Longhurst, A. R. 2007. Ecological geography of the sea. - Academic Press.

Longhurst, A. R. and Pauly, D. 1987. Ecology of tropical oceans. - Academic Press.

Looijen, R. C. 1995. On the distinction between habitat and niche, and some implications for species' differentiation. - Poz St Phil Sci Hum. 45: 87–108.

Louzao, M. et al. 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. - Ecol. Appl. 16: 1683–1695.

Lumaret, J.-P. and Jay-Robert, P. 2002. Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. - Glob. Ecol. Biogeogr. 11: 265–277.

Lutjeharms, J. R. E. et al. 2003. Modelling the shear edge eddies of the southern Agulhas Current. - Cont. Shelf Res. 23: 1099–1115.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. - Am. Nat.: 603–609.

MacLeod, C. D. et al. 2004. Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. - J. Mar. Biol. Assoc. UK 84: 469–474.

MacLeod, C. D. et al. 2005. Known and inferred distributions of beaked whale species (Cetacea: Ziphiidae). - J. Cetacean Res. Manag. 7: 271.

Mannocci, L. et al. 2013a. Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic. - J. Mar. Syst. 111–112: 208–222.

Mannocci, L. et al. 2013b. Predicting top predator habitats in the Southwest Indian Ocean. - Ecography: 1–18.

Marques, F. F. C. and Buckland, S. T. 2004. Covariate models for the detection function. - In: Advanced Distance Sampling. Oxford, pp. 31–47.

Martin, T. G. et al. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. - Ecol. Lett. 8: 1235–1246.

Martinez, E. and Maamaatuaiahutapu, K. 2004. Island mass effect in the Marquesas Islands: Time variation. - Geophys. Res. Lett. 31: L18307.

Martinez, E. et al. 2009. Central South Pacific thermocline water circulation from a high-resolution ocean model validated against satellite data: Seasonal variability and El Niño 1997–1998 influence. - J. Geophys. Res. 114: 16.

Matheron, G. 1971. The theory of regionalized variables and its applications. Les cahiers du centre de morphologie mathématique de Fontainebleau. - École national supérieure des mines.

McAlpine, C. A. et al. 2008. Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. - J. Appl. Ecol. 45: 558–567.

McGillicuddy, D. J. et al. 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. - Nature 394: 263–266.

McPhaden, M. J. 2004. Evolution of the 2002/03 El Niño. - Bull. Am. Meteorol. Soc. 85: 677.

McPhaden, M. J. et al. 2006. ENSO as an integrating concept in Earth science. - science 314: 1740–1745.

Ménard, F. et al. 2007. Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. - Mar. Biol.: 141–152.

Menkes, C. E. et al. 2002. A whirling ecosystem in the equatorial Atlantic. - Geophys. Res. Lett. 29: 48–1.

Mignucci-Giannoni, A. A. 1998. Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. - Caribb. J. Sci. 34: 173–190.

Miller, J. R. et al. 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. - BioScience 54: 310–320.

Miller, P. J. O. et al. 2008. Stereotypical resting behavior of the sperm whale. - Curr. Biol. 18: R21–R23.

Minamikawa, S. et al. 2013. Diving behavior of a false killer whale, *Pseudorca crassidens*, in the Kuroshio–Oyashio transition region and the Kuroshio front region of the western North Pacific. - Mar. Mammal Sci. 29: 177–185.

Monestiez, P. et al. 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. - Ecol. Model. 193: 615–628.

Moore, S. E. 2008. Marine mammals as ecosystem sentinels. - J. Mammal. 89: 534–540.

Moore, D. M. et al. 1991. A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. - Environ. Manage. 15: 59–71.

Moore, S. E. et al. 2002. Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. - Prog. Ocean. 55: 249–261.

Morris, D. W. 1987. Ecological scale and habitat use. - Ecology 68: 362–369.

Moura, A. E. et al. 2012. Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunity. - Acta Oecologica 38: 24–32.

Mueller, P. and Diamond, J. 2001. Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. - PNAS 98: 12550–12554.

Murphy, E. J. et al. 1988. Scales of Interaction Between Antarctic Krill and the Environment. - In: Sahrhage, P. D. D. (ed), Antarctic Ocean and Resources Variability. Springer Berlin Heidelberg, pp. 120–130.

New, A. L. et al. 2005. Physical and biochemical aspects of the flow across the Mascarene Plateau in the Indian Ocean. - Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 363: 151–168.

Oedekoven, C. S. et al. 2001. Variable responses of seabirds to change in marine climate: California Current, 1985-1994. - Mar. Ecol. Prog. Ser. 212: 265–281.

Officer, C. B. and Ryther, J. H. 1980. The possible importance of silicon in marine eutrophication. - Mar. Ecol. Prog. Ser. 3: 83–91.

Oleson, E. M. et al. 2010. Status review of Hawaiian insular false killer whales (*Pseudorca crassidens*) under the Endangered Species Act.

Olson, D. B. and Backus, R. H. 1985. The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. - J Mar Res 43: 113–137.

Oppel, S. et al. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. - Biol. Conserv. 156: 94–104.

Oschlies, A. and Garçon, V. 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. - Nature 394: 266–269.

Österblom, H. et al. 2008. Junk-food in marine ecosystems. - Oikos 117: 967–977.

Palialexis, A. et al. 2011. Fish distribution predictions from different points of view: comparing associative neural networks, geostatistics and regression models. - Hydrobiologia 670: 165–188.

Panigada, S. et al. 2005. Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. - J. Cetacean Res. Manag. 7: 137–145.

Panigada, S. et al. 2008. Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. - Remote Sens. Environ. 112: 3400–3412.

Papastavrou, V. et al. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. - Can. J. Zool. 67: 839–846.

Parsons, T. R. and Lalli, C. M. 2002. Jellyfish population explosions: revisiting a hypothesis of possible causes. - La mer 40: 111–121.

Pauly, D. et al. 1998. Diet composition and trophic levels of marine mammals. - ICES J. Mar. Sci. 55: 467–481.

Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? - Glob. Ecol. Biogeogr. 12: 361–371.

Penven, P. et al. 2001. A regional hydrodynamic model of upwelling in the Southern Benguela. - South Afr. J. Sci. 97: 472–475.

Perry, R. 1980. Wildlife Conservation in the Line Islands, Republic of Kiribati (formerly Gilbert Islands). - Environ. Conserv. 7: 311–318.

Pershing, A. J. et al. 2009. Model-based estimates of right whale habitat use in the Gulf of Maine. - Mar. Ecol. Prog. Ser. 378: 245–257.

Peterson, C. C. et al. 1990. Sustained metabolic scope. - Proc. Natl. Acad. Sci. 87: 2324–2328.

Pettex, E. et al. 2012. Multi-scale foraging variability in Northern gannet (*Morus bassanus*) fuels potential foraging plasticity. - Mar. Biol. 159: 2743–2756

Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. - Ecol. Model. 190: 231–259.

Piatt, J. F. et al. 2006. Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. - Deep Sea Res. Part II Top. Stud. Ocean. 53: 387–398.

Piatt, J. F. et al. 2007. Introduction: a modern role for seabirds as indicators. - Mar. Ecol. Prog. Ser. 352: 199–204.

Pidwirny, M. 2006. Surface and subsurface ocean currents: Ocean current map. - Univ Br. Columbia Okanagan BC CanadaAvailable Httpwww Phys. Netfundamentals8q1 Html

Pimm, S. L. et al. 1991. Food web patterns and their consequences. - Nature 350: 669–674.

Pinaud, D. and Weimerskirch, H. 2005. Scale-dependent habitat use in a long-ranging central place predator. - J. Anim. Ecol. 74: 852–863.

Pirotta, E. et al. 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. - Mar. Ecol. Prog. Ser. 436: 257–272.

Pitman, R. L. et al. 2001. Killer whale predation on sperm whales: observations and implications. - Mar. Mammal Sci. 17: 494–507.

Platt, T. 1972. Local phytoplankton abundance and turbulence. - Deep Sea Res. Ocean. Abstr. 19: 183–187.

Pollock, K. H. et al. 2006. Estimating Animal Abundance in Heterogeneous Environments: An Application to Aerial Surveys for Dugongs. - J. Wildl. Manag. 70: 255–262.

Praca, E. et al. 2009. Modelling the habitat suitability of cetaceans: Example of the sperm whale in the northwestern Mediterranean Sea. - Deep Sea Res. Part Ocean. Res. Pap. 56: 648–657.

Prince, E. D. and Goodyear, C. P. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. - Fish. Ocean. 15: 451–464.

Pyke, G. H. et al. 1977. Optimal foraging: a selective review of theory and tests. - Q. Rev. Biol.: 137–154.

Read, A. J. 2008. The looming crisis: interactions between marine mammals and fisheries. - J. Mammal. 89: 541–548.

Ready, J. et al. 2010. Predicting the distributions of marine organisms at the global scale. - Ecol. Model. 221: 467–478.

Redfern, J. V. et al. 2006. Technique of cetaceans-habitat modeling. - Mar. Ecol. Prog. Ser. 310: 271–295.

Redfern, J. V. et al. 2008. Absence of scale dependence in dolphin–habitat models for the eastern tropical Pacific Ocean. - Mar. Ecol. Prog. Ser. 363: 1–14.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. - Am. Sci. 46: 230A–221.

Regular, P. M. et al. 2013. Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. - Anim. Behav. 86: 545-552

Reid, J. L. 1997. On the total geostrophic circulation of the Pacific Ocean: Flow patterns, tracers, and transports. - Prog. Ocean. 39: 263–352.

Rendell, L. and Whitehead, H. 2001. Culture in whales and dolphins. - Behav. Brain Sci. 24: 309–382.

Reygondeau, G. et al. 2011. Biogeography of tuna and billfish communities. - J. Biogeogr. 39: 114–129.

Richardson, A. J. and Poloczanska, E. S. 2008. Under-resourced, under threat. - Sci. 320: 1294.

Ridoux, V. 1987. Feeding association between seabirds and killer whales, Orcinus orca, around subantarctic Crozet Islands. - Can. J. Zool. 65: 2113–2115.

Risien, C. M. and Chelton, D. B. 2008. A global climatology of surface wind and wind stress fields from eight years of QuikSCAT scatterometer data. - J. Phys. Ocean. 38: 2379–2413.

Robinson, L. M. et al. 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. - Glob. Ecol. Biogeogr. 20: 789–802.

Rodwell, L. D. et al. 2003. The importance of habitat quality for marine reserve fishery linkages. - Can. J. Fish. Aquat. Sci. 60: 171–181.

Rombouts, I. et al. 2009. Global latitudinal variations in marine copepod diversity and environmental factors. - Proc. R. Soc. B Biol. Sci. 276: 3053–3062.

Rosen, D. A. and Trites, A. W. 2000. Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. - Can. J. Zool. 78: 1243–1250.

Rossi-Santos, M. et al. 2006. Distribution and habitat use of small cetaceans off Abrolhos Bank, eastern Brazil. - Lat. Am. J. Aquat. Mamm. 5: 23–28.

Rougerie, F. and Rancher, J. 1994. The Polynesian south ocean: features and circulation. - Mar. Pollut. Bull. 29: 14–25.

Russell, R. W. et al. 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. - Landsc. Ecol. 7: 195–209.

Russell, R. W. et al. 1999. Foraging at a front: hydrography, zooplankton, and avian planktivory in the northern Bering Sea. - Mar. Ecol. Prog. Ser. 182: 77–93.

Sabarros, P. S. et al. 2009. Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. - Mar. Ecol. Prog. Ser. 395: 101–107.

Santora, J. A. et al. 2011. Spatial organization of krill and seabirds in the central California Current. - ICES J. Mar. Sci. J. Cons. 68: 1391–1402.

Schick, R. et al. 2011. Community structure in pelagic marine mammals at large spatial scales. - Mar. Ecol. Prog. Ser. 434: 165–181.

Schott, F. A. and McCreary, J. P. 2001. The monsoon circulation of the Indian Ocean. - Prog. Ocean. 51: 1–123.

Schouten, M. W. et al. 2003. Eddies and variability in the Mozambique Channel. - Deep Sea Res. II 50: 1987–2003.

Schröder, B. 2008. Challenges of species distribution modeling belowground. - J. Plant Nutr. Soil Sci. 171: 325–337.

Senina, I. et al. 2008. Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: Application to skipjack tuna. - Prog. Ocean. 78: 319–335.

Sequeira, A. et al. 2012. Ocean-scale prediction of whale shark distribution. - Divers. Distrib. 18: 504–518.

Shmueli, G. 2010. To explain or to predict? - Stat. Sci. 25: 289–310.

Sibert, J. et al. 2012. Shifting from marine reserves to maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*). - Proc. Natl. Acad. Sci. 109: 18221–18225.

Signorini, S. R. et al. 1999. Mixing and phytoplankton bloom in the wake of the Marquesas Islands. - Geophys. Res. Lett. 26: 3121–3124.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? - Biol. Conserv. 83: 247–257.

Smith, J. L. and Hyrenbach, K. D. 2003. Galapagos Islands to British Columbia: Seabird communities along a 9000 km transect from the tropical to the subarctic eastern Pacific Ocean. - Mar. Ornithol. 31: 155–166.

Smith, F. A. et al. 2008. Macroecology: more than the division of food and space among species on continents. - Prog. Phys. Geogr. 32: 115–138.

Spear, L. B. et al. 2007. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. - Stud. Avian Biol.: 1–99.

Spitz, J. et al. 2010. Prey selection by the common dolphin: Fulfilling high energy requirements with high quality food. - J. Exp. Mar. Biol. Ecol. 390: 73–77.

Spitz, J. et al. 2012. Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. - PLoS ONE 7: e50096.

Springer, A. M. et al. 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. - Fish. Ocean. 5: 205–223.

Steadman, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. - Science 267: 1123–1131.

Stewart, J. S. et al. 2012. Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones. - Deep Sea Res. Part II Top. Stud. Ocean. in press.

Stich, H.-B. and Lampert, W. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. - Nature 293: 396–398.

Strauss, B. and Biedermann, R. 2007. Evaluating temporal and spatial generality: How valid are species–habitat relationship models? - Ecol. Model. 204: 104–114.

Strindberg, S. and Buckland, S. T. 2004. Zigzag survey designs in line transect sampling. - J. Agric. Biol. Environ. Stat. 9: 443–461.

Surman, C. A. and Wooller, R. D. 2003. Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. - J. Zool. 259: 219–230.

Swartz, S. L. et al. 2003. Acoustic and visual survey of humpback whale (*Megaptera novaeangliae*) distribution in the eastern and southeastern Caribbean Sea. - Caribb. J. Sci. 39: 195–208.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. - Science 240: 1285–1293.

Sydeman, W. J. et al. 2010. Macro-ecology of plankton–seabird associations in the North Pacific Ocean. - J. Plankton Res. 32: 1697–1713.

Tasker, M. L. et al. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. - The Auk 101: 567–577.

Ter Braak, C. J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. - Ecology 67: 1167–1179.

Tew Kai, E. and Marsac, F. 2010. Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. - Prog. Ocean. 86: 214–223.

TewKai, E. and Marsac, F. 2009. Patterns of variability of sea surface chlorophyll in the Mozambique Channel: A quantitive aproach. - J. Mar. Syst.: 77–88.

Thibault, J.-C. and Bretagnolle, V. 2007. Atlas des oiseaux marins de Polynésie française et du Groupe Pitcairn. 84.

Thomas, L. et al. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. - J. Appl. Ecol. 47: 5–14.

Thorne, L. H. et al. 2012. Predictive modeling of spinner dolphin (*Stenella longirostris*) resting habitat in the Main Hawaiian Islands. - PLoS One 7: e43167.

Tittensor, D. P. et al. 2010. Global patterns and predictors of marine biodiversity across taxa. - Nature 466: 1098–1101.

Tomczak, M. and Godfrey, J. S. 2003. Regional oceanography: an introduction 2nd edition. - Daya Publishing House.

Torres, D. and Beasley, C. 2003. Pattern of use of a small bay in northern Brazil by Sotalia guianensis (Cetacea: Delphinidae). - Amazoniana 17: 583–594.

Torres, L. G. and Read, A. J. 2009. Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. - Mar. Mammal Sci. 25: 797–815.

Torres, L. G. et al. 2008. Fine-Scale Habitat Modeling of a Top Marine Predator: Do Prey Data Improve Predictive Capacity? - Ecol. Appl. 18: 1702-1717

Torres, L. G. et al. 2013. From exploitation to conservation: habitat models using whaling data predict distribution patterns and threat exposure of an endangered whale. - Divers. Distrib. in press.

Tremblay, Y. et al. 2009. Analytical approaches to investigating seabird-environment interactions: a review. - Mar. Ecol. Prog. Ser. 391: 153–163.

Trillmich, F. and Limberger, D. 1985. Drastic effects of El Niño on Galapagos pinnipeds. - Oecologia 67: 19–22.

Trites, A. and Donnelly, C. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. - Mammal Rev. 33: 3–28.

Turner, R. E. et al. 1998. Fluctuating silicate: nitrate ratios and coastal plankton food webs. - Proc. Natl. Acad. Sci. 95: 13048–13051.

Tyack, P. L. et al. 2006. Extreme diving of beaked whales. - J. Exp. Biol. 209: 4238–4253.

Tynan, C. T. et al. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. - Deep Sea Res. Part II 52: 145–167.

Uz, B. M. et al. 2001. Pumping of nutrients to ocean surface waters by the action of propagating planetary waves. - Nature 409: 597–600.

Vaillancourt, R. D. et al. 2003. Impact of a cyclonic eddy on phytoplankton community structure and photosynthetic competency in the subtropical North Pacific Ocean. - Deep Sea Res. Part Ocean. Res. Pap. 50: 829–847.

Van der Meer, J. and Leopold, M. F. 1995. Assessing the population size of the European storm petrel (*Hydrobates pelagicus*) using spatial autocorrelation between counts from segments of criss-cross ship transects. - ICES J. Mar. Sci. 52: 809–818.

Vandenabeele, S. P. et al. 2011. Tags on seabirds: how seriously are instrument-induced behaviours considered? - Anim. Welf.- UFAW J. 20: 559.

VanDerWal, J. et al. 2012. Package “SDMTools.”

Vanderwerf, E. A. et al. 2006. Pelagic seabird surveys in the Tuamotu and Gambier archipelagos, French Polynesia. - Mar. Ornithol. 34: 65–70.

Vaughan, I. P. and Ormerod, S. J. 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. - Conserv. Biol. 17: 1601–1611.

Vilchis, L. I. et al. 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. - Mar. Ecol. Prog. Ser. 315: 279–292.

Wackernagel, H. 2003. Multivariate Geostatistics. - Springer.

Wade, P. R. 1995. Revised estimates of incidental kill of dolphins (Delphinidae) by the purse-seine tuna fishery in the eastern Tropical Pacific, 1959-1972. - Fish. Bull. 93: 345–354.

Wagner, H. H. and Fortin, M. J. 2005. Spatial analysis of landscapes: concepts and statistics. - Ecology 86: 1975–1987.

Wanless, S. et al. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. - Mar. Ecol. Prog. Ser. 294: 8.

Wanless, S. et al. 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. - Prog. Ocean. 72: 30–38.

Ward, N. et al. 2001. Elements for the development of a marine mammal action plan for the wider Caribbean: A review of marine mammal distribution.

Waring, G. T. et al. 2001. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. - Mar. Mammal Sci. 17: 703–717.

Watkins, W. A. et al. 1993. Sperm whale dives tracked by radio tag telemetry. - Mar. Mammal Sci. 18: 55–68.

Wedekin, L. L. et al. 2010. Habitat preferences of Guiana dolphins, Sotalia guianensis (Cetacea: Delphinidae), in Norte Bay, southern Brazil. - J. Mar. Biol. Assoc. United Kingd. 90: 1561–1570.

Weichler, T. et al. 2004. Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. - ICES J. Mar. Sci. 61: 148–154.

Weilgart, L. S. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. - Can. J. Zool. 85: 1091–1116.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? - Deep Sea Res. Part II Top. Stud. Ocean. 54: 211–223.

Weimerskirch, H. et al. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. - Behav. Ecol. 8: 635–643.

Weimerskirch, H. et al. 2003. Flight performance: Frigatebirds ride high on thermals. - Nature 421: 333–334.

Weimerskirch, H. et al. 2004. Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. - Mar. Ecol. Prog. Ser. 275: 297–308.

Weimerskirch, H. et al. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? - Proc. R. Soc. B Biol. Sci. 272: 53–61.

Weimerskirch, H. et al. 2006. Postbreeding movements of frigatebirds tracked with satellite telemetry. - The Condor: 220–225.

Weimerskirch, H. et al. 2010. Foraging movements of great frigatebirds from Aldabra Island: Relationship with environmental variables and interactions with fisheries. - Prog. Ocean. 86: 204–213.

Whitehead, H. and Moore, M. J. 1982. Distribution and movements of West Indian humpback whales in winter. - Can. J. Zool. 60: 2203–2211.

Whitehead, H. et al. 2008. Diversity of deep-water cetaceans in relation to temperature: Implications for ocean warming. - Ecol. Lett. 11: 1198–1207.

Wiggins, S. 2003. Autonomous acoustic recording packages (ARPs) for long-term monitoring of whale sounds. - Mar. Technol. Soc. J. 37: 13–22.

Williams, T. M. and Yeates, L. 2004. The energetics of foraging in large mammals: a comparison of marine and terrestrial predators. - Int. Congr. Ser. 1275: 351–358.

Williams, R. and Thomas, L. 2007. Distribution and abundance of marine mammals in the coastal waters of British Columbia, Canada. - J. Cetacean Res. Manag. 9: 15–28.

Williams, T. et al. 1993. Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). 66: 383–394.

Willis, P. M. and Baird, R. W. 1998. Status of the dwarf sperm whale, *Kogia simus*, with special reference to Canada. - Can. Field-Nat. 112: 114–125.

Wilson, R. P. et al. 2012. Construction of energy landscapes can clarify the movement and distribution of foraging animals. - Proc. R. Soc. B Biol. Sci. 279: 975–980.

Winn, H. et al. 1975. Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. - J. Fish. Board Can. 32: 499–506.

Witman, J. D. and Roy, K. 2009. Marine macroecology. - University of Chicago Press.

Wittenberger, J. F. and Hunt, G. L. 1985. The adaptive significance of coloniality in birds. - Avian Biol. 8: 1–78.

Wood, S. N. 2006. Generalized Additive Models. - Chapman & Hall/CRC.

Wood, S. N. and Augustin, N. H. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. - Ecol. Model. 157: 157–177.

Woodworth, P. A. et al. 2012. Eddies as offshore foraging grounds for melon-headed whales (Peponocephala electra). - Mar. Mammal Sci. 28: 638–647.

Worm, B. et al. 2003. Predator diversity hotspots in the blue ocean. - Proc. Natl. Acad. Sci. 100: 9884–9888.

Worm, B. et al. 2005. Global patterns of predator diversity in the open oceans. - Science 309: 1365–1369.

Xing, X. et al. 2012. Quenching correction for in vivo chlorophyll fluorescence acquired by autonomous platforms: A case study with instrumented elephant seals in the Kerguelen region (Southern Ocean). - Limnol Ocean. Methods 10: 483–495.

Yazdi, P. et al. 1999. Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). - Mar. Biol. 134: 601–607.

Yen, P. P. W. et al. 2004a. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. - J. Mar. Syst. 50: 79– 100.

Yen, P. P. W. et al. 2004b. A large-scale model for the at-sea distribution and abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada. - Ecol. Model. 171: 395–413.

Yoshida, H. et al. 2010. Cetacean sightings in the eastern Caribbean and adjacent waters, spring 2004. - Aquat. Mamm. 36: 154–161.

Zacharias, M. A. and Roff, J. C. 2001. Use of focal species in marine conservation and management: a review and critique. - Aquat. Conserv. Mar. Freshw. Ecosyst. 11: 59–76.

Zador, S. G. et al. 2008. Determining spatial and temporal overlap of an endangered seabird with a large commercial trawl fishery. - Endang Species Res 5: 103–115.

Zaniewski, A. E. et al. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. - Ecol. Model. 157: 261–280.

ANNEXES

Photo credit: Observatoire PELAGIS / AAMP

ANNEX 1

Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic

Laura Mannocci, Pascal Monestiez, Jaime Bolaños-Jimènez, Ghislain Dorémus, Stéphane Jeremie, Sophie Laran, Renato Rinaldi, Olivier Van Canneyt, Vincent Ridoux

Journal of Marine Systems, 2013, 111-112 : 208-222

Journal of Marine Systems 111–112 (2013) 208–222

Contents lists available at SciVerse ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic

Laura Mannocci [a,*], Pascal Monestiez [b], Jaime Bolaños-Jiménez [c], Ghislain Dorémus [d], Stéphane Jeremie [e], Sophie Laran [d], Renato Rinaldi [f], Olivier Van Canneyt [d], Vincent Ridoux [a,d]

[a] Laboratoire Littoral Environnement et Sociétés, UMR 7266 Université de La Rochelle-CNRS, Institut du Littoral et de l'Environnement, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[b] INRA, UR0546, Unité Biostatistique et Processus Spatiaux, Domaine Saint Paul, Site Agroparc, 84914 Avignon, France
[c] Sociedad Ecológica Venezolana Vida Marina, AP 162, Cagua, Estado Aragua 2122, Venezuela
[d] Observatoire PELAGIS, Systèmes d'Observation pour la Conservation des Mammifères et des Oiseaux Marins, UMS 3462 Université de La Rochelle-CNRS, Pôle analytique, 5 allées de l'Océan, 17000 La Rochelle, France
[e] Société pour l'Etude, la Protection et l'Aménagement de la Nature à la Martinique, MBE 208 Mango Vulcin, 97288 Lamentin Cedex 02, France
[f] Association Evasion Tropicale, rue des palétuviers, 97125 Pigeon Bouillante, France

ARTICLE INFO

Article history:
Received 25 April 2012
Received in revised form 5 November 2012
Accepted 5 November 2012
Available online 15 November 2012

Keywords:
Megavertebrates
Cetaceans
Seabirds
Aerial survey
Antilles
Guiana
Productivity
Encounter rate
Community composition
Abundance
Density

ABSTRACT

Productivity was shown to structure megavertebrate communities, particularly in tropical oceans where they may be under selective pressure to maintain their foraging success in these low productivity environments. However, overall oligotrophic tropical oceans may encompass contrasting ecosystems. In the western tropical Atlantic, the Antilles and Guiana belong to two different biogeographic provinces and surface chlorophyll concentration is on average 10 times higher in Guiana. The aim of this study was to document megavertebrate communities in terms of encounter rates, species composition, abundance and spatial distribution and to compare them between these two contrasting regions. As part of an aerial census of cetaceans and other megavertebrates, line transect surveys were conducted across the French Antilles and Guiana. Both distance sampling and geostatistics were used to estimate abundance and geostatistics also provided maps of local density. Cetacean encounter rate was 3 times higher in Guiana (1.8 sightings/100 km) compared to the Antilles (0.6 sightings/100 km). Moreover, small delphinids strongly dominated in Guiana (representing 83% of the odontocete sightings) with a high abundance of bottlenose dolphins (*Tursiops truncatus*) (34,965 individuals, CV = 0.28). Seabird encounter rate was similar in both regions (4.7 sightings/100 km in the Antilles and 3.6 sightings/100 km in Guiana). Charadriiformes, mainly represented by terns, were abundant in both regions whereas Pelecaniformes were only abundant in the Antilles and represented by frigatebirds, tropicbirds and boobies. Additionally, cetaceans and seabirds were mainly distributed close to the islands in the Antilles and were more widely distributed in Guiana. This study provided new information about megavertebrates which are poorly documented in these waters and highlighted differences in communities between these contrasting ecosystems. In particular, odontocete communities appeared to respond to productivity and may be structured by a differential distribution of resources through the water column.

1. Introduction

Top marine predators, or upper trophic level predators, refer to large marine vertebrates which have no predators of their own (Pimm et al., 1991) and occupy a food's web highest trophic level (Estes et al., 2001). Along with some mid trophic level predators, they form the megavertebrates, which include a variety of taxa: marine mammals, seabirds, sea turtles, elasmobranches, predatory fishes… Megavertebrates (especially air breathing species), form one of the few components of pelagic biodiversity that can be seen from the surface of the ocean and be surveyed across large oceanic regions; it is therefore expected that their species assemblages reveal some of the major properties of the underlying ecosystems. This characteristic is referred to as the indicator value (Boyd et al., 2006; Zacharias and Roff, 2001).

Indeed, megavertebrates respond to the variability of the ecosystems in which they live. Notably, changes in prey abundance are thought to affect cetaceans and seabirds in many ecosystems (Furness and Tasker, 2000; MacLeod et al., 2007; Reid et al., 2005; Soto et al., 2004). However, as extensive sampling of prey is difficult, surface productivity is often used as a proxy for prey abundance over large spatial domains (*e.g.* Ballance et al., 1997). Surface productivity has been shown to structure cetacean and seabird communities over large spatial scales in the three oceans (Ballance et al., 1997;

* Corresponding author. Tel.: +33 5 46 50 76 48; fax: +33 5 46 50 76 63.
E-mail address: laura.mannocci@univ-lr.fr (L. Mannocci).

0924-7963/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jmarsys.2012.11.002

Hyrenbach et al., 2007; Schick et al., 2011; Smith and Hyrenbach, 2003). In the eastern tropical Pacific, seabird communities were structured along a surface productivity gradient (Ballance et al., 1997). In the Indian Ocean, Hyrenbach et al. (2007) observed changes in seabird density and community composition along a latitudinal gradient; seabird densities being higher in the cooler and productive sub-Antarctic waters compared to the less productive subtropical waters. Schick et al. (2011) studied cetacean community structure over three biogeographic provinces in the Atlantic Ocean and described two different groups of cetaceans along a surface chlorophyll gradient.

Tropical oceans, which represent 50% of total ocean area, are characterized by low productivity and hence scarce food resources (Longhurst and Pauly, 1987). Therefore, tropical species may be under selective pressure to maintain their foraging success in the face of these diminished feeding opportunities (Ballance and Pitman, 1999). Unfortunately, little is known about megavertebrates inhabiting tropical open oceans. While some regions have been intensively surveyed in space and time (*e.g.* the eastern tropical Pacific Ballance et al., 1997, 2006; Redfern et al., 2008), nearly nothing is known in certain regions (in general studies have focused on inshore areas whereas pelagic waters were poorly surveyed).

The REMMOA program (*REcensements des Mammifères marins et autre Mégafaune pélagique par Observation Aérienne*, Census of marine mammals and other pelagic megafauna by aerial survey) was implemented to establish a baseline knowledge on megavertebrates in French tropical waters. The first dedicated surveys were conducted in 2008, across the Exclusive Economic Zones (EEZs) of the Antilles and Guiana, in the western tropical Atlantic. Indeed, apart from the Gulf of Mexico, where large scale surveys resulted in a basic understanding of distribution, abundance and habitats of cetaceans and seabirds (*e.g.* Baumgartner et al., 2001; Davis et al., 2002; Fulling et al., 2003), little information is available on megavertebrates in the Caribbean and western tropical Atlantic.

The Antilles and Guiana belong to two connected biogeographic provinces, respectively the "Caribbean Province" including the Gulf of Mexico and the Northern Caribbean Sea and the "Guianas coastal province" running from Northern Brazil to Trinidad. Whereas Guiana is characterized by a high and seasonal productivity owing to the variability of river discharge, offshore waters are oligotrophic in the Antilles, where wind has a major influence on oceanographic processes (Longhurst, 2007). Hence, although they are geographically close to each other, the Antilles and Guiana are characterized by contrasting oceanographic conditions and productivity levels.

In this study, we document several aspects of megavertebrate communities in the Antilles and Guiana: encounter rates, species composition, density, abundance and spatial distribution. We used both distance sampling (Buckland et al., 2001; Thomas et al., 2010) and geostatistics (Bellier et al., 2011; Monestiez et al., 2006) to estimate density and abundance with associated uncertainties, relying on different assumptions. Geostatistics were implemented (1) to incorporate spatial autocorrelation between observations and transects in the estimation of density and abundance (Bellier et al., 2011) and (2) to provide maps of local density of sightings over the study regions (Monestiez et al., 2006). This study gives new insights about seabirds and cetaceans which are poorly documented as a whole in the Lesser Antilles and Guiana. Yet, cetaceans have been mainly documented through stranding records (Cardona-Maldonado and Mignucci-Giannoni, 1999), sightings (Gero et al., 2007; Swartz et al., 2003; Yoshida et al., 2010) or bycatch (VanWaerebeek, 1990) and seabirds, through censuses at breeding colonies (Boyé et al., 2009; Levesque and Mathurin, 2008) as well as satellite tracking studies (Weimerskirch et al., 2003, 2006). In addition, this work gives the opportunity to investigate differences in communities between these regions of contrasting oceanography and productivity and to discuss ecological mechanisms responsible for the observed patterns.

2. Material and methods

2.1. Study regions

In Guiana, the French EEZ (4–9°N, 49–54°W), spanning 132,000 km^2, extends 200NM into the Atlantic Ocean, including a broad continental shelf, a slope, wider on its western part and an abyssal plain where depths approach 4500 m (Fig. 1). Several rivers open into these waters (*Approuague*, *Oyapock*, and *Maroni*) as well as the Amazon plume. As a consequence, extensive mudflats are present along the coast and coastal waters are highly turbid (Froidefond et al., 1988). Local oceanography is strongly influenced by the variability of river discharge, maximum in May–June and minimum in November. The Amazon plume is retroflected during boreal summer (July to December) when the North Brazilian Current is the strongest (Longhurst, 2007, Fig. 1). Moreover, wind-driven coastal upwelling occurs, as indicated by the presence of cool water in the upper 10 m (Gibbs, 1980). Productivity is highly seasonal and maximal during summer. However, chlorophyll biomass inferred from remote sensing may be unreliable since the color of the water in the river plumes is dominated by dissolved organic matters rather than chlorophyll light absorption (Hu et al., 2004).

The French EEZ in the Antilles (14–19°N, 57–64°W), spanning 143,000 km^2, extends from Guadeloupe and Martinique Islands, 200NM into the Atlantic Ocean and 80NM into the Caribbean Sea and northward around St Barthélemy and St Martin islands (Fig. 1). These volcanic islands are characterized by narrow submarine shelves and a steep dropping of the sea floor, especially in the Caribbean Sea. Despite high biological productivity along the coasts, Caribbean pelagic waters are relatively oligotrophic and characterized by a permanent stratification (Longhurst, 2007). The regime of winds, influenced by the displacement of the Intertropical Convergence Zone, has a strong influence on oceanographic processes (Longhurst, 2007). The southern Caribbean shelf resembles ecologically the Guianean shelf, the turbid water from the Guyana Current passing along the southern Caribbean (near Trinidad and Tobago) to form the Caribbean Current (Johns et al., 1998, Fig. 1). However, water entering the Caribbean through the Lesser Antilles arc is largely dominated by the flow of the North Equatorial Current and of low surface chlorophyll concentration (Borstad, 1982). The seasonal cycle is of small amplitude but is complex with annual and seasonal variability and chlorophyll maxima in both boreal winter and summer (the second possibly induced by the Orinoco discharge plume passing in the southeastern Caribbean) (Longhurst, 2007).

As a result of these contrasting oceanographic processes, surface chlorophyll concentration is on average 10 times higher in Guiana compared to the Antilles. In 2008, the year of the aerial surveys, mean annual chlorophyll concentrations were 1.189 mg·m^{-3} in Guiana and 0.101 mg·m^{-3} in the Antilles (http://oceancolor.gsfc.nasa.gov/). We considered chlorophyll concentration to be a good indicator of primary production and later in the text we preferably use the term productivity (the rate at which primary producers fix the carbon).

2.2. Survey period and survey design

Aerial surveys were conducted from the 4 February to the 5 March 2008 (15 days on effort) across the French Antilles and from the 29 September to the 10 October 2008 (12 days on effort) off French Guiana. In the Antilles, the survey was stratified according to the windward/leeward side of the islands and depth, including three strata: inshore Caribbean, inshore Atlantic and offshore Atlantic (Fig. 1, Table 1). In Guiana, a stratified survey design was implemented according to approximate depth categories, including three strata: neritic (0–200 m), slope (200–2000 m) and oceanic (>2000 m) (Fig. 1, Table 1). Zigzag survey designs were implemented to provide

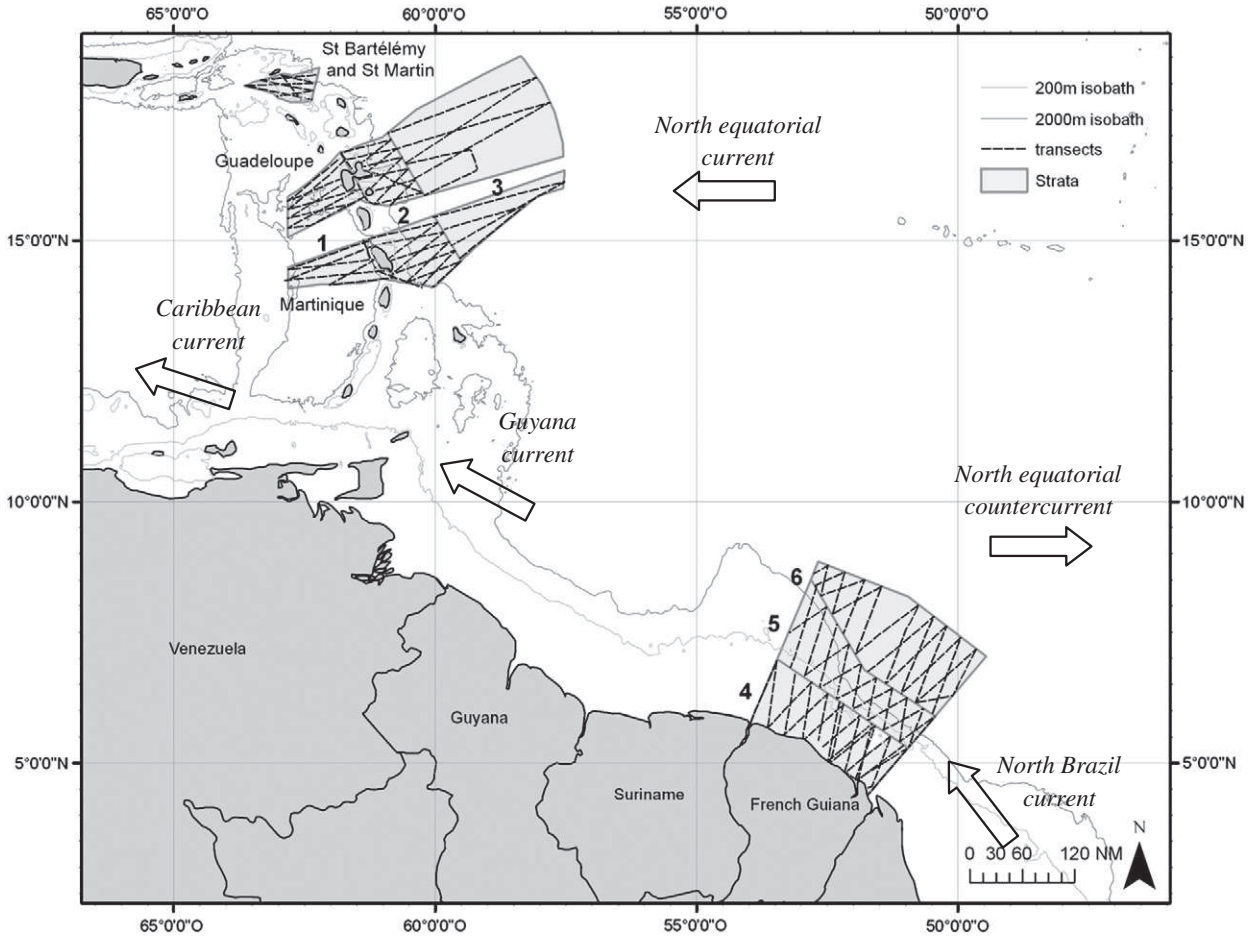


Fig. 1. Map of the study regions (French Antilles and French Guiana) in the western tropical Atlantic. Surveyed strata are shown in the Antilles (1: inshore Caribbean, including the Caribbean side of Martinique and Guadeloupe; 2: inshore Atlantic, including the Atlantic side of Martinique and Guadeloupe and St Bartélémy and St Martin islands and 3: offshore Atlantic) and in Guiana (4: neritic, 5: slope and 6: oceanic). Data source for bathymetry is GEBCO 08 1 min resolution grid (General Physiographic Chart of the Ocean; http://www.gebco.net/). Main currents are indicated according to (Johns et al., 1998).

a good spatial coverage within strata and improved flight efficiency (maximizing flight time spent on effort) (Buckland et al., 2001).

2.3. Aerial survey methods

Aerial surveys were based on standard line transect sampling (Buckland et al., 2001). Transects were sampled at a target altitude of 182 m (600 ft) and a ground speed of 90 knots (167 $km \cdot h^{-1}$). Survey platform was a Partenavia P68, a high-wing, double-engine aircraft equipped with bubble windows so that observers could scan right underneath the plane. Survey crew consisted in two trained observers observing with naked eyes and a flight leader in charge of data collection on a laptop computer. A GPS, logged to a computer equipped with 'VOR' software (designed for the aerial survey of the SCANS-II program Hammond et al., 2006), collected positional information every 2 s. Additionally, Beaufort Sea state, turbidity, glare, cloud coverage as well as an overall subjective assessment of sighting conditions were collected at the beginning of each track line and whenever any of these values changed.

The general protocol corresponded to published protocols prepared for small cetaceans (*e.g.* SCANS programs, Hammond et al., 2002, 2006). In addition to this, presence and group size of larger cetaceans, seabirds, sea turtles and elasmobranches were collected as well. Information recorded included identification to the taxonomic level, group size and angle to the track line, measured with a hand-held clinometer. Together with the altitude of the aircraft, the angle provided the perpendicular distance of the animal from the track line, which allowed distance sampling analyses to be conducted (Buckland et al., 2001). However, for seabirds, data was collected using the strip transect methodology based on the assumption that all seabirds within the strip are detected (Eberhardt 1978; Tasker et al. 1984). This methodology was used in an attempt to avoid disrupting the attention of the observers from the target species (cetaceans) in areas of high seabird densities. Strip width was 500 m on both sides of the track line in the Antilles and 150 m in Guiana. Identification was made to the lowest taxonomic level whenever possible, but groupings were inevitable for animals that could not be told apart from the air. Brown terns and brown boobies are examples of such groupings in the Antilles (see footnotes in Tables 2 and 3).

Table 1
Realized effort and surface area for each stratum during the aerial surveys.

Study region	Stratum	Transect length (km)	Surface area (km^2)
Antilles	Inshore Caribbean	2609	26,179
	Inshore Atlantic	3237	36,692
	Offshore Atlantic	2640	79,699
	All strata	8486	142,570
Guiana	Neritic	2826	39,409
	Slope	2405	38,062
	Oceanic	2544	55,009
	All strata	7775	132,480

Table 2
Number of sightings and individuals recorded on effort in the Antilles. Number of individuals refers to the total number of recorded individuals for each taxon.

	Taxon	Number of sightings	Number of individuals
Cetacea	Unidentified Cetacea	2	2
Mysticetes	*Balaenoptera edeni/Balaenoptera edeni borealis*	1	1
	Balaenoptera acutorostrata	2	2
	Megaptera novaeangliae	7	9
Sperm and beaked whales	Unidentified Ziphiidae	4	8
	Ziphius cavirostris	2	3
	Physeter macrocephalus	7	13
	Kogia spp.	2	4
Large delphinids	*Globicephala macrorhynchus*	5	54
	Pseudorca crassidens	2	11
	Orcinus orca	2	4
Small delphinids	Unidentified small delphinid	7	98
	Tursiops truncatus	2	34
	Lagenodelphis hosei	4	116
Total cetaceans		49	359
Procellariiformes	Unidentified Procellariidae	2	2
	Puffinus puffinus/P. lherminieri	4	13
	Unidentified Hydrobatidae	8	8
Pelecaniformes	*Fregata magnificens*	19	24
	Phaethon aethereus/Phaethon lepturus	171	187
	Sula sula/Sula leucogaster [a]	57	134
Charadriiformes	*Catharacta spp.*	6	6
	Sterna fuscata/Sterna anaethetus [b]	110	657
	Sterna dougalii/Sterna hirundo/Sterna antillarium	6	13
	Sterna maxima	3	3
	Anous stolidus	13	17
Total seabirds		399	1064
	Unidentified Cheloniidae	12	12
	Dermochelys coriacea	4	4
Total sea turtles		16	16
	Unidentified sharks	6	10
Total elasmobranches		6	10

[a] Referred to as brown boobies in text.
[b] Referred to as brown terns in text.

2.4. Analytical methods

We used both distance sampling (Buckland et al., 2001; Thomas et al., 2010) and geostatistics (Bellier et al., 2011; Monestiez et al., 2006) to estimate density and abundance in our study regions. In addition, geostatistics allowed mapping local density of sightings.

2.4.1. The distance sampling approach

Distance sampling (Buckland et al., 2001; Thomas et al., 2010) provides estimates of abundance and density in a study region with associated uncertainties (*e.g.* Williams & Thomas 2007; Hammond et al., 2002). It relies on 2 stages. First, one has to fit a detection function to distance data in order to estimate the proportion of missed animals in the covered region. In conventional distance sampling (Buckland et al., 2001), as implemented here, detection probability depends only on the distance from the track line. The second stage consists in extrapolating the number of animals seen in the covered region to the whole study region, the so-called design based estimate of abundance. For this, it is crucial that the lines be placed randomly with respect to the distribution of animals. Indeed, random line placement justifies the extrapolation of the sample statistics to the population and ensures that the surveyed lines are representative of the study region. Additionally, three assumptions are critical: (1) the probability of detecting an animal on the transect is certain, referred as the $g(0)=1$ assumption, (2) no responsive movement occurred prior to detection and (3) distances are measured accurately.

Here, we applied conventional distance sampling on portions of transects with homogeneous detection conditions. We truncated 5% of the sightings detected at the largest distances (Buckland et al., 2001). Then, detection models (uniform, hazard rate and half normal) were fitted to the distribution of perpendicular distances. The model that minimized the Akaike Information Criterion (AIC) was selected. For seabirds, for which data was collected using the strip transect methodology, a uniform detection function was used. Buckland et al. (2001) recommend at least 60 sightings for detection function fit, although a reliable detection model can be obtained from smaller samples, depending on the data.

Density of sightings (number of sightings per unit area) was estimated in the study region as:

$$\hat{D} = \frac{n}{2\hat{\mu}L}$$

where n is the number of detected sightings, L the total length of the transects and $\hat{\mu}$ the effective strip width. Density of individuals (number of individuals per unit area) was obtained by multiplying $\hat{D}$ by the expected group size $\left(\hat{E}(s)\right)$, estimated as the arithmetic mean of group sizes. The mean was calculated separately for each stratum only when group sizes differed significantly between strata and there were at least 10 sightings per stratum. Then, abundance (number of individuals) was estimated by multiplying density of individuals by the surface area of the study region (A):

$$\hat{N} = \frac{n\hat{E}(s)A}{2\hat{\mu}L}$$

Table 3
Number of sightings and individuals recorded on effort in Guiana. Number of individuals refers to the total number of recorded individuals for each taxon.

	Taxon	Number of sightings	Number of individuals
Cetacea	Unidentified Cetacea	2	4
Mysticetes	Unidentified Balenopteridae	1	1
	Balaenoptera physalus	2	2
Sperm and beaked whales	Unidentified Ziphiidae	2	2
	Mesoplodon spp.	2	4
	Ziphius cavirostris	3	5
	Physeter macrocephalus	3	10
Large delphinids	*Grampus griseus*	1	1
	Peponocephala electra/Feresa attenuata	3	50
	Globicephala macrorhynchus	8	162
	Globicephala macrorhynchus/Pseudorca crassidens	1	1
Small delphinids	Unidentified small delphinid	19	178
	Tursiops truncatus	68	1277
	Sotalia guianensis	22	59
Total cetaceans		137	1756
Procellariiformes	Unidentified Procellariidae	3	3
	Unidentified Hydrobatidae	1	5
Pelecaniformes	*Fregata magnificens*	58	128
	Phaethon aethereus/Phaethon lepturus	4	4
	Sula spp.	1	1
Charadriiformes	*Catharacta skua*	1	1
	Unidentified Laridae	3	40
	Larus atricilla	6	18
	Sterna fuscata	87	688
	Sterna sandvicensis/Sterna maxima/Sterna hirundo/Sterna dougallii/Sterna albifons[a]	116	438
	Anous stolidus	3	5
Total seabirds		283	1331
	Unidentified Cheloniidae	30	30
	Dermochelys coriacea	2	2
Total sea turtles		32	32
	Unidentified shark	17	19
	Sphyrna spp.	7	7
	Unidentified ray	10	14
	Manta birostris	100	127
Total elasmobranches		134	167

[a] Referred to as gray terns in text.

The uncertainty of density and abundance was described by the coefficient of variation (CV). It had an encounter rate component, a detection function component and a group size component and was computed analytically using the delta method (Buckland et al., 2001).

2.4.2. The geostatistical approach

We also implemented a geostatistical approach (Bellier et al., 2011; Monestiez et al., 2006) for two reasons. First, zigzag designs employed in our non rectangular study regions produced a non homogeneous distribution of transects (Strindberg and Buckland, 2004) and the distribution of animals may not be independent of the positions of transects. Geostatistics take into account the spatial autocorrelation between observations and transect segments in density and abundance estimations (Van der Meer and Leopold, 1995). Second, geostatistics allowed mapping local density of sightings (Monestiez et al., 2006). Basically, the geostatistical approach has two stages. First, one has to model the spatial dependence in the data and estimate its parameters (variographic analysis). The second stage consists in kriging the density of sightings over the study region in order to obtain a map of local density of sightings that minimizes the interpolation error given the spatial dependence. Multiplying this local density of sightings by mean group size and integrating it over the study region provides an estimate of abundance. The choice of the spatial dependence model is a crucial stage. The underlying hypothesis is stationarity of the animal's distribution (*i.e.* processes that leads to the spatial distribution are independent of localization or direction) (Wackernagel, 2003). A consequence is that covariance between two observations only depends on the distance between them.

As detection probability was not directly accessible from the geostatistical methodology, it necessarily relied on the detection function fitted in the distance sampling approach to estimate the proportion of missed animals in the covered region. Prior to the analysis, transects were split into 10 km segments. We used the modified kriging described by Monestiez et al. (2006) that includes a Poisson modeling of the observation process, to map local density of sightings. Then we used block kriging (Bellier et al., 2011) to estimate density of sightings and abundance in the study regions.

The first stage was the variographic analysis. The variogram corresponds to half of the squared difference between two observations separated by a distance h. Estimating a classical variogram from count data, that tend to be positively skewed and depart from normality, may lead to poor variogram estimates. Hence, we estimated a modified variogram as described in Monestiez et al. (2006) as:

$$\gamma^*(h) = \frac{1}{2N(h)} \sum_{\alpha,\beta} \left\{ \frac{l_\alpha l_\beta}{l_\alpha + l_\beta} \left(\frac{Z_\alpha}{l_\alpha} - \frac{Z_\beta}{l_\beta} \right)^2 - m \right\}$$

where l_α and l_β are the effort traveled on segment α and β and Z_α and Z_β are the number of sightings observed on segment α and β separated by distance h, m is the mean density in the study area and $N(h)$ is a normalizing constant. Subsequently, we fitted a variogram model (pure nugget effect, exponential, Gaussian or spherical model) and its parameters were estimated using the least squared method. Variograms were fitted for each taxon by using the data of the entire region (except for

Cheloniidae in Guiana for which variogram models were fitted for each stratum separately).

The second stage was spatial interpolation. In contrast to Bellier et al. (2011), which considered non stationarity in the process, we assumed constant mean and variance within each stratum and we applied the block kriging in each stratum. We defined a 0.1° of longitude by 0.1° of latitude grid over the area to krige in the Antilles and Guiana. We considered a stationary random field $Y(x)$ of density and a sample of n points, x_α, where the count variable Z_α is measured, and where Z_α follows a Poisson distribution with density Y_α as parameter. Given the known variogram $\gamma(h)$, the kriging estimator is the best linear predictor of $Y(x_0)$ in a non observed location x_0 of the form:

$$Y_0^* = \sum_{\alpha=1}^{n} \lambda_\alpha \frac{Z_\alpha}{l_\alpha}$$

where λ_α are the weights obtained by solving the following kriging system of $(n+1)$ equations:

$$\sum_{\beta=1}^{n} \lambda_\beta \gamma\left(Y_\alpha - Y_\beta\right) + \lambda_\alpha \frac{m}{l_\alpha} + \mu = \gamma(Y_\alpha - Y_0) \text{ for } \alpha = 1, \ldots, n$$

$$\sum_{\alpha=1}^{n} \lambda_\alpha = 1$$

with μ the Lagrangian multiplier. The minimized prediction variance was expressed as:

$$\mathrm{Var}(Y_0^* - Y_0) = {\sigma_Y}^2 - \sum_{\alpha=1}^{n} \lambda_\alpha \gamma(Y_\alpha - Y_0) - \mu.$$

In both distance sampling and geostatistical approaches, density of sightings, abundance and their associated uncertainties were estimated for each stratum and for the whole study regions. The overall density of sightings was calculated as the sum of the estimates for each stratum weighted by the surface areas. The overall abundance was calculated as the sum of the abundances of each stratum. Overall CVs were computed according to the delta method, assuming independence between strata (Buckland et al., 2001). The analyses were conducted for taxa for which there were at least 20 sightings. Distance sampling analyses were performed in Distance software (Thomas et al., 2010) and geostatistical analyses were entirely programmed in R.

2.4.3. Relation to physiographic features

Together with the maps of local density provided by geostatistics, we used simple physiographic variables to describe megavertebrates' distribution. We used ARCGIS 10 to co-locate the position of 10 km segments with depth and distance from the coast, based on the values at the mid points of the segments. Depth was derived from GEBCO 08 1 min resolution grid (General Physiographic Chart of the Ocean; http://www.gebco.net/). The coastline was isolated with XToolsPro 7.1.0 extension for ArcGIS 10 (Data East 2010, available from http://www.xtoolspro.com/). We compiled descriptive statistics (mean, standard deviation and range) of depth and distance from the coast associated with the segments where each taxon was present, as well as the statistics for the covered region (considering all segments).

3. Results

3.1. General description

During the Antilles survey, sea state was suboptimal (62% of effort was flown with a Beaufort sea state of 3 or lower and 33% with a Beaufort sea state of 4) in spite of the survey being planned after the trade wind season. These weather limitations prevented from fully covering the offshore Atlantic stratum. The survey covered 8486 km (or 71 h) of effort. A total of 49 sightings of cetaceans were collected on effort, representing 359 individuals. 67% of the sightings were identified to species level and 9 species were identified including 2 mysticetes, 2 sperm and beaked whales, 3 large delphinids and 2 small delphinids (Table 2, Appendix A.1). Humpback whales (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*) were the most sighted cetacean species (both encountered on 7 occasions). A total of 399 seabird sightings were recorded (1064 individuals), comprising 11 taxa including 3 Procellariiformes, 3 Pelecaniformes and 5 Charadriiformes (Table 2, Appendix A.2). Tropicbirds (*Phaethon aethereus* and *Phaethon lepturus*) were the most frequently encountered (171 sightings) followed by *Sterna fuscata* and *Sterna anaethetus* (referred to as brown terns) (110 sightings) and *Sula sula* and *Sula leucogaster* (referred to as brown boobies) (57 sightings). Additionally, we recorded 16 sightings of sea turtles (12 of Cheloniidae and 4 of the leatherback turtle, *Dermochelys coriacea*) and 6 sightings of unidentified sharks (Table 2, Appendix A.3).

During the Guiana survey, sea state was excellent (90% of effort was flown with a Beaufort sea state of 2 or lower) although water turbidity sometimes limited the aerial observation in the very coastal waters. Achieved effort was 7775 km (or 63 h). A total of 137 sightings of cetaceans were collected on effort, representing 1756 individuals. 78% of the sightings were identified to species level and 7 species were identified, including 1 mysticete, 2 sperm and beaked whales, 3 large delphinids and 2 small delphinids (Table 3, Appendix A.1). Bottlenose dolphins (*Tursiops truncatus*) were by far the most frequently sighted species (68 sightings), followed by Guiana dolphins (*Sotalia guianensis*) (22 sightings). A total of 283 seabird sightings were collected (1331 individuals), comprising 11 taxa, including 2 Procellariiformes, 3 Pelecaniformes and 6 Charadriiformes (Table 3, Appendix A.2). *Sterna sandvicensis, Sterna maxima, Sterna hirundo, Sterna dougallii* and *Sterna albifons* (referred to as gray terns) and the Sooty tern (*S. fuscata*) were the most frequently seen (respectively 116 and 87 sightings). Magnificent Frigatebird (*Fregata magnificens*) was also a frequently seen species (58 sightings). Additionally, we recorded 32 sea turtles (30 Cheloniidae and 2 leatherback turtles) and 134 sightings of elasmobranches; manta ray (*Manta birostris*) being the most commonly sighted species (100 sightings) (Table 3, Appendix A.3).

3.2. Encounter rates

In Guiana, the encounter rate of cetaceans (1.76 sightings/100 km) was 3 times greater than in the Antilles (0.58 sightings/100 km); this difference was even more pronounced in terms of individuals (respectively 22.59 and 4.23 individuals/100 km). In the Antilles, 0.12 sightings of mysticetes and 0.44 sightings of odontocetes were encountered per 100 km of effort. In Guiana, 0.04 sightings of mysticetes and 1.70 sightings of odontocetes were encountered per 100 km of effort. Overall, the encounter rate of sperm and beaked whale was higher in the Antilles (0.18 sightings/100 km) compared to Guiana (0.13 sightings/100 km). Large delphinid encounter rate was higher in Guiana (0.17 sightings/100 km) compared to the Antilles (0.11 sightings/100 km). Finally, the encounter rate of small delphinids was almost 10 times higher in Guiana (1.40, compared to 0.15 sightings/100 km in the Antilles).

The encounter rate of seabirds was slightly greater in the Antilles (4.70 sightings/100 km, 12.54 individuals/100 km) compared to Guiana (3.64 sightings/100 km, 17.12 individuals/100 km). Procellariiformes were rarely encountered in both regions. Charadriiformes were more frequently encountered in Guiana (2.82 sightings/100 km) compared to the Antilles (1.56 sightings/100 km). The encounter rate of Pelecaniformes was 4 times higher in the Antilles (2.92 sightings/100 km) compared to Guiana (0.81 sightings/100 km).

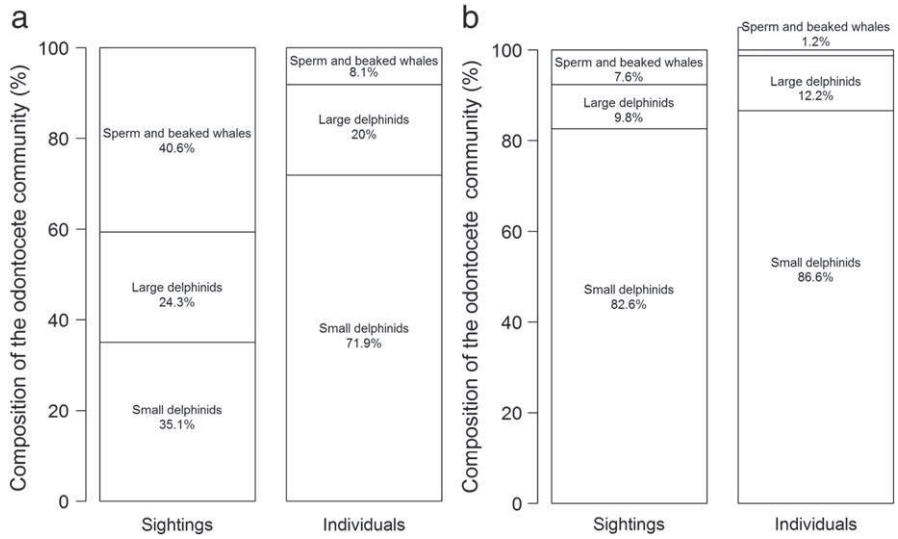


Fig. 2. Composition of the odontocete community (sightings and individuals) in the Antilles (a) and in Guiana (b).

Sea turtles and elasmobranches were more frequently encountered in Guiana (respectively 0.46 and 2.07 sightings/100 km) than in the Antilles (respectively 0.25 and 0.07 sightings/100 km).

3.3. Composition of odontocete and seabird communities

In the Antilles, odontocete sightings were almost equally partitioned between small delphinids, large delphinids and sperm and beaked whales, the later being slightly more frequently recorded (40.5% of the sightings) (Fig. 2a). However, in terms of individuals, small delphinids dominated (representing 71.9% of the individuals). In Guiana, the composition of the odontocete community was different. Small delphinids (mostly represented by bottlenose dolphins) dominated in terms of sightings (82.6%) and individuals (86.6%) (Fig. 2b). Subsequently, sightings were almost equally partitioned between large delphinids and sperm and beaked whales.

In the Antilles, Pelecaniformes dominated in terms of sightings (61.9%) (Fig. 3a) and were represented by 69.2% of tropicbirds, 23.1% of boobies and 7.7% of frigatebirds. Charadriiformes totalized 34.6% of the sightings and were mainly represented by terns. However, in terms of individuals, Charadriiformes dominated. In Guiana, the seabird community was strongly dominated by Charadriiformes (76.3% of the sightings and 89.4% of the individuals) (Fig. 3b), within which, as in the Antilles, terns accounted for more than 95%. Pelecaniformes totalized 22.3% of the sightings and were almost exclusively represented by frigatebirds.

3.4. Abundance

Analytical details are given in Appendix B for distance sampling and Appendix C for geostatistics. Overall, both approaches provided similar estimates of abundance for the analyzed taxa in the Antilles and Guiana (Tables 4 and 5). For Cheloniidae, abundance estimates from both approaches were equal. However, for Magnificent Frigatebird in Guiana, the overall geostatistical estimate was lower. Additionally, when there was no sighting in a stratum, distance sampling estimated an abundance of 0 and a CV of 0 whereas geostatistics estimated a non zero abundance and a relatively high CV (for example for Guiana dolphin). Distance sampling results only are presented in the text.

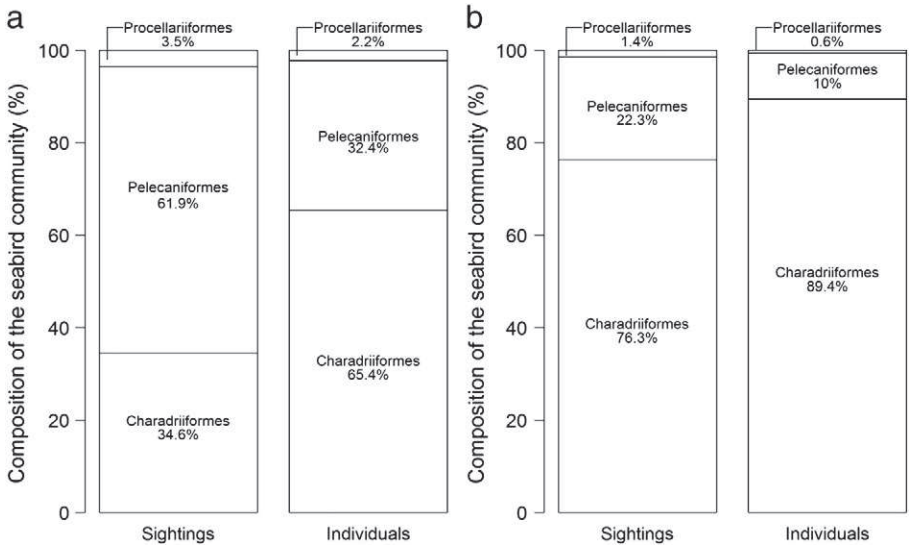


Fig. 3. Composition of the seabird community (sightings and individuals) in the Antilles (a) and in Guiana (b).

Table 4
Estimated abundance and density of sightings from distance sampling and geostatistics in the Antilles. Brown boobies include *Sula sula* and *Sula leucogaster*, brown terns include *Sterna fuscata* and *Sterna anaethetus* and tropicbirds, *Phaethon aethereus* and *Phaethon lepturus*. We provide by stratum and combined estimates. Coefficients of variation are given in parentheses. Geostatistics were not applied to Magnificent frigatebirds due to low sighting numbers.

		Magnificent frigatebird	Tropicbirds	Brown bobbies	Brown terns
		Descriptive results			
Number of sightings	Inshore Caribbean	4	41	27	32
	Inshore Atlantic	12	106	26	65
	Offshore Atlantic	3	24	4	13
	TOTAL	19	171	57	110
Mean group size	Inshore Caribbean				9.5 (0.34)
	Inshore Atlantic	1.26 (0.08)	1.09 (0.02)	2.35 0.18)	5.04 (0.18)
	Offshore Atlantic				1.92 (0.35)
		Conventional distance sampling			
Abundance (individuals)	Inshore Caribbean	56 (0.51)	493 (0.22)	698 (0.29)	3345 (0.44)
	Inshore Atlantic	172 (0.32)	1318 (0.14)	695 (0.26)	3729 (0.25)
	Offshore Atlantic	121 (0.67)	836 (0.24)	300 (0.51)	797 (0.44)
	TOTAL	349 (0.30)	2647 (0.11)	1693 (0.23)	7870 (0.23)
Density of sightings (sightings / 100 km²)	Inshore Caribbean	0.17 (0.51)	1.72 (0.22)	1.13 (0.23)	1.34 (0.28)
	Inshore Atlantic	0.37 (0.31)	3.28 (0.15)	0.80 (0.19)	2.01 (0.17)
	Offshore Atlantic	0.12 (0.67)	0.96 (0.24)	0.16 (0.47)	0.52 (0.26)
	TOTAL	0.19 (0.29)	1.69 (0.11)	0.50 (0.15)	1.06 (0.13)
		Geostatistical analysis			
Abundance (individuals)	Inshore Caribbean		504 (0.15)	598 (0.16)	3049 (0.21)
	Inshore Atlantic		1055 (0.09)	653 (0.18)	3787 (0.11)
	Offshore Atlantic		1466 (0.16)	829 (0.35)	1244 (0.37)
	TOTAL		3025 (0.13)	2080 (0.24)	8080 (0.22)
Density of sightings (sightings / 100 km²)	Inshore Caribbean		1.76 (0.15)	0.97 (0.16)	1.23 (0.21)
	Inshore Atlantic		2.64 (0.09)	0.76 (0.18)	2.05 (0.11)
	Offshore Atlantic		1.69 (0.16)	0.44 (0.35)	0.81 (0.37)
	TOTAL		1.95 (0.13)	0.62 (0.24)	1.21 (0.22)

In the Antilles, cetacean sightings were too low to fit detection functions and provide species-specific estimates of abundance. However, in Guiana, sighting numbers were appropriate for bottlenose dolphin and Guiana dolphin (Table 5). Bottlenose dolphin was the most abundant cetacean, with an estimation of 34,965 individuals (CV = 0.28). For Guiana dolphin, the overall estimate was of 2076 individuals (CV = 0.44), all located in the neritic stratum.

We estimated abundances for several taxa of seabirds in both regions (Tables 4 and 5). In the Antilles, the abundance of brown terns was estimated at 7870 individuals (CV = 0.23). For brown boobies, we estimated 1693 individuals (CV = 0.23). For both taxa, abundance was lower in the offshore Atlantic stratum. The estimate for tropicbirds was of 2647 individuals (CV = 0.11). Additionally, we estimated an abundance of 349 Magnificent Frigatebirds (CV = 0.30). In Guiana, Sooty terns appeared to be the most abundant species (40,996 individuals (CV = 0.27)) and their abundance was greater in the oceanic strata. In contrast, Magnificent Frigatebirds and gray terns were abundant in the neritic stratum (respectively 5389 individuals (CV = 0.52) and 16,999 individuals (CV = 0.34)).

In Guiana, we also obtained abundance estimates for manta rays and Cheloniidae (Table 5).

3.5. Distribution

In the Antilles, cetaceans were mainly encountered over the inshore Atlantic and Caribbean strata, with more numerous sightings in slope habitat, especially in the Atlantic (Appendix A.1). In Guiana, cetacean sightings were fairly evenly distributed across all strata albeit sightings were more numerous in the neritic stratum (Appendix A.1). The geostatistical analysis was applied to bottlenose dolphins and Guiana dolphins. Bottlenose dolphins were widely sighted and their distribution seemed to be random (pure nugget effect in the variogram, Appendix C). Geostatistics estimated a constant density (1.27 sightings/100 km^2) across all strata (Table 5); as a result we obtained a flat map (Fig. 4a). Bottlenose dolphins showed no preference for the analyzed physiographic features (Table 6) but they were not observed closer than 14 km from the coast. In contrast, Guiana dolphins had a very coastal distribution (Fig. 4b). Most sightings were within the first 10 km, with only one sighting located further offshore (36 km from the coast). Mean depth used by Guiana dolphins was 7.5 m (sd = 11.2 m; Table 6).

In the Antilles, seabirds were more frequently encountered in the inshore Atlantic and Caribbean strata (Appendix A.2). Tropicbirds were mainly aggregated around the islands, with a lower density of sightings offshore (Fig. 5a). Brown boobies were sighted in both inshore Atlantic and Caribbean strata but density of sightings was higher in the latter. They were aggregated around the islands (notably East of Martinique, West of Guadeloupe) (Fig. 5b). Brown terns were recorded in all strata with noticeable aggregations in the South of the region. Density of sightings was the highest in the inshore Atlantic stratum and the lowest in the offshore Atlantic stratum (Fig. 5c). In Guiana, seabirds were mainly distributed along the coast and in the oceanic strata. The deeper part of the continental shelf and the inner slope were poorly frequented (Appendix A.2). Sooty terns were exclusively distributed in slope and oceanic strata, with a higher density of sightings in oceanic waters (Fig. 6a). They used the offshore part of the study region

Table 5
Estimated abundance and density of sightings from distance sampling and geostatistics in Guiana. Gray terns include *Sterna sandvicensis, Sterna maxima, Sterna hirundo, Sterna dougallii* and *Sterna albifons*. We provide by stratum and combined estimates. Coefficients of variation are given in parentheses.

		Bottlenose dolphin	Guiana dolphin	Magnificent Frigatebird	Sooty tern	Gray terns	Cheloniidae	Manta ray
Descriptive results								
Number of sightings[a]	Neritic	27	20	45	0	91	20	82
	Slope	22	0	1	15	6	3	13
	Oceanic	16	0	0	51	4	5	1
	TOTAL	65	20	46	66	101	28	96
Mean group size	Neritic	6.22 (0.16)			_			
	Slope	27.13 (0.25)	2.45 (0.11)	2.46 (0.44)	3.13 (0.40)	3.83 (0.27)	1 (0)	1.28 (0.06)
	Oceanic	30.62 (0.27)			10.23 (0.21)			
Conventional distance sampling								
Abundance (individuals)	Neritic	3449 (0.30)	2076 (0.44)	5389 (0.52)	0 (0)	16,999 (0.34)	366 (0.23)	2712 (0.49)
	Slope	16,533 (0.42)	0 (0)	162 (1.04)	3091 (0.49)	1512 (0.57)	76 (0.71)	588 (0.39)
	Oceanic	14,983 (0.40)	0 (0)	0 (0)	37,905 (0.29)	1113 (0.53)	136 (0.42)	49 (0.98)
	TOTAL	34,965 (0.28)	2076 (0.44)	5551 (0.52)	40,996 (0.27)	19,624 (0.33)	576 (0.20)	3350 (0.41)
Density of sightings (sightings/100 km^2)	Neritic	1.40 (0.26)	2.14 (0.43)	5.56 (0.29)	0 (0)	11.25 (0.21)	0.93 (0.23)	5.37 (0.49)
	Slope	1.60 (0.34)	0 (0)	0.17 (0.94)	2.59 (0.29)	1.03 (0.45)	0.19 (0.71)	1.18 (0.38)
	Oceanic	0.88 (0.29)	0 (0)	0 (0)	6.73 (0.20)	0.52 (0.45)	0.25 (0.42)	0.06 (0.98)
	TOTAL	1.24 (0.20)	0.63 (0.43)	1.70 (0.28)	3.54 (0.17)	3.86 (0.19)	0.43 (0.20)	1.96 (0.40)
Geostatistical analysis								
Abundance (individuals)	Neritic	3122 (0.13)	1968 (0.16)	3440 (0.17)	603 (1.47)	17,102 (0.78)	365 (25)	2480 (0.12)
	Slope	13,154 (0.13)	21 (15.73)	366 (1.71)	3130 (0.30)	2101 (0.68)	74 (0.67)	691 (0.43)
	Oceanic	21,456 (0.13)	38 (8.11)	14 (60.89)	32,066 (0.13)	1638 (1.17)	136 (0.51)	101 (4.39)
	TOTAL	37,732 (0.13)	2027 (0.54)	3820 (0.53)	35,799 (0.23)	20,841 (0.22)	575 (0.38)	3272 (0.40)
Density of sightings (sightings/100 km^2)	Neritic	1.27 (0.13)	2.04 (0.16)	3.55 (0.17)	0.49 (1.47)	11.33 (0.78)	0.93 (0.25)	4.91 (0.12)
	Slope	1.27 (0.13)	0.02 (15.73)	0.39 (1.71)	2.63 (0.30)	1.44 (0.68)	0.19 (0.67)	1.41 (0.43)
	Oceanic	1.27 (0.13)	0.04 (8.11)	0.01 (60.89)	5.70 (0.13)	0.78 (1.17)	0.25 (0.51)	0.14 (4.39)
	TOTAL	1.27 (0.13)	0.63 (0.54)	1.17 (0.53)	3.27 (0.23)	4.11 (0.22)	0.43 (0.38)	1.93 (0.40)

[a] Number of sightings are given after truncation for cetaceans.

(mean = 260.1 km, sd = 66.6 km; Table 6). In contrast, Magnificent Frigatebirds and gray terns used inshore waters (respectively means of 21.46 km and 63.55 km, Table 6). Density of Magnificent Frigatebirds was high between the *Approuague* and *Oyapock* rivers and around *Grand Connétable* Island (Fig. 6b). High densities of gray terns were found along the coast, with some sightings in the outer continental shelf and further offshore (Fig. 6c).

In the Antilles, other megavertebrates were more commonly seen close to the islands (Appendix A.3). Sea turtles were mainly encountered around Martinique and Guadeloupe. In Guiana, sea turtles and elasmobranches were preferentially distributed in the neritic and slope strata (Appendix A.3). Sea turtles were seen throughout the continental shelf and occasionally on the inner slope and further offshore. Manta rays were almost exclusively distributed in the neritic stratum and were highly aggregated (Fig. 4c).

4. Discussion

4.1. Methodological considerations

4.1.1. Survey methods

A dedicated aerial survey methodology was chosen for its capacity to cover vast areas at a much lower cost than dedicated ship surveys and for its flexibility of implementation which allows a quick reaction to changing weather conditions, hence resulting in a higher rate of platform usage in optimal detection conditions.

A combination of two components makes our abundance estimates negatively biased. First, animals under the surface while in the observation area are not detected by observers (availability bias, Pollock et al., 2006). Second, observers may miss some animals at the surface, given that they are available for detection (perception bias, Pollock et al., 2006). Availability bias can be estimated from a double platform methodology (aircrafts flying in tandem, Hiby and Lovell, 1998), from the deployment of time depth recorders on individuals (Pollock et al., 2006) or the observation of diving behavior (Laake et al. 1997). Perception bias can be estimated using a tandem team of two observers on either side of the aircraft (Pollock et al., 2006). However, our objective was more to investigate differences in communities than to conduct a thorough quantitative analysis.

Survey conditions were not homogeneous between both regions. In Guiana, the high turbidity of the very coastal waters (Froidefond et al., 1988) could have prevented the detection of animals swimming under the surface. In addition, sea state was higher in the Antilles compared to Guiana. Animals swimming at or under the surface could have been missed and the consequence is an underestimation of their abundance in the Antilles. Hence, sea state could have contributed to the observed differences in communities between regions.

For seabirds, sometimes encountered in high densities and strongly aggregated, the strip transect methodology has proven to be more adapted and useful for monitoring populations at very large scales (Certain and Bretagnolle, 2008). In our surveys, the strip width was reduced from 500 m in the Antilles to 150 m in Guiana. Certain and Bretagnolle (2008) showed that variation of detection probability in aerial surveys of pelagic seabirds did not occur in a strip of 150 m and that the effect up to 230 m was very weak. Hence, seabird abundance may have been under-evaluated in the Antilles, albeit this may be less the case for large species like frigatebirds or boobies, frequent in this region.

Although observers were trained to recognize local species, surveying different species at the same time is not easy. First, an overestimation of detectable species compared to cryptic ones can occur (Ballance, 2008). Then, particularly for seabirds, identification to the species level was rarely possible from the aircraft. In the case of high density situations quickly gathering data is difficult, so we decided to focus on cetaceans. This could have caused an underestimation of seabird abundance, notably in coastal waters.

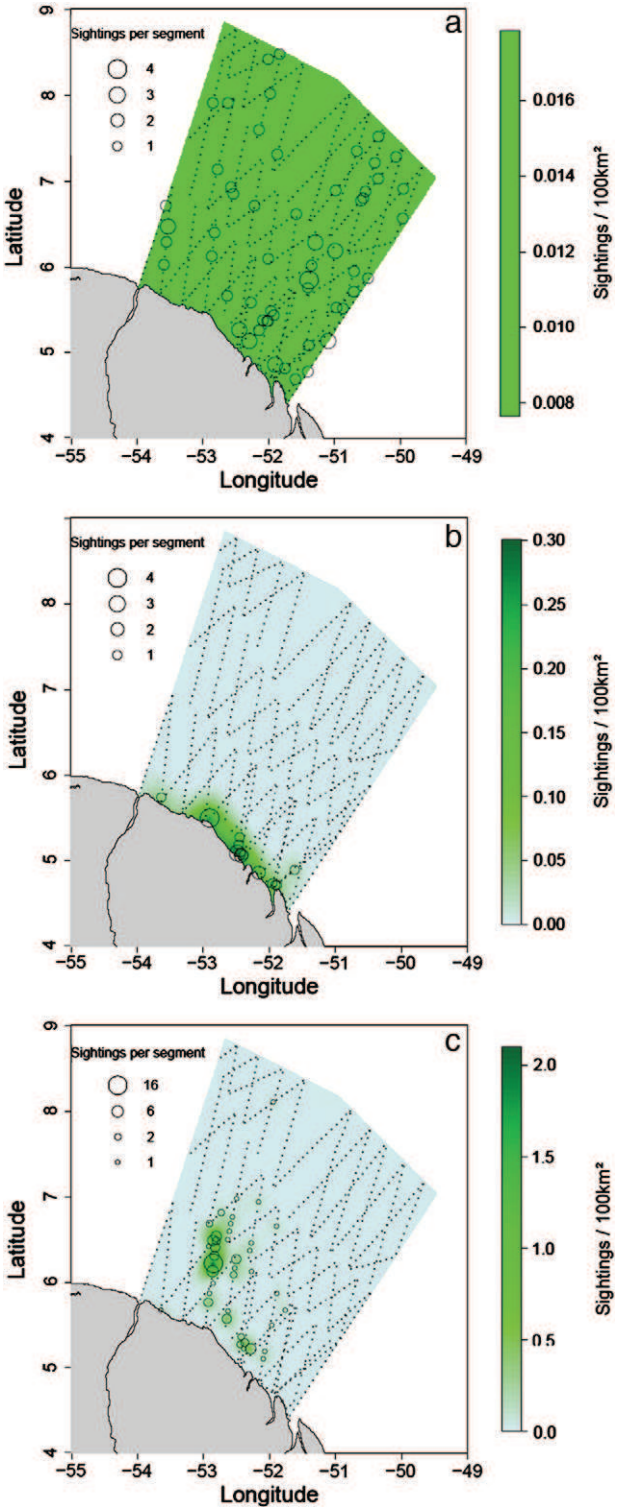


Fig. 4. Local density of sightings for bottlenose dolphin (a), Guiana dolphin (b) and manta ray (c) in Guiana. For bottlenose dolphin, density of sightings was constant over the study region (1.27 sightings/100 km^2). Transects were divided in 10 km segments for the analysis. Analytical details of the geostatistical approach are given in Appendix C.

The aerial surveys were carried out in two different seasons. In the Antilles, it coincided with the migration of humpback whales (Clapham, 2002), thus leading to a higher encounter rate of mysticetes compared to Guiana. However, in our analysis of community composition we were mainly interested in odontocetes, which may be resident in the region. Additionally, the dependence of seabirds on colonies may have caused a "colony effect" (Hyrenbach et al., 2007) if surveys were conducted during the breeding period. Hence, our surveys provided a real-time picture of communities but only reflect a given situation of the environment (*i.e.* snapshot). For this reason, results on distribution and abundance should be related to the sampled periods.

4.1.2. Analytical methods

We used both distance sampling and geostatistics to estimate density and abundance in our study regions. When sightings were not uniformly distributed and this distribution was not independent from the distribution of transects, geostatistics corrected the estimates (*e.g.* for Magnificent Frigatebirds in Guiana, Table 5). When there were no sightings in a stratum, distance sampling estimated an abundance of 0 and a CV of 0 whereas geostatistics estimated a non zero abundance and a very high CV (*e.g.* for Guiana dolphins, Table 5). However, the zero abundance estimated by distance sampling is still included in the confidence interval of geostatistics, which probably give a more realistic result. Nevertheless, due to low sighting numbers, we were close to the limit of utilization of both approaches. As they rely directly on the effective strip width estimated from detection function fitting, geostatistics cannot be used independently from distance sampling. Geostatistics allow mapping local density across a study region, giving information on an animal distribution. Hence, geostatistics are a good complement to distance sampling (Bellier & Monestiez 2008).

Despite these methodological considerations, it is clear that these multispecific surveys added new knowledge on megavertebrates inhabiting these poorly documented regions. Indeed, we provided for the first time an integrated and large scale vision of the diversity and distribution of megavertebrates inhabiting the French EEZ of the Antilles and Guiana. Furthermore, we derived estimates of abundance for two cetacean species in Guiana and for several seabird taxa in the Antilles and Guiana. This provided a useful baseline, in particular for cetaceans for which few estimates of abundance exist in the western tropical Atlantic (Waring et al., 2000).

4.2. Comparison with previous studies in the Caribbean and western tropical Atlantic

4.2.1. Cetaceans

Dedicated effort has been limited in the Caribbean and western tropical Atlantic, excepted in the Gulf of Mexico and quantitative information is rare. Nevertheless according to strandings (Cardona-Maldonado and Mignucci-Giannoni, 1999) and sightings (Gero et al., 2007; Swartz et al., 2003; Yoshida et al., 2010), the region appear to be inhabited by a diverse cetacean fauna. All cetacean species identified during our surveys had been previously reported in the Wider Caribbean (Ward et al., 2001). We will focus on the most commonly encountered species.

In Guiana the most frequently seen cetaceans were Guiana dolphins and bottlenose dolphins. Guiana dolphin, *S. guianensis*, is the marine species of the genus *Sotalia*, recently separated from the riverine species (*Sotalia fluviatilis*) (Caballero et al., 2007; Cunha et al., 2005; Monteiro-Filho et al., 2002). It is continuously distributed from southern Brazil to Honduras (Da Silva et al., 2010; Flores and DaSilva, 2008) and its ecological niche is defined as a narrow strip of coastal waters (Wedekin et al., 2010). This is consistent with our results as they were restricted to coastal and shallow waters and aggregated close to river mouths and estuaries (Edwards and Schnell, 2001; Rossi-Santos et al., 2006). Our estimate was of 2076 individuals (CV = 44.32). The only published abundances are from studies of portions of Brazilian coastal waters (Cantor et al., 2012; Torres and Beasley, 2003), not comparable with the extent of the area prospected during our survey. Bottlenose dolphins were widely distributed in Guiana and showed no preferences for specific physiographic features. The same pattern was observed in Abrolhos Bank (Brazil) where they were widespread and using various depth, whereas Guiana dolphins were the only species using waters

Table 6
Descriptive statistics (mean, standard deviation (sd) and range) of depth and distance from the coast associated with the sightings.

Study region	Taxon	Depth (m)			Distance from the coast (km)		
		Mean	sd	Range	Mean	sd	Range
Antilles	Magnificent Frigatebird	1870.0	2051.5	6259–18	52.24	72.04	0.68–262.15
	Tropicbirds	2191.1	1795.6	6242–12	60.61	67.68	1.69–321.91
	Brown boobies	2330.3	1460.1	5295–34	61.83	40.62	4.18–157.16
	Brown terns	2548.3	1467.5	5923–27	70.34	63.93	4.187–315.18
	Covered region	2927.7	1806.3	6539–4	101.99	92.91	0.684–370.19
Guiana	Bottlenose dolphin	1737.0	1806.6	4823–10	164.20	110.13	14.43–358.51
	Guiana dolphin	7.5	11.2	44–2	9.35	8.50	3.02–36.03
	Magnificent Frigatebird	43.2	135.1	731–0	21.46	38.46	0.11–203.43
	Sooty tern	3373.5	1252.2	4920–10	260.07	66.63	23.02–358.66
	Gray terns	614.7	1384.7	4823–2	63.55	96.60	3.021–358.51
	Manta ray	323.8	808.3	3982–8	89.09	61.34	1.58–314.94
	Covered region	1852.8	1797.4	4959–0	169.13	109.37	0.11–363.60

within 10 km from the coast (Rossi-Santos et al., 2006). They potentially overlapped with Guiana dolphins as some sightings co-occurred in inshore waters. Although bottlenose dolphins are widely distributed in the western tropical Atlantic, there is very little information on their abundance apart from a few local sightings. Our abundance estimate (34,965 individuals (CV = 0.28)) is the first for Guiana. In the Gulf of Mexico, bottlenose dolphins are also abundant, with 50,247 individuals (CV = 0.18) estimated for the outer continental shelf stock (Waring et al., 2000). Recently, the presence of A 'worldwide distributed form' and 'inshore' ecotypes was demonstrated in the Wider Caribbean (Caballero et al., 2012). However, there is no evidence of differential habitat use and true ecotype specialization in Guiana.

The only published line transect survey carried out in the Lesser Antilles (Yoshida et al., 2010) suggested that cetacean density was lower in offshore waters beyond the insular shelf. During our survey, cetacean sightings were also common in slope habitats. Humpback whales and sperm whales were the most commonly sighted cetaceans. Humpback whales migrate to the eastern Caribbean for mating and calving in the winter season (Clapham, 2002) with a peak in February and March (Mignucci-Giannoni, 1998). Breeding areas occur on offshore banks and off insular coasts of the Atlantic margins of the Antilles (Whitehead and Moore, 1982; Winn et al., 1975). Our sightings were almost exclusively in inshore waters on the Atlantic side of the islands. Sperm whales were sighted on 7 occasions, notably around Guadeloupe. The Lesser Antilles population was estimated at 145 individuals (95% CI 94–219), known to undertake inter-island movements (Gero et al., 2007).

4.2.2. Seabirds

Since there had been no seabirds at-sea surveys in the Lesser Antilles and Guiana, we will make a broad comparison with censuses at breeding colonies (*e.g.* Boyé et al., 2009), considering that our at-sea abundance estimates include immatures, breeding adults and non breeding adults, as we could not differentiate them from the air. Such a comparison has successfully been done using demographic parameters to subtract the non breeding component of the at-sea population (Clarke et al., 2003; Van der Meer and Leopold, 1995). Feeding communities represent the at-sea component of seabird community ecology and often comprise individuals that come from scattered breeding colonies (Ballance, 2008).

Grand Connétable Island is the only seabird breeding site between the Amazon and the Orinoco and hosts important colonies during the breeding season (between April and September), including 1500 pairs of *S. maxima*, 8000 pairs of *S. sandvicensis* and several hundreds of pairs of *S. fuscata* (Bird Life International, 2012). Hence, *S. maxima* and *S. sandvicensis* may represent a significant amount of our gray terns category. Additionally, approximately 650 pairs of Magnificent Frigatebirds nest there year-round (Bird Life International, 2012; Weimerskirch et al., 2006). In general, our at-sea abundance estimates were in the order of magnitude of breeding pairs, considering that our survey was conducted at the end of the breeding season when adults as well as dispersing seabirds may be present. *S. fuscata* is completely pelagic and highly gregarious (Hertel and Ballance, 1999; Surman and Wooller, 2003). This is well reflected in our maps of local density. However, our abundance estimate was high related to breeding numbers, indicating that non breeders probably represented a significant amount of the at-sea population. Our abundance estimate for gray terns was in concordance with breeding numbers and their density was high along the coast, where roosting sites are probably numerous. Finally, Magnificent Frigatebirds were aggregated around *Grand Connétable* Island; hence a significant amount of the population was probably breeding during the survey.

In the Antilles, seabird densities were higher close to the islands and probably related to the proximity of colonies. Indeed, depending on survey synchrony with the breeding season, location of breeding colonies was shown to have a strong influence on seabird at-sea distribution (Ballance et al., 1997; Ford et al. 2004; Jaquemet et al. 2005; Smith and Hyrenbach, 2003). In contrast, offshore aggregations could be related to feeding opportunities. For example, there was a high density of brown terns South of Martinique where there are important colonies (*Ilets et falaises de St Anne* and *Rocher du Diamant*) hosting 7000 to 24,000 *S. fuscata* (Lemoine and Dubief, 2008). The aggregation of tropicbirds observed around Marie Galante can be related to a known colony hosting 450 to 900 *P. aethereus* (Levesque and Mathurin, 2008). Similarly, the high density of brown boobies East of Guadeloupe might be due to the vicinity of a *S. leucogaster* colony (Levesque and Mathurin, 2008). The distribution of brown terns and tropicbirds was much more pelagic compared to brown boobies, which are mainly inshore feeders (Harrison, 1991).

4.2.3. Elasmobranchs and sea turtles

In Guiana, we had some data on manta rays' distribution. Their strong aggregation could be related to a local feeding opportunity. In Venezuela, aerial surveys showed that manta ray occurrence was highly predictable and related to an enhanced productivity (Luiz et al., 2009; Notarbartolo-di-Sciara and Hillyer, 1989). We documented sea turtle distribution in both regions. The estuary of the Maroni River at the border of French Guiana and Surinam hosts one of the world's largest leatherback turtle nesting populations (Fossette et al., 2008). However, sea turtles studies in Guiana have mainly focused on nest monitoring (Kelle et al., 2007), demography (Rivalan et al., 2006) and foraging and diving strategy based on tagging (Fossette et al., 2008).

4.3. Contrasting communities in the Antilles and Guiana

Our study revealed differences in megavertebrate communities between two regions of contrasted oceanography and productivity

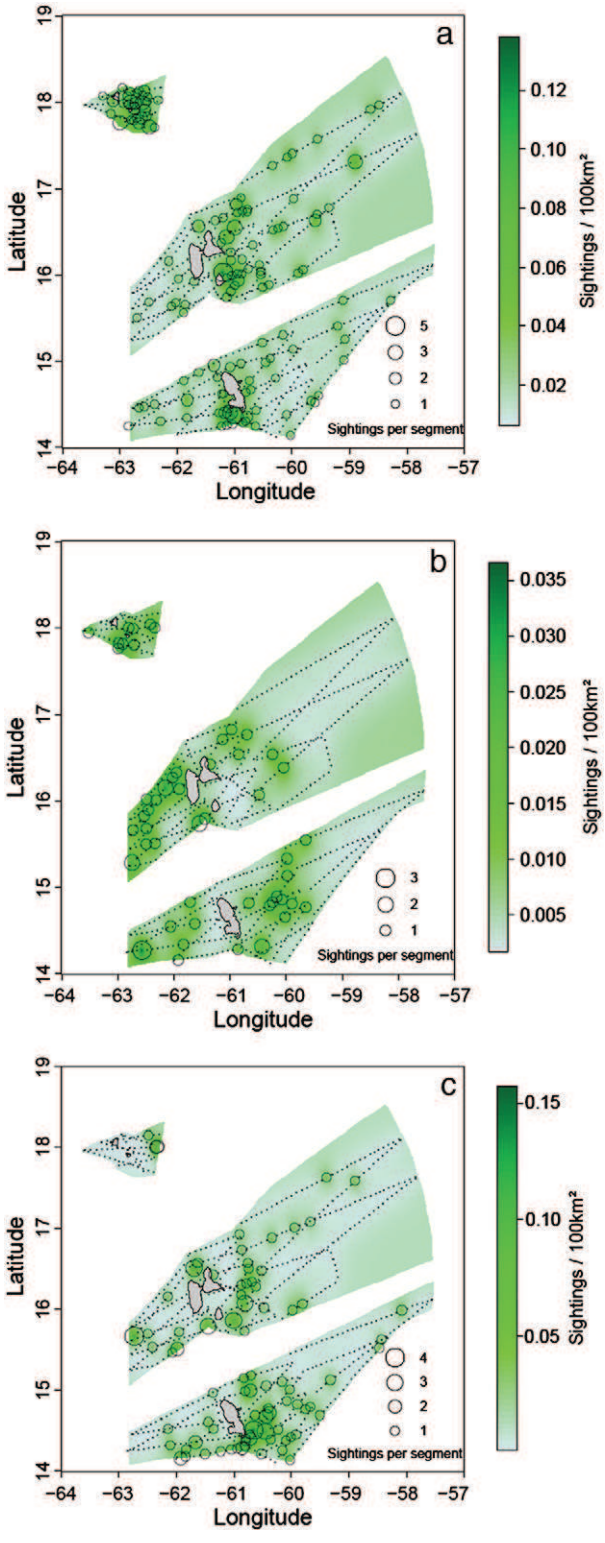


Fig. 5. Local density of sightings for tropicbirds (a), brown boobies (b) and brown terns (c) in the Antilles. Transects were divided in 10 km segments for the analysis. Analytical details of the geostatistical approach are given in Appendix C.

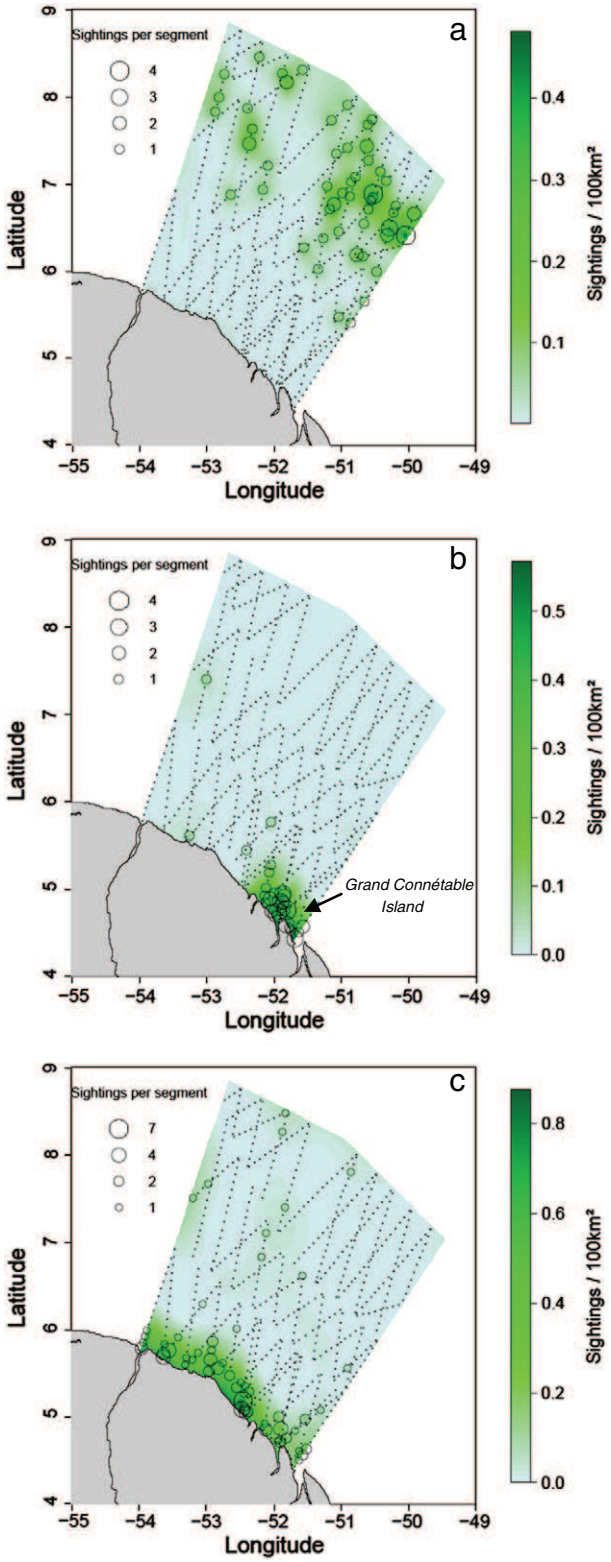


Fig. 6. Local density of sightings for Sooty tern (a), Magnificent Frigatebird (b) and gray terns (c) in Guiana. Transects were divided in 10 km segments for the analysis. Analytical details of the geostatistical approach are given in Appendix C.

in the western tropical Atlantic. We focus our discussion on seabirds and odontocetes.

Seabird encounter rate was similar in the Antilles and Guiana. Charadriiformes were frequently encountered and dominated by terns in both regions. Procellariiformes were rare in both regions. However, Pelecaniformes were more frequently encountered in the Antilles and represented by frigatebirds, boobies and tropicbirds, whereas they were mainly represented by frigatebirds in Guiana.

Previous studies have shown that productivity affected seabird community structure at the macro scale (1000 s of km) (Ballance et al., 1997; Hyrenbach et al., 2007; Schick et al., 2011; Smith and Hyrenbach, 2003). For example, Ballance et al. (1997) studied seabird

communities along a productivity gradient in the eastern tropical Pacific. Sooty terns foraged in waters of low productivity, Juan Fernandez Petrels (*Pterodroma externa*) and Wedge tailed shearwaters (*Puffinus pacificus*) in waters of intermediate productivity and red footed (*S. sula*) and masked boobies (*Sula dactylatra*) in waters of higher productivity. This was in accordance with costs of flight values which were the lowest for Sooty terns, intermediate for Procellariiformes and high for red footed boobies (Ballance, 1995; Flint and Nagy, 1984). They concluded that this community was structured by energetic constraint. In contrast, in our study, Sooty terns were abundant in both high productivity (Guiana) and low productivity (Antilles) regions and boobies were only abundant in the low productivity region. Hence our results appear to be in discordance with Ballance et al. (1997). However, the high proportion of tropicbirds within the Antillean seabird community seems to be in accordance with (Vichis et al. (2006)) who showed that tropicbirds selected habitats with low surface chlorophyll.

Nevertheless, productivity is not the only factor affecting seabird distribution. Indeed, as seabirds are constrained to breed on land, the availability of substrate and the size of the colonies may also be strong determinants of at sea communities during the breeding season (Hertel and Ballance, 1999). This could strongly influence the patterns of seabird distribution and at-sea community composition. In particular, the limited space available to breeding seabirds in Guiana (only represented by the *Grand Connétable* Island from the Amazon to the Orinoco, Bird Life International, 2012) may have promoted competition for nest sites. Hence the low abundance of boobies and tropicbirds in Guiana may be related to the absence of appropriate breeding sites. Nevertheless, this does not alter the fact that both regions are inhabited by seabirds with flight patterns based on energy saving (*e.g.* Magnificent Frigatebirds and red footed boobies), which can exploit at low costs the overall low and scattered food resources of tropical oceans (Weimerskirch et al., 2003, 2005).

The encounter rate of cetaceans was 3 times higher in Guiana compared to the Antilles (5 times higher in terms of individuals). In Guiana, small delphinids strongly dominated the odontocete community (representing 82.6% of the sightings), with bottlenose dolphins being particularly abundant. In contrast, in the Antilles, the odontocete community was more equally partitioned between small delphinids, large delphinids and sperm and beaked whales. However, we must keep in mind that physiographic habitats were different in both regions (seafloor topography was complex around the Antilles with narrow insular shelf and slope whereas the continental shelf was wide in Guiana).

Many studies have shown that high productivity areas are associated with high densities of cetaceans (*e.g.* Ballance et al., 2006; Cañadas et al., 2005; Jaquet and Whitehead, 1996; Tynan et al., 2005). Conversely, oligotrophic regions are characterized by a low density of cetaceans (*e.g.* the Bahamas, MacLeod et al., 2004). Hence the much higher encounter rate of cetaceans in Guiana may be related to the higher productivity in that region.

The structure of cetacean communities may change according to productivity. For example, Schick et al. (2011) studied the cetacean community from Nova Scotia to the Gulf of Mexico and described two groups of cetaceans separated along a surface chlorophyll gradient. Piscivorous were found in the cooler, more productive waters of the continental shelf and teuthophagous in offshore, warmer and less productive waters at the shelf break. In Guiana, the dominance of small delphinids, which are limited by their physiology to shallow diving (Williams et al., 1993) and are mainly piscivorous (Pauly et al., 1998), may be related to more abundant food resources in the epipelagic layer. Furthermore, the dominance of bottlenose dolphins within small delphinids in Guiana may result from a competitive exclusion of similar species, as seen in the Bahamas (MacLeod et al., 2004). In contrast, in the Antilles, sperm and beaked whales accounted for a greater proportion of the odontocete community. Sperm whales, which feed on deep squids, were shown to be positively correlated with the intensity and thickness of middle and deep scattering layers (Jaquet and Whitehead, 1996). Hence, despite the oligotrophy of the epipelagic waters in the Caribbean province (Longhurst, 2007), secondary productivity may be greater in deeper layers, promoting feeding opportunities for deep diving teuthophagous cetaceans. Hence, the observed patterns of odontocetes communities between both regions may be the result of a differential location of prey resources (in surface waters in Guiana and in deeper layers in the Antilles).

As raised by Ballance et al. (1997), the energetic cost of foraging may be a strong determinant of community structure. Unfortunately, few studies on cetacean metabolic rates are available (mostly for dolphins in captivity, Kastelein et al., 2002) compared to seabirds. Small delphinids, characterized by a small size and a high cost of transport (Costa and Williams, 1999), may have greater costs of foraging compared to sperm and beaked whales. Moreover, diet studies have shown that a small delphinid, the common dolphin (*Delphinus delphis*) selected high energy density preys to meet its energetically expensive life style (Spitz et al., 2010). We can extrapolate this at the spatial scale and hypothesize that small delphinids may be constrained to forage in the most productive habitats of the oceans to meet their high energetic needs.

4.4. Conclusion

This study provided new information about megavertebrates which are poorly documented in the Antilles and Guiana and also highlighted differences in odontocete and seabird communities between these contrasting ecosystems. In order to obtain a more complete picture of communities, it would be useful to implement the aerial survey regionally, from Guiana to the whole Antillean Arc. This would allow investigating communities along a more continuous productivity gradient. Further, we could examine community structure in relation to micronekton, which is at a higher trophic level than productivity. Unfortunately, micronekton sampling, either from trawling or acoustics studies is not available at the scale of the region. However, ecosystemic models, which estimate the biomass of micronekton in different depth layers (Lehodey et al., 2010), can provide information on prey biomasses available to deep diving and shallow diving cetaceans. This would allow testing if the contrasted cetacean communities between the Antilles and Guiana could be effectively related to a differential distribution of resources through the water column.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jmarsys.2012.11.002.

Acknowledgments

The French Ministry in charge of the environment (Ministère de l'Écologie, du Développement durable, des Transports et du Logement, MEDDTL) and the Agency for marine protected areas (Agence des aires marines protégées, AAMP) funded the project. We are indebted to the aircraft crew members of Air Key West, Florida, USA. We are thankful to Gregoire Certain for a preliminary work on distribution and abundance of megafauna in the Antilles and Guiana. We wish to thank our colleagues of Laboratoire LIENSs for fruitful exchanges regarding analyses and interpretations. Finally, we are grateful to Lisa Ballance and an anonymous reviewer who provided valuable comments on the manuscript.

References

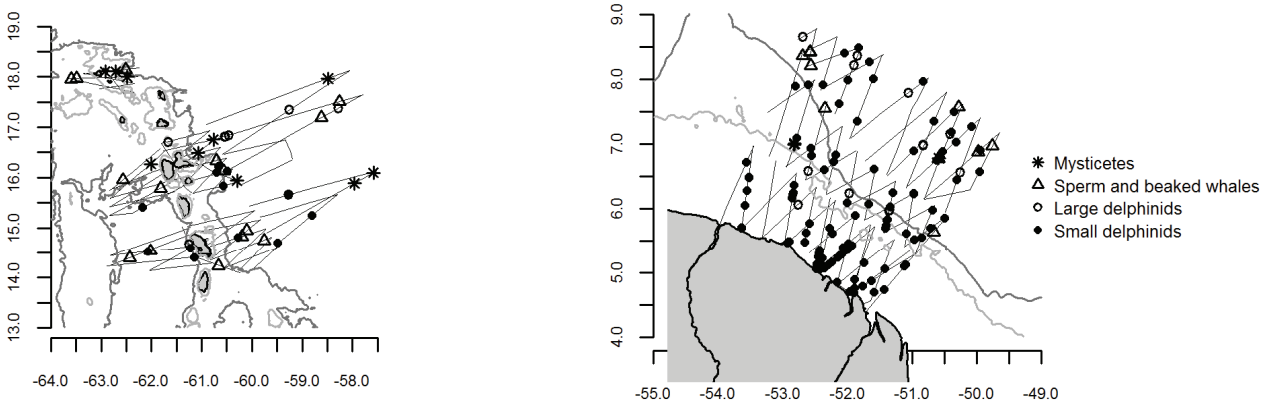
Ballance, L.T., 1995. Flight energetics of free-ranging red-footed boobies (*Sula sula*). Physiol. Zool. 68 (5), 887–914.
Ballance, L.T., 2008. Understanding seabirds at sea: why and how. Mar. Ornithol. 35, 127–135.

Ballance, L.T., Pitman, R.L., 1999. Foraging Ecology of Tropical Seabirds. Proceedings of the 22nd International Ornithological Congress, Durban. BirdLife South Africa, Johannesburg, pp. 2057–2071.
Ballance, L.T., Pitman, R.L., Reilly, S.B., 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78 (5), 1502–1518.
Ballance, L.T., Pitman, R.L., Fiedler, P.C., 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 360–390.
Baumgartner, M.F., et al., 2001. Cetacean habitats in the northern Gulf of Mexico. Fish. Bull.-NOAA 99 (2), 219–239.
Bellier, E., Monestiez, P., 2008. Model based block kriging to estimate spatial abundance of wildlife populations from count data. In: Proceedings of the Eighth International Geostatistics Congress. Julian Ortiz & Xavier Emery, pp. 119–128.
Bellier, E., et al., 2011. Decomposing the heterogeneity of species distributions into multiple scales: a hierarchical framework for large-scale count surveys. Ecography (Available at: http://onlinelibrary.wiley.com/doi/10.1111/j.1600-0587.2011.06456.x/full).
Bird Life International, 2012. Important Bird Areas Factsheet: Connétable. (Downloaded from http://www.birdlife.org).
Borstad, G., 1982. The influence of the meandering Guiana Current and Amazon River discharge on surface salinity near Barbados. J. Mar. Res. 40 (2), 421–433.
Boyd, I.L., Wanless, S., Camphuysen, C.J., 2006. Introduction. In: Boyd, I.L., Camphuysen, C.J. (Eds.), Top Predators in Marine Ecosystems: Their Role in Monitoring and Management. Cambridge University Press, pp. 1–10 (Cambridge).
Boyé, A., et al., 2009. Important Bird Areas — French Overseas Départements and Territories. Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/AmCntryPDFs/French_Guiana.pdf.
Buckland, S.T., et al., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, New York.
Caballero, S., et al., 2007. Taxonomic status of the genus *Sotalia*: species level ranking for "tucuxi" (*Sotalia fluviatilis*) and "costero" (*Sotalia guianensis*) dolphins. Mar. Mamm. Sci. 23 (2), 358–386.
Caballero, S., et al., 2012. Phylogeography, genetic diversity and population structure of common bottlenose dolphins in the Wider Caribbean inferred from analyses of mitochondrial DNA control region sequences and microsatellite loci: conservation and management implications. Anim. Conserv. 15 (1), 95–112.
Cañadas, A., et al., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquat. Conserv. Mar. Freshwat. Ecosyst. 15 (5), 495–521.
Cantor, M., et al., 2012. Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): an eight-year mark-recapture study. Mar. Mamm. Sci. 28 (1), 63–83.
Cardona-Maldonado, M.A., Mignucci-Giannoni, A.A., 1999. Pygmy and dwarf sperm whales in Puerto Rico and the Virgin Islands, with a review of *Kogia* in the Caribbean. Caribb. J. Sci. 35 (1–2), 29–37.
Certain, G., Bretagnolle, V., 2008. Monitoring seabirds population in marine ecosystem: the use of strip-transect aerial surveys. Remote. Sens. Environ. 112 (8), 3314–3322.
Clapham, 2002. Humpback whale. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals, pp. 589–592.
Clarke, E., et al., 2003. Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. J. Appl. Ecol. 40 (2), 278–292.
Costa, D.P., Williams, R., 1999. Marine mammals energetics. In: Reynolds, J.J., Rommel, S.A. (Eds.), Biology of Marine Mammals.
Cunha, H., et al., 2005. Riverine and marine ecotypes of *Sotalia* dolphins are different species. Mar. Biol. 148 (2), 449–457.
Da Silva, V., et al., 2010. Report of the Working Group on distribution, habitat characteristics and preferences, and group size. Lat. Am. J. Aquat. Mamm. 8 (1–2), 31–38.
Davis, R.W., et al., 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Res. Part I 49 (1), 121–142.
Eberhardt, L., 1978. Appraising variability in population studies. J. Wildlife Manage. 42 (2), 207–238.
Edwards, H.H., Schnell, G.D., 2001. Status and ecology of *Sotalia fluviatilis* in the Cayos Miskito Reserve, Nicaragua. Mar. Mamm. Sci. 17 (3), 445–472.
Estes, J., Crooks, K., Holt, R., 2001. Predators, Ecological Role Of. Encyclopedia of Biodiversity, 4. Academic Press, pp. 857–878.
Flint, E.N., Nagy, K.A., 1984. Flight energetics of free-living sooty terns. Auk 101, 288–294.
Flores, P.A.C., DaSilva, V.M.F., 2008. Tucuxi and Guiana dolphin, In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals, 2nd Edition. Academic Press, pp. 1188–1192 (Amsterdam, Netherlands).
Ford, R.G., et al., 2004. The biogeographic patterns of seabirds in the central portion of the California Current. Mar. Ornithol. 32, 77–96.
Fossette, S., et al., 2008. The world's largest leatherback rookeries: a review of conservation-oriented research in French Guiana/Suriname and Gabon. J. Exp. Mar. Biol. Ecol. 356 (1), 69–82.
Froidefond, J., Pujos, M., Andre, X., 1988. Migration of mud banks and changing coastline in French Guiana. Mar. Geol. 84 (1–2), 19–30.
Fulling, G.L., Mullin, K.D., Hubard, C.W., 2003. Abundance and distribution of cetaceans in outer continental shelf waters of the US Gulf of Mexico. Fish. Bull. 101 (4), 923–932.
Furness, R.W., Tasker, M.L., 2000. Seabird–fishery interactions: quantifying the sensitivity of seabirds to reductions in sand eel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar. Ecol. Prog. Ser. 202, 253–264.
Gero, S., et al., 2007. Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the Eastern Carribbean Sea. J. Cetacean Res. Manage. 9 (2), 143–150.
Gibbs, R.J., 1980. Wind-controlled coastal upwelling in the western equatorial Atlantic. Deep-Sea Res. Part I 27 (10), 857–866.
Hammond, P., et al., 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. J. Appl. Ecol. 39 (2), 361–376.
Hammond, P.S., Mc Leod, K., Scheidat, M., 2006. Small Cetaceans in the European Atlantic and North Sea (SCANS-II). Final Report, Saint Andrews.
Harrison, P., 1991. Seabirds: An Identification Guide. Houghton Mifflin Company, Boston.
Hertel, F., Ballance, L.T., 1999. Wing ecomorphology of seabirds from Johnston Atoll. Condor 101 (3), 549–556.
Hiby, L., Lovell, P., 1998. Using aircraft in tandem formation to estimate abundance of harbour porpoise. Biometrics 54 (4), 1280–1289.
Hu, C., et al., 2004. The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: observation from space and S-PALACE floats. Deep-Sea Res. Part II 51 (10–11), 1151–1171.
Hyrenbach, K.D., et al., 2007. Community structure across a large-scale ocean productivity gradient: marine bird assemblages of the Southern Indian Ocean. Deep-Sea Res. Part I 54 (7), 1129–1145.
Jaquemet, S., et al., 2005. Foraging habitats of the seabird community of Europa Island (Mozambique Channel). Mar. Biol. 147, 573–582.
Jaquet, N., Whitehead, H., 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Mar. Ecol. Prog. Ser. 135, 1–9.
Johns, W., et al., 1998. Annual cycle and variability of the North Brazil Current. J. Phys. Oceanogr. 28 (1), 103–128.
Kastelein, R.A., et al., 2002. Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Mar. Environ. Res. 53 (2), 199–218.
Kelle, L., et al., 2007. Monitoring of nesting Leatherback Turtles (*Dermochelys coriacea*): contribution of remote sensing for real-time assessment of beach coverage in French Guiana. Chelonian Conserv. Biol. 6 (1), 142–147.
Laake, J., et al., 1997. Probability of detecting harbor porpoise from aerial surveys: estimating g(0). J. Wildlife Manage. 61 (1), 63–75.
Lehodey, P., Murtugudde, R., Senina, I., 2010. Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. Prog. Oceanogr. 84, 69–84.
Lemoine, V., Dubief, L., 2008. Important Bird Areas in the Caribbean — Martinique. Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/CaribCntryPDFs/martinique_%28to_france%29.pdf.
Levesque, A., Mathurin, A., 2008. Important Bird Areas in the Caribbean — Guadeloupe. Downloaded from http://www.birdlife.org/datazone/userfiles/file/IBAs/CaribCntryPDFs/guadeloupe_%28to_france%29.pdf.
Longhurst, A.R., 2007. Ecological Geography of the Sea. Academic Press, Oxford.
Longhurst, A.R., Pauly, D., 1987. Ecology of Tropical Oceans. Academic Press, Oxford.
Luiz, O.J., et al., 2009. Seasonal occurrences of *Manta birostris* (Chondrichthyes: Mobulidae) in southeastern Brazil. Ichthyol. Res. 56 (1), 96–99.
MacLeod, C.D., Hauser, N., Peckham, H., 2004. Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. J. Mar. Biol. Assoc. UK 84 (02), 469–474.
MacLeod, C.D., et al., 2007. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? Biol. Lett. 3 (2), 185–188.
Mignucci-Giannoni, A.A., 1998. Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. Caribb. J. Sci. 34 (3–4), 173–190.
Monestiez, P., et al., 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. Ecol. Model. 193 (3–4), 615–628.
Monteiro-Filho, E.L.A., Monteiro, L.R., Reis, S.F., 2002. Skull shape and size divergence in dolphins of the genus *Sotalia*: a tridimensional morphometric analysis. J. Mammal. 83 (1), 125–134.
Notarbartolo-di-Sciara, G., Hillyer, E.V., 1989. Mobulid rays off eastern Venezuela (Chondrichthyes, Mobulidae). Copeia 607–614.
Pauly, D., Christensen, V., Trites, A.W., 1998. Diet composition and trophic levels of marine mammals. ICES J. Mar. Sci. 55, 467–481.
Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food web patterns and their consequences. Nature 350 (6320), 669–674.
Pollock, K.H., et al., 2006. Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. J. Wildl. Manage. 70 (1), 255–262.
Redfern, J.V., et al., 2008. Absence of scale dependence in dolphin-habitat models for the eastern tropical Pacific Ocean. Mar. Ecol. Prog. Ser. 363, 1–14.
Reid, K., et al., 2005. Antarctic Ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES J. Mar. Sci. 62 (3), 366–373.
Rivalan, P., et al., 2006. Demographic scenario inferred from genetic data in leatherback turtles nesting in French Guiana and Suriname. Biol. Conserv. 130 (1), 1–9.
Rossi-Santos, M., Wedekin, L.L., Sousa-Lima, R.S., 2006. Distribution and habitat use of small cetaceans off Abrolhos Bank, eastern Brazil. Lat. Am. J. Aquat. Mamm. 5 (1), 23–28.
Schick, R., et al., 2011. Community structure in pelagic marine mammals at large spatial scales. Mar. Ecol. Prog. Ser. 434, 165–181.
Smith, J.L., Hyrenbach, K.D., 2003. Galapagos Islands to British Columbia: seabird communities along a 9000 km transect from the tropical to the subarctic eastern Pacific Ocean. Mar. Ornithol. 31 (2), 155–166.
Soto, K.H., Trites, A.W., Arias-Schreiber, M., 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. J. Zool. 264 (4), 419–428.
Spitz, J., et al., 2010. Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. J. Exp. Mar. Biol. Ecol. 390 (2), 73–77.

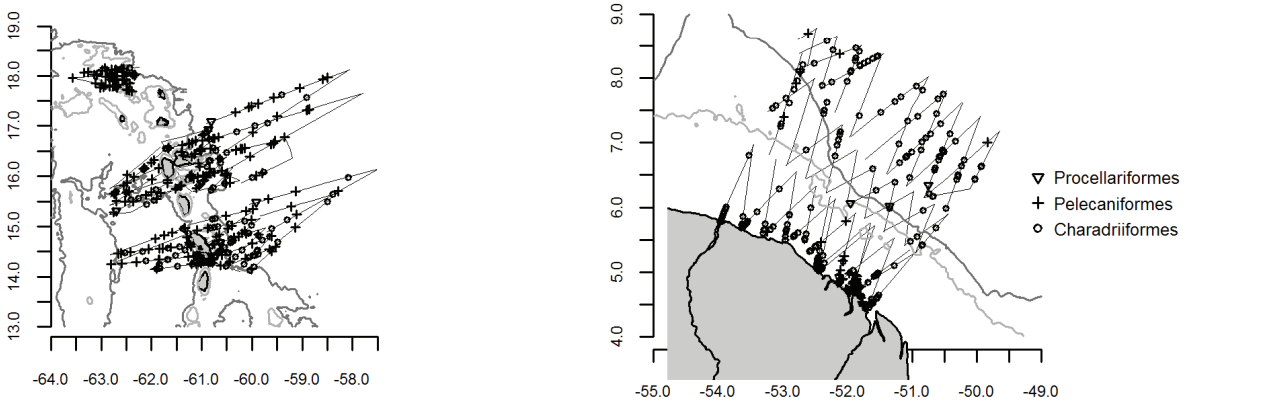
Strindberg, S., Buckland, S.T., 2004. Zigzag survey designs in line transect sampling. J. Agric. Biol. Environ. Stat. 9 (4), 443–461.
Surman, C., Wooller, R., 2003. Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. J. Zool. 259 (3), 219–230.
Swartz, S.L., et al., 2003. Acoustic and visual survey of humpback whale (*Megaptera novaeangliae*) distribution in the eastern and southeastern Caribbean Sea. Caribb. J. Sci. 39 (2), 195–208.
Tasker, M.L., et al., 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. The Auk 101 (3), 567–577.
Thomas, L., et al., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. 47 (1), 5–14.
Torres, D., Beasley, C., 2003. Pattern of use of a small bay in northern Brazil by *Sotalia guianensis* (Cetacea: Delphinidae). Amazoniana 17 (3), 583–594.
Tynan, C.T., et al., 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep-Sea Res. Part II 52 (1–2), 145–167.
Van der Meer, J., Leopold, M.F., 1995. Assessing the population size of the European storm petrel (*Hydrobates pelagicus*) using spatial autocorrelation between counts from segments of criss-cross ship transects. ICES J. Mar. Sci. 52 (5), 809–818.
VanWaerebeek, K., 1990. Preliminary notes on the existence of a dolphin by-catch off French Guiana. Aquat. Mamm. 16 (2), 71–72.
Vilchis, L.I., Ballance, L.T., Fiedler, P.C., 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. Mar. Ecol. Prog. Ser. 315, 279–292.
Wackernagel, H., 2003. Multivariate Geostatistics, 3rd éd. Springer Verlag, Berlin Heidelberg.
Ward, N., Moscrop, A., Carlson, C., 2001. Elements for the development of a marine mammal action plan for the wider Caribbean: a review of marine mammal distribution. UNEP document. First Meeting of the Contracting Parties (COP) to the Protocol Concerning Specially Protected Areas and Wildlife (SPAW) in the Wider Caribbean Region. United Nations Environment Programme, (Havana, Cuba).
Waring, G.T., et al., 2000. US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments — 2002. US Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Region, Northeast Fisheries Science Center.
Wedekin, L.L., Daura-Jorge, F.G., Simões-Lopes, P.C., 2010. Habitat preferences of Guiana dolphins, *Sotalia guianensis* (Cetacea: Delphinidae), in Norte Bay, southern Brazil. J. Mar. Biol. Assoc. U. K. 90 (8), 1561–1570.
Weimerskirch, H., et al., 2003. Flight performance: frigatebirds ride high on thermals. Nature 421 (6921), 333–334.
Weimerskirch, H., et al., 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? Proc. R. Soc. Lond. B Biol. Sci. 272 (1558), 53–61.
Weimerskirch, H., et al., 2006. Postbreeding movements of frigatebirds tracked with satellite telemetry. Condor 108 (1), 220–225.
Whitehead, H., Moore, M.J., 1982. Distribution and movements of West Indian humpback whales in winter. Can. J. Zool. 60 (9), 2203–2211.
Williams, T., et al., 1993. Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). Symposia of the Zoological Society of London, pp. 383–394.
Williams, R., Thomas, L., 2007. Distribution and abundance of marine mammals in the coastal waters of British Columbia. Canada. J. Cetacean Res. Manage. 9 (1), 15–28.
Winn, H., Edel, R., Taruski, A., 1975. Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. J. Fish. Res. Board Can. 32 (4), 499–506.
Yoshida, H., et al., 2010. Cetacean sightings in the eastern Caribbean and adjacent waters, spring 2004. Aquat. Mamm. 36 (2), 154–161.
Zacharias, M.A., Roff, J.C., 2001. Use of focal species in marine conservation and management: a review and critique. Aquat. Conserv. Mar. Freshwat. Ecosyst. 11 (1), 59–76.

Appendix A: Distribution of cetaceans (1), seabirds (2) and other megavertebrates (3) in the Antilles (right) and in Guiana (left). 200m (light gray) and 2000m (dark gray) isobaths are shown.

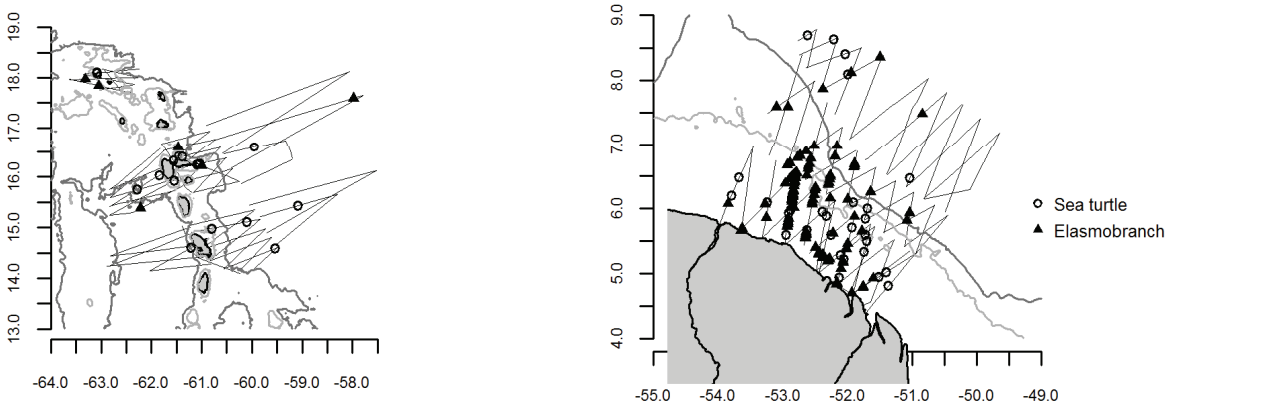
1



2



3



Appendix B: Analytical details of the distance sampling approach

Study region	Taxon	Truncation distance (m)	Fitted detection model	Effective strip width (m)	Mean group size
Antilles	Magnificent frigatebird	500	Uniform	500	Calculated for the whole region
	Tropicbirds	500	Uniform	500	Calculated for the whole region
	Brown bobbies	500	Uniform	500	Calculated for the whole region
	Brown terns	500	Uniform	500	Calculated per stratum
Guiana	Bottlenose dolphin	500	Hazard rate (σ=305.2, β=3.364)	356.21	Calculated per stratum
	Guiana dolphin	300	Half normal (σ=142.8)	172.63	Calculated for the whole region
	Magnificent frigatebird	150	Uniform	150	Calculated for the whole region
	Sooty tern	150	Uniform	150	Calculated per stratum
	Gray terns	150	Uniform	150	Calculated for the whole region
	Manta ray	450	Hazard rate (σ=232.4, β=3.110)	283.25	Calculated for the whole region
	Cheloniidae	400	Uniform	400	Calculated for the whole region

Formula for the fitted detection models:

$$Uniform: g(x) = 1, x \le w$$

$$Half-normal: g(x) = \exp\left\{-x^2 / 2\sigma^2\right\}, x \le w$$

$$Hazard-rate: g(x) = 1 - \exp\left\{-(x/\sigma)^{-\beta}\right\}, x \le w$$

Appendix C: Analytical details of the geostatistical approach

Study region	Taxon	Fitted variogram model	Variogram parameters		
			c_0	c_1	a
Antilles	Tropicbirds	Exponential	0	$7.92.10^{-4}$	10
	Brown bobbies	Exponential	0	$1.2.10^{-4}$	20
	Brown terns	Exponential	0	$1.03.10^{-3}$	15.36
Guiana	Bottlenose dolphin	Pure nugget effect	$1.7\ 10^{-4}$	_	_
	Guiana dolphin	Exponential	0	0.0020	78.07
	Magnificent frigatebird	Spherical and	0	0.0019	17
		Gaussian	0	0.023	100
	Sooty tern	Exponential	0	0.0074	18.92
	Gray terns	Spherical and	0	0.0041	14
		Gaussian	0	0.063	100
	Manta ray	Exponential	0	0.0209	23.12
	Cheloniidae*	Pure nugget effect	$2.5\ 10^{-4}$ (neritic) $8.7\ 10^{-5}$ (slope) $9.7\ 10^{-5}$(oceanic)	_	_

*For Cheloniidae due to non stationarity, a variogram model was fitted for each stratum

Formula for the fitted variogram models:

$$\text{Pure Nugget Effect}: \gamma(h) = c_0 \text{ if } h > 0;\ \gamma(h) = 0 \text{ if } h = 0$$

$$\text{Exponential}: \gamma(h) = c_0 + c_1(1 - \exp(-|h|/a))$$

$$\text{Gaussian}: \gamma(h) = c_0 + c_1(1 - \exp(-|h|/a)^2)$$

$$\text{Spherical}: \gamma(h) = c_0 + c_1(3|h|/2a - |h|^3/2a^3) \text{ if } h \le a;\ \gamma(h) = c_0 + c_1 \text{ if } h > a$$

ANNEX 2

Predicting top predator habitats in the Southwest Indian Ocean

Laura Mannocci, Sophie Laran, Pascal Monestiez, Ghislain Dorémus, Olivier Van Canneyt, Pierre Watremez, Vincent Ridoux

Ecography, 2013, 36 : 001-018

Ecography 36: 001–018, 2013
doi: 10.1111/j.1600-0587.2013.00317.x

Subject Editor: Mikko Mönkkönen. Accepted 30 July 2013

Predicting top predator habitats in the Southwest Indian Ocean

Laura Mannocci, Sophie Laran, Pascal Monestiez, Ghislain Dorémus, Olivier Van Canneyt, Pierre Watremez and Vincent Ridoux

L. Mannocci (laura.mannocci@univ-lr.fr) and V. Ridoux, Laboratoire Littoral Environnement et Sociétés, UMR 7266 Univ. de La Rochelle-CNRS, Inst. du Littoral et de l'Environnement, FR-17000 La Rochelle, France. – S. Laran, G Dorémus, O. Van Canneyt and VR, Observatoire PELAGIS, UMS 3462 Univ. de La Rochelle-CNRS, Systèmes d'Observation pour la Conservation des Mammifères et des Oiseaux Marins, FR-17000 La Rochelle, France. – P. Monestiez, INRA, UR0546, Unité Biostatistiques et Processus Spatiaux, Domaine Saint-Paul, FR-84914 Avignon, France. – P. Watremez, Agence des Aires Marines Protégées, 44 bis quai de la douane, FR-29229 Brest cedex 2, France.

Top predators need to develop optimal strategies of resources and habitats utilization in order to optimize their foraging success. At the individual scale, a predator has to maximize his intake of food while minimizing his cost of foraging to optimize his energetic gain. At the ecosystem scale, we hypothesized that foraging strategies of predators also respond to their general energetic constraints. Predators with energetically costly lifestyles may be constrained to select high quality habitats whereas more phlegmatic predators may occupy both low and high quality habitats. The objectives of this study were 1) to investigate predator responses to heterogeneity in habitat quality with reference to their energetic strategies and 2) to evaluate their responses to contemporaneous versus averaged habitat quality. We collected cetacean and seabird data from an aerial survey in the Southwest Indian Ocean, a region characterized by heterogeneous oceanographic conditions. We classified cetaceans and seabirds into energetic guilds and described their habitats using remotely sensed covariates at contemporaneous and time-averaged resolutions and static covariates. We used generalized additive models to predict their habitats at the regional scale. Strategies of habitat utilization appeared in accordance with predators energetic constraints. Cetaceans responded to the heterogeneity in habitat quality, with higher densities predicted in more productive areas. However, the costly Delphininae appeared to be more dependent on habitat quality (showing a 1-to-13 ratio between the lowest and highest density sectors) than the more phlegmatic sperm and beaked whales (showing only a 1-to-3 ratio). For seabirds, predictions primarily reflected colony locations, although the colony effect was stronger for costly seabirds. Moreover, our results suggest that predators may respond better to persistent oceanographic features. To provide a third dimension to habitat quality, cetacean strategies of utilization of the vertical habitat could be related to the distribution of micronekton in the water column.

Top marine predators, such as cetaceans and seabirds, are large marine vertebrates which occupy food webs' highest trophic levels (Estes et al. 2001). Top predators need to develop optimal strategies of resources and habitats utilization in order to optimize their foraging success. Indeed, this may represent the principal selection pressure on these organisms for which the risk of predation is generally low (Pimm et al. 1991). According to the optimal foraging theory (MacArthur and Pianka 1966), a predator has to maximize its intake of food while minimizing its cost of foraging in order to optimize its energetic gain.

At the individual scale, Spitz et al. (2012) showed that energetically costly cetaceans, such as the common dolphin *Delphinus dephis*, select high quality preys (i.e. of high energetic content) whereas the more phlegmatic sperm and beaked whales, meet their needs by feeding on lower quality preys. At the ecosystem scale, energetic constraints may also shape the selection of habitat. For example, Ballance et al. (1997) showed that seabirds were structured along a productivity gradient in the eastern tropical Pacific; seabirds with the highest costs of flight selecting high quality habitats (i.e. of high productivity).

As data on prey resources are often limited, lower trophic levels (phytoplankton) and other oceanographic parameters which can be inferred from remote sensing sources (surface productivity, sea surface temperature, sea level anomaly… etc.), have been widely used to characterize habitat quality (Vilchis et al. 2006, Becker et al. 2010). In addition, in the highly dynamic marine ecosystems, spatial variability is observed from several to hundreds of kilometers and temporal variability, from diel to decadal scales. The choice of resolution, either spatial or temporal, is critical when modeling habitat and depends on the data collected and the question being addressed (Redfern et al. 2006). The influence of spatial resolution in habitat models has been more investigated (Redfern et al. 2008) than the influence of temporal

resolution, which is nevertheless an important issue. Indeed, pelagic habitats are distinguished by different predictabilities in time and characterized by static (geographically fixed), persistent (high predictability) and ephemeral (low predictability) features (Hyrenbach et al. 2000). Hence, we can wonder if top predators better respond to either short-term variations of oceanographic conditions or time-averaged situations.

In this study, we hypothesize that foraging strategies of top predators over large spatial domains are in accordance with their general energetic constraints. Thus, predators with energetically costly life styles may be constrained to select high quality habitats and conversely, more phlegmatic predators may occupy both low and high quality habitats. The first objective of this study, focusing on cetaceans and seabirds, was to investigate their responses to spatial heterogeneity in habitat quality and relate these distributional properties to energetic strategies. Heterogeneity was defined here as the spatially structured variability of the property of interest (Wagner and Fortin 2005). As central place foragers, seabirds are constrained to colonies during the breeding season and their at-sea distributions may primarily reflect colony locations (Hyrenbach et al. 2007). Nevertheless, the largest colonies should be situated in areas where recurrent resources are easily accessible year after year and thus colony locations may reflect long-term habitat quality. As a result, seabirds may exhibit more complex responses to habitat quality compared to cetaceans. The second objective was to evaluate cetacean and seabird responses to different levels of temporal integration of habitat covariates, and more precisely to investigate their responses to contemporaneous versus averaged habitat quality.

We collected cetacean and seabird data during a multispecific aerial survey in the Southwest Indian Ocean (SWIO). As a tropical region, it has an overall low productivity and scarce food resources (Longhurst and Pauly 1987). Nevertheless, the SWIO encompasses three biogeographic provinces characterized by heterogeneous oceanographic conditions (Longhurst 2007). The Mozambique Channel is characterized by very dynamic mesoscale eddies (De Ruijter et al. 2004), generating productivity enhancements (TewKai and Marsac 2009). Surface productivity is contrasted in the rest of the region, with oligotrophic waters in the south (oceanic waters located east of Madagascar and around the Mascarene Islands) and richer waters to the north (around the Seychelles plateau) (New et al. 2005). We relied on remotely sensed covariates as well as static covariates to characterize top predator habitats.

In order to classify seabirds and cetaceans into energetic guilds, either direct metabolic measurements or reliable indicators of energetic costs can be used. For seabirds, direct energetic measurements are available (Flint and Nagy 1984). Conversely, there are very few direct measures of cetacean metabolic rates (mostly for dolphins in captivity, Kastelein et al. 2002); or a few cases of trained animals performing measurable effort in the wild (Williams et al. 1993). Nevertheless, diving performances of cetaceans are closely related to their capacity to save oxygen owing to reduced metabolic rates (Boyd 1997), and hence can be considered as a good indicator of energetic costs. On a different yet related point of view, it was also shown that cetaceans could be categorized as having high, medium or low costs of living on the basis of muscular mitochondrial density and lipid content (Spitz et al. 2012).

In this study, we used generalized additive models (GAMs) along with time-averaged oceanographic covariates and static covariates in order to predict cetacean and seabird habitats at the regional scale in the SWIO. We evaluated their responses to the heterogeneity in habitat quality within this vast region in order to test our energetic hypothesis. Then, we investigated top predator reactions to shorter term variations in oceanographic conditions.

Material and methods

Study region

Our study region covers more than 1.4 million km² in the SWIO and encompasses the Exclusive Economic Zone of the five countries of the Indian Ocean Commission: Comoros, Madagascar, Mauritius, Reunion (France) and the Seychelles, as well as waters around the Island of Mayotte and the Scattered Islands (Fig. 1a).

The Indian Ocean is characterized by a seasonal reversal of the monsoon winds which has resulting effects on surface currents (Tomczak and Godfrey 2003). During the northwest monsoon (austral summer), the East African coast current (EACC) meets the Somali Current (SC) and supplies the South Equatorial Countercurrent (SECC) flowing westeast. The South Equatorial Current (SEC) separates into two branches at the coast of Madagascar (near 17°S), generating the Northeast Madagascar Current (NEMC), passing to the north of Madagascar and the Southeast Madagascar Current (SEMC) (Schott and McCreary 2001). The SEC forms a strong boundary between low nutrient subtropical waters in the south (around the Mascarene Islands) and richer waters to the north (Seychelles plateau) (New et al. 2005), where enhanced productivity is associated to mid ocean shallow banks (Longhurst 2007)

The Mozambique Channel is characterized by an important mesoscale activity, notably in its central and southern part. A large anticyclonic cell is present in the Comoros basin and then, along the coasts of Mozambique, a train of anticyclonic and cyclonic eddies (with diameters of 300 km and a frequency of 4 yr^{-1}) propagate to the south (Schouten et al. 2003, De Ruijter et al. 2004). High chlorophyll biomass is almost permanently associated with this eddy field, with slightly higher values during the northwest monsoon. Submarine topography and coastal blooms induced in river plumes around Madagascar likely influence biological enhancements generated by mesoscale activity (Longhurst 2007).

Therefore, the SWIO is characterized by a large range of oceanographic conditions and can be divided into three ecoregions: the Mozambique Channel, the Seychelles and the Mascarenes (including pelagic waters to the east of Madagascar and the Mascarene Islands).

Energetic guilds

We classified cetaceans and seabirds into energetic guilds on the basis of either direct metabolic measurements or

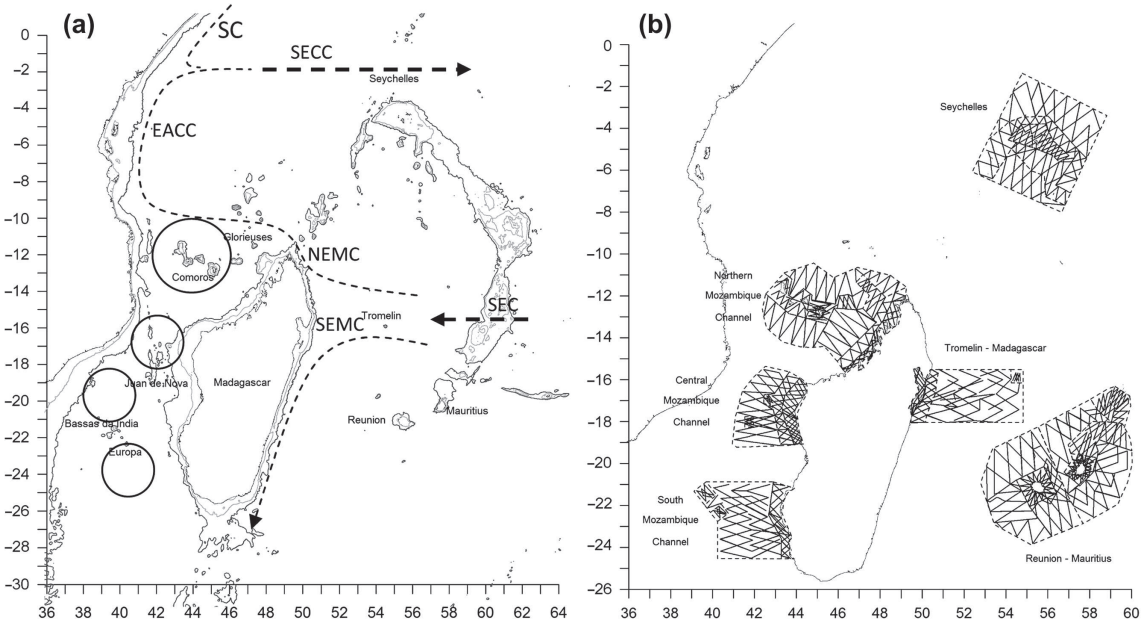


Figure 1. (a) Main surface currents in the Southwest Indian Ocean during austral summer (from Schott and McCreary 2001). SC: Somali Current; EACC: East African coast current; SECC: South Equatorial Countercurrent; SEC: South Equatorial Current; NEMC: Northeast Madagascar Current, SEMC: Southeast Madagascar Current. Circles symbolize major eddies. 200 m (light grey) and 2000 m (dark grey) isobaths are shown. (b) Transects conducted within the six geographic sectors during the aerial survey.

indicators of costs of living from the literature. This general classification of top predator energetic lifestyles may reflect both physiological efficiency and foraging success rate, as these two components are difficult to disentangle in the overall cost of living.

For seabirds, direct metabolic measurements include basal metabolic rate (BMR, measuring resting metabolism) and field metabolic rate (FMR, representing the cost of overall daily activities) (Flint and Nagy 1984). To classify seabirds into energetic guilds, we relied on the FMR/BMR ratio, referred to as sustained metabolic scope (Peterson et al. 1990, which is the capacity to increase metabolism above resting levels). This ratio ranges from 2.8 to 4.2 in tropical seabirds (Ellis and Gabrielsen 2002). From the most phlegmatic to the most energetically costly, we obtained: sooty terns, petrels and shearwaters, boobies, noddies, grey terns and tropicbirds. The FMR/BMR ratio was not available for frigatebirds as no metabolic measurements were made for this guild. However, the extremely low wing loading of frigatebirds (large wing area for a comparatively low body mass) suggests much reduced costs of flight (Weimerskirch et al. 2003). Hence, frigatebirds are considered here as the guild with the lowest cost of living.

For cetaceans, there are few direct metabolic measurements, thus we relied on their diving performances, which are closely related to their capacity to save oxygen and reduce their energetic costs (i.e. hypometabolism, Boyd 1997). The vast majority of cetacean sightings during the survey (conducted in the austral summer) were of odontocetes, so our classification focuses on odontocetes, simply named cetaceans thereafter. Sperm and beaked whales, albeit few data are available for some species, have remarkable abilities for breath-hold diving and can reach depths greater than 1000 m, demonstrating an efficient locomotion behavior during transit to and from foraging depth (Tyack et al. 2006, Watwood et al. 2006) . They should exhibit the lowest costs of living . Globicephalinae generally engage in fairly deep and long dives, as exemplified by the short-finned pilot whale *Globicephala macrorhynchus*; however this species, and perhaps other Globicephalinae, has also been reported to use burst and glide strategies when foraging (Aguilar de Soto et al. 2008). They should have intermediate costs of living. Conversely, Delphininae, such as *Stenella* spp. or bottlenose dolphins, generally engage in shorter and shallower dives no deeper than 300 m (Baird et al. 2001) and their foraging tactic largely relies on active swimming, in particular for cooperative feeding (Benoit-Bird and Au 2009). Hence Delphininae constitute the guild of cetaceans with the most costly lifestyle. This classification is corroborated by indicators of cost of living based on muscle performance as expressed by muscular mitochondrial density and lipid content (Spitz et al. 2012). Twenty-two species of seabirds and seventeen species of cetaceans are represented in the energetic guilds considered in this study (Table 1).

Field methodology

Survey period and survey design

We collected top predator data from a dedicated aerial survey in the SWIO during the austral summer (from December 2009 to April 2010). The study area was stratified into six geographic sectors: Northern Mozambique Channel (NMC, including Comoro and Glorioso Islands), Central Mozambique Channel (CMC, including Juan de Nova), Southern Mozambique Channel (SMC, including Europa and Bassas da India), Seychelles (SE),

Table 1. Description of energetic guilds, ordered from the most phlegmatic to the most energetically costly, for seabirds and cetaceans.

Seabird guilds	
Frigatebirds	great frigatebird *Fregata minor*, lesser frigatebird *Fregata ariel*
Brown terns	sooty tern *Onychoprion fuscatus**, bridled tern *Onychoprion anaethetus*
Petrels and shearwaters	wedge tailed shearwater *Puffinus pacificus*, Barau's petrel *Pterodroma baraui*, Audubon shearwater *Puffinus lherminieri*, mascarene petrel *Pseudobulweria aterrima*, herald petrel *Pterodroma arminjoniana*, flesh-footed shearwater *Puffinus carneipes***
Boobies	red footed booby *Sula sula*, masked booby *Sula dactylatra*, brown booby *Sula leucogaster*
Noddies	brown noddy *Anous stolidus*, lesser noddy *Anous tenuirostris*
Grey terns	lesser crested tern *Sterna bengalensis***, roseate tern *Sterna dougallii*, Caspian tern *Sterna caspia*, black-napped tern *Sterna sumatrana*, crested tern *Thalasseus bergii*
Tropicbirds	white tailed tropicbird *Phaethon lepturus*, red tailed tropicbird *Phaethon rubricauda*
Cetacean guilds	
Sperm and beaked whales	Blainville's beaked whale *Mesoplodon densirostris*, Cuvier's beaked whale *Ziphius cavirostris*, Longman's beaked whale *Indopacetus pacificus*, sperm whale *Physeter macrocephalus*, pygmy sperm whale *Kogia breviceps*, dwarf sperm whale *Kogia sima*
Globicephalinae	pygmy killer whale *Feresa attenuata*, melon-headed whale *Peponocephala electra*, short finned pilot whale *Globicephala macrorhynchus*, false killer whale *Pseudorca crassidens*, Risso's dolphin *Grampus griseus*
Delphininae	Indo Pacific humpback dolphin *Sousa chinensis*, pantropical spotted dolphin *Stenella attenuata*, spinner dolphin *Stenella longirostris*, common bottlenose dolphin *Tursiops truncatus*, Indo-Pacific bottlenose dolphin *Tursiops aduncus*, Fraser's dolphin *Lagenodelphis hosei*

*Largely dominant, **non breeder in the region.

Tromelin – Madagascar (TM) and Reunion – Mauritius (RM) (Fig. 1b). Each sector was subdivided into bathymetric strata corresponding roughly to shelf (0–200 m), slope (200–2000 m) and oceanic domains (> 2000 m). A zigzag survey design was implemented to provide a good spatial coverage within each strata and improved flight efficiency (Buckland et al. 2001).

Aerial survey methods

Transects were flown at a target altitude of 182 m (600 feet) and a ground speed of 167 km h^{-1} (90 knots). Survey platforms were two Britten Norman 2, high-wing, double-engine aircrafts equipped with bubble windows. Survey crew consisted in two trained observers observing with naked eyes and a navigator in charge of data collection on a laptop computer. A GPS, logged to a computer equipped with 'VOR' software (designed for the aerial parts of the SCANS-II survey (Hammond et al. 2013)), collected positional information every 2 s. Beaufort Sea state, glare severity, turbidity, cloud coverage and an overall subjective assessment of detection conditions (good, moderate or poor as for small delphinids) were recorded at the beginning of each transect and whenever any of these values changed.

For cetaceans, we collected data following a distance sampling protocol. Information recorded included identification to the lowest possible taxonomic level, group size and declination angle to the group when it passed at right angle to the aircraft (measured with a hand-held clinometer). Together with the altitude of the aircraft, angles provided perpendicular distances, which allowed distance sampling analyses to be conducted (Buckland et al. 2001). For seabirds, we collected data using the strip transect methodology, with the assumption that all seabirds within the strip were detected (Tasker et al. 1984). Strip width was fixed at 200 m on both sides of the transect. Identification was made to the lowest taxonomic level whenever possible, but groupings were inevitable for seabirds that could not be told apart from the air (e.g. brown terns, composed of the sooty *Onychoprion fuscatus* and the bridled tern and *O. anaethetus*).

Detection function modeling

We used multiple covariate distance sampling (Marques and Buckland 2004) to model the effect of detection covariates on cetacean detection probability, in addition to distance. Before fitting detection functions, we truncated 5% of the most distant sightings, as recommended by Buckland et al. (2001). For each cetacean guild, hazard rate and half normal models were fitted to perpendicular distances and the model that minimized the Akaike information criterion (AIC) was selected. Then, we tested the influence of sea state, glare severity and subjective conditions and retained the detection covariate if it provided a significantly smaller AIC. If a detection covariate was significant, we estimated an effective strip width (ESW) for each of the covariate levels, if not, we estimated a unique ESW. For all seabirds, the ESW was 200 m (a uniform detection function was used, as implied by the strip transect methodology). These analyses were conducted in R with the mrds package (Laake et al. 2011).

Data organization

Surveyed transects were split into legs of identical detection conditions, further divided into 10 km long segments, so that variability in detection conditions and geographic location was small within segments. Over 70% of segments were equal to 10 km but segment lengths varied between 2 and 15 km. To maximize the quality of data for habitat modeling, we ignored segments flown under a deteriorated sea state (greater than 5) and segments shorter than 3 km, and performed the analysis on the remaining 8385 segments. In each segment we compiled the total number of individuals for each top predator guild. Then, we used ArcGIS 10 (ESRI 2010) to co-locate the position of segments with habitat covariates, based on values at their mid points.

Habitat covariates

To model top predator habitats we used oceanographic as well as static covariates (Table 2). As the aerial methodology did not allow the collection of simultaneous in situ oceanographic measurements, we relied on remote sensing data. We considered three temporal resolutions: 1) a short-term or contemporaneous resolution, corresponding to a weekly time period (our finest resolution), 2) a medium-term or seasonal resolution, corresponding to oceanographic conditions averaged over the season of the survey (December 2009–April 2010) and 3) a long-term or climatological resolution, corresponding to oceanographic conditions averaged over the same season (December to April) from 2003 to 2010.

From Ocean color website (<http://oceancolor.gsfc.nasa.gov/>), we obtained surface chlorophyll-a concentration (CHL), sea surface temperature (SST) and photosynthetically available radiation (PAR), derived from aqua-MODIS sensor (4 km spatial resolution). Weekly, seasonal and climatological composites were directly available from the website. We obtained net primary production (NPP) with Windows Image Manager Software (Kahru 2010) using CHL, SST, PAR and the vertically generalized productivity model (Behrenfeld and Falkowski 1997).

Additionally, we used sea level anomalies (SLAs) (0.25 decimal degree spatial resolution), an altimetry product produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<www.aviso.oceanobs.com/duacs/>). We considered the standard error of SLAs as an indicator of mesoscale activity (areas with a high standard error would have a high mesoscale activity; areas with a low standard error would have a low mesoscale activity). Based on weekly SLAs available from the website, we calculated standard errors for the season and the climatology. Oceanographic covariates are mapped on Fig. 2a–d (the climatological resolution is shown).

In addition, we used slope and distance to the nearest colony as static covariates, the latter only for seabirds. Slope was previously identified as a good predictor of cetacean (Ferguson et al. 2006) and seabird (Yen et al. 2004) habitats. We derived slope from GEBCO one minute bathymetric grid (General Physiographic Chart of the Ocean; <www.gebco.net/>) and compiled it in ArcGIS 10 using Spatial Analyst (ESRI 2010). Colony locations have a strong influence on seabird at-sea distribution (Hyrenbach et al. 2007) and distance to colony was shown to be an important predictor in seabird habitat models (Ford et al. 2004). We calculated distance to the nearest colony (D_{colony}) as the shortest distance between the midpoint of each segment and colony location.

For seabirds which disperse outside the breeding season (petrels and shearwaters, tropicbirds (Le Corre et al. 2012) and sooty terns (Jaquemet et al. 2008)), we retained only colonies of summer and year-round reproduction. For sedentary seabirds (boobies, noddies (Le Corre et al. 2012)), we considered all breeding colonies regardless of their seasonality. We also included roosting sites for frigatebirds, as they are known to roost on some islands (Weimerskirch et al. 2006). There may be a large amount of non breeding individuals within grey terns; in particular lesser crested terns *Sterna bengalensis* which do not breed in the SWIO but are abundant along Madagascar coastlines (wintering habitat) (Le Corre pers. comm.). Therefore, for grey terns we preferably used distance to the coast (D_{coast}) instead of distance to the colony. Seabird colonies are located in Fig. 2e and described in Supplementary material Appendix 1.

Table 2. Covariates used to model top predator habitats. Abbreviations and units are provided. Contemporaneous resolution corresponds to a weekly time period, seasonal resolution corresponds to oceanographic conditions averaged over the season of the survey (December 2009–April 2010) and climatological resolution refers to oceanographic conditions averaged over the same season (December to April) from 2003 to 2010.

Oceanographic covariates	
CHL_{cont}	Contemporaneous chlorophyll concentration (mg m^{-3})
CHL_{seas}	Seasonal chlorophyll concentration (mg m^{-3})
CHL_{clim}	Climatological chlorophyll concentration (mg m^{-3})
NPP_{cont}	Contemporaneous net primary production (mgC m^{-3} d^{-1})
NPP_{seas}	Seasonal net primary production (mgC m^{-3} d^{-1})
NPP_{clim}	Climatological net primary production (mgC m^{-3} d^{-1})
SST_{cont}	Contemporaneous sea surface temperature (°C)
SST_{seas}	Seasonal sea surface temperature (°C)
SST_{clim}	Climatological sea surface temperature (°C)
SLA_{cont}	Contemporaneous sea level anomaly (cm)
SLA_{seas}	Seasonal standard error of sea level anomaly (cm)
SLA_{clim}	Climatological standard error of sea level anomaly (cm)
Static covariates	
Slope	Slope (%)
D_{colony}	Distance from the nearest seabird colony (km)
D_{coast}	Distance from the coast (km)

Habitat modeling

Model development

Generalized additive models (GAMs) have been successfully used to model non linear relationships between top predators and environmental covariates and predict their distributions (Ferguson et al. 2006, Vilchis et al. 2006, Becker et al. 2010, Forney et al. 2012). We used GAMs to relate the number of cetaceans and seabirds per segment to habitat covariates. In GAMs, the link function $g()$ relates the mean of the response variable given the covariates $\mu = E(Y|X_1,\ldots,X_p)$ to the additive predictor $\alpha + \sum fi(X_i)$:

$$g(\mu) = \alpha + \sum fi(X_i)$$

The components $fi(X_i)$ of the additive predictor include non parametric smooth functions (splines) of the covariates (Wood and Augustin 2002).

Our response variable Y was the number of individuals. As count data are often characterized by heavy tailed

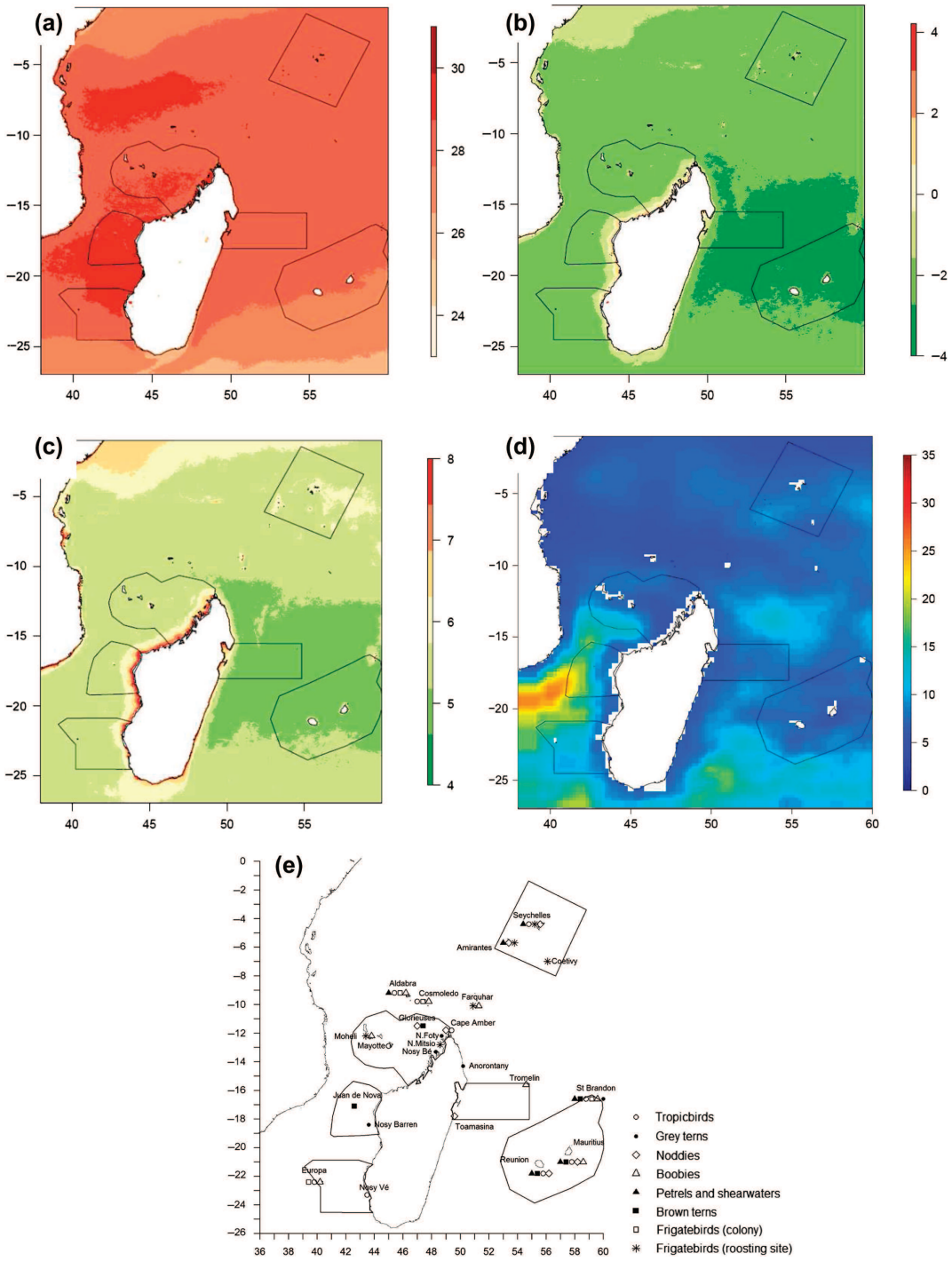


Figure 2. (a–d) Oceanographic covariates used to model top predator habitats ((a) sea surface temperature in °C, (b) chlorophyll concentration (Log) in mg m^{-3}, (c) net primary production (Log) in mgC m^{-3} d^{-1}, (d) standard error of sea level anomaly in cm). The climatological resolution is shown (the seasonal resolution provides very similar maps). (e) Location of seabird colonies (according to: Bretagnolle et al. 2000, Burger and Lawrence 2001, Le Corre 2001, Le Corre et al. 2002, Rocamora et al. 2003, Jaquemet et al. 2004, 2008, Le Corre and Jaquemet 2005, Weimerskirch et al. 2005b, 2010, Feare et al. 2007, Kojadinovic et al. 2008, Catry et al. 2009b, Le Corre and Bemanaja 2009, Russell and Le Corre 2009).

distributions, we used an overdispersed Poisson distribution with variance proportional to the mean and a logarithmic link function. Accounting for non constant effort, we used the logarithm of segment area as an offset, calculated as segment length multiplied by twice the ESW. GAMs were fitted in R using the mgcv package in which degrees of freedom for each smooth function are determined internally in model fitting and thin plate regression splines are the default (Wood 2006). We limited the amount of smoothing to 3 degrees of freedom for each spline to model non linear trends but to avoid overfitting that would have no ecological meaning (Forney 2000).

Model selection

Candidate covariates for model selection were time-averaged oceanographic covariates (seasonal and climatological), as well as static covariates. NPP and CHL were log-transformed, slope was square-root-transformed. For each top predator guild, we fitted the models containing all possible combinations of four covariates, excluding combinations of collinear covariates (i.e. with a Spearman coefficient < 0.6 and > -0.6). We retained the model which had the lowest generalized cross validation (GCV) score. We used explained deviance to evaluate each model's fit to the data. The selected models were used to predict cetacean and seabird distributions.

Predictions

We generated a grid of habitat covariates with a 0.2×0.2 decimal degree resolution. We limited the predictions to a convex hull including the sampled geographic sectors, in which oceanographic conditions encompassed those encountered during the survey. Consequently, we did not predict top predator distributions at the southern tip of Madagascar, characterized by a strong upwelling (Ho et al. 2004), nor for pelagic waters off Kenya and Tanzania. We predicted cetacean and seabird habitats in this convex hull, allowing geographical (between sectors) extrapolation, but without predicting beyond the range of covariates used in model fitting. In addition, for each guild we provided an uncertainty map, as measured by the coefficient of variation. Uncertainty estimations were derived from the Bayesian covariance matrix of the model coefficients within the mgcv package (Wood 2006).

Response to contemporaneous versus averaged oceanographic conditions

In order to investigate top predator responses to contemporaneous versus time-averaged oceanographic conditions, we compared the selected models built with averaged (seasonal and climatological) oceanographic covariates with models built with the same covariates, but at the contemporaneous (weekly) resolution. We replaced time-averaged oceanographic covariates by their contemporaneous equivalents, refitted the models and compared explained deviances (static covariates were unchanged). Better deviance for contemporaneous models would mean that top predators respond to short-term variation of their environment. Conversely, worse deviances would mean that top predators respond better to averaged oceanographic conditions.

Results

Survey effort and detection conditions

The aerial survey covered 83 726 km of transects within the SWIO, with the majority of effort implemented in slope and oceanic strata (Table 3). Overall, detection conditions were very good, with 70% of effort flown at sea state 2 or lower and more than 85% with good to very good subjective conditions. Glare severity was medium to low in 81% of effort. However, sea state was not homogeneous within the region. It was better in the Seychelles (94% of effort with sea state 2 or lower) and in the Mozambique Channel (on average 77%) and comparatively poorer in Tromelin-Madagascar (71%) and Reunion-Mauritius (52%).

Top predator sightings

During the survey a total of 21 317 sightings of seabirds and 1103 sightings of cetaceans were collected, of which 15 725 and 1017 respectively were used in the analyses. Among cetaceans, Delphininae represented the most commonly sighted guild (643 sightings, 9845 individuals), followed by Globicephalinae (232 sightings, 7559 individuals) and sperm and beaked whales (142 sightings, 275 individuals) (Fig. 3, Supplementary material Appendix 2). Delphininae encounter rates were the highest in central Mozambique Channel (1.55 sightings 100 km^{-1}) and in the Seychelles (1.31) and the lowest in Reunion-Mauritius (0.30) and Tromelin-Madagascar (0.18). Globicephalinae were most often encountered in the Mozambique Channel, especially in its central part (0.53 sightings 100 km^{-1}) and the least encountered around Reunion-Mauritius (0.05). In contrast, the probability to find sperm and beaked whales was much less variable between sectors. Encounter rates were the highest in the Seychelles (0.24 sightings 100 km^{-1}) and central Mozambique Channel (0.23) and the lowest in Reunion-Mauritius (0.10).

The most frequently encountered seabirds were brown terns (5990 sightings, 31 109 individuals) and grey terns (4813 sightings, 19 086 individuals) whereas boobies (300 sightings, 535 individuals) and frigatebirds (162 sightings, 519 individuals) were the least commonly sighted (Fig. 3, Supplementary material Appendix 2). Tropicbird encounter rates were the highest in the Seychelles (2.55 sightings 100 km^{-1}) and Reunion-Mauritius (1.86). Grey terns were common in the neritic strata of all sectors and their encounter rate was the highest in the Seychelles (12.77 sightings 100 km^{-1}). However, white terns *Gygis alba* were not differentiated from grey terns in the Seychelles (and therefore

Table 3. Survey effort per geographic sector and bathymetric stratum.

Geographic sector	Neritic	Slope	Oceanic	Total
Northern Mozambique Channel (NMC)	2258 km	6292 km	6648 km	15 198 km
Central Mozambique Channel (CMC)	2445 km	3329 km	4002 km	9776 km
Southern Mozambique Channel (SMC)	–	3549 km	6236 km	9785 km
Seychelles (SE)	2783 km	4658 km	7007 km	14 448 km
Tromelin – Madagascar (TM)	1647 km	6161 km	2624 km	10 432 km
Reunion – Mauritius (RM)	909 km	9548 km	13 630 km	24 087 km
Total	10 042 km	33 537 km	40 147 km	83 726 km

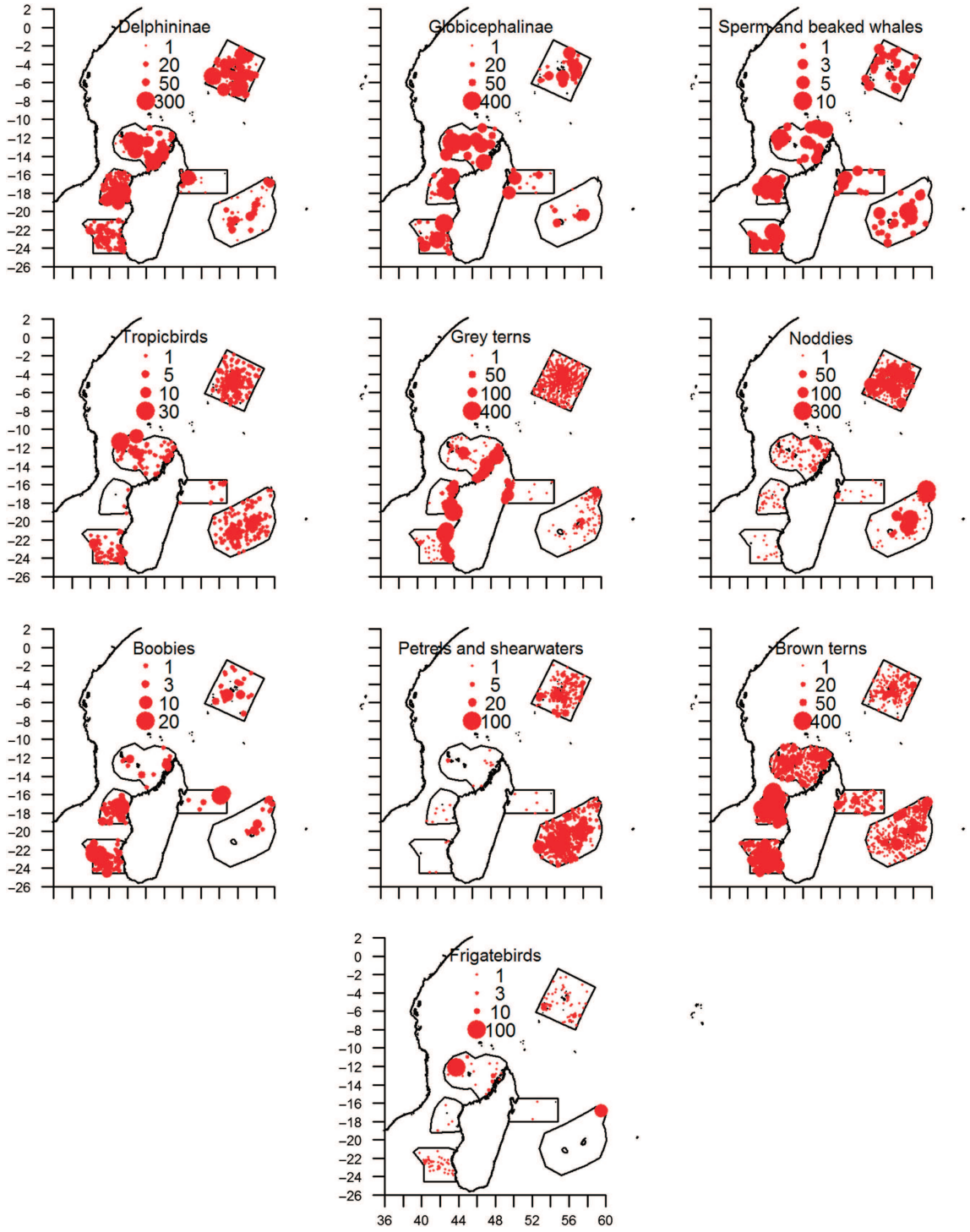


Figure 3. Observed distribution (numbers of individuals per segment) for cetacean and seabird guilds.

we excluded the Seychelles from the prediction of grey terns). Noddies were present in all sectors but more frequent in the Seychelles (6.54 sightings 100 km^{-1}) and Reunion-Mauritius (2.00). Boobies were more frequently encountered in central (1.04 sightings 100 km^{-1}) and southern (1.02) Mozambique Channel. Petrels and shearwaters were almost exclusively encountered around Reunion-Mauritius (5.91 sightings 100 km^{-1}), followed by the Seychelles (1.52). Sooty terns were frequent in all sectors with by far the highest encounter rate in central Mozambique Channel (29.35 sightings 100 km^{-1}). Frigatebirds were more frequently seen in southern Mozambique Channel (0.58 sightings 100 km^{-1}) and around the Seychelles (0.41).

Detection function modeling

Best fitting detection models were half normal for Delphininae and Globicephalinae and hazard rate for sperm and beaked whales (Table 4, Supplementary material

Table 4. Detection models and effective strip widths (ESWs) estimated for cetacean guilds.

Cetacean guild (sightings after truncation)	Truncation distance	Detection model	Effect of covariate on detection	
			Detection covariate	ESW
Delphininae (612)	500 m	half normal	glare severity	Low: 245.9 m Medium: 220.7 m High: 197.4 m
Globicephalinae (217)	500 m	half normal	no significant detection covariate	247.6 m
Sperm and beaked whales (128)	600 m	hazard rate	sea state	0: 509.4 m 1–2: 281.4 m 3–4–5: 121.2 m

Appendix 3). Glare severity significantly affected the detection of Delphininae. No detection covariate had a significant effect on Globicephalinae. Sea state significantly affected the detection of sperm and beaked whales. There is no detection function for seabirds, as they were sampled using a strip transect methodology.

Habitat modeling

Model selection

The selected model for Delphininae included NPP_{clim}, SST_{seas} and SLA_{seas} (Fig. 4). For Globicephaline, CHL was preferred over NPP. For sperm and beaked whales, only climatological covariates were selected (NPP_{clim}, SST_{clim} and SLA_{clim}). We can notice the higher NPP optimum for Delphininae (close to 2.7 in log scale) compared to sperm and beaked whales (2.4). Overall, cetacean densities increased with SST. Sperm and beaked whales densities increased in areas of higher standard error of sea level anomaly, suggesting an affinity for higher mesoscale activity. Slope was not significant for Delphininae, densities of Globicephalinae decreased with slopes greater than 4% and there was a positive linear relationship between slope and sperm and beaked whales. Explained deviances for cetaceans were comprised between 10.7 and 4%.

For seabirds, explained deviances were higher and ranged from 19.6% (boobies) to 39.7% (grey terns) (Fig. 4). Distance to the nearest colony was an important predictor, explaining between 6.6% (boobies) and 32.1% (petrels and shearwaters) of deviance. Based on the interpretation of curves, we can notice a colony effect up to about 200 km for tropicbirds and frigatebirds and 500 km for petrels and shearwaters and brown terns. Either seasonal or climatological covariates were selected depending on the guild. Many seabirds showed unimodal relationships with CHL. Densities of brown terns and grey terns increased with SST. Noddies, boobies and petrels and shearwaters showed increasing relationships with the standard error of sea level anomaly, whereas tropicbirds and grey terns showed decreasing relationships. Slope was selected only for brown terns, with a decreasing relationship for higher slope values

Predictions

Prediction maps were different for the three cetacean guilds (Fig. 5). Ecoregions with the highest predicted densities of Delphininae were the Mozambique Channel, especially its center and south and the Seychelles. In contrast low densities were predicted around the Mascarenes (including Tromelin-Madagascar and Reunion-Mauritius sectors). For Globicephalinae, maximum densities were predicted in the Mozambique Channel, particularly in the slope strata, as well as around the Seychelles and predicted densities were lower in the Mascarenes. For sperm and beaked whales predicted densities were less contrasted between the three ecoregions. They were the highest in the high mesoscale activity area in the center of the Mozambique Channel. As for Delphininae and Globicephalinae, predicted densities were lower around the Mascarenes but to a lesser extent. Indeed, the variability of predicted densities in the six sectors differed for the three guilds. For Delphininae, predicted densities showed a 1-to-13 variability between the highest (CMC) and lowest density sectors (RM) (Fig. 6a). For Globicephalinae, there was a 1-to-7 variability (Fig. 6b) and for sperm and beaked whales, only a 1-to-3 variability (Fig. 6c). Predicted densities (standardized for each guild by its mean density) showed a positive relationship with the climatology of net primary production (NPP_{clim}): for the three cetacean guilds density increased with increasing primary production (Fig. 6d). However, the slope of the regression line was the highest for Delphininae, intermediate for Globicephalinae and the lowest for sperm and beaked whales, indicating than Delphininae were responding more strongly to primary production compared to Globicephalinae and sperm and beaked whales.

For seabirds, prediction maps strongly reflected colony locations (Fig. 5). Tropicbird predicted densities were high around Reunion, Mauritius, the Seychelles, Europa, Nosy Vé, Cape Amber , as well as outside sampled sectors, around Aldabra and Cosmoledo. There were high predicted densities of grey terns along Madagascar coastlines. Noddy densities were predicted to be the highest around the Seychelles, Glorieuses and Saint Brandon. For boobies, densities were the highest around Tromelin and Europa, as well as in the high mesoscale activity area. For petrels and shearwaters, densities were the highest around Reunion and Mauritius. High densities of brown terns were predicted in the Mozambique Channel with particularly high values around Juan de Nova Island. Intermediate densities were also predicted in pelagic waters, in the whole Mozambique Channel and to the north of Madagascar. Frigatebird densities were the highest around Europa, the Seychelles (including Amirantes) and Comoros.

Predictions appeared in accordance with the observed distributions of cetacean and seabird guilds (Fig. 3) Uncertainty maps showed that high predicted densities were associated with a low uncertainty, whereas low predicted densities were associated with a higher uncertainty

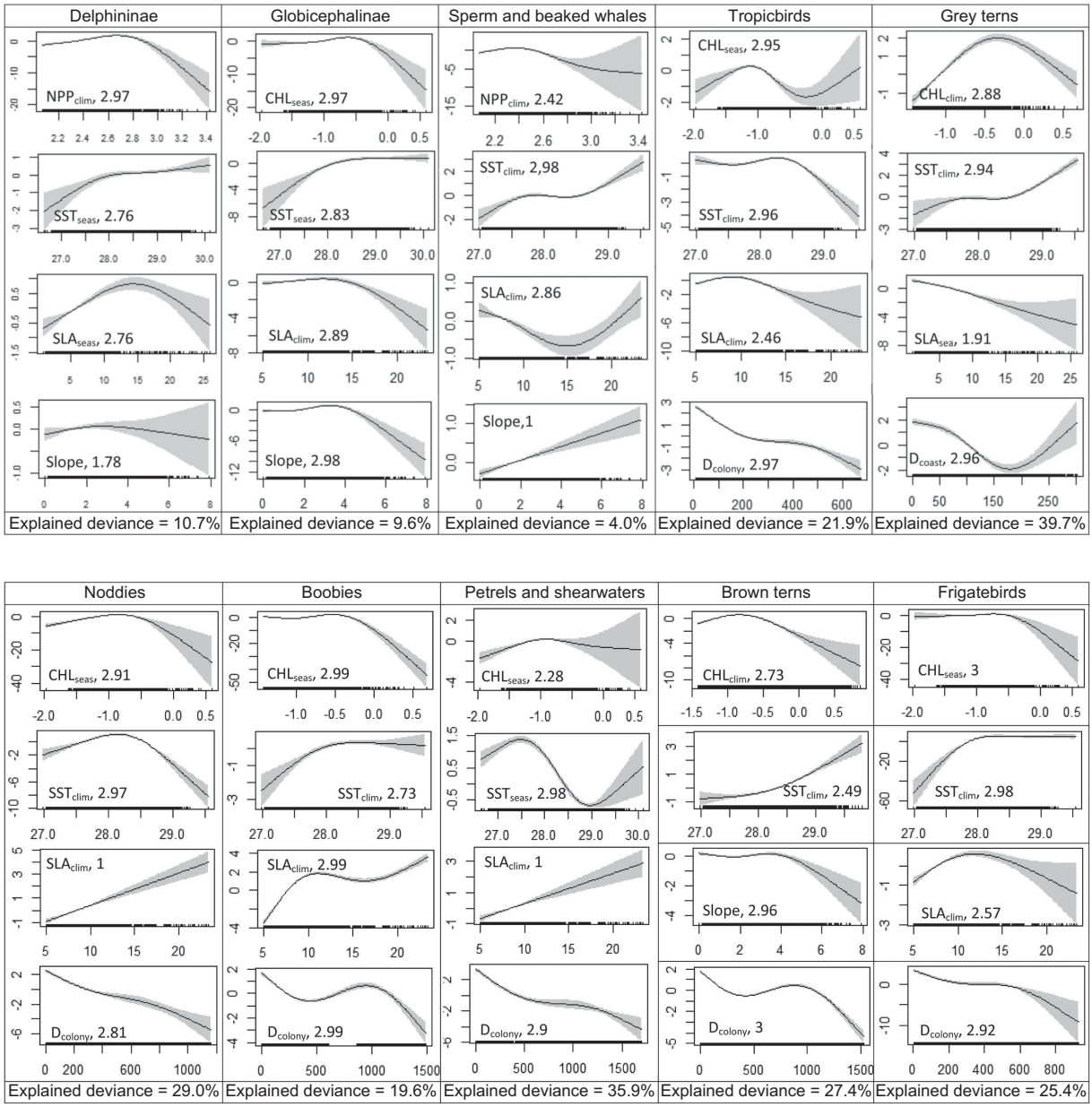


Figure 4. Forms of smooth functions for the selected covariates for each top predator guild. CHL and NPP were log-transformed, slope was square-root-transformed. Estimated degrees of freedom are provided for each smoother. The solid line in each plot is the smooth function estimate and shaded regions represent approximate 95% confidence intervals. Zero on the y-axis indicates no effect of the covariate (given that the other covariates are included in the model).

(Supplementary material Appendix 4). In addition, uncertainty in seabird predicted densities increased with distance from the colony, as illustrated for tropicbirds and noddies.

Response to contemporaneous versus averaged oceanographic conditions

Replacing time-averaged covariates in the selected models by their contemporaneous equivalents always negatively altered model deviances. For all guilds, deviance was always higher for models built with time-averaged covariates (Fig. 7). This indicates that top predators may not primarily react to short term variations of their environment but may respond better to time-averaged oceanographic conditions.

Discussion

Methodological considerations

The aerial methodology allowed to cover this vast region at lower costs and with better flexibility relative to weather conditions compared to a dedicated boat-based methodology. However, two sources of biases are inherent to our data. First, weather related covariates affected

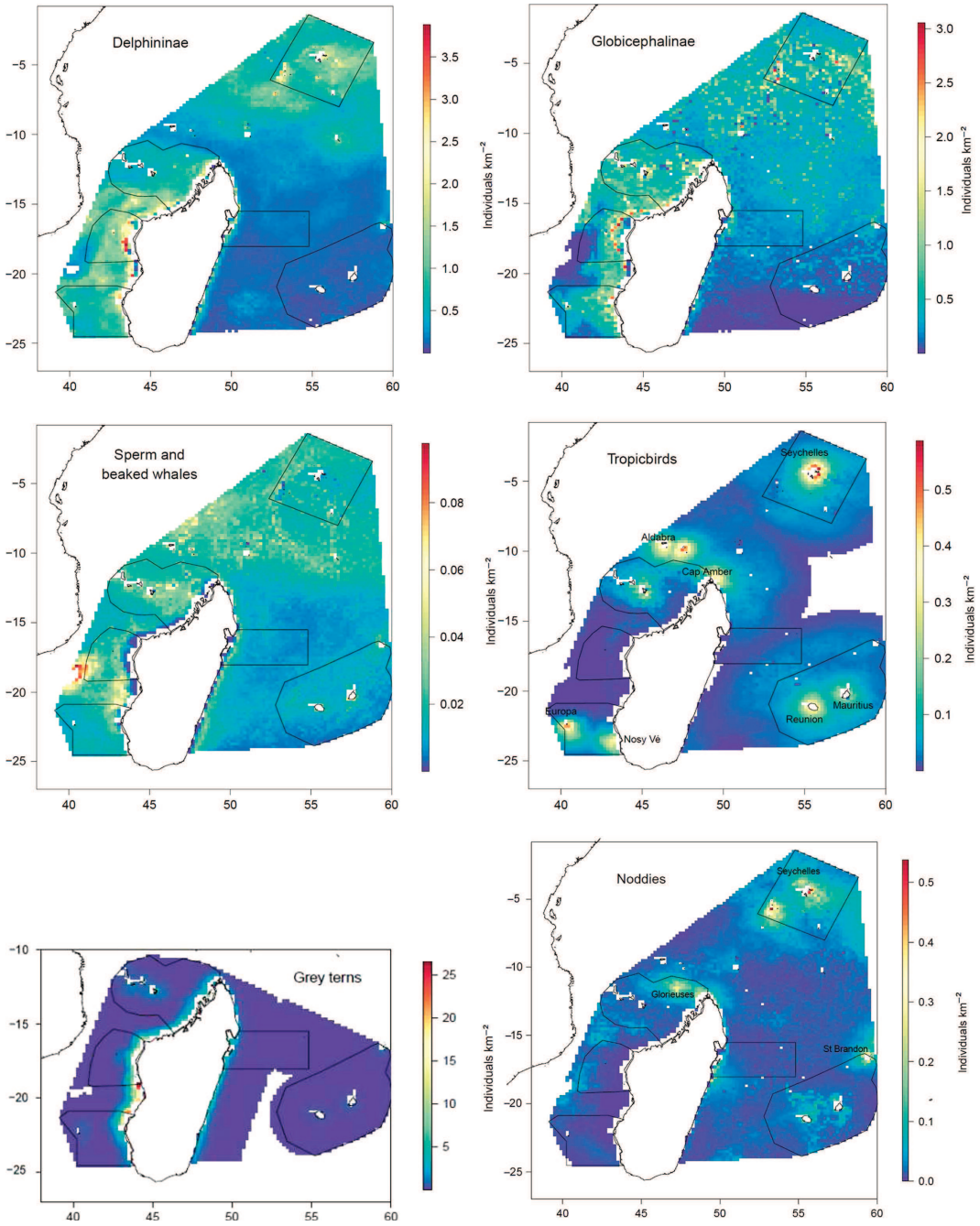


Figure 5. Predicted relative density (individuals km^{-2}) for each top predator guild in the Southwest Indian Ocean. Predictions are in a convex hull encompassing the surveyed sectors. The absence of predictions beyond the range of covariates used in model fitting resulted in white areas on certain maps. For grey terns the prediction map was truncated to the north as white terns *Gygis alba* were not differentiated from grey terns in the Seychelles.

the detection of predators and generated perception bias (observers failing to detect animals although they are available for detection, Pollock et al. 2006). We found a significant effect of sea state on sperm and beaked whale detection. Their characteristic resting dives just below the surface (e.g. for sperm whales, Miller et al. 2008) may explain this negative effect of deteriorated sea state. On the other hand, sea state did not have a significant effect on the detection of Delphininae and Globicephalinae. Nevertheless, it may have biased the estimated numbers of individuals. For cetaceans, the estimation of condition-specific ESWs, allowed to incorporate the non homogeneous spatial distribution of detection covariates (such as sea state) in habitat modeling. For seabirds, we assumed all individuals within the strip were detected (Tasker et al. 1984) but some seabirds were undoubtedly missed within the strip.

The second bias was availability bias (when animals are unavailable for detection, Pollock et al. 2006). It can be estimated from a double platform methodology (two aircrafts flying in tandem, Hiby and Lovell 1998) or dive pattern data documented by time depth recorder experiments

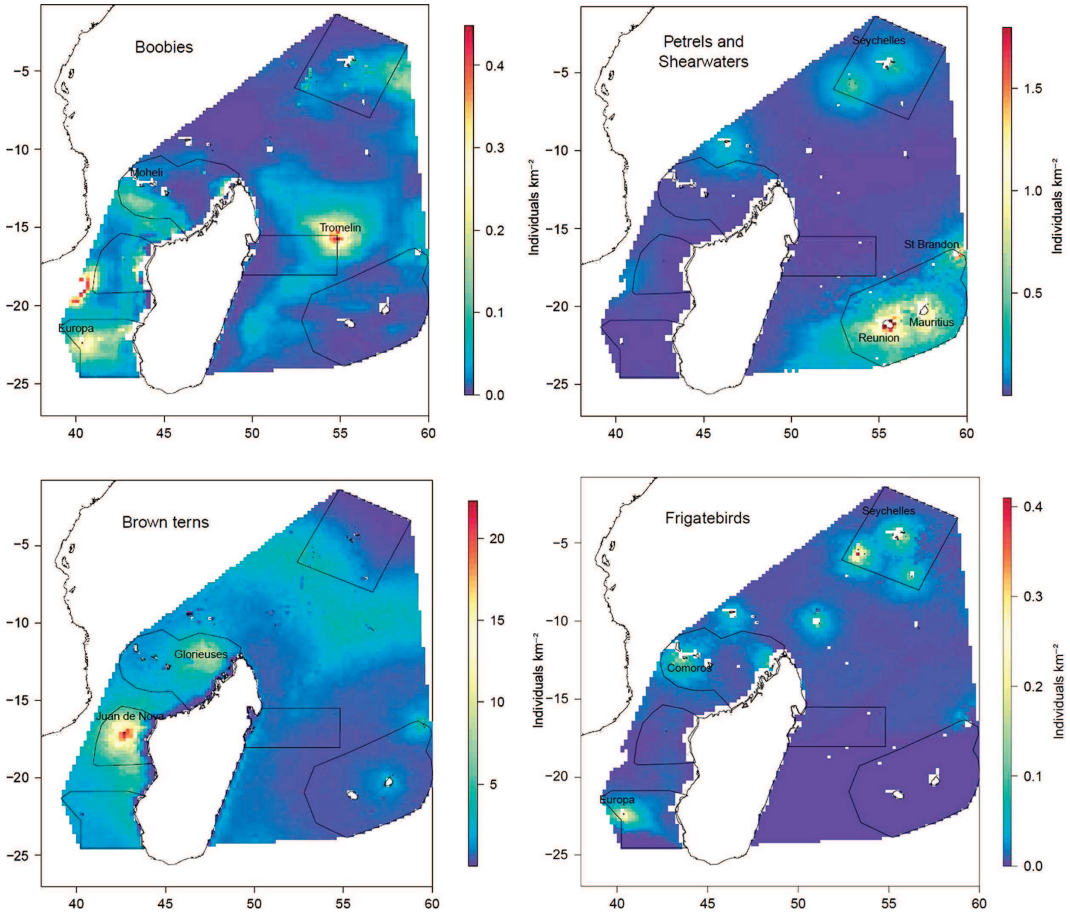


Figure 5. (Continued).

(Pollock et al. 2006). Considering it would have only resulted in multiplying densities by a given factor for each cetacean guild. This was less relevant here, as we did not aim at comparing densities between guilds, but at investigating the variability of predicted densities between sectors within each cetacean guild.

In this study, we used GAMs as tools to model top predator habitats. GAMs have been successfully used to examine cetacean and seabird habitats (Ferguson et al. 2006, Vilchis et al. 2006, Becker et al. 2010). They offer a flexible framework for developing species-habitat models without imposing a linear form to the underlying relationships. Indeed, Forney (2000) found that most cetacean-habitat relationships were non linear. GAMs result in higher fidelity to data (they are data driven) compared to other regression methods (Guisan et al. 2002). Drawbacks of these models include overfitting the data and a lack of transferability (Elith and Leathwick 2009) which is an issue when predicting outside the study area. To avoid overfitting, we limited the degrees of freedom for each smoother. Besides, we proposed a geographical extrapolation (predictions between surveyed sectors), but we did not allow predictions outside the range of covariates used in model fitting.

Our models explained little variability in the observed data (i.e. a lot of noise remained unexplained by the models), especially for cetaceans. Low explained deviances are common in GAMs. For example, in the eastern tropical Pacific, deviances for GAMs of cetacean encounter rates ranged between 5 and 38% but were mostly around 10% (Forney et al. 2012). Our low deviances may be the consequence of modeling rare species (characterized by a lot of zeros, Welsh et al. 1996), as well as using indirect oceanographic covariates rather than more causal ones (Austin 2002) (such as the distribution of resources through the water column). This is especially true for deep divers which may show a weak dependence to surface characteristics inferred from remote sensing, but a stronger relationship with water column features. Nevertheless, remote sensing remains the only means to provide indicators of oceanographic features and resources availability over such an extensive region. In addition, when habitat models are built for individual species, explained deviances increase notably compared to deviances obtained for the corresponding guild (Supplementary material Appendix 5). Hence, our low deviances may also result from grouping species into guilds.

Evaluating the predictive power of a model is an important step in the modeling process (Guisan and Zimmermann 2000). However, as we conducted the aerial survey only once, we were not able to evaluate the predictive power of our habitat models on an independent dataset (e.g. collected in the same region but during another year). We leave it to experts and future studies to evaluate the reliability of our prediction maps.

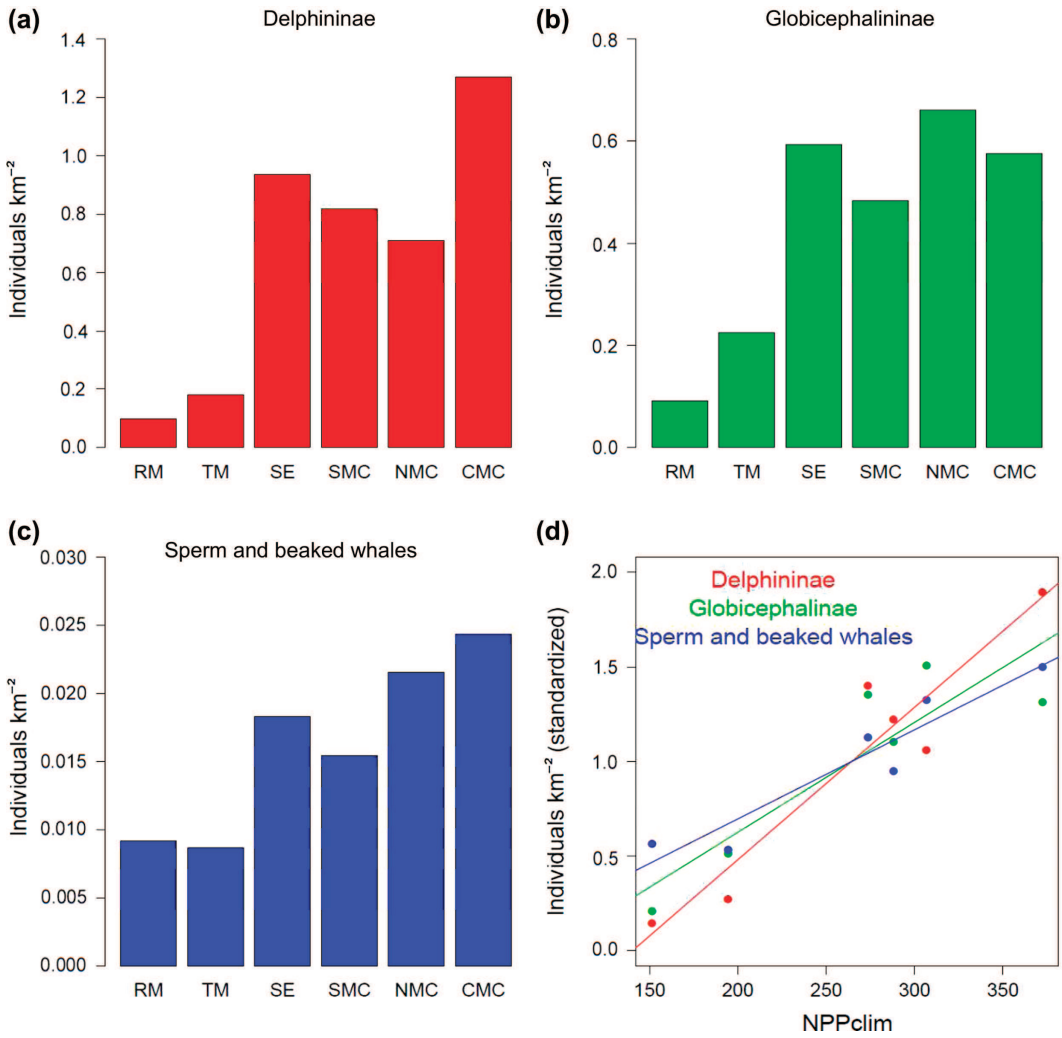


Figure 6. Predicted relative densities in the six geographic sectors for each cetacean guild (Delphininae (a), Globicephalinae (b) and sperm and beaked whales (c)) and plotted against the climatology of primary production (NPP_{clim}), after standardization for each guild by the mean density (d). Regression lines are overlaid to materialize each guild relationship to primary production. NMC: Northern Mozambique Channel, CMC: Central Mozambique Channel, SMC: Southern Mozambique Channel, SE: Seychelles, TM: Tromelin-Madagascar, RM: Reunion-Mauritius.

Acquisition of new data

With this multispecific aerial survey, an extensive pelagic region was covered for the first time in the SWIO, encompassing contrasting oceanographic conditions. It provided new and valuable data on top predator distributions in the austral summer and gave the opportunity to investigate their responses to the heterogeneity in habitat quality.

Most seabird studies in the SWIO relied on telemetry and focused on the breeding component of populations. Telemetry studies, in which each tracked individual is known (sex, status, breeding colony), provided information about their movements, activity patterns (Weimerskirch et al. 2004, Catry et al. 2009a) and feeding ecology (Jaquemet et al. 2008, Catry et al. 2009b). Seabird–environment relationships have previously been demonstrated from tracked individuals. For example, Weimerskirch et al. (2010) used GAMs to highlight a positive effect of cyclonic eddies on the foraging of frigatebirds. Le Corre et al. (2012) combined tracking data for seven pelagic seabirds to identify foraging hotspots in the western Indian Ocean and highlighted three breeding areas: the Seychelles, the southern Mozambique Channel and the Mascarene archipelago. Boobies and frigatebirds were generally distributed close to their breeding colonies whereas Procellaridae and tropicbirds had wider distributions and used different habitats when breeding or dispersing. These three places also appeared as high density areas in our prediction maps but our aerial survey did not allow differentiating breeding from dispersing seabirds. Nonetheless, the two approaches appear complementary: tracking studies give a real time picture of an individual while it moves in its environment, and aerial or boat-based studies provide a real time picture of seabird at-sea populations while the platform moves (Ballance 2008).

Cetacean studies in the SWIO mainly relied on boat-based surveys in inshore areas. Although effort was limited in comparison to our survey, they provided useful information on cetacean communities and species diversity around some islands (Kiszka et al. 2011). The most extensive previous survey in terms of effort (9784 km, mostly located in

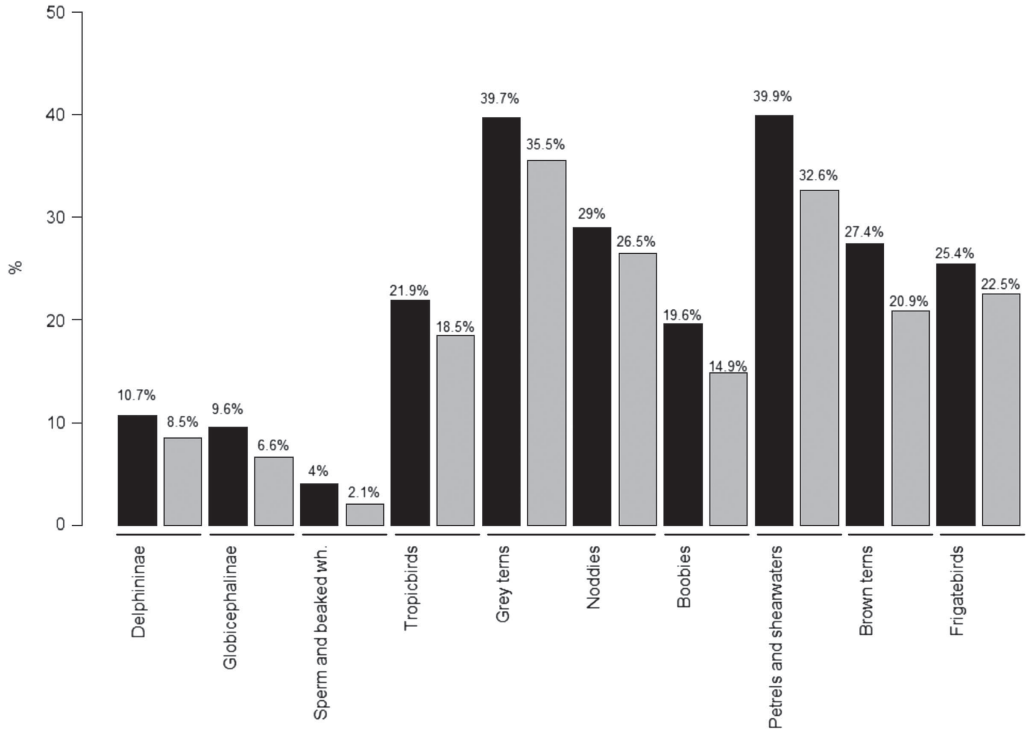


Figure 7. Explained deviances of models built with time-averaged (black) versus contemporaneous (grey) oceanographic covariates for each top predator guild.

the Arabian Sea) characterized twelve widespread species and proposed relative abundances for several cetaceans (the spinner dolphin dominated in terms of sighted individuals and the sperm whale, in terms of groups) (Ballance and Pitman 1998). Although this survey covered pelagic waters, it was based on a ship of opportunity, resulting in a non standard design and an inhomogeneous coverage and thus, may not be fully comparable with our dedicated aerial survey.

Top predator distributions are contrasting within the SWIO

The SWIO encompasses a range of oceanographic conditions: the Mozambique Channel is characterized by very dynamic mesoscale eddies, the Seychelles are influenced by the monsoon and have productive surface waters while the Mascarenes remain oligotrophic year-round (Longhurst 2007). Cetacean predicted distributions are contrasting across these three ecoregions: densities are the highest in the Mozambique Channel and the Seychelles and the lowest around the Mascarenes. Thus, cetaceans quite logically appear more abundant in productive regions. This is also true for other top predators, such as tunas, as reflected in fisheries data. Indeed, catches of bigeye tuna (longline fisheries) and yellowfin tuna (purse seine fisheries) are mostly distributed in the equatorial area to the north of Madagascar and in the Mozambique Channel, but not in the Mascarenes (Ménard et al. 2007).

Our models predicted high densities of cetaceans in the Mozambique Channel. In particular, Delphininae densities were the highest in the center and southern Mozambique Channel where mesoscale activity is the most dynamic (Tew Kai and Marsac 2010). Top predators, including tunas (Tew Kai and Marsac 2010) and frigatebirds (TewKai and Marsac 2009, Weimerskirch et al. 2010), are known to associate with mesoscale eddies in the Mozambique Channel. According to Sabarros et al. (2009), advection of coastal nutrient-rich waters and eddy-eddy interactions enhance biological production, which sustains the stocks of micronekton through bottom-up processes and in turn shape the distribution of top predators.

Top predator strategies of habitat utilization seem in accordance with their costs of living

We classified cetaceans and seabirds into energetic guilds to investigate whether their strategies of habitat utilization at the ecosystem scale responded to their general energetic constraints. For cetaceans, the overall cost of living may primarily reflect the physiological efficiency of diving. Foraging success is the other component of the cost of living. For sperm and beaked whales, foraging success has been approximated by echolocation click buzzes, marking capture attempts (Miller et al. 2004). However, there is very few information regarding foraging success rates of small cetaceans. In this study, we present a general classification of top predator energetic lifestyles in which the overall cost of living encompasses both physiological efficiency and foraging success rate, as these two components are not easily disentangled. This classification represents a simplified image of the reality and there may be differences within guilds. For example, the extensive use of wind and gliding behavior of red footed booby (Weimerskirch et al. 2005a) may induce lower costs of flight compared to other boobies. Similarly, there are some

differences within Delphininae, as illustrated by the common dolphin *Delphinus delphis* and striped dolphin *Stenella coeruleaolalba* in the Bay of Biscay, characterized by different costs of living (measured with muscular indicators) in spite of having very similar body shapes (Spitz et al. 2012). Nevertheless, differences within a guild are likely smaller than differences between guilds.

The link between energetic costs and habitat quality is not new and was previously documented in both marine and terrestrial habitats. In the eastern tropical Pacific, seabirds were distributed along a productivity gradient, in accordance with their costs of flight (Ballance et al. 1997). Otariids, which have an expensive foraging strategy, are found in highly productive areas whereas the more phlegmatic phocids inhabit both high and low productive areas (Costa 1993). Mueller and Diamond (2001) studied five species of mice originating from very different habitats and noticed a correlation between metabolic rate and the primary production of their habitat, high metabolism mice occupying the most productive habitats.

In this study, energetically costly Delphininae seemed to be more dependent on productivity than the other cetacean guilds. Indeed, high Delphininae densities were predicted in the most productive habitats (Mozambique Channel and the Seychelles) and conversely, low densities (as much as 13 times lower) were predicted around the Mascarenes. In contrast, the more phlegmatic sperm and beaked whales were present in both high and low productivity habitats and seemed less dependent on habitat quality (they showed only a 1-to-3 variability between the highest and lowest density sectors). Globicephalinae, with a 1-to-7 variability, appeared intermediate. Therefore, cetacean distributions at the ecosystem scale seemed in accordance with their costs of living.

Sooty terns, characterized by low energetic costs, were observed in all sectors and occupied all habitats. As for sperm and beaked whales, they may not heavily depend on productivity. However this pattern was not strongly reflected in our prediction map, showing a very high density area around Juan de Nova colony. Indeed, distance to the nearest colony explained a significant amount of deviance for some seabirds and prediction maps reflected colony locations. Seabird at-sea distributions strongly depend on where they breed (Le Corre et al. 2012) and the colony effect (Hyrenbach et al. 2007) was predominant in our predictions. Differences in seabird energetic costs were partly reflected in this colony effect. Tropicbirds, which have the highest energetic costs, were tightly related to their colonies (influence of the colony up to 200 km). Conversely, sooty terns and petrels and shearwaters showed a broader colony effect (up to 500 km). This illustrates that energetically costly seabirds may be constrained to forage closer to their colonies.

Top predators respond to persistent oceanographic features

Following our results, top predators appeared to be distributed according to averaged oceanographic features and did not seem to react to short-term oceanographic variability. Either seasonal or climatological covariates were selected in the models depending on guilds, indicating no strong preference for the medium or long-term resolutions. Indeed, oceanographic conditions during the survey period did not differ much from the climatology, and both resolutions may bring similar information. When relying on large scale surveys, evaluating top predator responses to time-averaged environmental parameters has proven useful to build habitat models and provide worldwide distribution maps (Kaschner et al. 2006). A technical advantage is that composites (averaged) remote sensing products are less affected by cloud coverage. On the other hand, responses to instantaneous environmental conditions can be better evaluated by telemetry studies (Weimerskirch et al. 2010).

Our study showed that cetaceans and seabirds may respond better to persistent (highly predictable) compared to ephemeral (less predictable) environmental situations. This is consistent with memory-based foraging strategy (Davoren et al. 2003). Especially in tropical oceans where resources are dispersed, top predators may have learned to exploit oceanographic features that determine recurrent access to food resources.

For seabirds, colony locations explained an important amount of their distribution. Since colony locations are static and breeding at a colony can only carry on if food resources are sufficient and recurring year after year around this colony (as described by the climatology), seabirds may respond to long-term oceanographic features. Conversely, cetaceans are not constrained to colonies but, owing to their foraging mode, they likely respond better to persistent features. Indeed, compared to seabirds, which locate prey by observing the activity of sub surface predators (Ballance et al. 1997, Jaquemet et al. 2004), or congeners, resulting in a network foraging (Wittenberger and Hunt 1985), cetaceans forage by visual or acoustic detection within a smaller radius than seabirds can do when foraging in network. Therefore, cetaceans may be able to sample a smaller area of the ecosystem and thus probably take better advantage of persistent or recurring oceanographic situations for foraging.

Conclusions and perspectives

In this study, we used top predator data collected from a dedicated aerial survey in the SWIO and oceanographic and static covariates along with GAMs to highlight their responses to time-averaged oceanographic conditions and propose regional habitat predictions. For cetaceans, predictions stressed different responses to the heterogeneity in habitat quality and the dependence of the energetically costly Delphininae to productivity. For seabirds, predictions primarily reflected the locations of colonies, although the colony effect was stronger for energetically costly seabirds. Thus, strategies of habitat utilization at the ecosystem scale appeared in accordance with top predator energetic costs. Finally, we emphasized the importance of predictable oceanographic features for cetaceans and seabirds.

Owing to their cheap and easy accessibility and their extensive spatial coverage, remote sensing data can be useful for identifying potential Marine Protected Areas (MPAs) (Game et al. 2009). Especially for far ranging pelagic vertebrates, MPAs should be designed according to large scale oceanographic features which are temporally and spatially

predictable (Hyrenbach et al. 2000). In this study, we demonstrated the responses of top predators to persistent oceanographic features and produced prediction maps according to the form of these responses. We believe this could help managers in designing pelagic MPAs.

In the SWIO, where the food chain is relatively short (Potier et al. 2004), lower trophic levels probably represent unbiased indicators of prey. Nevertheless, examining top predator habitats in relation to mid trophic levels (micronekton) would be useful. Unfortunately, micronekton sampling is not available on our study region but ecosystemic models (Lehodey et al. 2010) can estimate the biomass of micronekton for different depth layers. This would provide a third dimension to habitat quality, which could be correlated with the distribution of cetaceans and their foraging in different depth layers.

Acknowledgements – The French Ministry in charge of the environment (Ministère de l'Ecologie, du Développement Durable, du Logement et du Transport, MEDDLT) and the Agency for marine protected areas (Agence des aires marines protégées, AAMP) funded the project. The Indian Ocean Commission (IOC), the Governments of all Member States (Comoros, Reunion, Madagascar, Mauritius, Seychelles) and the prefecture of the Terres Australes et Antarctiques Françaises considerably facilitated the regional approach conducted in the SW Indian Ocean. We thank all observers: Norbert Andrianarivelo, Adele Cadinouche, Violaine Dulau-Drouot, Rebecca Guezel, Aurélie Hermans, François-Xavier Mayer, Devis Monthy, Morgane Perri, Claire Pusineri, Yvette Razafindrakoto and Anli Toilibou from organizations: CetaMada, Collectivité Départementale de Mayotte, Globice, Mauritius Marine Conservation Society, Megaptera, Naturalistes de Mayotte and World Conservation Society, who were very professional in the air and friendly project mates on land. We are indebted to all aircraft crew members of Aerosotravia, France and Madagascar Trans Air, for their continuous high level of professionalism and enthusiasm despite hundreds of hours flying in strait lines over the ocean. We wish to thank Mathieu Le Corre and Sebastien Jaquemet for their help on seabird colonies and Jerome Spitz for fruitful exchanges regarding analyses and interpretations.

References

Aguilar de Soto, N. et al. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). – J. Anim. Ecol. 77: 936–947.

Austin, M. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – Ecol. Model. 157: 101–118.

Baird, R. W. et al. 2001. Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. – Can. J. Zool. 79: 988–996.

Ballance, L. T. 2008. Understanding seabirds at sea: why and how. – Mar. Ornithol. 35: 127–135.

Ballance, L. T. and Pitman, R. L. 1998. Cetaceans of the western tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. – Mar. Mamm. Sci. 14: 429–459.

Ballance, L. T. et al. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. – Ecology 78: 1502–1518.

Becker, E. A. et al. 2010. A comparison of California current cetacean habitat models developed using in situ and remotely sensed sea surface temperature data. – Mar. Ecol. Prog. Ser. 413: 163–183.

Behrenfeld, M. J. and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. – Limnol. Oceanogr. 42: 1–20.

Benoit-Bird, K. J. and Au, W. W. L. 2009. Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. – J. Acoust. Soc. Am. 125: 125–137.

Boyd, I. 1997. The behavioural and physiological ecology of diving. – Trends Ecol. Evol. 12: 213–217.

Bretagnolle, V. et al. 2000. Audubon's shearwaters *Puffinus lherminieri* on Reunion Island, Indian Ocean: behaviour, census, distribution, biometrics and breeding biology. – Ibis 142: 399–412.

Buckland, S. T. et al. 2001. Introduction to distance sampling: estimating abundance of biological populations. – Oxford Univ. Press.

Burger, A. E. and Lawrence, A. D. 2001. Census of wedge-tailed shearwaters *Puffinus pacificus* and Audubon's shearwaters *P. lherminieri* on Cousin Island, Seychelles using call-playback. – Mar. Ornithol. 29: 57–64.

Catry, T. et al. 2009a. Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. – Mar. Ecol. Prog. Ser. 391: 231–242.

Catry, T. et al. 2009b. Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. – Mar. Ecol. Prog. Ser. 374: 259–272.

Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. – Symp. Zool. Soc. Lond. 66: 293–314.

Davoren, G. K. et al. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. – Mar. Ecol. Prog. Ser. 256: 229–242.

De Ruijter, W. P. M. et al. 2004. Eddies and dipoles around south Madagascar: formation, pathways and large-scale impact. – Deep-Sea Res. I: 383–400.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Ellis, H. I. and Gabrielsen, G. W. 2002. Energetics of free-ranging seabirds. – In: Schreiber, E. A. and Burger, J. (eds), Biology of marine birds. CRC Marine Biology Series, pp. 359–407.

ESRI 2010. ArcGIS desktop. – Environmental Systems Research Inst.

Estes, J. et al. 2001. Predators, ecological role of. – In: Levin, S. (ed.), Encyclopedia of biodiversity. Academic Press, pp. 857–878.

Feare, C. J. et al. 2007. An inventory of sooty terns (*Sterna fuscata*) in the western Indian Ocean with special reference to threats and trends. – Ostrich 78: 423–434.

Ferguson, M. C. et al. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. – Ecol. Model. 193: 645–662.

Flint, E. N. and Nagy, K. A. 1984. Flight energetics of free-living sooty terns. – Auk 101: 288–294.

Ford, R. G. et al. 2004. The biogeographic patterns of seabirds in the central portion of the California Current. – Mar. Ornithol. 32: 77–96.

Forney, K. A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. – Conserv. Biol. 14: 1271–1286.

Forney, K. A. et al. 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. – Endangered Species Res. 16: 113–133.

Game, E. T. et al. 2009. Pelagic protected areas: the missing dimension in ocean conservation. – Trends Ecol. Evol. 24: 360–369.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – Ecol. Model. 135: 147–186.

Guisan, A. et al. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. – Ecol. Model. 157: 89–100.
Hammond, P. S. et al. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. – Biol. Conserv. 164: 107–122.
Hiby, L. and Lovell, P. 1998. Using aircraft in tandem formation to estimate abundance of harbour porpoise. – Biometrics 54: 1280–1289.
Ho, C. R. et al. 2004. SeaWiFs observations of upwelling south of Madagascar: long-term variability and interaction with East Madagascar Current. – Deep Sea Res. Part II 51: 59–67.
Hyrenbach, K. D. et al. 2000. Marine protected areas and ocean basin management. – Aquat. Conserv. 10: 437–458.
Hyrenbach, K. D. et al. 2007. Community structure across a large-scale ocean productivity gradient: marine bird assemblages of the Southern Indian Ocean. – Deep Sea Res. Part I 54: 1129–1145.
Jaquemet, S. et al. 2004. Seabird community structure in a coastal tropical environment: importance of associations with sub-surface predators and of Fish Aggregating Devices (FADs). – Mar. Ecol. Prog. Ser. 268: 281–292.
Jaquemet, S. et al. 2008. Comparative foraging ecology and ecological niche of a superabundant tropical seabird: the scooty tern *Sterna fuscata* in the southwest Indian Ocean. – Mar. Biol. 155: 505–520.
Kahru, M. 2010. Window Image Manager 1991–2010, ver. 6.63. – <www.wimsoft.com>.
Kaschner, K. et al. 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. – Mar. Ecol. Prog. Ser. 316: 285–310.
Kastelein, R. A. et al. 2002. Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. – Mar. Environ. Res. 53: 199–218.
Kiszka, J. et al. 2011. Ecological niche segregation within a community of sympatric dolphins around a tropical island. – Mar. Ecol. Prog. Ser. 433: 273–288.
Kojadinovic, J. et al. 2008. Trophic ecology of marine birds and pelagic fishes from Reunion Islands as determined by stable isotope analysis. – Mar. Ecol. Prog. Ser. 361: 239–251.
Laake, J. L. et al. 2011. "mrds" (mark–recapture distance sampling) package. – R package ver. 2.0.0, <http://GRAN.R-project.org/package = mrds>.
Le Corre, M. 2001. Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. – J. Zool. 254: 239–249.
Le Corre, M. and Jaquemet, S. 2005. Assessment of the seabird community of the Mozambique Channel and its potential use as indicator of tuna abundance. – Estuarine Coastal Shelf Sci. 63: 421–428.
Le Corre, M. and Bemanaja, E. 2009. Discovery of two major seabird colonies in Madagascar. – Mar. Ornithol. 37: 153–158.
Le Corre, M. et al. 2002. Light-induced mortality of petrels: a 4-year study from Réunion Island (Indian Ocean). – Biol. Conserv. 105: 93–102.
Le Corre, M. et al. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. – Biol. Conserv. 156: 83–93.
Lehodey, P. et al. 2010. Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. – Prog. Oceanogr. 84: 69–84.
Longhurst, A. R. 2007. Ecological geography of the sea. – Academic Press.
Longhurst, A. R. and Pauly, D. 1987. Ecology of tropical oceans. – Academic Press.
MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.
Marques, F. F. C. and Buckland, S. T. 2004. Covariate models for the detection function. – In: Buckland, S. T. et al. (eds), Advanced distance sampling. Oxford Univ. Press, pp. 31–47.
Ménard, F. et al. 2007. Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. – Mar. Biol. 153: 141–152.
Miller, P. J. et al. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes "creaks" in prey capture. – Proc. R. Soc. B 271: 2239–2247.
Miller, P. J. O. et al. 2008. Stereotypical resting behavior of the sperm whale. – Curr. Biol. 18: R21–R23.
Mueller, P. and Diamond, J. 2001. Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. – Proc. Natl Acad. Sci. USA 98: 12550–12554.
New, A. L. et al. 2005. Physical and biochemical aspects of the flow across the Mascarene Plateau in the Indian Ocean. – Phil. Trans. R. Soc. A 363: 151–168.
Peterson, C. C. et al. 1990. Sustained metabolic scope. – Proc. Natl Acad. Sci. USA 87: 2324–2328.
Pimm, S. L. et al. 1991. Food web patterns and their consequences. – Nature 350: 669–674.
Pollock, K. H. et al. 2006. Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. – J. Wildl. Manage. 70: 255–262.
Potier, M. et al. 2004. Feeding partitioning among tuna taken in surface and mid-water layers: the case of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) in the Western Tropical Indian Ocean. – Western Indian Ocean J. Mar. Sci. 3: 51–62.
Redfern, J. V. et al. 2006. Technique of cetaceans-habitat modeling. – Mar. Ecol. Prog. Ser. 310: 271–295.
Redfern, J. V. et al. 2008. Absence of scale dependence in dolphin-habitat models for the eastern tropical Pacific Ocean. – Mar. Ecol. Prog. Ser. 363: 1–14.
Rocamora, G. et al. 2003. The breeding avifauna of Cosmoledo Atoll (Seychelles) with special reference to seabirds: conservation status and international importance. – Bird Conserv. Int. 13: 151–174.
Russell, J. C. and Le Corre, M. 2009. Introduced mammal impacts on seabirds in the Îles Éparses, Western Indian Ocean. – Mar. Ornithol. 37: 121–129.
Sabarros, P. S. et al. 2009. Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. – Mar. Ecol. Prog. Ser. 395: 101–107.
Schott, F. A. and McCreary, J. P. 2001. The monsoon circulation of the Indian Ocean. – Prog. Oceanogr. 51: 1–123.
Schouten, M. W. et al. 2003. Eddies and variability in the Mozambique Channel. – Deep Sea Res. II 50: 1987–2003.
Spitz, J. et al. 2012. Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. – PLoS One 7: e50096.
Tasker, M. L. et al. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. – Auk 101: 567–577.
TewKai, E. and Marsac, F. 2009. Patterns of variability of sea surface chlorophyll in the Mozambique Channel: a quantitive aproach. – J. Mar. Syst. 77: 77–88.
Tew Kai, E. and Marsac, F. 2010. Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. – Prog. Oceanogr. 86: 214–223.
Tomczak, M. and Godfrey, J. S. 2003. Regional oceanography: an introduction, 2nd ed. – Daya Publishing House.
Tyack, P. L. et al. 2006. Extreme diving of beaked whales. – J. Exp. Biol. 209: 4238–4253.
Vilchis, L. I. et al. 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. – Mar. Ecol. Prog. Ser. 315: 279–292.

Wagner, H. H. and Fortin, M. J. 2005. Spatial analysis of landscapes: concepts and statistics. – Ecology 86: 1975–1987.
Watwood, S. L. et al. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). – J. Anim. Ecol. 75: 814–825.
Weimerskirch, H. et al. 2003. Flight performance: frigatebirds ride high on thermals. – Nature 421: 333–334.
Weimerskirch, H. et al. 2004. Foraging strategy of top predator in tropical waters: great frigate birds in the Mozambique Channel. – Mar. Ecol. Prog. Ser. 275: 297–308.
Weimerskirch, H. et al. 2005a. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? – Proc. R. Soc. B 272: 53–61.
Weimerskirch, H. et al. 2005b. Foraging strategy of tropical seabird, the red-footed booby in a dynamic marine environnement. – Mar. Ecol. Prog. Ser. 288: 251–261.
Weimerskirch, H. et al. 2006. Postbreeding movements of frigatebirds tracked with satellite telemetry. – Condor 108: 220–225.
Weimerskirch, H. et al. 2010. Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. – Prog. Oceanogr. 86: 204–213.
Welsh, A. H. et al. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. – Ecol. Model. 88: 297–308.
Williams, T. M. et al. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. – J. Exp. Biol. 179: 31–46.
Wittenberger, J. F. and Hunt Jr, G. L. 1985. The adaptive significance of coloniality in birds. – Avian Biol. 8: 1–78.
Wood, S. N. 2006. Generalized additive models. – Chapman and Hall/CRC.
Wood, S. N. and Augustin, N. H. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. – Ecol. Model. 157: 157–177.
Yen, P. P. W. et al. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. – J. Mar. Syst. 50: 79– 99.

Supplementary material (Appendix ECOG-00317 at <www.oikosoffice.lu.se/appendix>). Appendix 1–5.

Appendix 1: Main breeding colonies for each seabird guild

We describe the main breeding colonies for each seabird guild. For each colony, we provide estimated numbers of breeding pairs of each species with associated references.

Tropicbirds	References
Europa (*4500 RTT, 1000 WTT*), Cosmoledo (*2000 WTT, 2000 RTT*), Reunion (*2000-3000 WTT*), Aldabra (*2500 WTT, 1900 RTT*), Mauritius (*2600 RTT, 1500 WTT*), Cousin (*860-1540 WTT*), Aride (*276-972 WTT*), Cousine (*440-850 WTT*), Cap Amber (*?WTT*), Mayotte (*>100 WTT*), Nosy Vé (*YR, 250*)	Le Corre 2001 ; Rocamora et al. 2003; Le Corre & Jaquemet 2005; Kojadinovic et al. 2008; Catry et al. 2009a ; Le Corre & Bemanaja 2009; Le Corre pers. com., BirdLife International 2012
Grey terns	References
Nosy Foty (*10840 CT*), Nosy Bé (*4000 RT*), Anorontary (*3200 CT, 500 RT*), Nosy Barren (*1480 RT*), St Brandon (*400 RT*)	Le Corre & Bemanaja 2009 ; Le Corre pers. com.
Noddies	References
Aride (*110000 LN, 4000-11000 BN*), Cousin (*71900-90000 LN, ?BN*), Cousine (*47800-71200 LN*), Mauritius (*30000 LN, 30000 BN),* St Brandon (*15000 LN, 4500 BN*), Bird (*10000 BN*), Amirantes (*2000-5900 BN*), Reunion (*500 BN*), Glorieuses (*300 BN*), Toamasina (*100 BN*), Cape Amber (*?BN*)	Le Corre & Jaquemet 2005 ; Kojadinovic et al. 2008 ; Catry et al. 2009a; Le Corre and Bemanaja 2009b; Le Corre pers. com.; BirdLife International 2012
Boobies	References
Cosmoledo (*15000 RFB, 5000-6000 MB, ?BB*), Aldabra (*6000-7000 RFB*), Europa (*2800-3800 RFB*), Tromelin (*500 RFB, 300 MB*), St Brandon (*200 MB*), Mitsio (*250 MB*), Farquhar (*50-70 RFB*), Mauritius (*60 MB*), Moheli (*<50 MB*), Nosy Bé (*30 BB*)	Le Corre 2001 ; Rocamora et al. 2003 ; Le Corre & Jaquemet 2005 ; Weimerskirch et al. 2005a; Le Corre and Bemanaja 2009b; Russell and Le Corre 2009; Le Corre pers. com., BirdLife International 2012
Petrels and shearwaters	References
Mauritius (*80000 WTS*), Reunion (*4000-6500 BP, 3000-5000 AS, 250 MP, ?WTS*), Aride (*20000 WTS, 12000 AS*), Cousin (*24000 WTS, 5000 AS*), Amirantes (*20000 WTS, 100-1000 AS*), Aldabra (*100-1000 AS*), Mauritius (*200 HD*), St Brandon (*100 WTS*)	Bretagnolle et al. 2000; Burger and Lawrence 2001; Le Corre et al. 2002; Catry et al. 2009b; Jaquemet et al. 2004; Le Corre pers. com.
Brown terns	References
Juan de Nova (*2000000 ST*), Glorieuses (*270000 ST*), Mauritius (*200000-300000 ST*), St Brandon (*20000 ST*)	Le Corre & Jaquemet 2005; Feare et al. 2007 ;Jaquemet et al. 2008
Frigatebirds	References
Europa (*1100 GF, 1200 LF*), Aldabra (*6000 LF, 4000 GF*), St Brandon (*50 GF, 50 LF*), roosting sites (Moheli, Mitsio, Amirantes, Seychelles, Farquhar, Coetivy)	Le Corre 2001; Le Corre & Jaquemet 2005; Weimerskirch et al. 2010; Le Corre pers. com.

WTT: White tailed tropicbird, RTT: Red tailed tropicbird, RT: Roseate tern, CT: Crested tern, BN: Brown noddy, LN: Lesser noddy, RFB: Red footed booby, MB: Masked booby, BB: Brown booby, WTS: Wedge tailed shearwater, AS: Audubon's shearwater, BP: Barau's petrel, MP: Mascarene petrel, HP: Herald petrel, ST: Sooty tern, GF: Great frigatebird, LS: Lesser frigatebird.

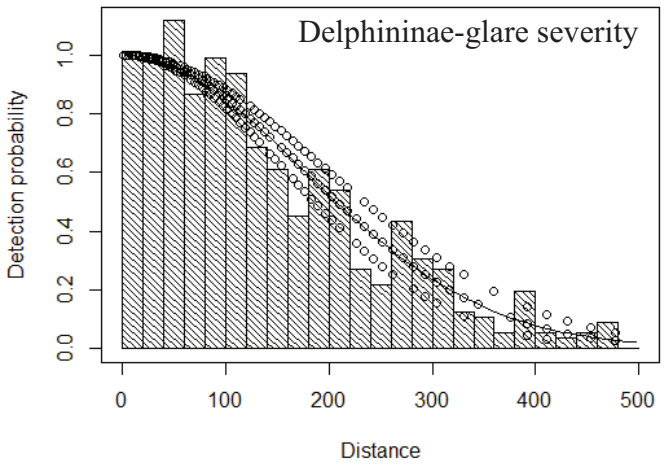
Appendix 2: Details of cetacean and seabird sightings

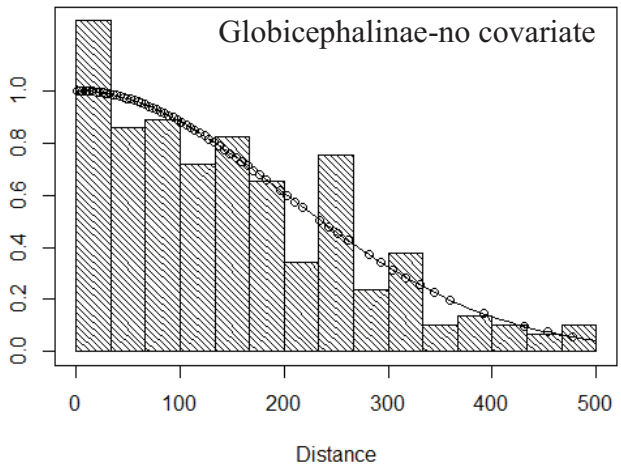
In this table we report the number of groups and individuals sighted during the aerial survey and overall encounter rates of cetacean and seabird guilds.

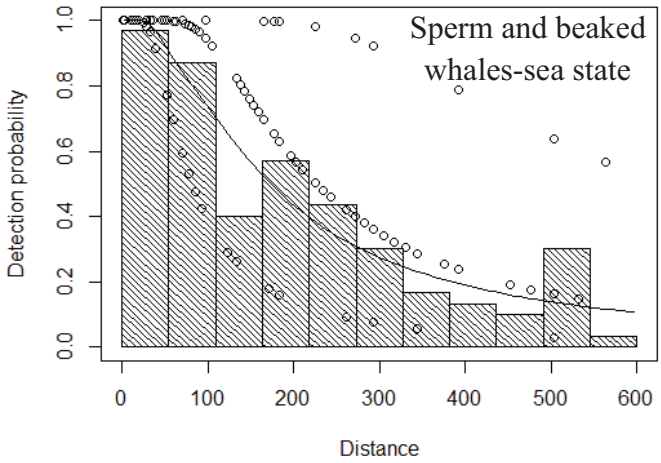
	Number of groups	Number of individuals	Encounter rate (groups / 100km)	Encounter rate (individuals / 100km)
CETACEANS				
Delphininae	**643**	**9 846**	**0.768**	**11.760**
Indo Pacific humpback dolphin *Sousa chinensis*	9	30		
Pantropical spotted dolphin *Stenella attenuata*	2	160		
Spinner dolphin *Stenella longirostris*	16	1 260		
Stenella spp	195	4 361		
Common bottlenose dolphin *Tursiops truncatus*	195	2 235		
Unidentified bottlenose dolphin	225	1 600		
Fraser's dolphin *Lagenodelphis hosei*	1	200		
Globicephalinae	**232**	**7 559**	**0.277**	**9.028**
Pygmy killer whale *Feresa attenuata* / Melon-headed whale *Peponocephala electra*	27	283		
Melon-headed whale *Peponocephala electra*	63	5 704		
Short finned pilot whale *Globicephala macrorynhus*	19	239		
False killer whale *Pseudorca crassidens* / Short finned pilot whale *Globicephala macrorynhus*	19	85		
False killer whale *Pseudorca crassidens*	51	495		
Risso's dolphin *Grampus griseus*	53	753		
Sperm and beaked whales	**142**	**275**	**0.170**	**0.328**
Blainville's beaked whale *Mesoplodon densirostris*	4	6		
Unidentified Mesoplodon	20	42		
Cuvier's beaked whale *Ziphius cavirostris*	26	61		
Longman's beaked whale *Indopacetus pacificus*	3	4		
Unidentified beaked whale	32	77		
Sperm whale *Physeter macrocephalus*	29	50		
Unidentified Kogia	28	35		
SEABIRDS				
Tropicbirds	**1 112**	**1 253**	**1.328**	**1.497**
White tailed tropicbird *Phaeton lepturus*	428	454		
Red tailed tropicbird *Phaeton rubricauda*	45	51		
Unidentified tropicbirds	639	748		
Grey terns	**4 813**	**19 086**	**5.749**	**22.796**
Noddies	**1 661**	**9 323**	**1.984**	**11.136**
Bobbies	**300**	**535**	**0.358**	**0.639**
Red footed booby *Sula sula*	91	171		
Masked booby *Sula dactylatra*	8	14		
Unidentified boobies	201	350		
Petrels and shearwaters	**1 669**	**3 078**	**1.993**	**3.676**
Brown terns	**5 990**	**31 109**	**7.154**	**37.156**
Frigatebirds	**162**	**519**	**0.193**	**0.620**

Appendix 3: Detection models for cetaceans according to multiple covariate distance sampling

Glare severity significantly affected the detection of Delphininae and sea state significantly affected the detection of sperm and beaked whales (the detection model fitted for each level of the covariate is shown). No covariate affected the detection of Globicephalinae.

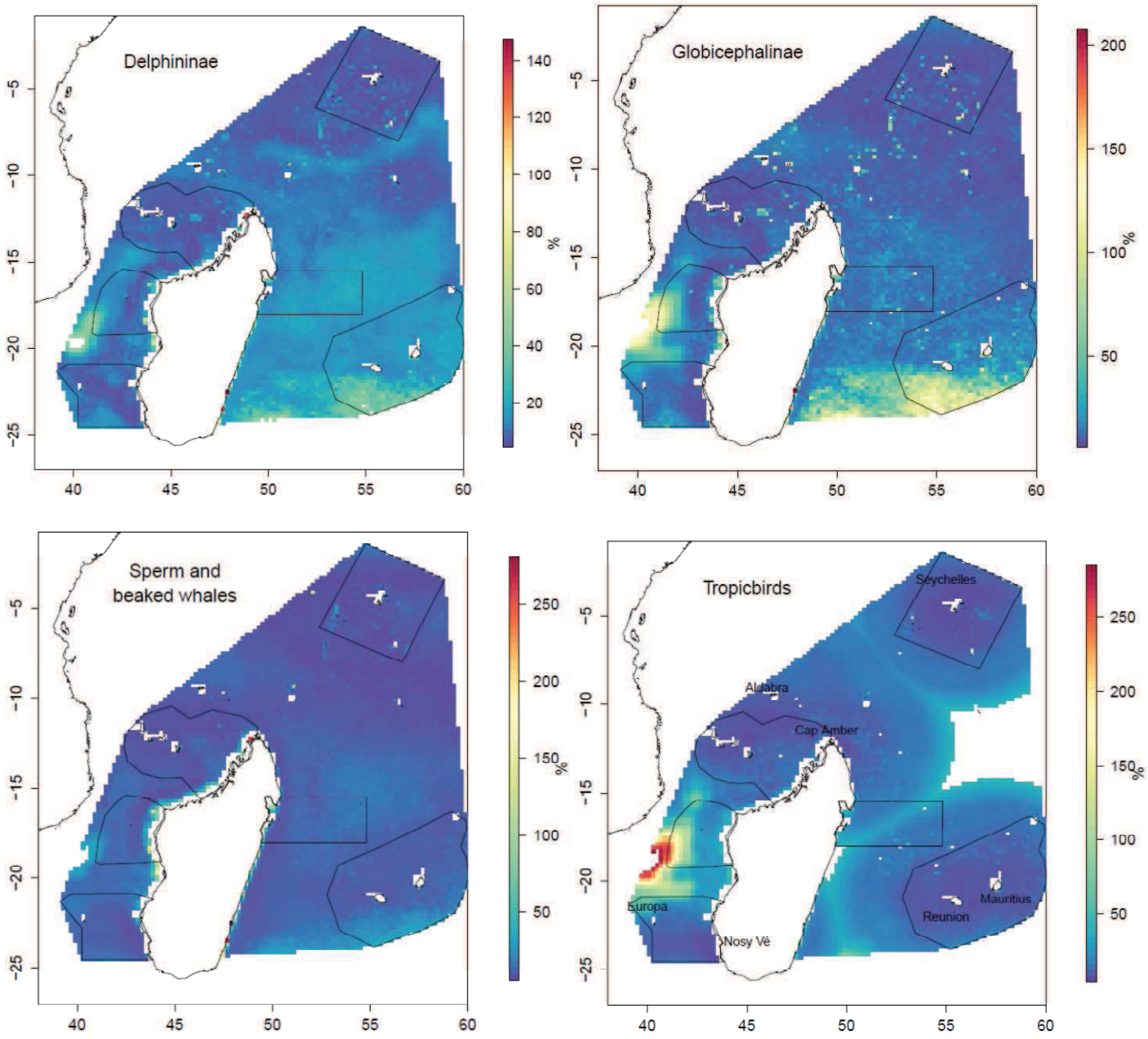


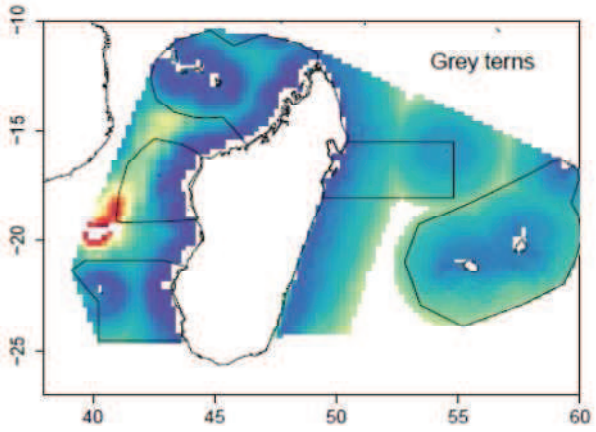


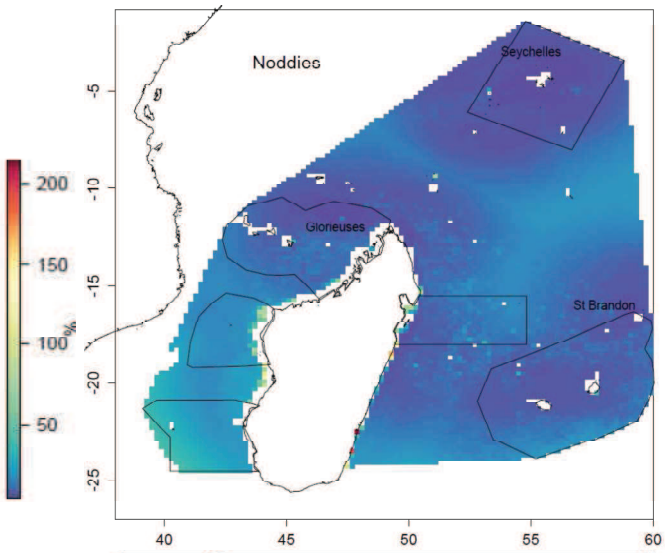


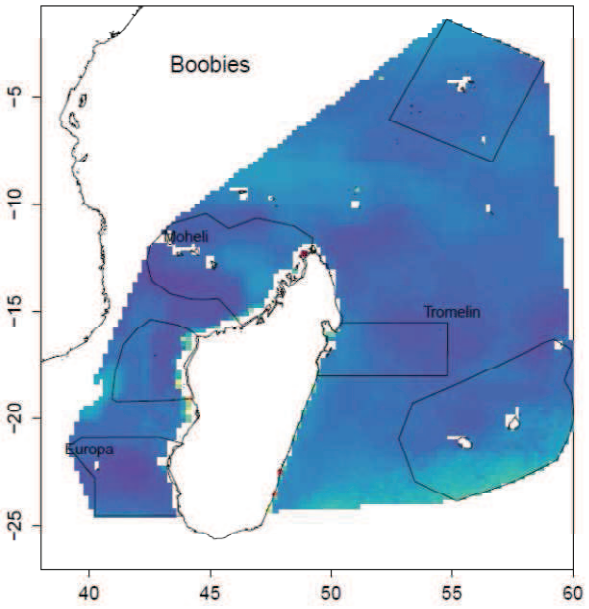
Appendix 4: Uncertainty maps for each top predator guild

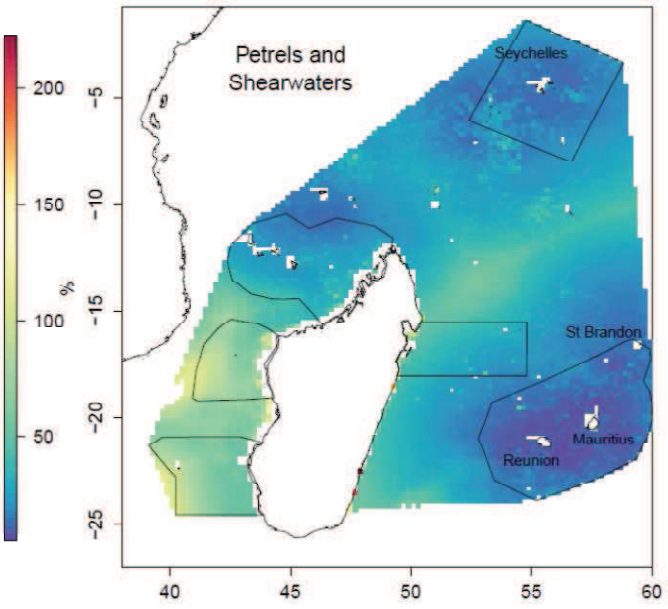
We provide uncertainty maps for each guild, as measured by the coefficient of variation (expressed in %). High predicted densities are associated with a low uncertainty whereas low predicted densities are associated with a higher uncertainty.

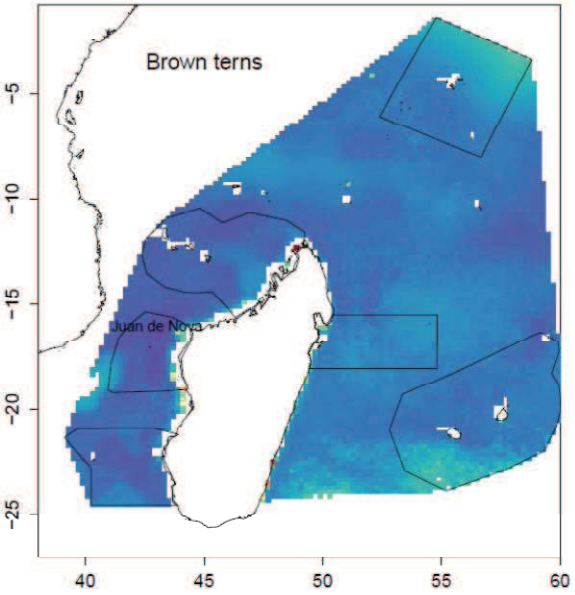


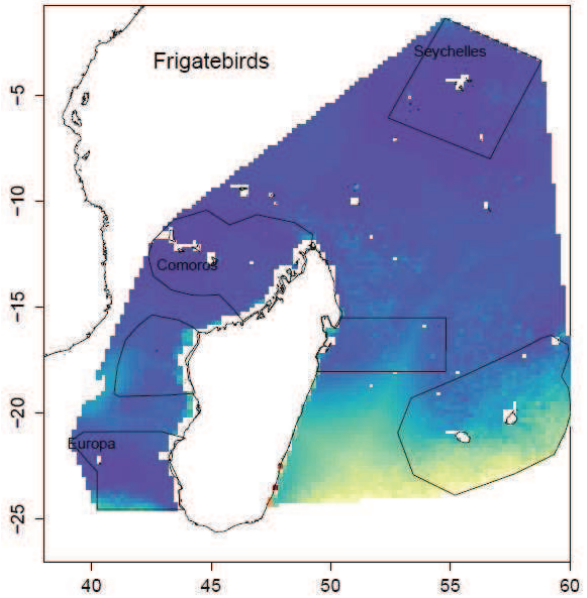

Grey terns
-10
-15
-20
-25
40
45
50
55
60


Noddies
Seychelles
Glorieuses
St Brandon
200
150
100
50
%
400
300
200
100
%
-5
-10
-15
-20
-25
40
45
50
55
60


Boobies
Moheli
Tromelin
Europa
-5
-10
-15
-20
-25
40
45
50
55
60


Petrels and
Shearwaters
Seychelles
St Brandon
Mauritius
Reunion
200
150
100
50
%
100
80
60 %
40
20
-5
-10
-15
-20
-25
40
45
50
55
60

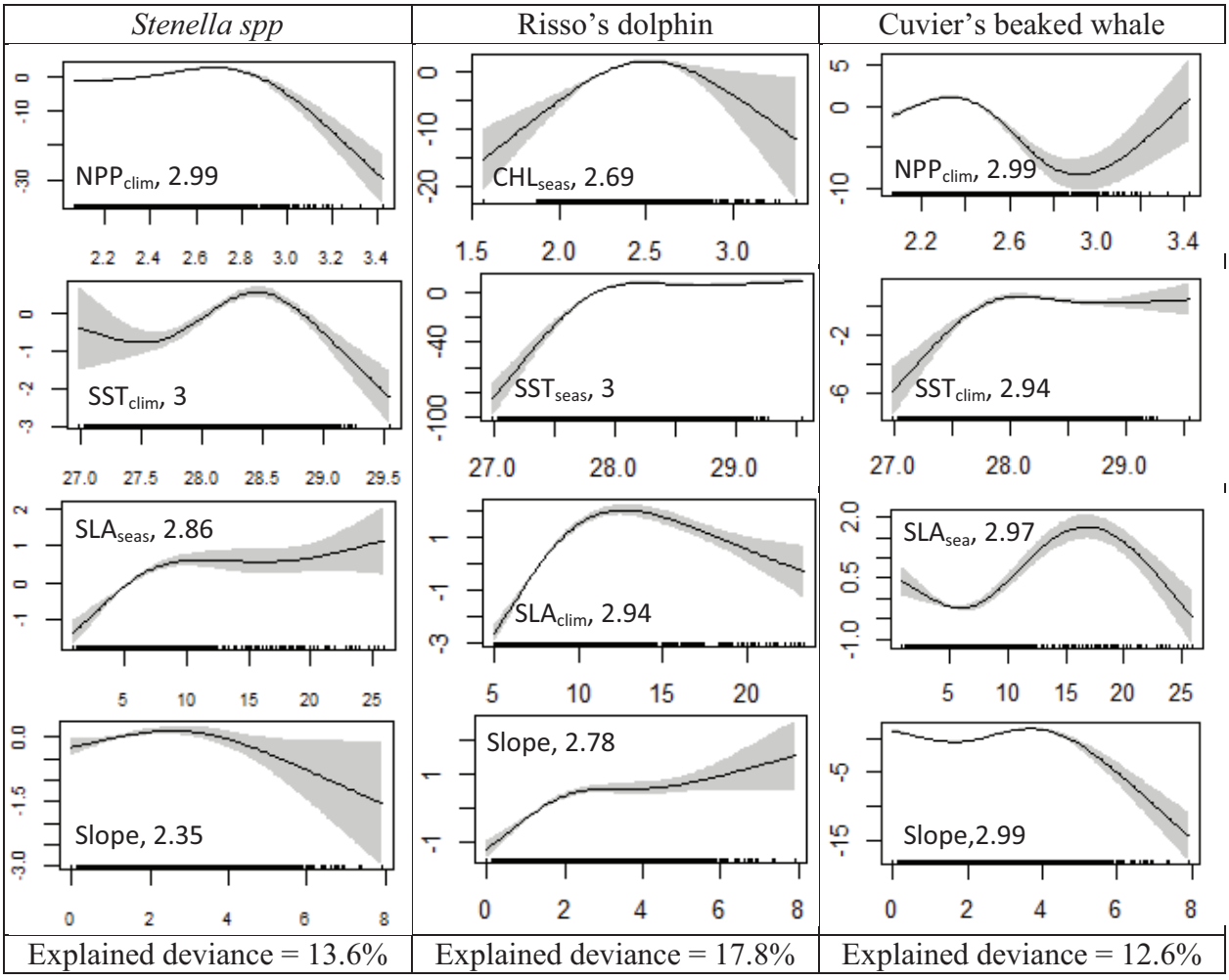

Brown terns
Juan de Nova
140
120
100
80
%
60
40
20
-5
-10
-15
-20
-25
40
45
50
55
60


Frigatebirds
Seychelles
Comoros
Europa
1000
800
600
%
400
200
-5
-10
-15
-20
-25
40
45
50
55
60

Appendix 5: Habitat models for three cetaceans: *Stenella spp*, Risso's dolphin and Cuvier's beaked whale

Here we present habitat modeling results for three cetaceans (forms of smooth functions for the selected covariates, prediction maps and uncertainty maps). Explained deviances are higher for individual species compared to deviances obtained for the corresponding guild.

Table 1: Forms of smooth functions for the selected covariates for each cetacean.



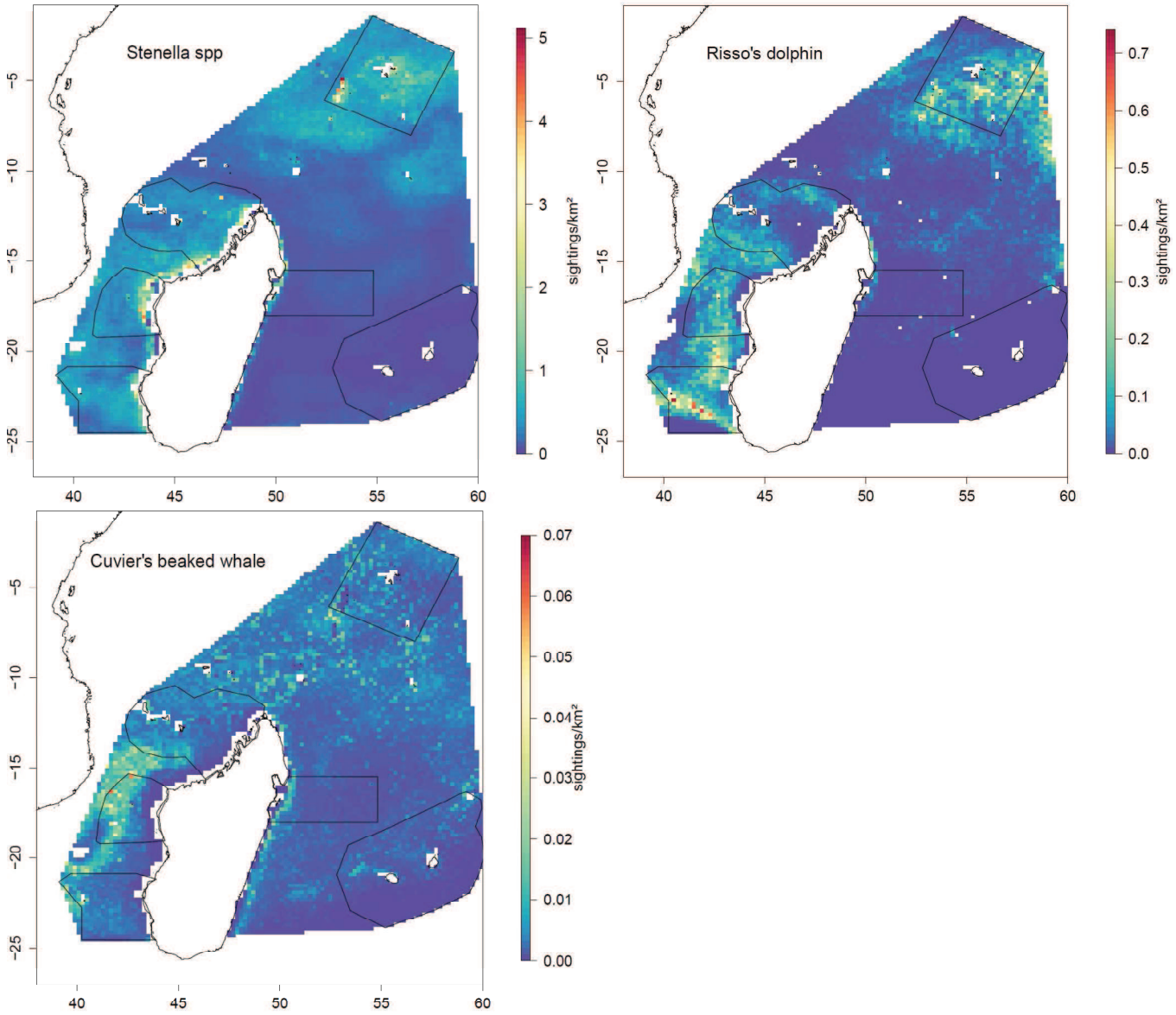


Figure 1: Predicted relative density (individuals/km²) for each cetacean.

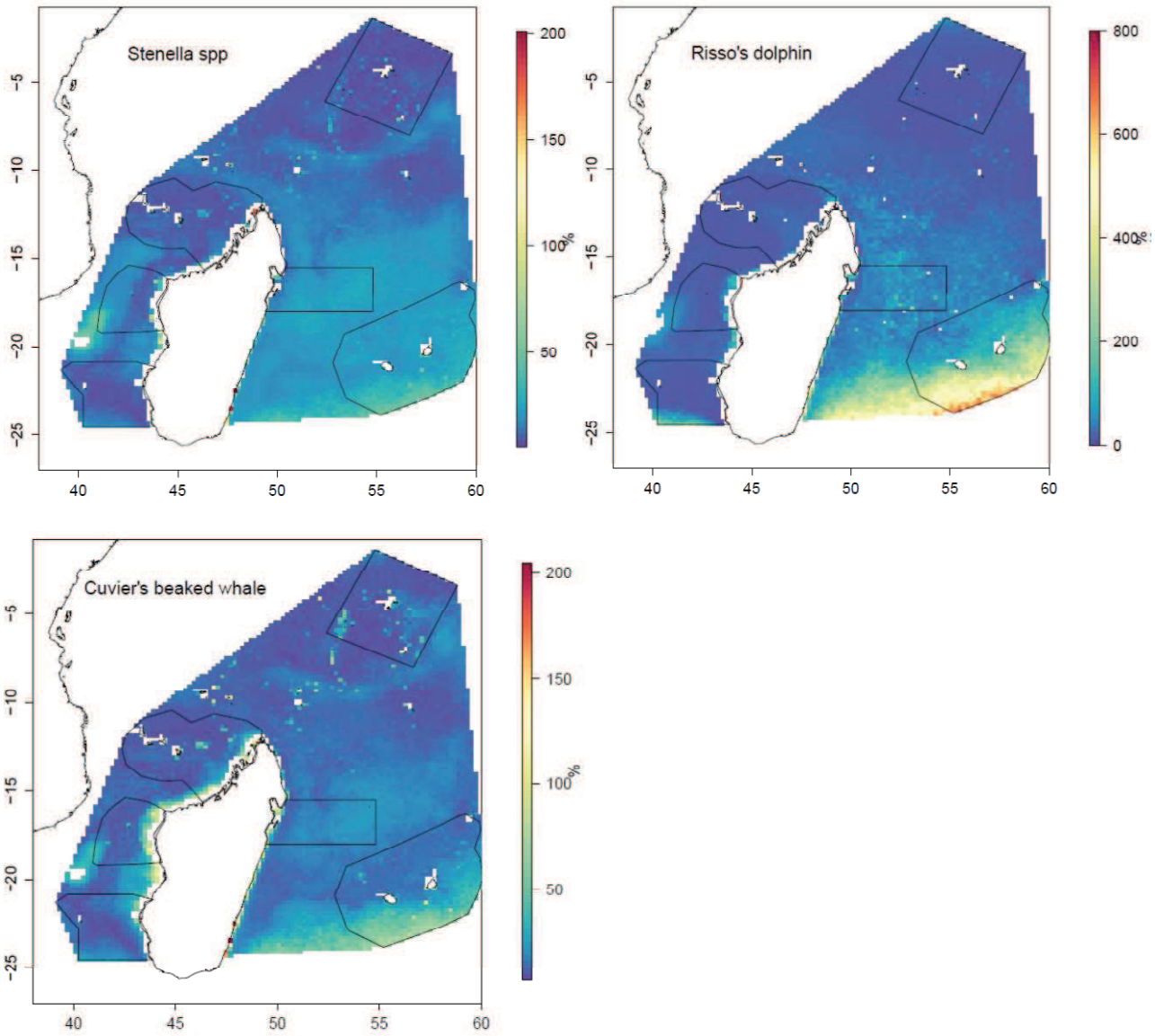


Figure 2: Uncertainty map for each cetacean.

ANNEX 3

Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre

Laura Mannocci, Maxime Catalogna, Ghislain Dorémus, Sophie Laran, Patrick, Lehodey, Pascal Monestiez, Olivier Van Canneyt, Pierre Watremez, Vincent Ridoux

In revision in *Progress in Oceanography*

Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre

Laura Mannocci *(1), Maxime Catalogna (1), Ghislain Dorémus (2), Sophie Laran (2), Patrick Lehodey (3), Wendy Massart (2), Pascal Monestiez (4), Olivier Van Canneyt (2), Pierre Watremez(5) and Vincent Ridoux (1,2).

(1) Laboratoire Littoral Environnement et Sociétés, UMR 7266 Université de La Rochelle-CNRS, Institut du Littoral et de l'Environnement, 2 rue Olympe de Gouges, 17000 La Rochelle, France.

(2) Observatoire PELAGIS, UMS 3462 Université de La Rochelle-CNRS, Systèmes d'Observation pour la Conservation des Mammifères et des Oiseaux Marins, Pôle analytique, 5 allées de l'océan, 17000 La Rochelle, France.

(3) Marine Ecosystems Modeling and Monitoring by Satellites, CLS, Space Oceanography Division, 8-10 rue Hermes, 31520 Ramonville, France.

(4) INRA, UR0546, Unité Biostatistiques et Processus Spatiaux, Domaine Saint-Paul, Site Agroparc, 84914 Avignon, France.

(5) Agence des Aires Marines Protégées, 44 bis quai de la douane, 29229 Brest cedex 2, France.

Abstract

Oligotrophic regions are expected to host low densities of top predators. Nevertheless, top predators with contrasting energetic costs might respond differently to the productivity of their habitat. Energetically costly predators might be constrained to select the most productive habitats to match their high energetic requirements, whereas less active predators would be able to satisfy their needs by exploiting either high or low productivity habitats. In addition, to locate the most profitable habitats, predators can either track the contemporaneous situation of their environment or rely on their past experience to locate areas recurrently favorable to them. Although situated in the core of the South Pacific oligotrophic gyre, French Polynesia is characterized by a fairly marked productivity gradient from the extremely oligotrophic Australs area to the more productive Marquesas area. During the austral summer 2011, concurrent with a moderate La Niña episode, we conducted an aerial survey to collect cetacean and seabird data across the five archipelagos of French Polynesia. The objectives of this study were: (1) to investigate top predator distributions with reference to their energetic constraints and (2) to evaluate their responses to the contemporaneous *versus* average oceanographic situation. We classified cetaceans and seabirds into energetic guilds according to the literature. We used generalized additive models with oceanographic covariates at seasonal and climatological resolutions, as well as static covariates, to predict their distributions. We provided regional habitat predictions for Delphininae, Globicephalinae, sperm and beaked whales, tropicbirds, grey terns, noddies, white terns, boobies, petrels and shearwaters, sooty terns and frigatebirds. Explained deviances ranged from 5% to 30% for cetaceans and from 14% to 29% for seabirds. Cetaceans clearly responded to the productivity gradient, with the highest predicted densities around the Marquesas. However, the energetically costly Delphininae and Globicephalinae depended more strongly on productivity, showing a ratio of 1–26 and 1–31 between their lowest and highest density areas respectively, compared to the less active sperm and beaked whales (showing only a ratio of 1–3.5 in predicted densities). In contrast, seabird distributions appeared more governed by the availability of nesting and roosting sites than by energetic constraints. Top predators did not respond strongly to the contemporaneous situation of the survey, but appeared to exploit areas recurrently favorable to them.

Keywords: South Pacific gyre, productivity gradient, French Polynesia, cetaceans, seabirds, energetic guilds, spatial predictions.

1. Introduction

The South Pacific gyre is an entirely oceanic province, characterized by nutrient-depleted waters and often denoted as the most uniform and stable region of the open oceans, reflecting the origin of the name Pacific ocean (Longhurst, 2007). Although there is a growing knowledge on the physicochemical properties of water masses and circulation features from oceanographic cruises (Rougerie and Rancher, 1994), remote sensing (Martinez and Maamaatuaiahutapu, 2004) and physical models (Sudre and Morrow, 2008), how top predators respond to oligotrophy and exploit this province is poorly known. Top predators, such as seabirds, marine mammals and large predatory fishes, representing the food web's highest trophic levels (Estes et al., 2001) are usually suggested as ecosystem composition indicators, since their presence or abundance can denote a particular habitat or biological community (Zacharias and Roff, 2001). Indeed, top predators often reflect the abiotic characteristics of the ecosystems in which they live, including salinity, temperature, nutrients or productivity. This is illustrated by the global distribution of tuna and billfishes, which mirrors the biogeochemical divisions of the oceans (Reygondeau et al., 2011). According to the concept of ecosystem composition indicators, we would expect low densities of top predators in the South Pacific oligotrophic gyre, as reported in other regions of low productivity and scarce resources (MacLeod et al., 2004; Mannocci et al., 2013).

However, various guilds of top predators might respond differently to the productivity of their ecosystems. In particular, energetic constraints might shape top predator strategies of habitat use. For example, Ballance et al. (1997) showed that seabirds responded to a productivity gradient in the eastern tropical Pacific in accordance with their costs of flight.

Energetically costly seabirds, such as the red-footed booby (*Sula sula*), were only abundant in the most productive habitats and when productivity subsequently dropped, only species with energetically cheaper flights, such as the sooty tern (*Onychoprion fuscatus*), were abundant. We hypothesized that predators with energetically costly life styles might be constrained to select the most productive habitats to match their high energetic requirements, whereas less active predators would be able to satisfy their needs by exploiting either high or low productivity habitats. This should hold especially true in oligotrophic provinces, such as the South Pacific gyre, where top predators might have adapted their foraging strategies to exploit these extremely poor environments (Ballance and Pitman, 1999).

The first objective of this study was to investigate top predator responses to a productivity gradient in an oligotrophic region in relation to their energetic costs. We relied on an aerial survey, which collected cetacean and seabird data in the Exclusive Economic Zone of French Polynesia, in the core of the South Pacific oligotrophic gyre. Remote sensing highlights a productivity gradient in French Polynesia, with nutrient-depleted waters in the south, around the Australs archipelago and more productive waters to the north, near the Marquesas, where an island mass enhances productivity (Signorini et al., 1999). We classified

cetaceans and seabirds into energetic guilds according to the literature and predicted their distributions across French Polynesian waters using habitat models based on static and oceanographic covariates.

To exploit a resource, animals must know where this resource is located (Clark and Mangel, 1984). Some animals might continuously track high quality habitats that are the most valuable for foraging, thus responding to the contemporaneous situation of their environment. However, in long-lived animals such as top predators, foraging probably relies on experience acquired after years or even generations, if foraging culture can be transmitted as is the case in some cetaceans (Rendell and Whitehead, 2001). This is referred to as memory-based foraging strategy (Davoren et al., 2003). Such animals might have learned to exploit oceanographic features that determine recurrent access to food resources, and might respond better to the average oceanographic situation.

Our aerial survey provided a snapshot of top predator distributions in French Polynesia in the austral summer 2011, which was concurrent with a moderate La Niña episode, as indicated by slightly cooler sea surface temperatures across the equatorial Pacific (Climate Prediction Center, 2011). The second objective of this study was to evaluate the capacity of cetaceans and seabirds to respond to the contemporaneous (reflected by the seasonal situation of this survey) *versus* the average (or climatological) oceanographic situation. We predict that if top predators responded to the seasonal situation during the survey, then contemporaneous rather than climatological oceanographic covariates would be selected in the final habitat models. Alternatively, if top predators responded better to recurrent oceanographic features, climatological oceanographic covariates would be preferred over contemporaneous ones.

2. Materials and methods

2.1. Study region

The study region encompassed more than 1.7 million km² in the Economical Exclusive Zone (EEZ) of French Polynesia (4.8 million km²) and spanned over 20 degrees in latitude and longitude. It included five archipelagos, generally oriented northwest-southeastward. The largest Tuamotu archipelago comprises a high density network of islands and atolls and is extended to its southeast by the more dispersed Gambier archipelago. The Society and Australs archipelagos as well as the Marquesas in the north, form three groups of steep islands separated by deep passages (Martinez et al., 2009).

The South Pacific anticyclonic system results from the pressure difference between the southeastern Pacific (high pressure) and the low-pressure system in the central and western equatorial zone. This generates easterly trade winds over the north and westerly trade winds over the south, influencing large-scale oceanic circulation through surface friction. Owing to the rotation of the Earth, Ekman force causes a leftward deviation in ocean currents, producing western and eastern boundary currents, which complete a vast anticyclonic gyre,

bounded by the equator to the north, Australia to the west, the Antarctic Circumpolar Current to the south, and South America to the east. In the center of the gyre, Ekman convergence of the surface water flow induces downwelling. This phenomenon prevents the upward migration of nutrients and generates a permanent decoupling between the oligotrophic euphotic layer and the nutrient-rich deep layer (Longhurst, 2007; Rougerie and Rancher, 1994).

Oceanic circulation generates strong spatial patterns of oceanographic features in French Polynesia (**Figure 1a**). The South Equatorial Current (SEC) flows westwards to the north of French Polynesia. The SEC follows a seasonal cycle: it strengthens during the austral winter and slows down during the austral summer, when the South Equatorial Countercurrent (SECC) appears (Martinez et al., 2009). The Marquesas form an important topographic obstacle to the SEC, inducing turbulent mixing and advection, which, in combination with the iron-enriched waters (from land drainage and hydrothermal supplies), creates an island mass effect (Signorini et al., 1999). Therefore, a significant enhancement of phytoplankton production occurs and is an important contributor to the productivity of this otherwise oligotrophic region. Around the Marquesas, the chlorophyll concentration is higher than 0.2 mg m^{-3} throughout the year and a seasonal bloom occurs between June and December (Martinez and Maamaatuaiahutapu, 2004). As a result of dispersion by SEC, chlorophyll concentration is the highest on the lee side of the archipelago (Signorini et al., 1999). South of the Marquesas, a countercurrent (Marquesas Countercurrent, MCC) flows eastward in the summer (Martinez et al., 2009).

South of 17°S, the Subtropical Countercurrent (STCC), flows eastwards and is characterized by a strong eddy activity, which creates westward and eastward perturbations, decreasing to the east. Eddy kinetic energy is maximum in the summer. The Regional Ocean Modeling System (ROMS) highlighted two regions of strong eddy activity in French Polynesia: south of 22°S (in the STCC) and north of 6–7°S (the northern part of the SEC); between these regions, mesoscale variability is weak (Martinez et al., 2009).

This oceanic circulation scheme is modified by aperiodic ENSO anomalies. During El Niño (as in 1997–1998), the trade winds reverse and consequently, SEC weakens, while SECC strengthens. During La Niña, due to the strengthening of trade winds, SEC reinforces and SECC moves to the southwest. La Niña-related blooms have been reported around the Marquesas (Martinez and Maamaatuaiahutapu, 2004). During both episodes, STCC appears to strengthen and MCC to disappear (Martinez et al., 2009).

2.2. Energetic guilds

We classified cetaceans and seabirds into energetic guilds on the basis of either direct metabolic measurements or indicators of costs of living from the literature. Seabirds are easy to observe and to capture in colonies, allowing a variety of direct metabolic measurements.

This includes basal metabolic rate (BMR, measuring resting metabolism) and field metabolic rate (FMR, representing the overall cost of daily activities) (*e.g.* Flint and Nagy 1984). To classify seabirds into energetic guilds, we relied on the FMR/BMR ratio, referred to as sustained metabolic scope (Peterson et al., 1990), which is the capacity to increase metabolism above resting levels. This ratio ranges from 2.8 to 4.2 in tropical seabirds (Ellis and Gabrielsen, 2002). From the most to the least energetically expensive life styles, we obtained the following guilds: tropicbirds, grey terns, noddies, boobies, petrels and shearwaters and the sooty tern. The FMR/BMR ratio was not available for frigatebirds and white terns, as no metabolic measurements were available for these guilds. However, the extremely low wing loading of frigatebirds (large wing area for a comparatively low body mass), suggests much reduced costs of flight (Weimerskirch et al., 2003). Hence, frigatebirds are considered here as the guild with the lowest cost of living. White terns have a wing loading similar to that of noddies (Hertel and Ballance, 1999); thus, regarding flight energetics, we assumed that they were analogous to noddies.

In contrast to seabirds, very few direct metabolic measurements for cetaceans exist. We relied on their diving performances, which are closely related to their capacity to save oxygen by reducing their energetic costs (Boyd, 1997). The vast majority of cetaceans observed during the survey (austral summer) were odontocetes; hence, our classification focuses on this suborder only, simply named cetaceans in the text. Although limited data are available for some species, sperm and beaked whales generally have remarkable abilities for breath-hold diving, reaching depths greater than 1 000 m for durations of up to over one hour (Tyack et al., 2006; Watkins et al., 1993). They are considered to have the lowest costs of living. Globicephalinae generally engage in fairly deep and long dives, as exemplified by the short-finned pilot whale, *Globicephala macrorhynchus*; however, this species, and perhaps other Globicephalinae, has also been reported to use burst and glide strategies when foraging (Aguilar de Soto et al., 2008). Therefore, Globicephalinae are considered here to form an intermediate energetic guild. Conversely, Delphininae generally engage in shorter and shallower dives, no deeper than 300 m (Baird et al., 2001; Klatsky et al., 2007) and their foraging tactic largely relies on active swimming, in particular for cooperative feeding (Benoit-Bird and Au, 2009). Consequently, in this study, Delphininae constitute the guild of cetaceans with the most costly lifestyle. This classification is supported by indicators of the cost of living based on muscle performance as expressed by muscular mitochondrial density and lipid content (Spitz et al., 2012). Thirty-two species of seabirds and 16 species of cetaceans are represented in the energetic guilds considered in this study (**Table 1)**.

2.3. Field methodology

2.3.1. Survey period and survey design

We collected top predator data from a dedicated aerial survey in French Polynesia during the austral summer (from January to early May 2011). The study area was divided into

six geographic sectors: Society, Australs, North Tuamotu, South Tuamotu, Gambier, Marquesas (**Figure 1b**). Most of the effort was deployed in the oceanic domain (depths ≥ 2 000 m), referred to as the oceanic stratum. In addition, around North Tuamotu and the elevated islands of the Society, Australs, Gambier and Marquesas, a slope stratum was defined (depths < 2 000 m).

2.3.2. Aerial survey methods

Transects were flown at a target altitude of 182 m (600 feet) and a ground speed of 167 km h^{-1} (90 knots). Survey platforms were three Britten Norman 2, high-wing, double-engine aircraft equipped with bubble windows. The survey crew consisted of two trained observers observing with naked eyes and a navigator in charge of data collection on a laptop computer. A fourth, off-duty crew member was also present to enable the rotation of crew members every two hours in an attempt to limit loss of vigilance due to tiredness in long flights (on average five hours without interruption). A GPS, logged to a computer equipped with 'VOR' software (designed for the aerial parts of the SCANS-II survey (Hammond et al., 2013)), collected positional information every two seconds. Beaufort Sea state, glare severity, turbidity, cloud coverage and an overall subjective assessment of the detection conditions (good, moderate or poor as for small delphinids), were recorded at the beginning of each transect and whenever any of these values changed.

For cetaceans, we collected data following a distance sampling protocol. Information recorded included species identification to the lowest possible taxonomic level, group size and declination angle to the group when it passed at right angle to the aircraft (measured with a hand-held clinometer). Together with the altitude of the aircraft, angles provided perpendicular distances, which allowed distance sampling analyses to be conducted (Buckland et al., 2001). For seabirds, we collected data using strip transect methodology, under the assumption that all seabirds within the strip were detected (Tasker et al., 1984). The strip width was fixed at 200 m on both sides of the transect. Identification was performed to the lowest taxonomic level whenever possible, but groupings were inevitable for seabirds that could not be distinguished from the air (*e.g.* frigatebirds, composed of the Great frigatebird, *Fregata minor* and the Lesser frigatebird, *F. ariel*).

2.4. Detection function modeling

We used multiple covariate distance sampling (Marques and Buckland, 2004) to model the effect of detection covariates on cetacean detection probability, in addition to distance. Before fitting detection functions, we truncated 5% of the most distant sightings (w being the truncation distance). For each cetacean guild, hazard rate ($g(x)=1-\exp(-(x/\sigma)^{-\beta})$, $x \leq w$) and half normal models ($g(x)=\exp(-x^2/2\sigma^2)$, $x \leq w$) were fitted to perpendicular distances and the model that minimized the Akaike Information Criterion (AIC) was selected (Buckland et al., 2001). We then tested the influence of sea state, glare severity, turbidity, cloud coverage and subjective conditions and retained the detection covariate if it provided a significantly

smaller AIC (*i.e.* delta AIC greater than two units). If a detection covariate was significant, we estimated an effective strip width (ESW) for each level of the covariate, if not, we estimated a unique ESW for use under all detection conditions. For seabirds, the strip width was 200 m (a uniform detection function was used, as implied by the strip transect methodology). These analyses were conducted in R with the mrds package (Laake et al., 2011).

2.5. Data organization

Surveyed transects were split into legs of identical detection conditions, further divided into 10 km-long segments, so that variability in survey conditions and geographic location was small within segments. More than 65% of segments were equal to 10 km, but lengths varied between 0.3 and 15 km. To maximize the quality of data for habitat modeling, we ignored segments shorter than 3 km and segments flown under deteriorated survey conditions (*i.e.* with sea state greater than five) and performed the analysis on the remaining 9 392 segments. For every segment, we compiled the total number of individuals for each cetacean and seabird guild. We used ArcGIS 10 (Environmental Systems Research Institute, 2010) to co-locate the position of segments with habitat covariates, based on values at their mid points.

2.6. Habitat covariates

To model top predator habitats, we used oceanographic as well as static covariates (**Table 2**). As the aerial methodology did not allow the collection of simultaneous *in situ* oceanographic measurements, we relied on remotely sensed data, which provided coverage of the ocean surface in our survey region. We considered two temporal resolutions: (1) a seasonal resolution, corresponding to contemporaneous oceanographic conditions averaged over the duration of the survey (January–May 2011) and (2) a climatological resolution, corresponding to oceanographic conditions averaged over the same season (January–May) from 2003 to 2011. In this study, the seasonal resolution was the most instantaneous resolution that was available for consideration in the analyses. Using a finer (for example weekly) temporal resolution would have led to a high proportion of missing data, as cloud coverage was significant during the survey. In addition, the survey period corresponded to an established austral summer situation. In the central South Pacific, oceanographic variability is mostly seasonal (Wang et al., 2000), so oceanographic conditions were probably not very variable over this time period.

From the ocean color website (http://oceancolor.gsfc.nasa.gov/), we obtained surface chlorophyll-*a* concentration (CHL), sea surface temperature (SST) and photosynthetically available radiation (PAR), derived from the aqua-MODIS sensor (4 km spatial resolution). We used daily data along with Wimsoft Automation Module (Kahru, 2010) to derive seasonal and climatological composites. We obtained net primary production (NPP) using CHL, SST, PAR and the Vertically Generalized Productivity Model (Behrenfeld and Falkowski, 1997).

Additionally, we used sea level anomaly (SLA) (0.25° spatial resolution), an altimetry product produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/). We considered the standard error of SLA as an indicator of mesoscale activity (areas with a high standard error would have a high mesoscale activity; areas with a low standard error would have a low mesoscale activity). Indeed, vigorous variation in sea surface height denotes significant mesoscale activity (Stammer and Wunsch, 1999). Based on weekly SLAs available from the website, we calculated the standard errors of SLA for the survey season and the same season's climatology averaged over 2003–2011. The spatial and temporal variability of oceanographic covariates is described in **Appendix A**.

In addition to oceanographic covariates, we considered static covariates: slope and depth for cetaceans and slope and either distance to the nearest colony or to the nearest coast for seabirds. We obtained bathymetric data from the GEBCO one minute grid (General Physiographic Chart of the Ocean; http://www.gebco.net/). We derived slope via Spatial Analyst in ArcGIS 10 (Environmental Systems Research Institute, 2010). Bottom slope interacts with water circulation, inducing physical processes that either enhance primary production or influence the availability and aggregation of prey (e.g. at island shelf edges) (Springer et al., 1996). We calculated the distance to the nearest colony (D_{colony}) and distance to the nearest coast (D_{coast}), respectively, as the shortest distance between the midpoint of each segment and colony location or the coast.

Thibault and Bretagnolle (2007) summarized the baseline knowledge on seabird colonies in French Polynesia (**Appendix B)**. Due to the remoteness of some islands, an exhaustive prospection of colonies was difficult. For seabirds for which there was a fairly good knowledge of colony locations, we used distance to the nearest colony. This was the case for frigatebirds, boobies, noddies and petrels and shearwaters. For seabirds for which there was an incomplete knowledge of colony locations (tropicbirds and sooty terns) or which use roosting sites outside the breeding season (grey terns and white terns), we used distance to the nearest coast. This implied that every coast could potentially be used for reproduction or roosting.

2.7. Habitat modeling

2.7.1. Model development

Regressions are commonly used to model the relationships between an animal's distribution and its environment. They encompass a range of methods that differ in their assumptions regarding the statistical distribution of variables and the functional forms of relationships. Generalized additive models (GAMs), which are semi parametric extensions of generalized linear models, have two underlying assumptions: predictors are additive and their components are smooth. They are often referred to as data-driven because data determine the

nature of the relationships without any assumptions concerning their functional form (Guisan et al., 2002).

We used GAMs to relate the numbers of cetaceans and seabirds per segment to habitat covariates. In GAMs, the link function $g()$ relates the mean of the response variable given the covariates $\mu=E(Y|X_1,...,X_p)$ to the additive predictor $\alpha + \sum fi(Xi)$:

$$g(\mu) = \alpha + \sum fi(Xi)$$

The components $fi(Xi)$ of the additive predictor are non parametric smooth functions (splines) of the covariates (Wood and Augustin, 2002).

The response variable Y was the number of individuals. As count data are often characterized by skewed distributions, we used an overdispersed Poisson distribution with a variance proportional to the mean and a logarithmic link function. Accounting for non-constant effort, we used the logarithm of strip area as an offset, calculated as segment length multiplied by twice the ESW. GAMs were fitted in R using the mgcv package, in which degrees of freedom for each smooth function are determined internally in model fitting and thin plate regression splines are the default (Wood, 2006). We limited the amount of smoothing to three degrees of freedom for each spline to model non-linear trends, while avoiding overfitting with no ecological meaning (Forney, 2000).

2.7.2. Model selection

Candidate covariates for model selection were oceanographic covariates (at both seasonal and climatological resolution), as well as static covariates. NPP and CHL were log-transformed and slope was square-root-transformed. For each cetacean and seabird guild, we fitted the models containing all possible combinations of four covariates, excluding combinations of collinear covariates (*i.e.* with a Spearman coefficient < 0.7 and > -0.7). Four covariates were retained in the model to avoid excessive complexity, whilst providing a reasonable explanatory power. The models with the lowest generalized cross-validation (GCV) score were selected. We used explained deviance to evaluate the models' fit to the data. The selected models were then used to predict cetacean and seabird distributions.

2.7.3. Predictions

We used the selected models to predict relative densities of top predators in each cell of a $0.2° \times 0.2°$ grid of habitat covariates, including static and both seasonal and climatological oceanographic covariates. We limited the predictions to a convex hull including the surveyed geographic sectors in which oceanographic conditions encompassed those encountered during the survey. We predicted cetacean and seabird habitats in this convex hull, allowing geographic extrapolation (between survey blocks) but without predicting beyond the range of variables used in model fitting. For each guild, we also produced an uncertainty map, as measured by the coefficient of variation. Uncertainty

estimates were derived from the Bayesian covariance matrix of the model coefficients within the mgcv package (Wood 2006).

3. Results

3.1. Survey effort and detection conditions

The aerial survey covered 98 476 km of transects within the EEZ of French Polynesia, with the majority of effort implemented in oceanic waters (**Table 3**). Overall, detection conditions were good-to-moderate, with 62% of effort flown at sea state three or lower. However, sea state was not homogeneous within the region. It was the most deteriorated in the Marquesas (58% of effort with sea state four) and South Tuamotu (36%) and comparatively better in the Society (21%) and Gambier (only 9%).

3.2. Cetacean and seabird sightings

During the survey, 21 497 sightings of seabirds and 274 sightings of cetaceans were collected on effort. We retained 15 633 seabird sightings (recorded within the 200 m strip) and 260 cetacean sightings (identified to the genus) for the constitution of guilds. Among cetaceans, sperm and beaked whales were the most frequently sighted guild (100 sightings), followed by Delphininae (86) and Globicephalinae (74) (**Appendix C, Figure 2a**). However, in terms of individuals, Delphininae and Globicephalinae were more numerous (respectively 774 and 1 046 individuals sighted) compared to sperm and beaked whales (194 individuals). For the three cetacean guilds, encounter rates were the highest in the Marquesas (2.38 sightings/1 000 km for Delphininae, 1.78 for Globicephalinae and 2.26 for sperm and beaked whales). For Delphininae and Globicephalinae encounter rates were the lowest in the Australs (both equal to 0.13 sightings/1 000 km), whereas for sperm and beaked whales they were intermediate in the Australs (1.01) and the lowest in Gambier (0.54) and South Tuamotu (0.37). Thus, encounter rates of sperm and beaked whales appeared less variable between sectors.

The most frequently encountered seabirds were white terns by far (7 755 sightings, 13 063 individuals) followed by noddies (2 058 sightings, 14 005 individuals) and boobies (1 891 sightings, 6 782 individuals). Grey terns and frigatebirds were the least commonly sighted (respectively 105 and 295 sightings) (**Appendix C, Figure 3a**). Tropicbird encounter rates were the highest in the Marquesas (22.81 sightings/1 000 km). Grey terns were more frequently encountered in the Marquesas (2.14) and North Tuamotu (1.95). Noddies were more frequent in North Tuamotu (52.78). White terns were common in all sectors, with more numerous encounters in Tuamotu (116.26 sightings/1000 km in North Tuamotu and 141.14 in South Tuamotu). Booby encounter rates were the highest in the Society (31.52) and North Tuamotu (39.32). Petrels and shearwaters were the most frequently encountered in North Tuamotu (19.86) and the Society (19.95). Finally, sooty terns and frigatebirds were more

common around the Marquesas (respectively 43.96 and 9.92 sightings/1 000 km). For most seabirds, encounter rates were the lowest in the Australs and Gambier sectors.

3.3. Detection function modeling

Best-fitting detection models were half normal for the three cetacean guilds (**Table 4**, **Appendix D**). Turbidity significantly affected the detection of Delphininae. No detection covariate had a significant effect on Globicephalinae. Sea state significantly affected the detection of sperm and beaked whales. In addition, group size did not have a strong impact on cetacean detection, since ESWs were not significantly higher for larger group sizes (**Appendix E**). There is no detection function for seabirds as they were sampled using a strip transect methodology.

3.4. Habitat modeling

3.4.1. Model selection

For cetaceans, either climatological or seasonal covariates were selected in the best models (only climatological covariates for Globicephalinae and two seasonal and one climatological covariate for the other two guilds) **(Figure 4)**. Explained deviances varied between 4.9% for sperm and beaked whales and 29.9% for Globicephalinae. Sperm and beaked whales showed an increasing relationship with NPP. For Delphininae and Globicephalinae, in the core of sampled NPP values (indicated by the tenth and ninetieth quantiles), smooth functions suggested increasing relationships. Delphininae and sperm and beaked whales showed unimodal relationships with SST, although uncertainty was higher in cooler waters, as expressed by the large confidence intervals. For Globicephalinae, when considering the tenth and ninetieth quantiles of data, the smooth function suggested an optimum SST. Densities of Delphininae decreased for higher standard errors of SLA, whereas densities of sperm and beaked whales increased, indicating an affinity for areas of higher mesoscale activity. Globicephalinae densities increased with higher slope values. For Delphininae, there was a negative relationship with depth.

For seabirds, climatological covariates were primarily selected in the best models **(Figure 5)**. For noddies, white terns, sooty terns and frigatebirds, only climatological oceanographic covariates were selected. The guild of petrels and shearwaters was the only one for which only seasonal covariates were selected. Explained deviances ranged from 13.9% for petrels and shearwaters to 29.4% for frigatebirds. The distance to the nearest coast or colony explained between less than 2% of the deviance for petrels and shearwaters and sooty terns and 13.6% for boobies, indicating contrasting dependencies on colonies or roosting sites. Seabird density decreased with distance to the coast or distance to the colony, except for sooty terns, for which density was maximum at about 200 km from the coast. Many seabirds showed monotonically increasing relationships with NPP or CHL. Smooth functions suggested optimum SSTs for grey terns, white terns, frigatebirds, boobies and petrels and

shearwaters, although for the latter two, confidence intervals were large in cooler waters. The density of sooty terns increased with SST. The density of frigatebirds and boobies decreased with the standard error of SLA, whereas that of tropicbirds and sooty terns increased, suggesting an affinity for areas of higher mesoscale activity. Slope was selected for tropicbirds, grey terns, noddies and boobies, with either increasing or decreasing relationships.

In general, smooth functions were the least reliable at the extremes of the sampled data, where they were often associated with large confidence intervals, due to the limited amount of data at the edges of covariate ranges.

3.4.2. Predictions

Predicted distributions differed for the three cetacean guilds (**Figure 2b**). A latitudinal gradient was apparent for Delphininae, with the highest densities in the Marquesas (in particular in oceanic waters to the west of the archipelago), intermediate in the Society and Tuamotu and the lowest in the Australs. Mean predicted densities showed a 1–26 ratio between the Australs and the Marquesas (**Figure 2b, Figure 6**). For Globicephalinae, as for Delphininae, there was a latitudinal gradient in the predicted distribution. Predicted densities were the highest around the Marquesas, intermediate around Tuamotu and the Society and the lowest in the Australs. Mean predicted densities showed a 1–31 ratio between the Australs and the Marquesas (**Figure 2b, Figure 6**). For sperm and beaked whales, predicted densities were high around the Marquesas (to the west of the archipelago), low in a latitudinal band situated between 14 and 22°S, before increasing again south of 22°S, in the Australs (**Figure 2b**). In contrast to Delphininae and Globicephalinae, mean predicted densities showed only a 1–3.5 ratio between the lowest (Society) and highest (Marquesas) density sectors (**Figure 6)**.

Seabird predicted distributions also revealed a latitudinal gradient, with the lowest predicted densities around Gambier or the Australs (**Figure 3b, Figure 6**). Tropicbirds had an inshore distribution, with higher predicted densities around the Marquesas and the Society. For grey terns, higher densities were predicted inshore, notably around the Marquesas and Tuamotu and very low densities were predicted in southern French Polynesia. For noddies, the highest densities were predicted in North Tuamotu, followed by the Marquesas and very low densities were predicted south of 20°S. For white terns, the predicted map showed a wide distribution extending to offshore waters (although densities were maximum around the islands), with only a 1–4 ratio in predicted densities. Boobies had an inshore distribution with the highest densities predicted in Tuamotu and the lowest in the Australs. Petrels and shearwaters were mainly distributed north of 20°S, with the highest densities predicted in North Tuamotu and the Society. Sooty terns were principally distributed north of 14°S, with maximum densities offshore, at the limit of surveyed sectors. The highest densities of sooty terns were predicted around the Marquesas. Finally, frigatebirds had an inshore distribution around Tuamotu and Marquesas, with the highest densities predicted in the latter sector.

Overall, habitat predictions agreed with the observed distributions (**Figure 2a-b, Figure 3a-b**). The very large groups of Globicephalinae, notably around the Marquesas, were fairly well predicted by the model. Among seabirds, predictions were perhaps the least reliable for guilds, with the lowest sighting numbers (grey terns and frigatebirds) (**Figure 3**). Uncertainty maps, provided for each guild in **Appendix F**, showed that high predicted densities were associated with low uncertainty, whereas low predicted densities were associated with higher uncertainty, as illustrated by Delphininae and Globicephalinae. In addition, uncertainty in predicted seabird densities increased with distance from the islands. Typically, two roughly triangular areas located west and southeast of the Marquesas, further offshore from any island than the maximum distance flown by survey aircrafts, corresponded to poor predictions for most seabird guilds except for petrels and shearwaters.

4. Discussion

4.1. Limitations of the approach

Habitat models relate species distribution data with environmental predictors at sighting locations by using statistically derived response surfaces, then allowing predictions across an entire region (Barry and Elith, 2006; Elith and Leathwick, 2009). We collected top predator data from an aerial survey based on distance sampling (for cetaceans) and strip transect (for seabirds). Cetaceans might have been missed due to perception bias (animals missed while they are present at the surface, often as the result of bad survey conditions) and availability bias (animals not available at the surface) (Pollock et al., 2006). We did not account for the availability bias, as our objective was not to provide quantitative estimates of abundance, but to investigate for each energetic guild independently, the spatial distribution of predicted densities and their variability between the sampled sectors. However, we tested and modeled the effect of survey conditions on the detection of cetaceans, in addition to perpendicular distance, before incorporating it in habitat modeling. Sea state, which was more deteriorated around the Marquesas, significantly affected the detection of sperm and beaked whales. Accounting for this effect in habitat modeling strengthened the initial perception, based on uncorrected encounter rates, that the Marquesas were the sector of highest cetacean densities. Similar corrections could not be performed for seabirds, which were sampled with a strip transect methodology, implying equal detection probabilities across the survey band width. Therefore, possible seabird detection biases related to a deteriorated sea state around the Marquesas could not be accounted for.

In this study, we classified cetaceans and seabirds into energetic guilds to examine their distributions in relation to their general energetic constraints. Several limitations are inherent to this approach. Guilds might contain species with various body sizes and group sizes; so species within a guild might exhibit different detectabilities, as illustrated by the sperm and beaked whale guild, which combines sperm whales, *Kogia spp* and beaked whales. This affected the offsets used in the GAMs but probably did not impact cetacean-habitat

relationships. Guilds might also contain species with different habitat preferences, which might have contributed to the low explained deviances. Although grouping top predators into guilds raised some methodological issues, differences within a guild are probably smaller than differences between guilds and these guilds defined on general metabolic considerations have a clear heuristic value for our exploration of top predator habitat utilisation in relation to their energetic needs. In addition, this approach allowed the full exploitation of aerial survey data in which identification to the species level is not always possible.

Along with top predator data, we used indirect environmental predictors as proxies of resource availability (Guisan and Zimmermann, 2000). The objective was more to highlight statistical relationships between top predators and their environment to provide regional predictions (*i.e.* predictive models), than to elucidate precise mechanisms that drive the observed patterns (*i.e.* explanatory models) (Guisan et al., 2002). Model predictors identified in this study, either oceanographic (*e.g.* primary production, temperature) or static (depth, slope, distance from the nearest colony), were previously found to be relevant for top predators in the northeast and tropical Pacific, although environmental data were collected simultaneously with sightings (Becker et al., 2010, 2012; Ferguson et al., 2006; Redfern et al., 2008; Vilchis et al., 2006; Yen et al., 2004). However, for a given predictor, the forms of the relationships differed between French Polynesia and other regions of the Pacific. This probably results from the contrasting ranges of oceanographic covariates between these regions and suggests a limited model transferability (Elith and Leathwick, 2009). In addition, in French Polynesia, logistical constraints inherent to aerial surveys (including the obligate presence of an airport with an adequate aircraft maintenance) prevented us from sampling the whole range of environmental conditions present in the region. As a result, waters north of the Marquesas and around Rapa in the southeastern Australs, as well as some areas located between the main archipelagos could not be surveyed. These poorly sampled areas corresponded fairly well to the areas of higher uncertainty in predicted densities (**Appendix F**).

4.2. Modeling framework

In this study, we modeled the number of individuals using Poisson GAMs in which overdispersion was corrected using a quasilikelihood model. This method has successfully been used for species characterized by small group sizes (*e.g.*Redfern et al., 2013) and was appropriate for most of our guilds. The negative binomial is the other distribution recommended in case of heavy tailed count data (Ver Hoef and Boveng, 2007). Globicephalinae and noddies had larger and more variable group sizes. However, using a negative binomial distribution yielded similar results (not shown). Thus, we considered the Poisson distribution with overdispersion to be a good approximation, considering our approach of grouping species into guilds.

The rather low explained deviances of our models, in particular for cetaceans, appeared common in GAMs (Becker et al., 2010; Ferguson et al., 2006; Forney et al., 2012). They might reflect the use of indirect predictors rather than more causal ones (Austin, 2002), such as the availability of prey, as well as the probable high number of false absences in cetacean data, resulting from diving behavior which limit availability at the surface.

Model evaluation is an important step in the habitat modeling process (Guisan and Zimmermann, 2000). Since only one survey was conducted in French Polynesia, we could not evaluate the performance of our models based on an independent dataset. Nonetheless, we proceeded with caution since we allowed geographical extrapolation (between survey blocks) but did not predict beyond the range of habitat variables used in model fitting. In the survey blocks, predictions are supported by available data and can be visually compared with observations. Predictions are probably less reliable outside the survey blocks. Uncertainty in seabird predicted densities increased outside survey blocks, but this was not the case in cetacean predictions, where uncertainty was sometimes greater within sectors with very few sightings (for example for Delphininae, CV scores were highest in the Australs sector). Although these initial habitat predictions at the scale of French Polynesia are encouraging, it would be worth validating them with future surveys. However, obtaining data from outside the sectors is logistically challenging, as these areas are situated far from any large islands.

4.3. Top predator responses to the spatial variability of oceanographic features

Our survey provided for the first time insights into the distribution of cetaceans and seabirds in one of the most oligotrophic regions of the tropical Pacific, which had remained poorly studied to date. Indeed, the understanding of top predator habitats in Pacific waters has primarily focused on eutrophic systems, such as the California Current (Ainley et al., 1995; Becker et al., 2010; Ford et al., 2004) or the Humboldt Current (Anderson, 1989; Weichler et al., 2004) and mesotrophic systems, such as the eastern tropical Pacific (ETP) (Ballance et al., 2006; Ferguson et al., 2006). In this study, we investigated cetacean and seabird responses to the spatial variability of oceanographic features in French Polynesia. Prediction maps highlighted the three principal oceanographic domains in the region: (1) the north (between 7 and 14°S), with high surface productivity, (2) the center (between 14 and 22°S), with low mesoscale activity and low surface productivity and (3) the south (between 22 and 26°S), with strong eddy activity but low productivity.

In the north of the region, densities were comparatively high for the three cetacean guilds and several seabird guilds (*e.g.* sooty terns). Gannier (2009) previously noted the high relative abundance of odontocetes around the Marquesas compared to the Society Islands. The north is characterized by an enhancement of phytoplankton production, occurring to the west of the Marquesas (Signorini et al., 1999). Bertrand et al. (1999) highlighted three micronekton zones from acoustic echo-sounding in French Polynesia and found a maximum abundance

south of the Marquesas, between 7 and 13°S. The highest tuna catches per unit effort were also reporded in this area (Bertrand et al., 2002). Thus, the high densities of top predators were probably related to more abundant prey resources.

Conversely, in the center, densities of all cetaceans were low, probably as a consequence of the low abundance of micronekton (Bertrand et al., 1999). In the southern part of the region, densities of cetaceans (except sperm and beaked whales) and seabirds were very low. This area is defined by strong eddy activity (Martinez et al., 2009) but low surface productivity, unlike what is often observed elsewhere (*e.g.* in the Mozambique Channel, TewKai and Marsac, 2009). Mesoscale eddies induce a productivity enhancement in the euphotic zone if (1) nutrients are available in sufficient quantities in the water column and (2) eddy energy is strong enough to drive nutrients to the surface (Uz et al., 2001). This is clearly not the case around the Australs, in the core of the oligotrophic gyre, as illustrated by the very low nitrate concentrations at 200 m (CSIRO Atlas of regional seas, 2009). Sperm and beaked whales were the only cetaceans present at comparatively intermediate densities around the Australs. With their long and deep dives (Tyack et al., 2006; Watkins et al., 1993) and less active lifestyles, they might be able to forage on more dispersed resources than cetaceans with more costly lifestyles. Alternatively, their presence might be related to more abundant deep resources, not accessible to other cetaceans. Thus, oceanographic data describing productivity in the epipelagic layer might be partly irrelevant to predict the distribution of deep divers, unlike suggested in previous studies conducted at very large spatial scales (*e.g.* Jaquet and Whitehead, 1996).

Barlow (2006) conducted an extended cetacean line transect survey in the EEZ of the Hawaiian Islands, characterized by low surface productivity and situated at a similar latitudinal range as French Polynesia in the northern hemisphere. Low densities of cetaceans, especially delphinids, were reported compared to the more productive waters of the ETP. However, densities of deep diving cetaceans, including sperm whales and beaked whales, were similar or even higher than in the ETP. This appeared consistent with our results in French Polynesia, where deep divers were present with fairly similar densities in both high and low productivity habitats, whereas delphinids might be constrained to forage in more productive habitats, owing to their expensive lifestyles.

4.4. Strategies of habitat use

The link between top predator energetics and the productivity of their habitat has been previously documented. Studies conducted along large scale productivity gradients (Ballance et al., 1997; Hyrenbach et al., 2007; Smith and Hyrenbach, 2003) or comparing distinct biogeographic provinces (Mannocci et al., 2013; Schick et al., 2011) found that top predator communities were possibly structured according to energetic constraints. For example, diving seabirds are absent from oligotrophic tropical waters where surface feeding seabirds with a less active foraging strategy dominate (Hyrenbach et al., 2007; Smith and Hyrenbach, 2003).

We documented the variability of predicted densities across surveyed sectors for each guild, to assess its dependence on habitat productivity. Cetaceans responded to the productivity gradient in French Polynesia. However, the energetically costly delphinids depended more strongly on productivity, showing respectively a 1–26 and a 1–31 ratio between the lowest and highest density sectors, compared to the less active sperm and beaked whales that only showed a 1–3.5 ratio.

Overall, seabirds responded to the productivity gradient, although less clearly than cetaceans did and apparently irrespective of their energetic costs, as illustrated by two guilds of terns. White terns, despite their supposedly intermediate costs of flight, were widely distributed and only showed a 1–4 ratio in their predicted densities. Unexpectedly, sooty terns, characterized by low costs of flight (Ellis and Gabrielsen, 2002), were concentrated in the most productive waters to the leeward side of the Marquesas and between 12° and 15°S to the north of the Society and Tuamotu archipelagos. Sooty terns are mostly winter breeders in the Marquesas (Thibault and Bretagnolle, 2007); thus, they were probably not bound to colonies during the survey, as suggested by maximum densities predicted 200 km offshore. This also disagrees with the study of Ballance et al (1997), in which sooty terns were abundant in the low productivity waters of the ETP. Nevertheless, productivity around the Marquesas is probably not greater than in the least productive waters of the ETP.

As central place foragers, seabirds also depend on colony locations, which strongly influence their at-sea distributions (Hyrenbach et al., 2007; Jaquemet et al., 2004; Le Corre et al., 2012). The availability of appropriate sites for nesting and roosting might be crucial determinants for seabirds. White terns usually lay one egg on a bare branch in a tree and form loose colonies, making their census difficult. About 60 000 pairs of white terns are reported in French Polynesia, with a majority of small colonies (Thibault & Bretagnolle 2007, **Appendix B**). These comparatively modest breeding numbers contrast with their at-sea dominance and might be due to an underestimation of colonies and/or a large proportion of dispersing individuals not bound to colonies. Conversely, sooty terns, which nest on the ground and form very dense colonies, find the most appropriate nesting habitats in the Marquesas (hundreds of thousand pairs reported by Thibault & Bretagnolle 2007, **Appendix B**). Sooty terns also breed on seven of the Line Islands, with 1 million pairs reported on Caroline atoll (Kepler et al., 1992), 3 million on Starbuck and up to 15 million on Christmas, the largest population in the Pacific (Perry, 1980). Interestingly, when extending the prediction region to the west, our model suggested high densities of sooty terns in offshore waters around Caroline atoll (9.937°S, 150.211°W).

Furthermore, the current locations of nesting sites might be heavily influenced by historical (concurrent with the arrival of the first Polynesians) and current anthropogenic pressures, including habitat destruction, direct exploitation and introduced predators (Steadman, 1995). For example, the absence of sooty tern colonies in southern French Polynesia might be the consequence of extirpations, notably in the Australs, where historical

colonies are documented but none remains today (Thibault & Bretagnolle 2007). As a ground-nesting species, the sooty tern is highly vulnerable to predation and direct exploitation. Hence, the current distribution of some seabirds in French Polynesia might better reflect past and present pressures on colonies than energetic constraints.

4.5. Response to contemporaneous versus average oceanographic conditions

Our survey in French Polynesia occurred during a moderate La Niña episode (Climate Prediction Center, 2011), characterized by slightly lower sea surface temperatures and eddy activity and higher productivity compared to the 10-year average (**Appendix A**). This 'experimental situation' gave us the opportunity to evaluate the capacity of top predators to respond to the contemporaneous *versus* average oceanographic situation.

For cetaceans, there was no clear pattern towards the selection of seasonal or climatological covariates in the best models. They did not appear to respond strongly to the conditions of the survey; however, sighting numbers were generally low and possibly impaired our capacity to highlight responses to rather subtle changes in oceanographic conditions. For most seabirds (all guilds but petrels and shearwaters), the climatological covariates were primarily selected. Hence, these guilds did not respond to the atypical situation observed during the survey but appeared to follow the climatological situation and continued to exploit areas that are on average favorable to them. Additionally, locations of the main colonies are generally not flexible between years. Breeders engaged in reproduction and individuals of species dependent on roosting sites, do not have the capacity to fully adapt their large scale distributions to yearly variations in oceanography. Rather, they might express this anomalous situation by an impaired breeding success or body condition (*e.g.* Anderson, 1989). Petrels and shearwaters were an exception, as only seasonal covariates were selected in the best model. There might be a large proportion of non-breeding procellariforms migrating through French Polynesia (Vanderwerf et al., 2006). They may be less constrained to the vicinity of colonies and more mobile than other primarily resident seabirds and are probably more responsive to climatic and oceanographic variations. This was previously noted for the sooty shearwater (*Puffinus griseus*) in the California Current (Oedekoven et al., 2001).

Our results in French Polynesia are different from findings in the California and Humboldt Current upwelling systems, where top predators responded to ENSO episodes by distribution shifts (Benson et al., 2002; Oedekoven et al., 2001), changes in body condition (Boersma, 1998), alteration of reproductive success (Ainley et al., 1995; Anderson, 1989), switching of prey (Oedekoven et al., 2001) or even mortality (Trillmich and Limberger, 1985). Upwellings are highly productive systems where anomalous climatic situations propagate through the food chain from lower to higher trophic levels (Barber and Chavez, 1983; Chavez et al., 2003). In contrast, French Polynesia is situated in one of the least productive regions of the Pacific and this La Niña episode was probably not sufficient to

enhance productivity and there was no significant biological effect through the food web, increasing resource availability and further impacting top predator distributions.

The aerial survey in French Polynesia was conducted only once. Ideally, to assess cetacean and seabird responses to contemporaneous *versus* average oceanographic conditions, the survey should be repeated during a normal and an El Niño situation. Fitting habitat models at the temporal scale of each survey and comparing predictions would show whether top predator distributions differed among these three situations. Alternatively, predicted densities derived from each individual survey could be averaged on a multiyear climatology to provide "densitologies", as performed in the eastern Pacific (Becker et al., 2012; Forney et al., 2012).

5. Conclusions

In this study, we used habitat models to relate cetacean and seabird data collected from an aerial survey, to oceanographic and static predictors and proposed regional predictions in French Polynesia. Since they are often referred to as ecosystem composition indicators (Zacharias and Roff, 2001), we expected low densities of top predators in this oligotrophic system. This appeared to be true for cetaceans, for which predicted densities were overall low; however, seabird densities encompassed those recorded in the mesotrophic waters of the eastern tropical Pacific (Vilchis et al., 2006).

Cetaceans responded positively to the productivity gradient in French Polynesia. However the energetically costly delphinids responded more strongly than sperm and beaked whales. Cetacean strategies of habitat use appeared to agree with their energetic constraints. For seabirds, the availability of colonies and roosting sites appeared the most crucial determinants. Top predators did not respond strongly to the contemporaneous situation of the survey, but seemed to exploit areas recurrently favorable to them.

Acknowledgements

The French Ministry in charge of the environment (*Ministère de l'Ecologie, du Développement Durable et de l'Energie*) and the Agency for marine protected areas (*Agence des Aires Marines Protégées*) funded the project. The Government of French Polynesia, the Ministry of Environment in French Polynesia and the councils of the different islands considerably facilitated the progress of this survey. We thank all observers: Ludwig Blanc, Adele Cadinouche, Pamela Carzon, Sylvie Geoffroy, Aurelie Hermans, Emmanuelle Levesque, Devis Monthy, Morgane Perri, Julie Petit, Guy Pincemin, Michael Poole, Richard Sears, Thierry Sommer and Jean-Luc Tison from organizations: *Groupe d'Etude des Mammifères marins*, *Société ornithologique de Polynesie Manu*, Mauritius Marine Conservation Society, *Te Mana o te Moana*, *Pa'e Pa'e No Te Ora*, Dolphin and Whale Watching Expedition and Mingan Island Cetacean Study, who were very professional in the air and friendly project mates on land. We are indebted to all aircraft crew members of

Aerosotravia, Unity Airlines and Great Barrier Airlines for their continuous high level of professionalism and enthusiasm despite hundreds of hours flying in strait lines over the ocean. We thank JC Thibault for his prompt answers to our questions about seabird colonies in French Polynesia and Henry Weimerskirch for his help regarding interpretations of seabird distributions.

References

Aguilar de Soto, N., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., Tyack, P., 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). Journal of Animal Ecology 77, 936–947.

Ainley, D.G., Sydeman, W.J., Norton, J., 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine ecology progress series. 118, 69–79.

Anderson, D.J., 1989. Differential responses of boobies and other seabirds in the Galápagos to the 1986-87 El Niño-Southern Oscillation event. Marine ecology progress series. 52, 209–216.

Austin, M., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological modelling 157, 101–118.

Baird, R.W., Ligon, A.D., Hooker, S.K., Gorgone, A.M., 2001. Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. Canadian Journal of Zoology 79, 988–996.

Ballance, L.T., Pitman, R.L., 1999. Foraging ecology of tropical seabirds, in: Proc. 22 Int. Ornithol. Congr. Adams, N.J. & Slotow, R.H., Durban, pp. 2057–2071.

Ballance, L.T., Pitman, R.L., Fiedler, P.C., 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Progress in Oceanography 69, 360–390.

Ballance, L.T., Pitman, R.L., Reilly, S.B., 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78, 1502–1518.

Barber, R.T., Chavez, F.P., 1983. Biological consequences of El Ninio. Science 222 1203–1210.

Barlow, J., 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. Marine Mammal Science 22, 446–464.

Barry, S., Elith, J., 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43, 413–423.

Becker, E.A., Foley, D.G., Forney, K.A., Barlow, J., Redfern, J.V., Gentemann, C.L., 2012. Forecasting cetacean abundance patterns to enhance management decisions. Endangered Species Research 16, 97–112.

Becker, E.A., Forney, K.A., Ferguson, M.C., Foley, D.G., Smith, R.C., Barlow, J., Redfern, J.V., 2010. A comparison of California current cetacean habitat models developped using in situ and remotely sensed sea surface temperature data. Marine Ecology Progress Series 413, 163–183.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42, 1–20.

Benoit-Bird, K.J., Au, W.W.L., 2009. Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. The Journal of the Acoustical Society of America 125, 125–137.

Benson, S.R., Croll, D.A., Marinovic, B.B., Chavez, F.P., Harvey, J.T., 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. Progress in Oceanography 54, 279–291.

Bertrand, A., Bard, F.-X., Josse, E., 2002. Tuna food habits related to the micronekton distribution in French Polynesia. Marine Biology 140, 1023–1037.

Bertrand, A., Le Borgne, R., Josse, E., 1999. Acoustic characterisation of micronekton distribution in French Polynesia. Marine Ecology Progress Series 191, 127–140.

Boersma, P.D., 1998. Population trends of the Galápagos penguin: impacts of El Niño and La Niña. Condor 100, 245–253.

Boyd, I., 1997. The behavioural and physiological ecology of diving. Trends in Ecology & Evolution 12, 213–217.

Buckland, S.T., Anderson, D.R., Burnham, H.P., Laake, J.L., D.L., B., Thomas, L., 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Ñiquen, M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299, 217–221.

Clark, C.W., Mangel, M., 1984. Foraging and flocking strategies: information in an uncertain environment. American Naturalist 626–641.

Climate Prediction Center, 2011. El niño/southern oscillation (enso) diagnostic discussion issued by climate prediction center/ncep/nws.

Davoren, G.K., Montevecchi, W.A., Anderson, J.T., 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series 256, 229–242.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40, 677–697.

Ellis, H.I., Gabrielsen, G.W., 2002. Energetics of free-ranging seabirds, in: Biology of Marine Birds. Schreiber, E.A. and Burger, J., Florida, USA.

Environmental Systems Research Institute, 2010. ArcGIS desktop. Redland, CA.

Estes, J., Crooks, K., Holt, R., 2001. Predators, ecological role of, in: Encyclopedia of Biodiversity. pp. 857–878.

Ferguson, M.C., Barlow, J., Fiedler, P., Reilly, S.B., Gerrodette, T., 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling 193, 645–662.

Flint, E.N., Nagy, K.A., 1984. Flight energetics of free-living sooty terns. The Auk 101, 288–294.

Ford, R.G., Ainley, D.G., Casey, J.L., Keiper, C.A., Spear, L.B., Ballance, L.T., 2004. The biogeographic patterns of seabirds in the central portion of the California Current. Marine Ornithology 32, 77–96.

Forney, K.A., 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. Conservation Biology 14, 1271–1286.

Forney, K.A., Ferguson, M.C., Becker, E.A., Fiedler, P.C., 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. Endangered Species Research 16, 113–133.

Gannier, A., 2009. Comparison of odontocete populations of the Marquesas and Society Islands (French Polynesia). Journal of the Marine Biological Association of the United Kingdom 89, 931–941.

Guisan, A., Edwards, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89–100.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.

Hammond, P.S., Mcleod, K., Berggren, P., Borchers, D.L., Burt, L., Canadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, R.G., Gordon, J., Hiby, L., Kuklik, I., Leaper, R., Lehnert, K., Leopold, M., Lovell, P., Oien, N., Paxton, G.M., Ridoux, V., Emer, R., Samara, F., Scheidat, M., Sequeira, M., Siebert, U., Skov, H., Swift, R., Tasker, M.L., Teilmann, J., Van Canneyt, O., Vasquez, J.A., 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biological Conservation 164, 107–122.

Hertel, F., Ballance, L.T., 1999. Wing ecomorphology of seabirds from Johnston Atoll. Condor 101, 549–556.

Hyrenbach, K.D., Veit, R.R., Weimerskirch, H., Metzl, N., Hunt Jr, G.L., 2007. Community structure across a large-scale ocean productivity gradient: Marine bird assemblages of the Southern Indian Ocean. Deep Sea Research Part I 54, 1129–1145.

Jaquemet, S., Le Corre, M., Weimerskirch, H., 2004. Seabird community structure in a coastal tropical environment: importance of associations with sub-surface predators and of Fish Aggregating Devices (FADs). Marine Ecology Progress Series 268, 281–292.

Jaquet, N., Whitehead, H., 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135, 1–9.

Kahru, M., 2010. Window Image Manager 1991–2010.

Kepler, C.B., Kepler, A.K., Ellis, D.H., 1992. Ecological Studies on Caroline Atoll, Republic of Kiribati, South-central Pacific Ocean Part 2. Seabirds, Other Terrestrial Animals, and Conservation, in: Results of the First Joint US-USSR Central Pacific Expedition (BERPAC) : Autumn 1988. Washington, DC : U.S. Fish and Wildlife Service, pp. 139–164.

Klatsky, L.J., Wells, R.S., Sweeney, J.C., 2007. Offshore bottlenose dolphins (*Tursiops truncatus*): Movement and dive behavior near the Bermuda Pedestal. Journal of Mammalogy 88, 59–66.

Laake, J.L., Borchers, D.L., Thomas, L., Miller, D., 2011. “mrds” (Mark-Recapture Distance Sampling) Package.

Le Corre, M., Jaeger, A., Pinet, P., Kappes, M.A., Weimerskirch, H., Catry, T., Ramos, J.A., Russell, J.C., Shah, N., Jaquemet, S., 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. Biological Conservation 156, 83–93.

Longhurst, A.R., 2007. Ecological geography of the sea. Academic Press, Oxford.

MacLeod, C.D., Hauser, N., Peckham, H., 2004. Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. Journal of the Marine Biological Association of the UK 84, 469–474.

Mannocci, L., Monestiez, P., Bolaños-Jiménez, J., Dorémus, G., Jeremie, S., Laran, S., Rinaldi, R., Van Canneyt, O., Ridoux, V., 2013. Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic. Journal of Marine Systems 111–112, 208–222.

Marques, F.F.C., Buckland, S.T., 2004. Covariate models for the detection function, in: Advanced Distance Sampling. Oxford, New York, pp. 31–47.

Martinez, E., Ganachaud, A., Lefèvre, J., Maamaatuaiahutapu, K., 2009. Central South Pacific thermocline water circulation from a high-resolution ocean model validated against satellite data: Seasonal variability and El Niño 1997–1998 influence. Journal of Geophysical Research 114, 16.

Martinez, E., Maamaatuaiahutapu, K., 2004. Island mass effect in the Marquesas Islands: Time variation. Geophysical Research Letters 31, L18307.

Oedekoven, C.S., Ainley, D.G., Spear, L.B., 2001. Variable responses of seabirds to change in marine climate: California Current, 1985-1994. Marine Ecology Progress Series 212, 265–281.

Perry, R., 1980. Wildlife Conservation in the Line Islands, Republic of Kiribati (formerly Gilbert Islands). Environmental Conservation 7, 311–318.

Peterson, C.C., Nagy, K.A., Diamond, J., 1990. Sustained metabolic scope. PNAS 87, 2324–2328.

Pollock, K.H., Marsh, H.D., Lawler, I.R., Allderdge, M., 2006. Estimating Animal Abundance in Heterogeneous Environments: An Application to Aerial Surveys for Dugongs. Journal of Wildlife Management 70, 255–262.

Redfern, J.V., Barlow, J., Ballance, L.T., Gerrodette, T., Becker, E.A., 2008. Absence of scale dependence in dolphin–habitat models for the eastern tropical Pacific Ocean. Marine Ecology Progress Series 363, 1–14.

Redfern, J.V., McKenna, M.F., Moore, T.J., Calambokidis, J., Deangelis, M.L., Becker, E.A., Barlow, J., Forney, K.A., Fiedler, P.C., Chivers, S.J., 2013. Assessing the risk of ships striking large whales in marine spatial planning. Conservation Biology 27, 292–302.

Rendell, L., Whitehead, H., 2001. Culture in whales and dolphins. Behavioral and Brain Sciences 24, 309–382.

Reygondeau, G., Maury, O., Beaugrand, G., Fromentin, J.M., Fonteneau, A., Cury, P., 2011. Biogeography of tuna and billfish communities. Journal of Biogeography 39, 114–129.

Rougerie, F., Rancher, J., 1994. The Polynesian south ocean: features and circulation. Marine Pollution Bulletin 29, 14–25.

Schick, R., Halpin, P., Read, A., Urban, D., Best, B., Good, C., Roberts, J., LaBrecque, E., Dunn, C., Garrison, L., others, 2011. Community structure in pelagic marine mammals at large spatial scales. Marine Ecology Progress Series 434, 165–181.

Signorini, S.R., McClain, C.R., Dandonneau, Y., 1999. Mixing and phytoplankton bloom in the wake of the Marquesas Islands. Geophysical Research Letters 26, 3121–3124.

Smith, J.L., Hyrenbach, K.D., 2003. Galapagos Islands to British Columbia: Seabird communities along a 9000 km transect from the tropical to the subarctic eastern Pacific Ocean. Marine Ornithology 31, 155–166.

Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., Ridoux, V., 2012. Cost of living dictates what whales, dolphins and porpoises eat: The importance of prey quality on predator foraging strategies. PLoS ONE 7, e50096.

Springer, A.M., McROY, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. Fish. Ocean. 5, 205–223.

Stammer, D., Wunsch, C., 1999. Temporal changes in eddy energy of the oceans. Deep Sea Research Part II: Topical Studies in Oceanography 46, 77–108.

Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.

Sudre, J., Morrow, R.A., 2008. Global surface currents: a high-resolution product for investigating ocean dynamics. Ocean Dynamics 58, 101–118.

Tasker, M.L., Jones, P.H., Dixon, T., Blake, B.F., 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. The Auk 101, 567–577.

TewKai, E., Marsac, F., 2009. Patterns of variability of sea surface chlorophyll in the Mozambique Channel: A quantitive aproach. Journal of Marine Systems 77–88.

Thibault, J.-C., Bretagnolle, V., 2007. Atlas des oiseaux marins de Polynésie française et du Groupe Pitcairn. Société d'Ornithologie de Polynésie et Direction de l'Environnement de la Polynésie française.

Trillmich, F., Limberger, D., 1985. Drastic effects of El Niño on Galapagos pinnipeds. Oecologia 67, 19–22.

Tyack, P.L., Johnson, M., Soto, N.A., Sturlese, A., Madsen, P.T., 2006. Extreme diving of beaked whales. Journal of Experimental Biology 209, 4238–4253.

Uz, B.M., Yoder, J.A., Osychny, V., 2001. Pumping of nutrients to ocean surface waters by the action of propagating planetary waves. Nature 409, 597–600.

Vanderwerf, E.A., Pierce, R., Gill, V.A., Wragg, G., Raust, P., Tibbits, T., 2006. Pelagic seabird surveys in the Tuamotu and Gambier archipelagos, French Polynesia. Marine Ornithology 34, 65–70.

Ver Hoef, J.M., Boveng, P.L., 2007. Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology 88, 2766–2772.

Vilchis, L.I., Ballance, L.T., Fiedler, P.C., 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. Marine Ecology Progress Series 315, 279–292.

Wang, B., Wu, R., Lukas, R., 2000. Annual adjustment of the thermocline in the tropical Pacific Ocean. Journal of Climate 13, 596–616.

Watkins, W.A., Daher, M.A., Dimarzio, N.A., Samuels, A., Wartzok, D., Fristrup, K.M., Howey, P.W., Maiefski, R.R., 1993. Sperm whale dives tracked by radio tag telemetry. Marine Mammal Science 18, 55–68.

Weichler, T., Garthe, S., Luna-Jorquera, G., Moraga, J., 2004. Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. ICES Journal of Marine Science 61, 148–154.

Weimerskirch, H., Chastel, O., Barbraud, C., Tostain, O., 2003. Flight performance: Frigatebirds ride high on thermals. Nature 421, 333–334.

Wood, S.N., 2006. Generalized Additive Models. Chapman & Hall/CRC.

Wood, S.N., Augustin, N.H., 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157, 157–177.

Yen, P.P.W., Sydeman, W., Hyrenbach, K.D., 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. Journal of Marine Systems 50, 79–99.

Zacharias, M.A., Roff, J.C., 2001. Use of focal species in marine conservation and management: a review and critique. Aquatic Conservation: Marine and Freshwater Ecosystems 11, 59–76.

Table 1: Description of seabird and cetacean guilds, ordered from the most energetically costly to the less active.

Seabird guilds	
Tropicbirds	White-tailed tropicbird *Phaeton lepturus,* Red-tailed tropicbird *Phaeton rubricauda*
Grey terns	Great Crested Tern *Sterna bergii*, Grey-backed tern *Sterna lunata*
Noddies	Brown noddy *Anous stolidus,* Black noddy *Anous minutus,* Blue Noddy *Procelsterna cerulean*
White tern	White tern *Gygis alba*
Bobbies	Red-footed booby *Sula sula,* Masked booby *Sula dactylatra,* Brown booby *Sula leucogaster*
Petrels and shearwaters	Black-winged Petrel *Pterodroma nigripennis*, Gould's Petrel *Pterodroma leucoptera*, Tahiti petrel *Pseudobulweria rostrata*, Murphy's petrel *Pterodroma ultima*, Bulwer's petrel *Bulweria bulwerii*, Kermadec petrel *Pterodroma neglecta*, Phoenix petrel *Pterodroma alba*, Herald petrel *Pterodroma heraldic*, White-necked petrel *Pterodroma exerna cervicalis**, Cook's petrel *Pterodroma cookii**, Stejneger's petrel *Pterodroma longirostris**, Parkinson's petrel *Procellaria Parkinsoni**, Wedge-tailed shearwater *Puffinus pacificus*, Christmas island shearwater *Puffinus nativitatis*, Audubon's shearwater *Puffinus lherminieri (Puffinus bailloni)**, Buller's shearwater *Puffinus bulleri**, Short-tailed shearwater *Puffinus tenuirostris**, Little shearwater *Puffinus assimilis**
Sooty tern	Sooty tern *Onychoprion fuscatus*
Frigatebirds	Great frigatebird *Fregata minor*, Lesser frigatebird *Fregata ariel*
Cetacean guilds	
Delphininae	Rough-toothed dolphin *Steno bredanensis,* Pantropical spotted dolphin *Stenella attenuata*, Spinner dolphin *Stenella longirostris*, Common bottlenose dolphin *Tursiops truncatus*, Fraser's dolphin *Lagenodelphis hosei*
Globicephalinae	Pygmy killer whale *Feresa attenuata*, Melon-headed whale *Peponocephala electra*, Short-finned pilot whale *Globicephala macrorynhus,* False killer whale *Pseudorca crassidens,* Risso's dolphin *Grampus griseus,* Killer whale *Orcinus orca*
Sperm and beaked whales	Blainville's beaked whale *Mesoplodon densirostris*, Cuvier's beaked whale *Ziphius cavirostris,* Sperm whale *Physeter macrocephalus*, Pygmy sperm whale *Kogia breviceps*, Dwarf sperm whale *Kogia sima*

* in migration in French Polynesia

Table 2: Environmental covariates used to model top predator habitats. Abbreviations and units are provided.

Oceanographic covariates	
CHL_{seas}	Seasonal chlorophyll concentration (mg m^3)
CHL_{clim}	Climatological chlorophyll concentration (mg m^3)
NPP_{seas}	Seasonal net primary production (mgC m^3 day)
NPP_{clim}	Climatological net primary production (mgC m^3 day)
SST_{seas}	Seasonal sea surface temperature (°C)
SST_{clim}	Climatological sea surface temperature (°C)
SLA_{seas}	Seasonal standard error of sea level anomaly (cm)
SLA_{clim}	Climatological standard error of sea level anomaly (cm)
Static covariates	
Slope	Slope (%)
Depth	Depth (m)
D_{colony}	Distance to the nearest seabird colony (km)
D_{coast}	Distance to the nearest coast (km)

Table 3: Survey effort per geographic sector and bathymetric stratum.

Geographic sector	Slope	Oceanic	Total
Society	1 571 km	14 819 km	16 390 km
Australs	1 745 km	20 981 km	22 726 km
North Tuamotu	7 877 km	7508 km	15 385 km
South Tuamotu	_	13 814 km	13 814 km
Gambier	250 km	13 035 km	13 285 km
Marquesas	2 270 km	14 606 km	16 876 km
Total	13 713 km	84 763 km	98 476 km

Table 4: Detection models and estimated effective strip widths (ESWs) for cetaceans

Cetacean guild (sightings after truncation)	Truncation distance	Detection model	Effect of detection covariates	
			Detection covariate	ESW
Delphininae (86)	400m	Half normal	Turbidity	0: 254 m 1: 143 m
Globicephalinae (72)	500m	Half normal	No significant detection covariate	234 m
Sperm and beaked whales (94)	600m	Half normal	Sea state	0-2 : 316 m 3 : 243 m 4-5 : 211 m

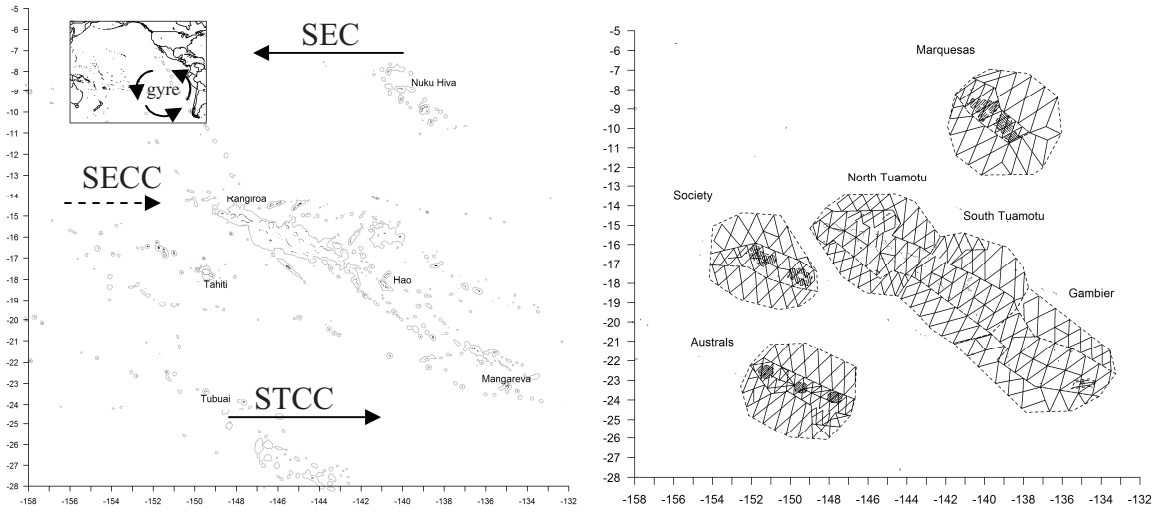


Figure 1. a: Main currents in French Polynesia, situated in the South Pacific oligotrophic gyre: the South Equatorial Current (SEC), the Subtropical Countercurrent (STCC) and the intermittent South Equatorial Countercurrent (SECC) (appearing in the austral summer). The 2000 m isobath is shown in grey. b: Transects conducted within the six geographic sectors during the aerial survey.

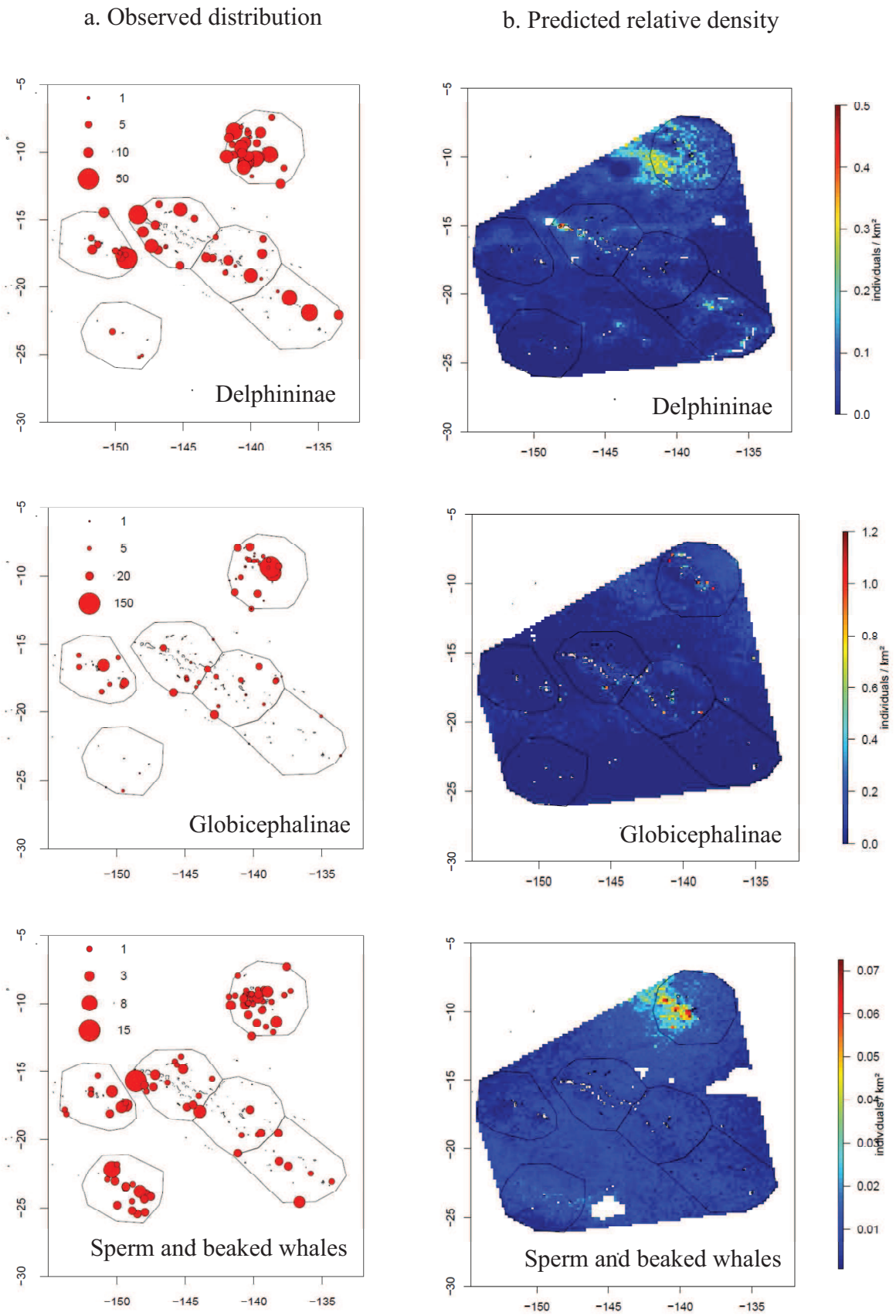


Figure 2. a: Observed distribution (number of individuals per segment) and b: predicted relative densities (number of individuals per km²) for cetacean guilds. Predictions are in a convex hull encompassing the surveyed sectors. White areas in predicted maps indicate the absence of predictions beyond the range of environmental covariates used in model fitting.

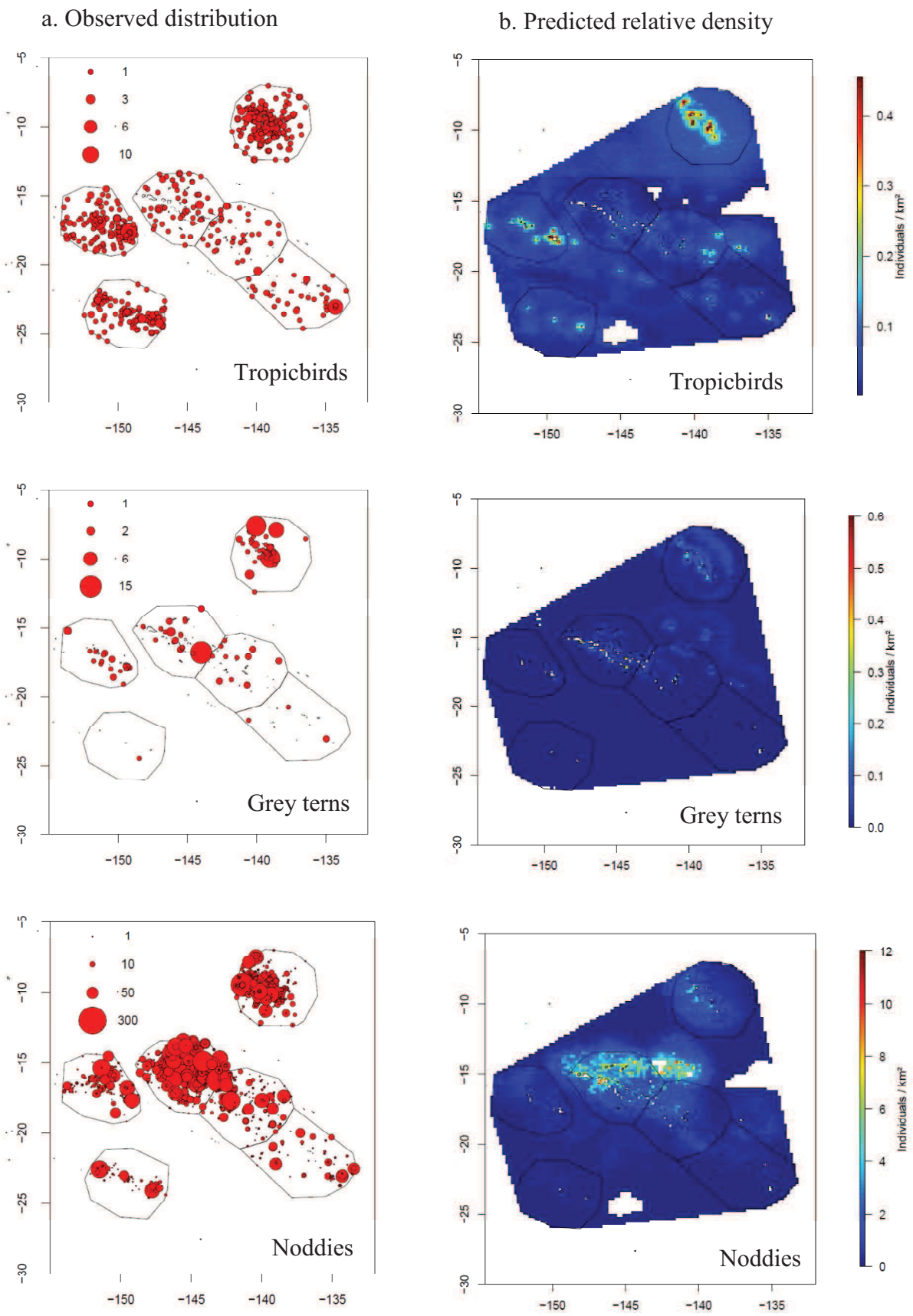


Figure 3. a: Observed distribution (number of individuals per segment) and b: predicted relative densities (number of individuals per km²) for seabird guilds. Predictions are in a convex hull encompassing the surveyed sectors. White areas in predicted maps indicate the absence of predictions beyond the range of environmental covariates used in model fitting.

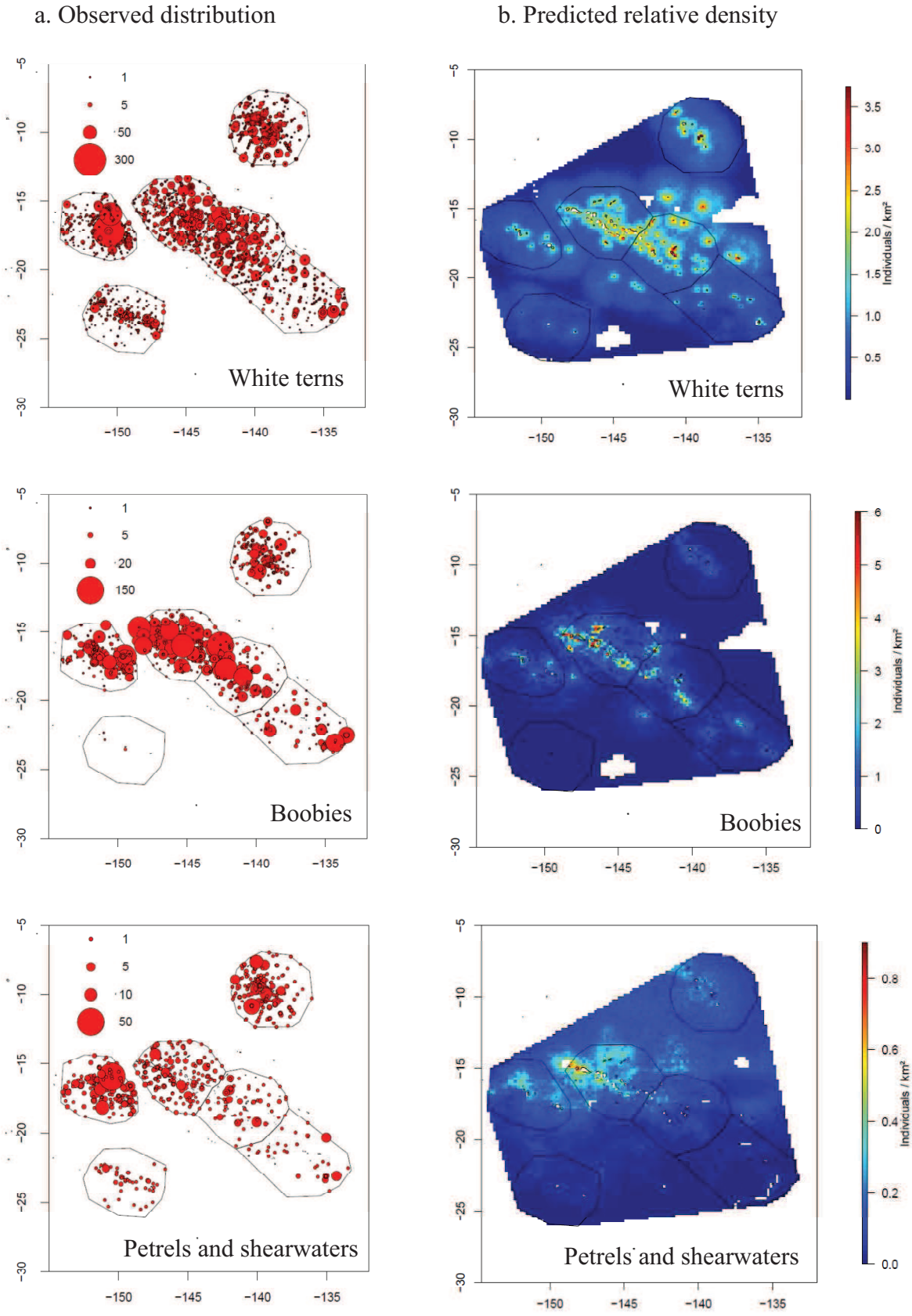


Figure 3 (continued).

a. Observed distribution

b. Predicted relative density

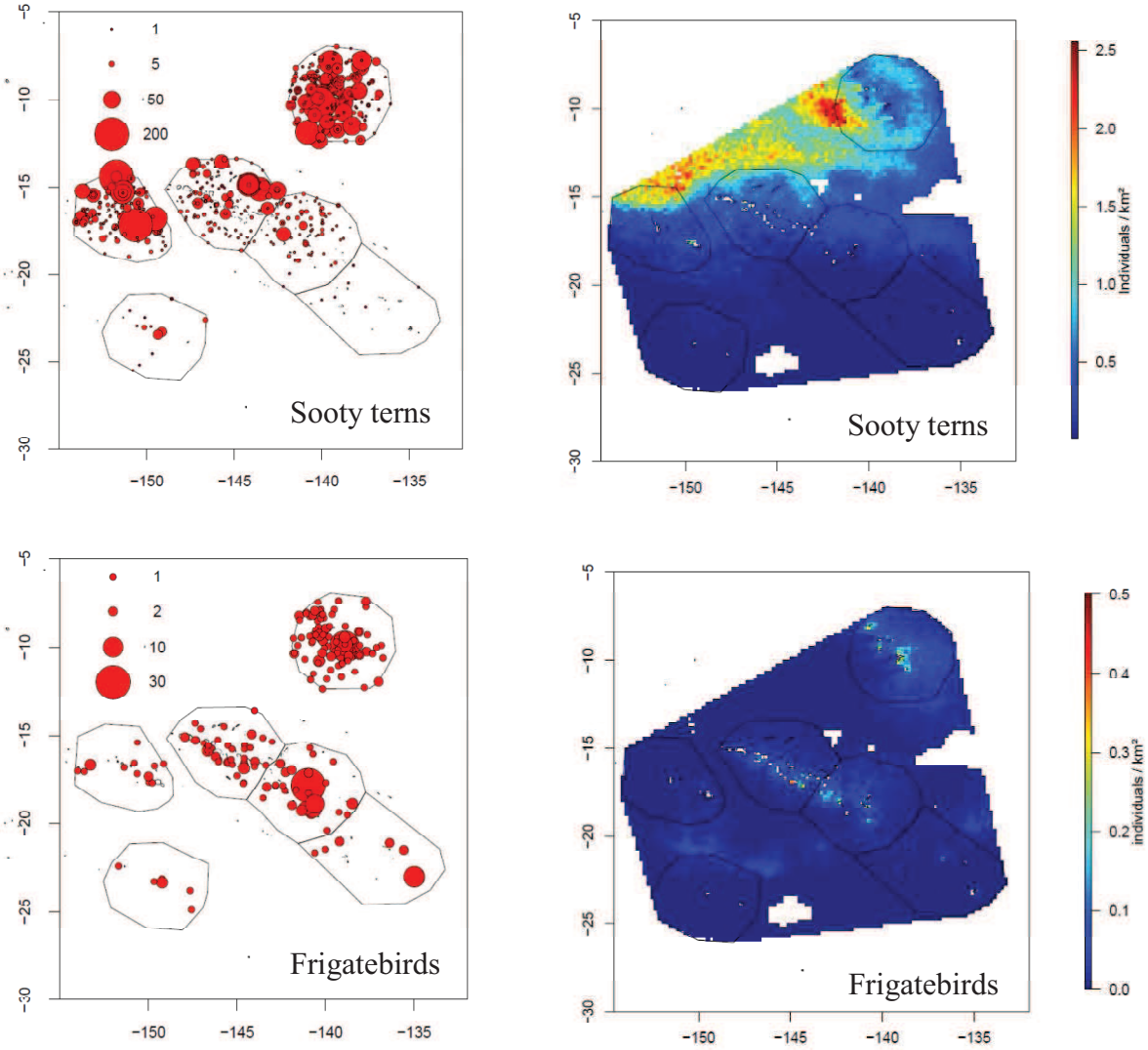


Figure 3 (continued).

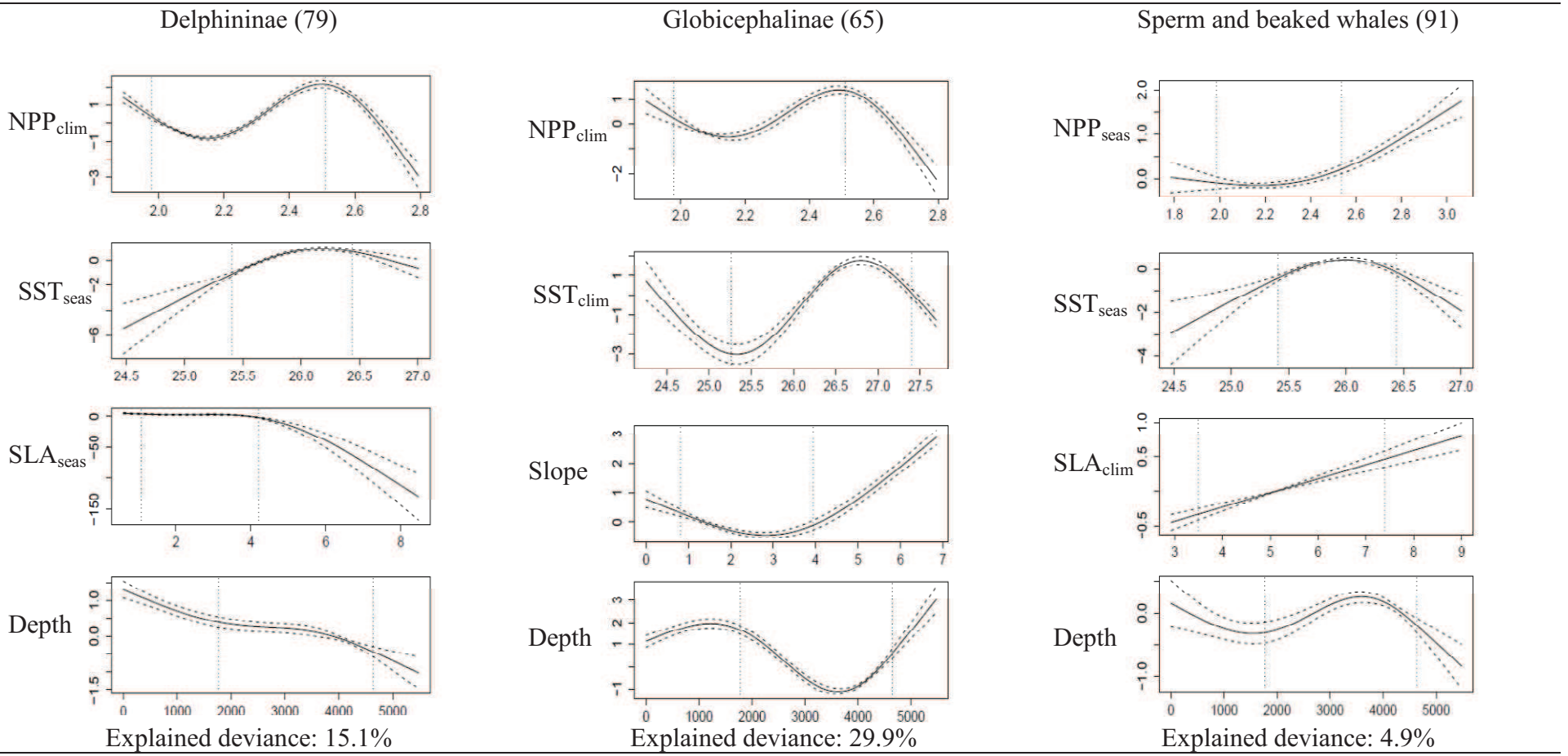


Figure 4: Forms of smooth functions for the selected covariates for cetacean guilds. Numbers of sightings used in habitat modeling are indicated in parentheses. CHL and NPP were log transformed, slope was square root transformed. Predictor variables are presented in the following order: chlorophyll (CHL), primary production (NPP), temperature (SST), standard error of sea level anomaly (SLA), slope, depth. The solid line in each plot is the smooth function estimate, dashed lines represent approximate 95% confidence intervals. Zero on the y axis indicates no effect of the predictor (given that the other predictors are included in the model). The tenth and nineteenth quantiles of data are provided as vertical dotted lines for each plot.

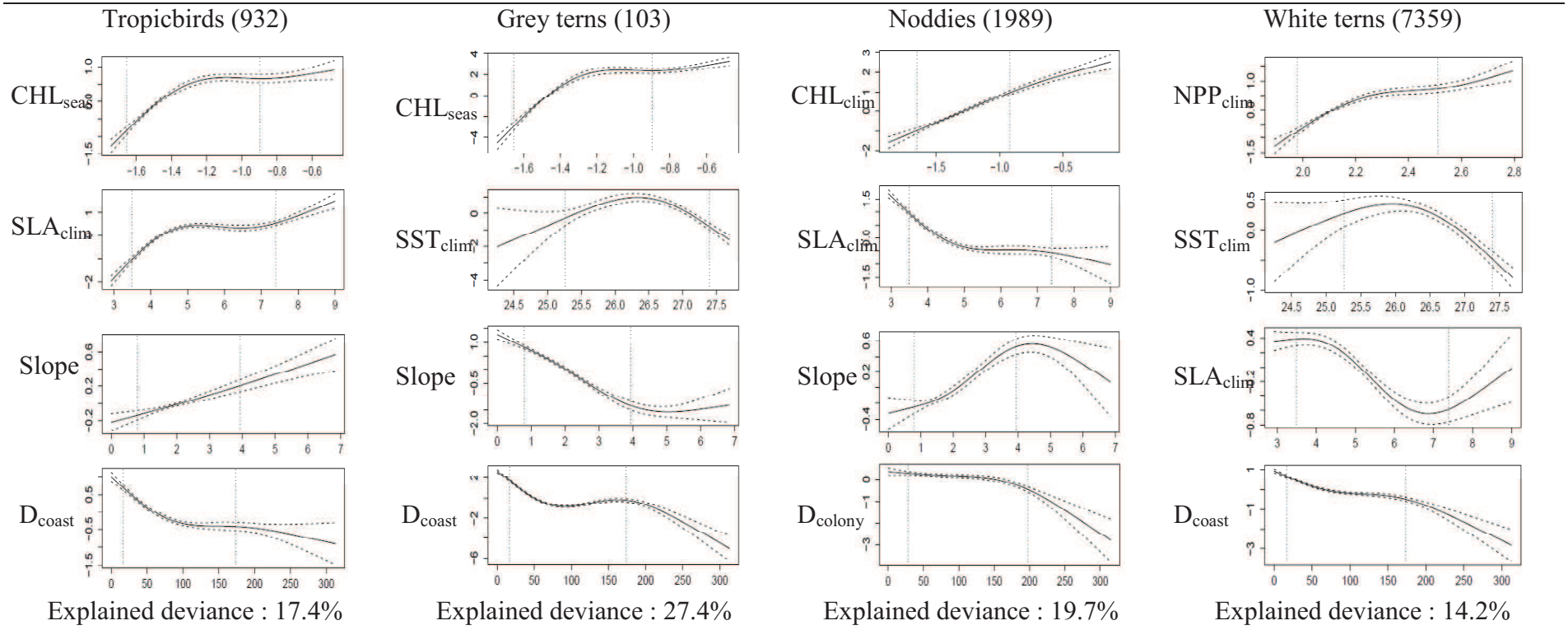


Figure 5: Forms of smooth functions for the selected covariates for seabird guilds. Numbers of sightings used in habitat modeling are indicated in parentheses. CHL and NPP were log transformed, slope was square root transformed. Predictor variables are presented in the following order: chlorophyll (CHL), primary production (NPP), temperature (SST), standard error of sea level anomaly (SLA), slope, distance to the coast (D_{coast}) and distance to the colony (D_{colony}). The solid line in each plot is the smooth function estimate, dashed lines represent approximate 95% confidence intervals. Zero on the y axis indicates no effect of the predictor (given that the other predictors are included in the model). The 10^{th} and 90^{th} quantiles of data are provided as vertical dotted lines for each plot.

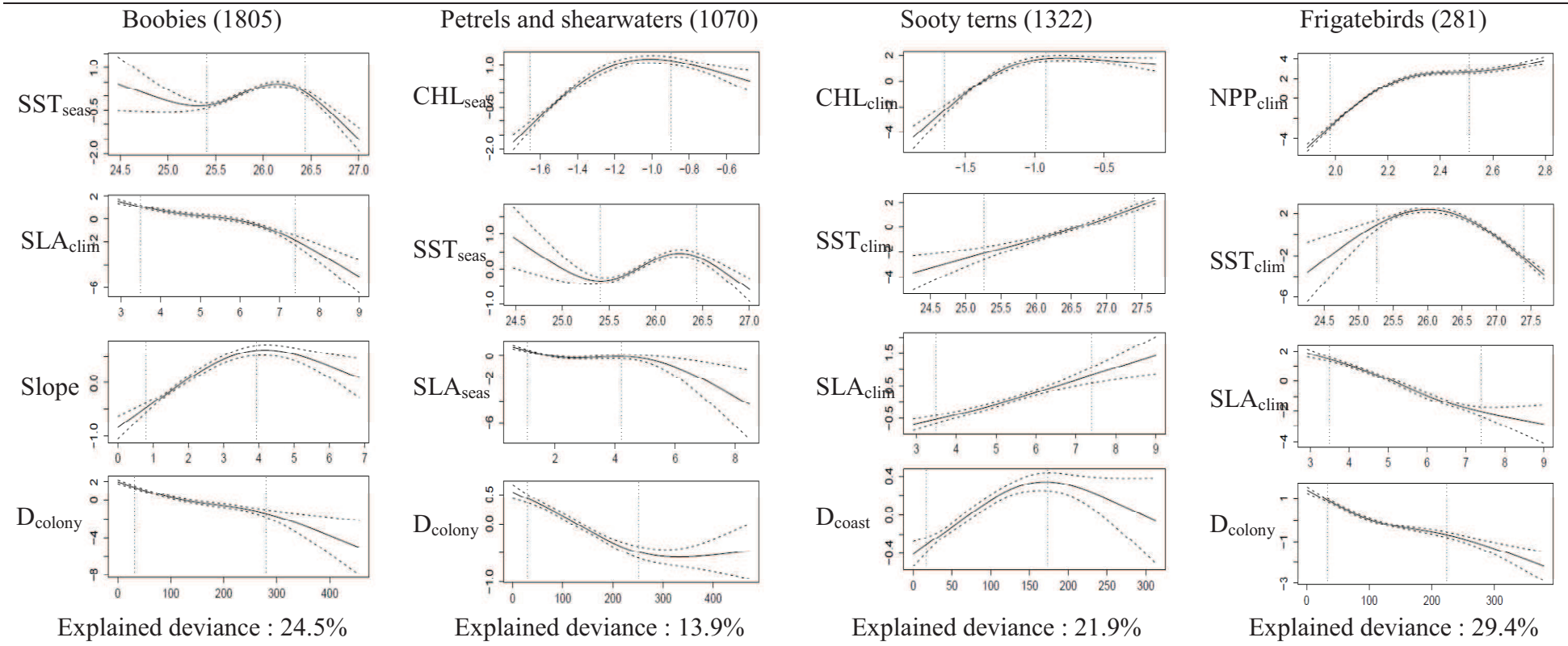


Figure 5 (continued).

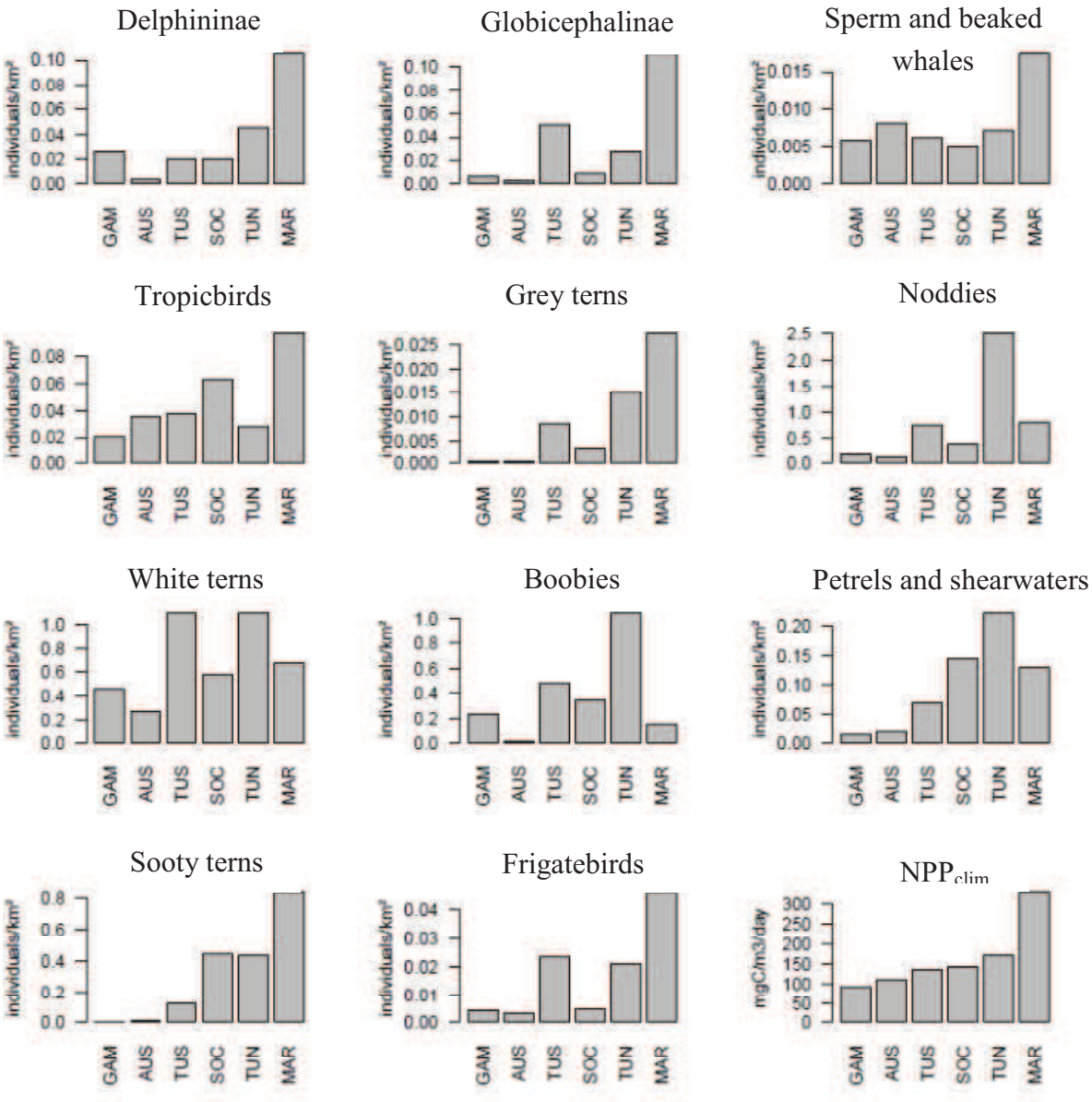
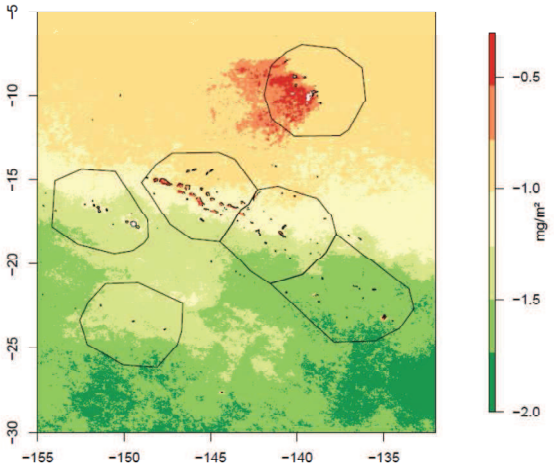


Figure 6: Mean predicted relative densities for cetacean and seabird guilds in the six geographic sectors (from the least productive to the left to the most productive to the right). GAM: Gambier, AUS: Australs, STU: South Tuamotu, SOC: Society, NTU: North Tuamotu, MAR: Marquesas.

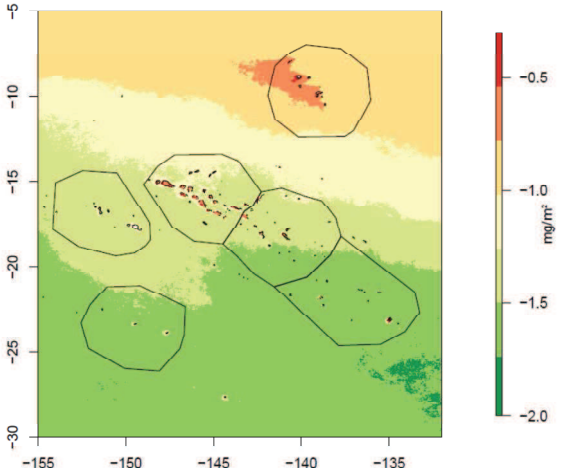
Appendix A: Oceanographic covariates used to model top predator habitats: spatial and temporal variability

Oceanographic covariates show strong spatial structures. There is a latitudinal productivity gradient throughout the study region, productivity being the highest around the Marquesas, intermediate around the Society and Tuamotu archipelagos and the lowest around the Australs and Gambier. Sea surface temperature is the highest in the northwest of French Polynesia. Mesoscale activity is greater around the Australs and Marquesas and much lower in between. The comparison of seasonal and climatological resolutions highlights the slightly unusual conditions encountered during the survey. Indeed, SST was approximately 1°C cooler in the austral summer 2011 compared to the 10 year average. The 2011 summer was also characterized by a slightly higher productivity, notably to the southwest of the Marquesas and a reduced mesoscale activity compared to the climatological situation.

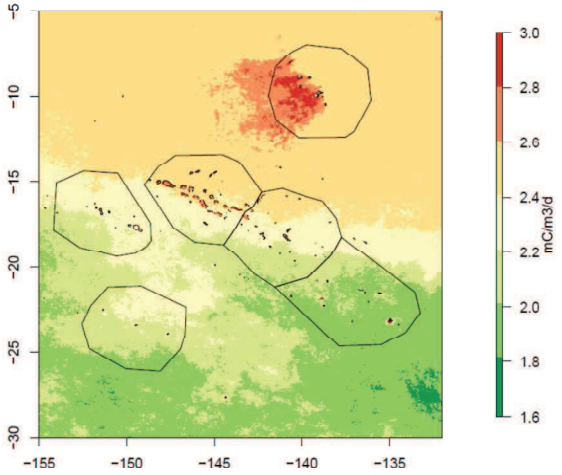
Seasonal chlorophyll concentration (Log)



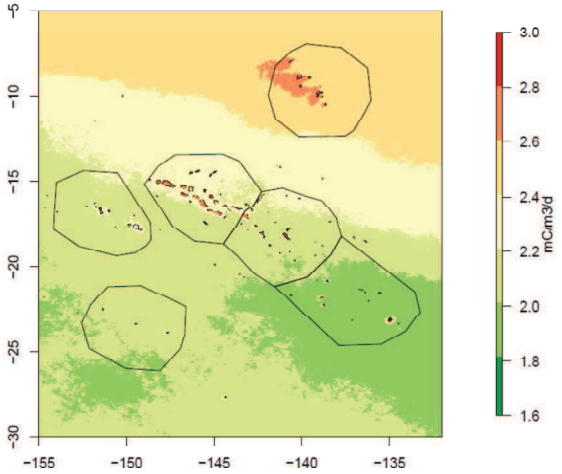
Climatological chlorophyll concentration



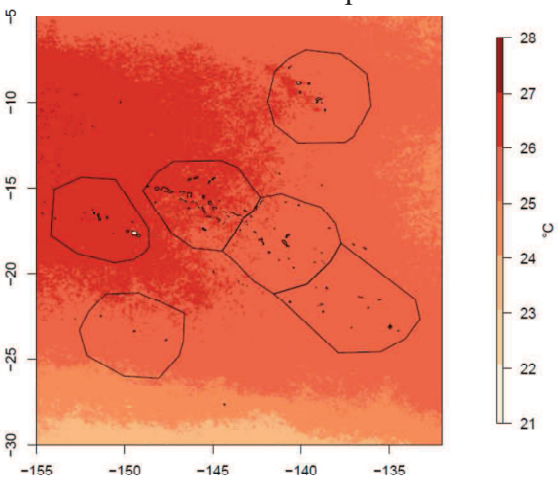
Seasonal net primary production (Log)



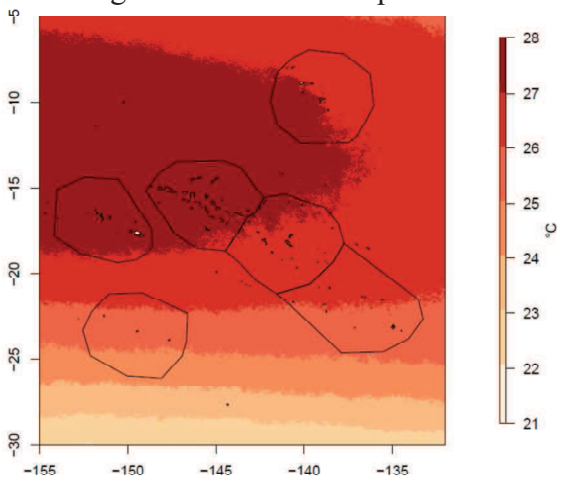
Climatological net primary production (Log)



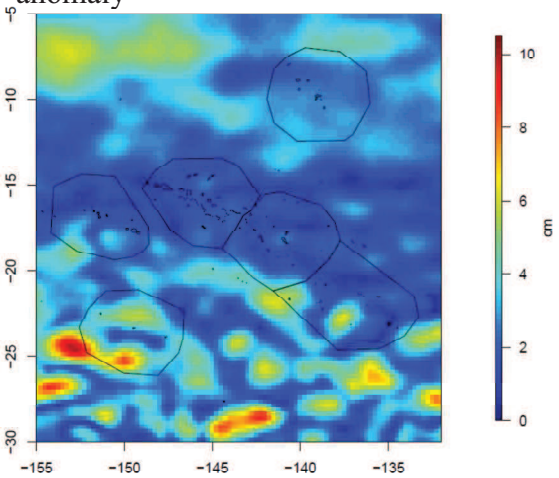
Seasonal sea surface temperature



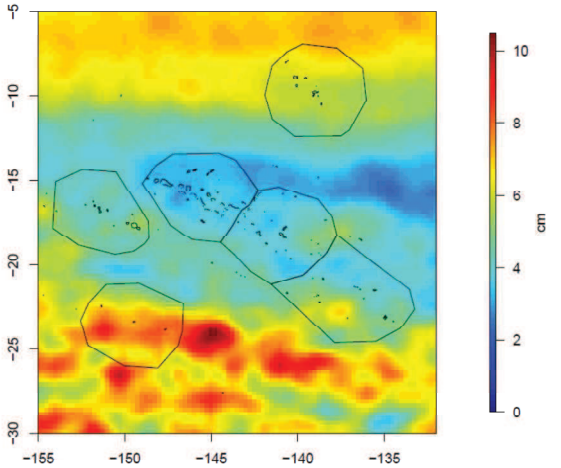
Climatological sea surface temperature



Seasonal standard error of sea level anomaly



Climatological standard error of sea level anomaly



Appendix B: Reported breeding colonies for each seabird guild (from Thibault and Bretagnolle 2007)

Sector	Island	Tropicbirds	Grey terns	Noddis	White terns	Boobies	Petrels and shearwaters	Sooty terns	Frigatebirds
Marquesas	EIAO	2	2	4	3	3	NA	2	3
	FATU HIVA	NA	2	2	3	2	NA	5	2
	FATU HUKU	2	2	2	3	3	1	3	2
	HATUTA A	2	2	2	3	3	3	3	3
	HIVA OA	3	2	2	3	2	NA	3	NA
	MOTANE	NA	2	3	4	2	X	3	3
	MOTO ITI	1	X	X	X	X	X	X	X
	NUKU HIVA	3	2	3	NA	2	NA	3	NA
	TAHUATA	NA	3	3	3	2	3	3	2
	UA HUKA	NA	3	4	3	2	NA	6	2
	UA POU	2	3	3	3	2	4	6	2
Australs	MARIA	3	X	2	NA	3	X	X	3
	MAROTIRI	2	NA	NA	NA	X	3	X	X
	RAIVAVAE	2	2	3	NA	NA	3	NA	NA
	RAPA	3	4	4	NA	NA	4	NA	NA
	RIMATARA	1	X	3	NA	X	X	X	NA
	RURUTU	2	2	3	NA	X	X	X	NA
	TUBUAI	2	X	2	NA	X	1	X	NA
Society	AVERA	X	X	X	X	X	NA	X	X
	BORA BORA	1	X	2	2	X	X	X	X
	HUAHINE	2	X	X	X	X	X	X	X
	MAIAO	1	NA	3	3	3	2	X	NA
	MANUAE MOTU ONE MAUPIHA A	NA	NA	X	X	3	X	X	2
	MAUPITI	2	X	X	2	3	X	X	X
	ME ETIA	1	NA	NA	2	2	NA	X	X
	MOOREA	NA	NA	3	2	NA	NA	X	NA

	MOPELIA	X	X	X	2	3	X	3	X
	MOTU ONE	X	X	X	X	2	X	X	3
	OPUNOHU	X	NA	X	X	X	NA	X	X
	RAIATEA	2	X	X	2	X	X	X	X
	TAHAA	2	X	X	1	4	X	X	X
	TAHITI	3	NA	4	2	1	NA	X	X
	TETIAROA	X	2	NA	3	4	X	3	3
	TUPAI	X	X	2	1	X	X	X	X
North Tuamotu	AHE	X	X	2	X	2	X	X	X
	ANAA	X	X	3	3	X	X	X	X
	ANUANURUNGA	X	X	X	X	X	X	X	2
	APATAKI ARUTUA KAUKURA	X	2	NA	2	NA	X	X	NA
	FAKARAVA	X	X	3	3	3	X	X	2
	HARAIKI	X	X	2	2	X	X	X	X
	HEREHERETUE	X	X	2	X	X	X	X	X
	KAUEHI	X	2	X	X	X	X	X	X
	MAKATEA	2	X	NA	4	3	X	X	X
	MANIHI	X	1	3	3	X	X	X	X
	MATAIVA	X	2	3	3	3	X	X	X
	MOTUTUNGA	X	X	X	X	1	X	X	X
	NAPUKA	X	X	2	2	X	X	X	X
	NIAU	X	X	3	4	X	X	X	X
	RANGIROA	X	2	4	3	3	X	2	2
	TAHANEA	X	NA	3	3	3	X	X	3
	TAKAPOTO	X	X	3	2	X	X	X	X
	TEPOTO	X	X	1	1	X	X	X	X
	TIKEHAU	X	2	4	4	3	X	X	X

South Tuamotu	AHUNUI	2	X	3	3	3	X	X	X
	ANUANURARO	3	X	2	2	X	X	X	X
	ANUANURUNGA	3	X	X	1	1	X	X	X
	FANGATAUFA	X	X	X	X	X	X	3	X
	HAO	X	1	3	X	2	X	X	X
	MANUHANGI	X	X	X	3	X	X	X	X
	NUKUTEPIPI	3	X	X	2	2	X	X	X
	PUKA PUKA	X	X	X	X	X	X	4	X
	PARAOA	2	X	X	3	2	X	X	2
	RAIROA	X	X	X	X	2	X	X	X
	REAO	X	X	2	2	X	X	X	X
	REITORU	X	X	NA	3	3	X	X	3
	TEKOKOTA	X	X	2	3	1	X	3	X
	TEMATANGI	X	X	2	X	X	X	X	X
Gambier	FANGATAUFA	3	X	3	3	2	2	X	2
	MANGAREVA	2	3	3	3	1	X	X	X
	MANUI KAMAKA MAKAROA	X	X	X	X	X	3	X	X
	MATUREIVAVAO	3	X	X	3	3	2	X	X
	MORANE	NA	X	NA	NA	NA	NA	X	NA
	MORUROA	X	2	3	3	2	1	X	2
	TEMATANGI	X	X	X	2	X	X	X	X
	TEMOE	3	2	X	3	3	3	X	3
	TENARARO	2	X	NA	X	3	X	X	2
	TENARUNGA	3	X	X	X	X	X	X	1
	VAHANGA	1	X	X	X	2	X	X	X

In this table, we describe seabird breeding colonies in French Polynesia, as reported by Thibault and Bretagnolle (2007). X: breeding seabirds not found NA: breeding seabirds reported but number of breeding pairs unknown. Number of breeding pairs: 1: 1-9, 2: 10-99, 3: 100-999, 4: 1 000-10 000, 5: 10 000-99 999, 6: > 10 0000

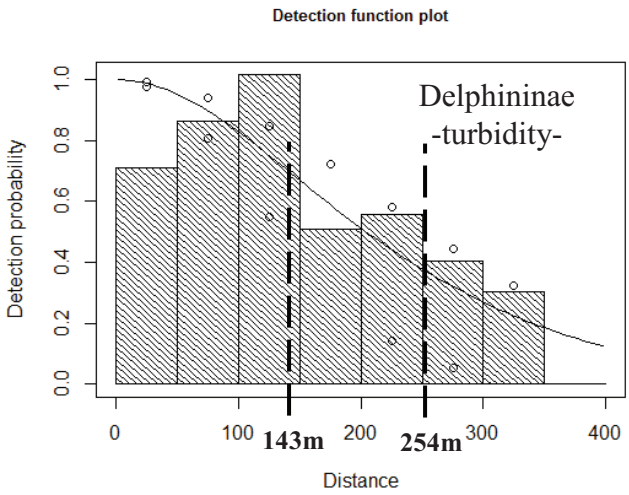
Appendix C: Details of cetacean and seabird sightings

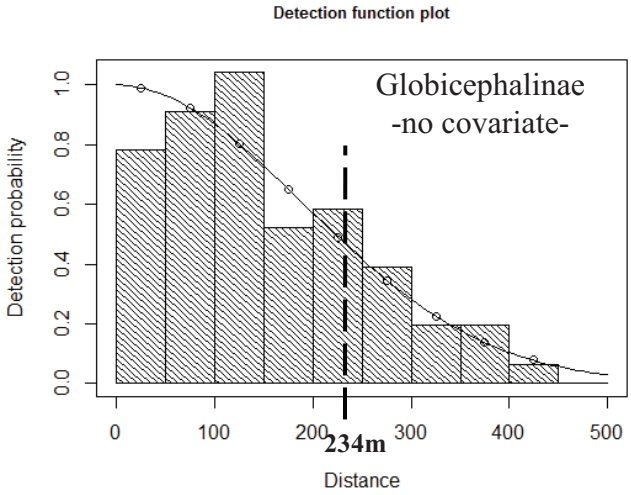
In this table we report numbers of groups and individuals sighted during the aerial survey for cetacean and seabird guilds and individual species (when identified), as well as overall encounter rates.

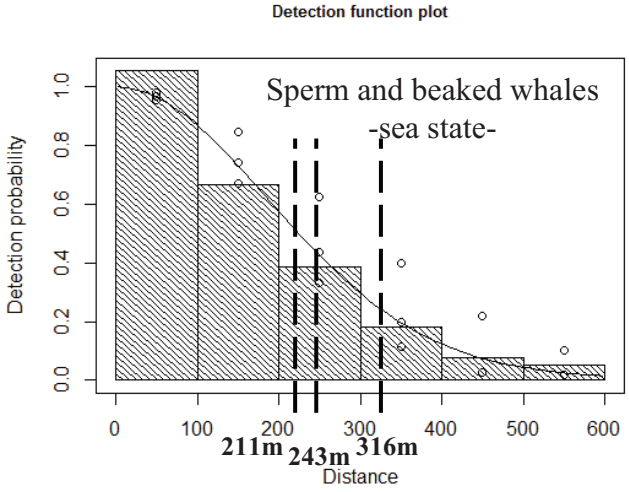
	Number of groups	Number of individuals	Encounter rate (groups / 1000km)	Encounter rate (individuals /
CETACEANS				
Delphininae	**86**	**774**	**0, 87**	**7,86**
Rough-toothed dolphin *Steno bredanensis*	9	52		
Pantropical spotted dolphin *Stenella attenuata*	1	20		
Small delphininae sp	27	353		
Bottlenose dolphin *Tursiops truncatus*	17	98		
Fraser's dolphin *Lagenodelphis hosei*	1	25		
Large delphininae	25	182		
Delphininae sp	6	44		
Globicephalinae	**74**	**1 046**	**0, 75**	**10,62**
Pygmy killer whale *Feresa attenuata* / Melon-	4	82		
Melon-headed whale *Peponocephala electra*	6	500		
Short-finned pilot whale *Globicephala*	19	122		
False killer whale *Pseudorca crassidens* / Short-	17	119		
False killer whale *Pseudorca crassidens*	1	20		
Risso's dolphin *Grampus griseus*	25	200		
Killer whale *Orcinus orca*	2	3		
Sperm and beaked whales	**100**	**194**	**1,02**	**1,97**
Blainville's beaked whale *Mesoplodon*	7	20		
Mesoplodon spp.	10	32		
Cuvier's beaked whale *Ziphius cavirostris*	28	48		
Ziphiidae sp	20	33		
Sperm whale *Physeter macrocephalus*	10	23		
Kogia spp.	25	38		
SEABIRDS				
Tropicbirds	**1 004**	**1 077**	**10,20**	**10,94**
White-tailed tropicbird *Phaeton lepturus*	684	730		
Red-tailed tropicbird *Phaeton rubricauda*	157	176		
Phaeton spp.	163	171		
Grey terns	**105**	**197**	**1,07**	**2,00**
Noddis	**2 058**	**14 005**	**20,90**	**142,22**
Anous spp.	1971	13 846		
Blue Noddy *Procelsterna cerulea*	87	159		
White tern *Gygis alba*	**7 755**	**13 063**	**78,75**	**132,65**
Bobbies	**1 891**	**6 792**	**19,20**	**68,97**
Red-footed booby *Sula sula*	1 760	6 527		
Masked booby *Sula dactylatra*	28	34		
Brown booby *Sula leucogaster*	67	117		
Sula spp.	36	114		
Petrels and shearwaters	**1 130**	**1 595**	**11,47**	**16,20**
Grey colored petrels	96	105		
Dark colored petrels	895	1 243		
Puffinus spp.	75	80		
Procellaridae sp	64	167		
Sooty tern *Onychoprion fuscatus*	**1 395**	**5 094**	**14,17**	**51,73**
Frigatebirds	**295**	**394**	**3,00**	**4,00**
Great frigatebird *Fregata minor*	36	47		
Lesser frigatebird *Fregata ariel*	21	21		
Fregata spp.	238	326		

Appendix D: Detection models for cetaceans according to multiple covariate distance sampling (Marques and Buckland, 2004)

A half normal detection model was selected for the three cetacean guilds. Turbidity significantly affected the detection of Delphininae; sea state significantly affected the detection of sperm and beaked whales (fitted detection models and estimated effective strip widths for each level of the covariate are provided). No covariate significantly affected the detection of Globicephalinae (the fitted detection model and the estimated effective strip width is provided). Effective strip widths are provided at the bottom of each graph.



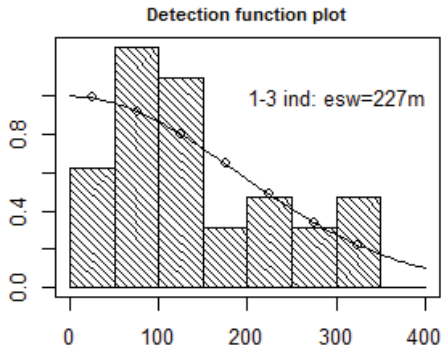


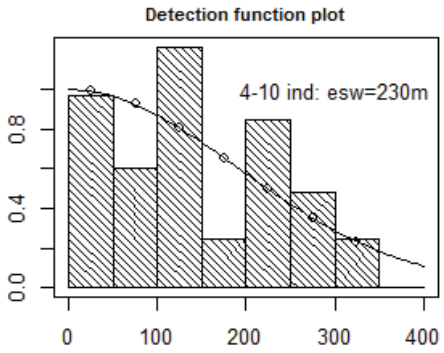


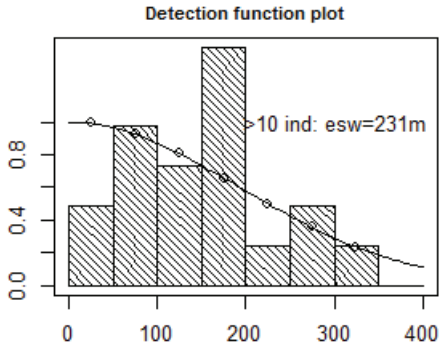
Appendix E: Impact of group sizes on cetacean detection

To investigate if group size impacted cetacean detection, we estimated detection functions for different group size categories for the three cetacean guilds. Group size categories were: 1 to 3, 4 to 10 and > 10 individuals for Delphininae; 1 to 4, 5 to 10 and > 10 individuals for Globicephalinae and 1 individual versus > 1 individual for sperm and beaked whales. Group size did not have a strong impact on cetacean detection as ESWs were not significantly higher for larger group sizes.

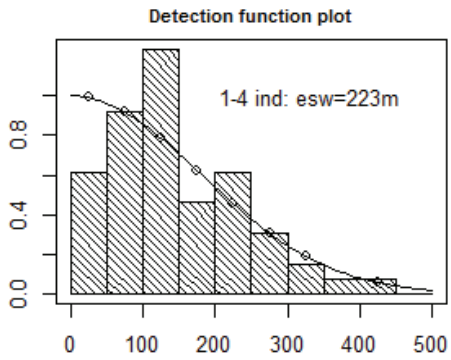
Delphininae

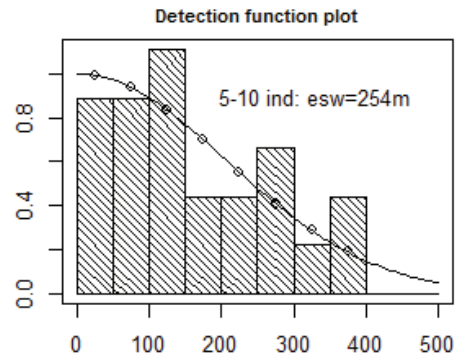


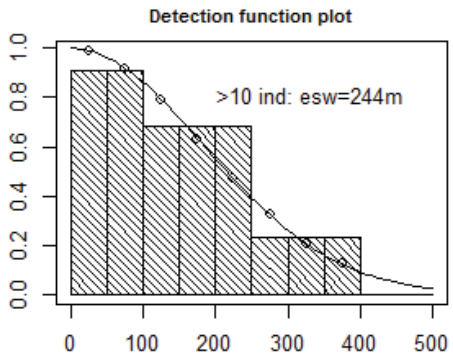




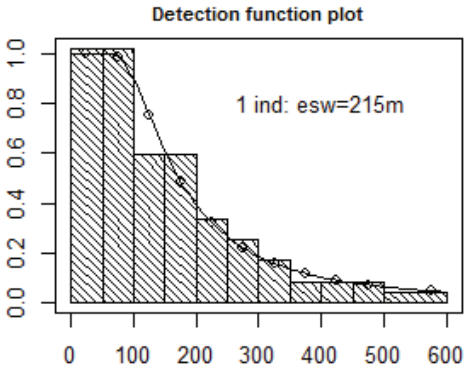
Globicephalinae

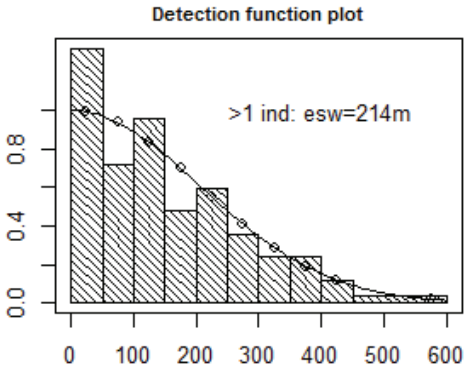






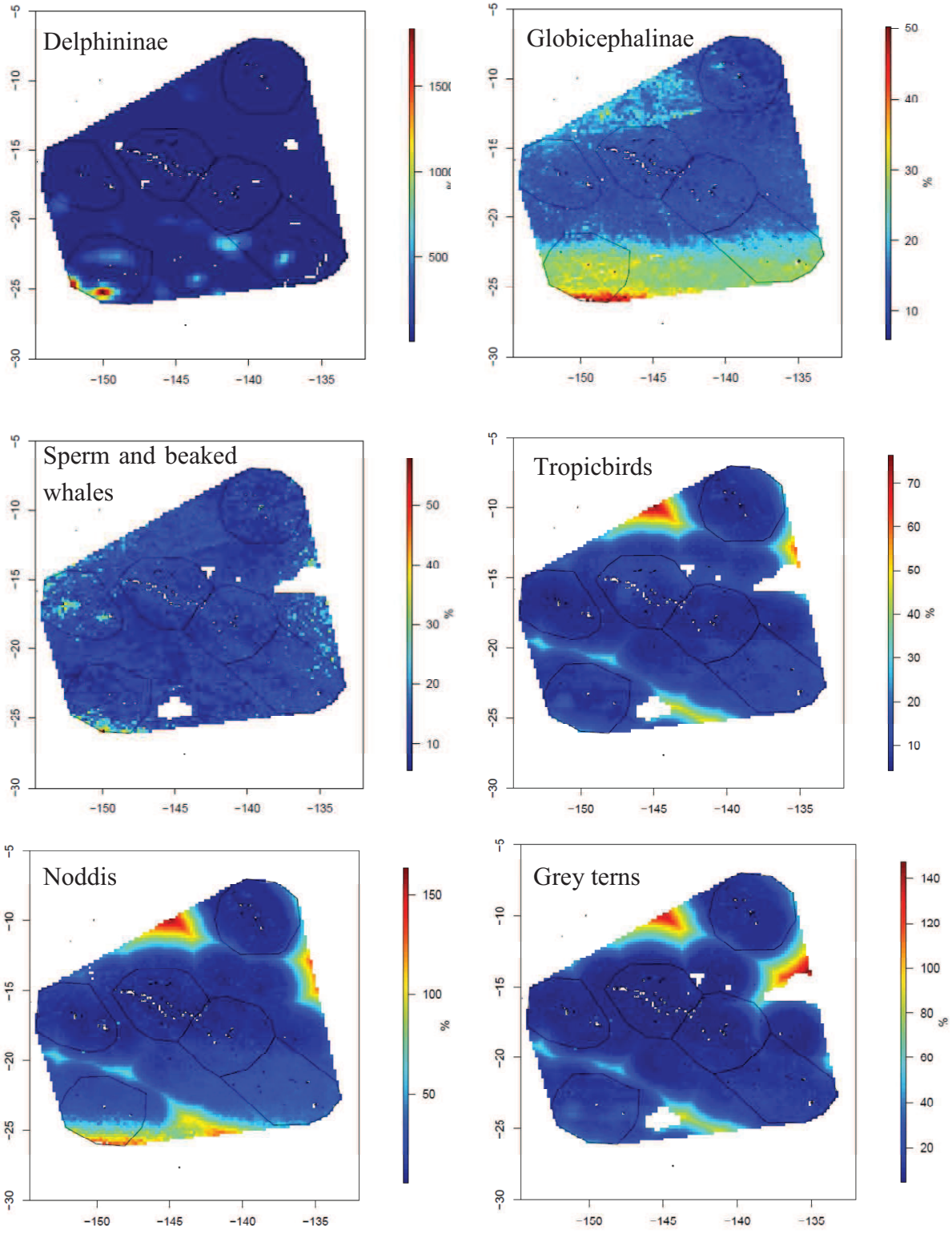
Sperm and beaked whales

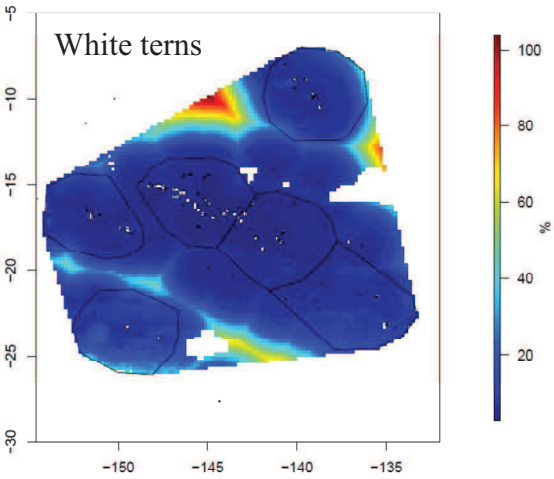


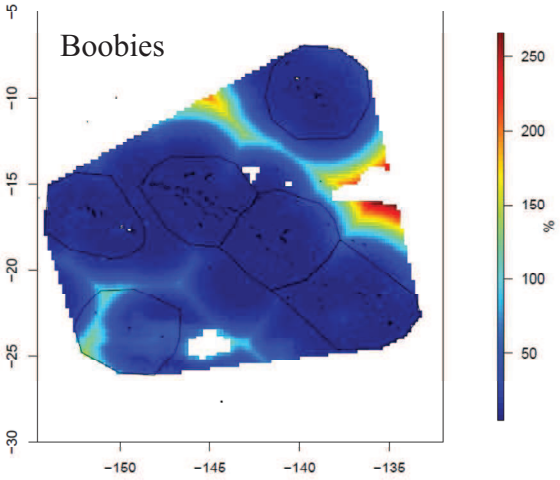


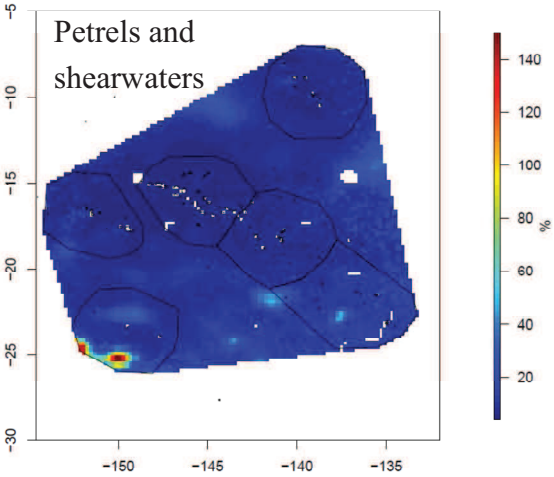
Appendix F: Uncertainty maps

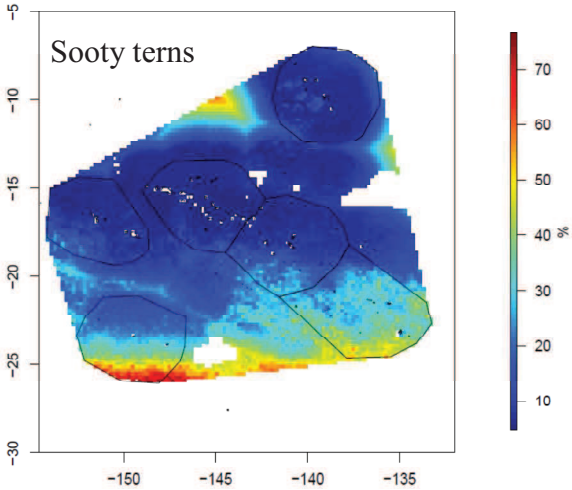
We provide uncertainty maps for cetacean and seabird guilds, as measured by the coefficient of variation (expressed in %). High predicted densities were associated with low uncertainty whereas low predicted densities were associated with high uncertainty. Uncertainty in seabird predicted densities increased with distance from the islands.

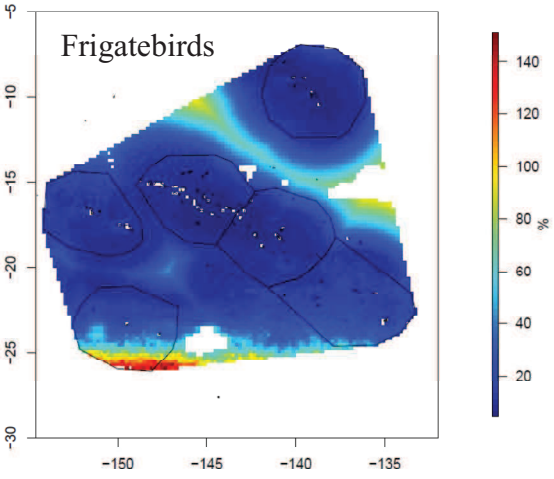



White terns
-5
-10
-15
-20
-25
-30
-150
-145
-140
-135
100
80
60
40
20
%


Boobies
-5
-10
-15
-20
-25
-30
-150
-145
-140
-135
250
200
150
100
50
%


Petrels and
shearwaters
-5
-10
-15
-20
-25
-30
-150
-145
-140
-135
140
120
100
80
60
40
20
%


Sooty terns
-5
-10
-15
-20
-25
-30
-150
-145
-140
-135
70
60
50
40
30
20
10
%


Frigatebirds
-5
-10
-15
-20
-25
-30
-150
-145
-140
-135
140
120
100
80
60
40
20
%

ANNEX 4

Predicting cetacean habitats from their energetic needs and the distributions of their prey in two contrasted tropical regions

Charlotte Lambert, Laura Mannocci, Patrick Lehodey, Vincent Ridoux

To be submitted to *Marine Ecology Progress Series*

Predicting cetacean habitats from their energetic needs and the distributions of their prey in two contrasted tropical regions

Lambert Charlotte[1], Mannocci Laura[1], Lehodey Patrick[3] Ridoux Vincent[1,2]

[1] Laboratoire Littoral Environnement et Sociétés, UMR 7266 Université de La Rochelle - CNRS, Institut du Littoral et de l'Environnement, 17000 La Rochelle, France.

[2] Observatoire PELAGIS, UMS 3462 Université de La Rochelle - CNRS, Systèmes d'Observation pour la Conservation des Mammifères et des Oiseaux Marins, 17000 La Rochelle, France.

[3] MEMMS (Marine Ecosystems Modeling and Monitoring by Satellites), CLS, Space Oceanography Division, 8-10 rue Hermes, 31520 Ramonville, France

Abstract

Modelling marine top predator distributions is a specific challenge, given the complexity of these ecosystems. So far, the majority of habitat modelling studies relied on static and oceanographic covariates, but very few related predator distributions to the distribution of their prey, often as the result of the unavailability of such information.

We investigated the distributions of 3 cetacean guilds with increasing costs of living (sperm and beaked whales, *Globicephalinae* and *Delphininae*) in relation to the biomass and production of micronekton in 2 contrasted regions, the Southwest Indian Ocean (SWIO) and French Polynesia (FP). We expected energetically costly cetaceans to forage preferentially in high quality habitats where they can easily meet their energetic needs, and less active cetaceans to forage in either low or high quality habitat.

Cetacean data were collected from dedicated aerial surveys. Biomasses and productions of 6 functional groups of micronekton between surface and ~1000 m were simulated by the SEAPODYM model at a resolution of ¼° x week using satellite data and physical outputs from an operational ocean circulation model. We examined cetacean distributions in relation to the distribution of micronekton groups through Generalized Additive Models and predicted their habitats in the SWIO and FP. The 3 guilds were related to micronekton in accordance with their diving abilities. Explained deviances ranged from 9 to 13% for sperm and beaked whales, from 18 to 47% for *Globicephalinae*, and from 19 to 22% for *Delphininae*.

In accordance with our hypothesis, the energetically costly *Delphininae* and *Globicephalinae* appeared to optimize their foraging success in each region by selecting areas where high micronekton biomass and/or production were available at shallow depth. At a broader scale, our models predicted higher densities in the productive SWIO (2.66 individuals/km² for *Delphininae*, 1.29 for *Globicephalinae*) compared to the oligotrophic FP (0.10 individuals/km² for *Delphininae*, 0.07 for *Globicephalinae*). In contrast, the less active sperm and beaked whales showed no clear habitat preferences (0.04 individuals/km² in both regions), indicating they can accommodate of both productive and oligotrophic areas.

Keywords: cetaceans, mid-trophic levels, SEAPODYM, direct predictors, Southwest Indian Ocean, French Polynesia, habitat modelling.

1. INTRODUCTION

Marine top predators represent the highest trophic levels of pelagic food webs (Estes *et al.* 2001). Several of them have been referred to as keystone species (Mills *et al.* 1993) since they exert strong influence over their ecosystems through top-down effects (Heithaus *et al.* 2008). Many marine top predators, especially cetaceans, are currently in decline, potentially linked to accidental mortality in fishing gears and pollution (Schipper *et al.* 2008). We are still not able to completely understand and predict the consequences of such declines on ecosystem functions and services (Heithaus *et al.* 2008). However, there are already strong evidences that a decrease in the abundance of upper-trophic levels could lead to disturbance of food webs at lower levels owing to trophic cascades. Studies in upwelling systems have demonstrated that decrease of top predators' abundance has led to a decrease of "keystoneness" of marine mammals in California, in favour of mid-trophic levels (Libralato *et al.* 2006).

Cetaceans are known to be very sensitive to the variability of their environment, and can notably respond through changes in their distributions (Forney 2000). Therefore, establishing models which correctly describe and predict cetacean preferred habitats is a critical need in the context of implementing good conservation and management strategies.

Pelagic marine systems are highly variable, both temporally and spatially, hence representing specific challenges for habitat modelling. More specifically, environmental predictors must be selected with care to be representative of ecological processes underlying cetacean distributions. Nevertheless, oceanographic processes are characterised by spatial and/or temporal lags between physical features and the resulting biological responses (Redfern *et al.* 2006).

Given those difficulties, habitat modelling should be performed with as much direct predictors as possible (Guisan and Zimmermann 2000). Typically, such predictors could be the distribution of cetaceans' prey (micronekton), since cetaceans are known to be very sensitive to variations in prey abundance or quality (Österblom *et al.* 2008). However, so far, cetacean habitat models were based on oceanographic features or primary production (Jaquet *et al.* 1996) because data on prey distribution were not available over time at large spatial scales. Consequently, top predator habitats have often been modelled by using indirect predictors (Baumgartner and Mate 2005, Cañadas *et al.* 2005, Ferguson *et al.* 2005) as proxies of prey distribution. These studies revealed that cetacean distributions mirror the abiotic characteristics of their ecosystems such as sea surface temperature, seafloor depth or slope, nutrients, and primary productivity.

Spitz and colleagues (2012) demonstrated that inherent energetic constraints (costs of living) governed cetacean foraging strategies according to the Optimal Foraging Theory (MacArthur and Pianka 1966). Assuming that this strategy of prey selection (prioritizing quality over quantity) can be extrapolated to habitat, Mannocci *et al.* (2013) recently

hypothesized that the energetic requirements of cetaceans governed habitat selection over large spatial scales. Hence, energetically costly cetaceans would preferentially distribute in high quality habitats to meet their high energy requirements, whereas less active cetaceans could meet their needs by exploiting either low or high quality habitats. These hypotheses have successfully been tested in the Southwest Indian Ocean (SWIO), characterized by 3 areas of contrasted primary productivity (Mannocci *et al.* 2013), and French Polynesia (FP), located in the oligotrophic South Pacific gyre (Mannocci *et al.* in revision). In both regions, cetaceans responded to the productivity of their habitats. Those habitat models were developed from cetacean sightings collected during aerial surveys and indirect static and oceanographic predictors.

In the present study, we aimed to extend these results with models based on direct predictors, *i.e.* prey distribution. In absence of synoptic datasets of micronektonic organisms at such large spatial scale, we turned to numerical models. This kind of model can provide a useful surrogate, even though their outputs and design require continuous evaluation and improvements. One original modelling approach of micronekton has been developed (Lehodey *et al.* 2010) as a component of the Spatial Ecosystem And Population Dynamics Model (SEAPODYM). This micronekton model describes six functional groups defined by their daily vertical migration patterns in 3 biological layers between the surface and ~1000 m. It has been successfully used to analyse tuna catch data (Briand *et al.* 2011), simulate habitat and movement of turtle (Abecassis *et al.* 2013) and predict large-scale population dynamics of several tuna species based on hindcast simulation from coupled physical-biogeochemical models (Lehodey *et al.* 2008, 2010; Senina *et al.* 2008; Sibert *et al.* 2012).

Here, we implemented habitat models based on the same cetacean sightings as Mannocci and colleagues in the SWIO and FP. Similarly, 3 guilds were defined on the basis of increasing costs of living (sperm and beaked whales, *Globicephalinae* and *Delphininae*) to explore their relationship to their habitat quality. However, in the present study habitat quality was characterized by the distribution of their prey, using the micronekton outputs of SEAPODYM. Generalized Additive Models were used to model the relationships between cetacean sightings and simulated micronekton distributions. We then predicted their habitats at the regional scale and compared their habitats between the SWIO and FP. Since SEAPODYM outputs represent prey directly consumed by cetaceans and match the survey periods, their use as predictors theoretically prevents any spatial and temporal lags with the response variable (cetacean distribution). Therefore, we expected more direct relationships between observed distributions and direct predictors.

As in Mannocci et al. (2013), we hypothesized that energetic requirements of cetaceans govern their habitat selection. We expected costly cetaceans to preferentially forage on high quality habitats to meet their high energetic requirements and less active cetaceans to meet their needs by foraging in habitats characterized by either high or low quality.

2. DATA AND METHODS

2.1. Aerial Surveys

Aerial surveys were conducted during the austral summer in the SWIO (December 2009 - April 2010) and FP (January – May 2011) (Figure 1). In the SWIO, the sampled region encompassed an area from 1 to 27°S and from 39 to 61°E. Six geographic sectors have been sampled: Northern, Central and Southern Mozambique Channel, Seychelles, Tromelin-Madagascar and Reunion-Mauritius. FP lies between 5 and 30°S, and 156 and 132°W. It includes five archipelagos oriented northwest-southeast, corresponding to the following sampled sectors: North and South Tuamotu, Gambier, Society, Marquesas and Australs Archipelagos.

Data were collected following the same standardized aerial protocol in both regions. It is based on a line transect methodology (Buckland *et al.* 2001), in which the angle to the track line is recorded for each observation. This angle, together with the flight altitude, informed about the perpendicular distance from the track line, required for detection function modelling (estimation of the effective strip width, ESW). Survey platforms were high-wing, double engine aircrafts equipped with bubble windows that allowed observers to scan the sea surface right underneath the plane. Observers recorded sightings and group size of cetaceans at the lowest possible taxonomic level. Beaufort sea-state, turbidity, glare severity, cloud coverage and an index of subjective conditions were also collected on board as detection covariates.

The total survey effort was 83 726 km in the SWIO (Mannocci *et al.* 2013) and 98 476 km in FP (Mannocci *et al.* in revision). In the SWIO, *Delphininae* and *Globicephalinae* encounter rates were the highest in the Central Mozambique Channel and in the Seychelles, and the lowest in Tromelin-Madagascar and Reunion-Mauritius (Appendix 1). In FP, encounter rates were far lower for the 2 guilds. The highest encounter rates were around the Marquesas, while the lowest were around the Australs. Compared to *Delphininae* and *Globicephalinae*, sperm and beaked whales showed lower and less variable encounter rates (Appendix 1). These encounter rates were consistent between sectors, and were similar in both regions (Mannocci *et al.* 2013, Mannocci *et al.* in revision).

2.2. Study regions

The 2 study regions have contrasted oceanographic conditions, which allowed predator distributions to be studied in a range of environmental conditions. The SWIO can be divided into 3 ecoregions: the Mozambique Channel, the Seychelles and the Mascarene Islands (including pelagic waters to the east of Madagascar and around the Mascarene Islands). The Mozambique Channel is characterized by a very dynamic system of mesoscale eddies (Schouten *et al.* 2003; de Ruijter *et al.* 2004), inducing a pronounced enhancement of phytoplankton production (Longhurst 2007). Enhanced productivity is also associated with

mid-ocean shallow banks of the Seychelles plateau (Longhurst 2007), whereas the Mascarene are characterized by low-nutrient subtropical waters (New *et al.* 2005).

FP is situated in the core of the South Pacific oligotrophic gyre where downwelling precludes any upward flow of nutrients. This results in a permanent decoupling between the euphotic layer and the richer deeper layers (Rougerie and Rancher 1994). This region is nonetheless characterised by a clear latitudinal productivity gradient. In the north, the Marquesas Islands are associated with a significant enhancement of phytoplankton production owing to an island mass effect (Signorini *et al.* 1999) and the proximity of the south equatorial current. In the south, extreme nutrient scarcity in the euphotic layer results in a very low primary production (Martinez *et al.* 2009).

2.3. SEAPODYM outputs

The SEAPODYM model (Lehodey *et al.* 2010), was initially developed to predict the distribution of tuna populations in tropical waters (Lehodey *et al.* 2008). It is based on physical and biogeochemical models describing the ocean to simulate 2 sub-models: a first model describing the prey populations (micronekton), and a second describing the predator populations. In the present study, we only used the first model simulating prey populations. Micronekton functional groups modelling is driven by the key variables temperature, currents, primary production and euphotic depth that can be provided from ocean models or all obtained directly or indirectly from space oceanography: infra-red radiometry and microwave for the temperature, altimetry for the currents and sea colour for the primary production.

Micronekton encompasses actively swimming organisms, ranging from plankton (< 2cm) to larger nekton (> 20cm), which includes cephalopods, crustaceans, fishes and jellyfishes (Brodeur *et al.* 2005). These mid-trophic levels represent a crucial link between oceanographic and biogeochemical processes of the global ocean and top predator distributions. The ultimate aim of SEAPODYM is to provide a realistic model of the complex marine ecosystem, including interactions between all species composing this trophic web, with both bottom-up and top-down controls.

SEAPODYM uses allometric relationships (linking size/weight to species abundance) to model several functional groups of micronekton corresponding to their size/weight window (Lehodey *et al.* 2010). Each functional group is modelled as a single multi-species population, with continuous mortality rates and recruitment. The model is based on the concept that primary production is transferred to upper-trophic levels through an energy efficiency coefficient. This energy feeds the eggs/larvae pool, inducing their development and recruitment into the upper size-window. Organisms are recruited in the forage population when they reach the minimal size, and disappear from it when they either die or exceed the maximum size. Production is then defined as the amount of energy transferred through the size-window. This parameterization of the model is based on biochemical or energetic

principles, such as metabolism at the cellular level, allowing the model to predict development time at a given temperature. This is a crucial element as it determines the time of growth and recruitment of organisms.

Micronekton is characterised by nycthemeral vertical migrations induced by daylight variations thanks to its ability to swim. Such behaviour is thought to be mainly a predator avoidance strategy: micronekton sinks to deeper layers during daytime where predation pressure is lower (Brodeur *et al.* 2005). SEAPODYM includes six functional groups defined on their migration patterns: epipelagic, non-migrant mesopelagic, migrant mesopelagic, non-migrant bathypelagic, migrant bathypelagic and highly migrant bathypelagic (Lehodey *et al.* 2010). Migrant mesopelagic and highly migrant bathypelagic organisms spend the night in the epipelagic layer, moving back to their respective layers during the day. Migrant bathypelagic organisms also perform a migration, but only between mesopelagic and bathypelagic layers.

The 3 layers are defined relative to the euphotic depth (Appendix 2). The boundary between the epipelagic and the mesopelagic layer is defined as 1.5 euphotic depths, whereas the limit between the mesopelagic and bathypelagic layers is at 5.5 euphotic depths and the lower bound of the bathypelagic layer is at 10.5 euphotic depths. Those layers have been recently updated following field observations, and therefore are different than those indicated in Lehodey and colleagues (2010). However, except those delimitations, nothing changed between the SEAPODYM model used for this study and the model described in the reference paper. The SEAPODYM prey population model has been parameterized and evaluated with biomass estimates from micronekton sampling cruises (e.g. ESTROPAC cruises; Hidaka *et al.* 2003).

2.4. Cetacean guilds

The vast majority of cetacean sightings during the survey (conducted in the austral summer) were of odontocetes, so our classification focuses on odontocetes, simply named cetaceans thereafter. 3 guilds of cetaceans were studied, with decreasing costs of living: *Delphininae*, *Globicephalinae* and sperm and beaked whales (see Mannocci *et al.* in revision for the species composition of these guilds in FP, and Mannocci *et al.* 2013 in the SWIO). This classification relied on cetaceans diving performances, closely related to their capacity to save oxygen and reduce their energetic costs, and is confirmed by Spitz and colleagues' study (Spitz *et al.* 2012) based on indicators of costs of living such as muscular performance.

2.5. Detection function modelling

Effective strip widths (ESWs) were estimated for each cetacean guild by fitting detection functions to perpendicular distances using multiple covariate distance sampling (Marques and Buckland 2004) to model the effect of both distance and detection conditions on detection probability. Results are presented in Mannocci *et al.* 2013 for the SWIO and Mannocci *et al.* in revision for FP.

2.6. Data processing

In order to model cetacean distributions, we used micronekton outputs from SEAPODYM as predictors. In addition to the 6 functional groups of micronekton, both in terms of biomass and production, the euphotic depth (provided by SEAPODYM) was included to consider the changing accessibility of micronekton to cetaceans between the different geographic sectors.

We averaged SEAPODYM outputs (provided at a weekly resolution) over the survey period in each sector (between 2 to 7 weeks), in order to have a close temporal match between the response variable and the predictors.

SEAPODYM outputs were provided at a 0.25°×0.25° spatial resolution. Using ArcGIS 10 (ESRI 2011), cetacean sightings and sampled surface areas were aggregated into this grid. Numbers of individuals as well as sampled surface areas were summed in each grid cell. The sampled surface area for each single transect was calculated as follows:

$$sampled\ area = transect\ length \times 2 \times ESW.$$

2.7. Habitat modelling

We used Generalized Additive Models (GAMs; Hastie and Tibshirani 1999) to model relative densities of the 3 cetacean guilds. We used a Poisson distribution family with variance proportional to the mean, because dispersion of our data was greater than predicted by the Poisson distribution (over-dispersion; McCullagh and Nelder 1989; Hedley *et al.* 1999). The mean of the response variable was related to the additive predictor with a log link function.

The relationship between the response variable (number of individuals per pixel *i*) and the additive predictor was modelled in both regions as:

$$\log(individual_i) = \alpha + \sum f_i\,(X_i) + \log(sampled\ area_i)$$

where $f_i(X_i)$ is a non-parametric smooth function (spline) of the covariate X, and $\log\,(sampled\ area_i)$ is the model offset. This offset allowed taking into account the variation in the amount of effort per pixel (Chambers and Hastie 1992). Micronekton biomasses and productions were log-transformed prior to model selection in order to limit outliers. To avoid over-fitting of the data while allowing the curve to be non-linear, we constrained the maximum number of degrees of freedom for each spline to 3.

A model selection procedure was implemented based on models with 4, 3, 2 or 1 covariates, excluding all combinations of covariates with a pair-wise correlation higher than 0.7 in the SWIO, and 0.8 in FP. These correlations were calculated with the Spearman correlation test implemented in R (R Core Team 2012), using the Hmisc package (Harrell Jr

2013). The selection criterion was the Generalized Cross-Validation score (GCV, the lower the better). The GCV score is a prediction error criterion: it estimates the average error, by removing each datum in turn and re-predicting it from the model fitted to the remaining data (Wood 2006). For each selected model, we quantified the contribution of each covariate to the linear predictor, in percent (Wood 2013).

Finally, prediction maps were produced for both regions based on the selected models, and using SEAPODYM outputs averaged over the period of each survey (3-4 months; Appendices 3 to 5). We predicted only inside the range of sampled covariate values (model-based interpolation; Elith and Leathwick 2009). Moreover, we mapped uncertainty on the model parameters with the coefficient of variation (CV). Models, model selection, quantification of contributions and predictions were performed in R using the mgcv package, especially gam and predict.gam functions (Wood 2006, 2013).

3. RESULTS

3.1. Micronekton outputs

Micronekton distributions provided by SEAPODYM were composed of 12 covariates for each region (6 micronekton functional groups, both in biomass and in production). For both regions, biomasses and productions were higher for the non-migrant bathypelagic, migrant bathypelagic and highly migrant bathypelagic groups compared to the 3 others micronekton groups, except for the epipelagic production in the SWIO, which showed higher maximum values than non-migrant bathypelagic production.

In the SWIO, the distributions of epipelagic and mesopelagic functional groups were quite contrasted, with high biomass and production in the Mozambique Channel, off Kenya and around the Seychelles, as opposed to the less variable bathypelagic micronekton groups (Appendix 3). In FP, all functional groups reflected the latitudinal gradient characterizing the region (Appendix 4). Higher biomass and production were found for all micronekton groups in the north of the region, although the production of the non-migrant bathypelagic and migrant bathypelagic functional groups was less variable than for the others groups. Epipelagic, non-migrant mesopelagic and migrant mesopelagic functional groups were also characterized by quite high biomass at the extreme south of FP.

3.2. Selected models

Delphininae

In the SWIO, the distribution of *Delphininae* was best predicted by a model containing, in order of decreasing contributions, euphotic depth (40%), non-migrant mesopelagic functional group (biomass; 27%), epipelagic functional group (biomass; 21%) and migrant bathypelagic functional group (production; 12%) (Figure 2a). This model explained 21.7% of the deviance. In the 5%-95% quantiles interval (corresponding to the core data), the

relationships were negative with the euphotic depth, positive with the non-migrant mesopelagic functional group and unimodal with the last 2 micronekton functional groups.

In FP, the selected model (19% of explained deviance) also contained euphotic depth, but as the least contributing covariate (11%) (Figure 2b). The other selected covariates were different from the SWIO model: non-migrant bathypelagic functional groups (both biomass and production; contribution of 42% and 18%) and epipelagic functional group (production; 29%). In the 5%-95% quantiles interval, relationships were positive with non-migrant bathypelagic (biomass) and epipelagic functional groups, but negative with non-migrant bathypelagic functional group (production) and euphotic depth.

Globicephalinae

For this guild in the SWIO, the selected model explained 18% of the deviance and contained, in order of decreasing contributions, epipelagic functional group (production; 30%), euphotic depth (28%), highly migrant bathypelagic functional group (production; 22%) and non-migrant mesopelagic functional group (biomass; 21%) (Figure 3a). In the 5-95% quantiles interval, relationships were negative (and linear) for euphotic depth and non-migrant mesopelagic functional group, positive for highly migrant bathypelagic functional group and unimodal for epipelagic functional group.

In FP, euphotic depth did not appear in the predictors, with a model explaining 47% of the deviance. The selected model contained non-migrant bathypelagic functional group (biomass; contribution of 60%), non-migrant mesopelagic functional groups (both biomass and production; contribution of 11% and 19% respectively) and migrant bathypelagic functional group (production; 10%) (Figure 3b). In the 5-95% quantiles interval, the relationship was positive with non-migrant bathypelagic functional group, but for the other 3 groups predicted density remained very close to zero, indicating a weak effect of these covariates.

Sperm and beaked whales

The model for sperm and beaked whales had the lowest explained deviances, both in the SWIO and in Polynesia, with 9% and 13%, respectively. In the SWIO, their distribution was best predicted by highly migrant bathypelagic functional group (production; contribution of 36%), euphotic depth (25%), migrant bathypelagic functional group (production; 24%) and epipelagic functional group (production; 16%) (Figure 4a). Relationships were globally negative for 3 of the covariates in the 5-95% quantiles intervals (euphotic depth, migrant bathypelagic and epipelagic functional groups) but positive with the highly migrant bathypelagic functional group.

In FP, the selected model included migrant mesopelagic functional group (biomass; contribution of 38%), migrant bathypelagic functional groups (biomass and production; 24% and 21% respectively) and euphotic depth (18%) (Figure 4b). Relationships were complex in

the 5-95% quantiles intervals, with unimodal relationships for the last 3 covariates, but a positive relationship with the migrant mesopelagic functional group.

3.3. Predicted distributions

Delphininae

In the SWIO, high densities of *Delphininae* were predicted in the north of the region (especially off Kenya and southeast of the Seychelles), in the Mozambique Channel and south of Madagascar (Figure 5a). Lowest predicted densities were around the Mascarene (Tromelin-Madagascar and Reunion-Mauritius). The mean predicted density was of 2.7 individuals per km² over the whole region (Table 1). Uncertainty was the lowest where predicted density was the highest (Figure 6a). Mean predicted densities showed a ratio of 16 between the highest and the lowest density sectors.

In FP, the model predicted much lower densities, with a mean predicted density over the region of only 0.1 individuals per km² (Table 1). The highest densities were predicted in the southwest of the Marquesas and the lowest in the south of the region (south 20°S, Figure 5b). Uncertainty was the lowest where predicted density was the highest (same range as in the SWIO, Figure 6b). Mean predicted densities showed a ratio of 19.5 between the highest and the lowest density sectors.

Globicephalinae

In the SWIO, the predicted distribution of *Globicephalinae* was similar with that of *Delphininae*: the highest densities were predicted off Kenya, south of Madagascar (close to the shelf) and in the Mozambique Channel (Figure 5a). The mean predicted density was of 1.3 individuals per km² over the region (Table 2). Lowest predicted densities were east of Madagascar, and east of the Mascarene. Uncertainty was low over the whole region, except close to Madagascar and Mascarene shelves or slopes (Figure 6a). Between-sector ratio was of 9.

In FP, the mean predicted density over the region was low (0.1 individuals per km², Table 2). The predictions were quite homogeneous (Figure 5b), especially in the north. The highest densities were predicted west of the Marquesas, and the lowest, in the south of the region (south 20°S). A low uncertainty was associated with high densities, but it reached high values in the south, where predicted densities were the lowest (Figure 6b). Between-sector ratio was of 25.5, the highest value of the 3 guilds.

Sperm and beaked whales

Sperm and beaked whales predicted distribution in the Southwest SWIO differed from the other 2 guilds, with a much lower mean (0.04 individuals per km², Table 3). The highest densities were predicted close to the slopes of Madagascar (Mozambique Channel and south of the island), the Seychelles and off Kenya. Predicted distribution was more homogenous than for *Delphininae* and *Globicephalinae*, with intermediate densities both in oligotrophic

and productive waters (Figure 5a). Between-sector ratio was low compared to the other 2 guilds, with a ratio of only 2.2 between the highest and the lowest density sector. An overall low uncertainty was associated with both high and low predicted densities (Figure 6a).

In FP, predicted densities were the lowest for sperm and beaked whales, with a mean of 0.04 individuals per km² (the same as in the SWIO, Figure 5b, Table 3). Sperm and beaked whales were homogenously distributed over FP, with the highest predicted densities in the north and south, and the lowest in the centre. Given the high densities predicted in the Marquesas compared to the other sectors, between-sector ratio was of 11. Uncertainties showed a different pattern compared to the other 2 guilds: low uncertainties were associated with both low and intermediate predicted densities (Figure 6b). An area of high uncertainty was found at the north-east corner of the region.

When compared to the numbers of individuals (Appendix 1), the predictions appeared consistent with the observed distribution. In the SWIO, *Delphininae* were mostly observed in the central and northern Mozambique Channel and around Seychelles, where our model predicted high densities. In FP, the observations show a latitudinal gradient, with more individuals observed around the Marquesas, reproduced by the model. Observations and predictions were also consistent for *Globicephalinae*, with high observed and predicted densities in the Mozambique Channel in the SWIO, and around the Marquesas in FP. Sperm and beaked whales showed a fairly uniform observed distribution both in the SWIO and in FP, a pattern also predicted by the models.

4. DISCUSSION

4.1. Modelling considerations

GAMs are common tools in habitat modelling, given their ability to model non-linear relationships (Redfern *et al.* 2006). However, it can be quite hard to interpret these complex relationships ecologically. Since the first goal of our models was to predict cetacean distributions, this limitation is not as important as it would have been for models with an explanatory goal. Nevertheless, our results can be interpreted on the basis of selected predictors and of their general trends. Our models are based on large sample sizes (about 1473 pixels are used for modelling in the SWIO and 1821 in FP), with a large number of presences, providing a good statistical basis.

Low explained deviances are common in GAMs, especially for cetaceans. For example, in the eastern tropical Pacific (ETP), Forney and colleagues (2012) and Becker and colleagues (2010) found similar deviances, ranging from 8 to 13% for delphinids and from 5 to 11% for the sperm whale. Deviances of the models built by Mannocci and colleagues were comprised between 9.6% and 30% for delphinids (*Delphininae* and *Globicephalinae*) and were around 5% for sperm and beaked whales. By comparison, our models resulted in higher explained deviances, ranging from 18% to 47% for *Delphininae* and *Globicephalinae*, and from 9% to

13% for sperm and beaked whales. Although these deviances cannot be directly compared due to the different modelling units between both studies, this seems to indicate that incorporating prey data improves cetacean habitat models. Furthermore, average uncertainties associated with our predictions were quite low, ranging from 14% to 35%.

Extrapolation outside the range of sampled environmental conditions and outside the sampled period must be avoided. Transferability of a model calls for 2 conditions, which are rarely fully met: a good understanding of the processes that underpin distributions and a good knowledge of differences between the region over which the model is calibrated and the region over which the prediction is made (Elith and Leathwick 2009). In this study, we were careful with extrapolations, since we provided predictions only within the range of micronekton biomasses and productions sampled over the surveyed sectors and within the sampled periods.

4.2. Comparison with previous studies

The SWIO and FP are regions of the world ocean where very few dedicated studies have been conducted to improve knowledge on abundances and distributions of cetaceans (Kaschner *et al.* 2012). Our aerial surveys therefore provided very valuable data to fill these gaps. Mannocci and colleagues conducted the first studies of cetacean habitat modelling at the scale of these regions. They relied on the same sightings, hypothesis and modelling procedure as presented here, but used oceanographic and static covariates as predictors instead of micronekton simulated distribution as done in the present study.

Their results can only be partially compared with our results, because modelling was done using a smaller sampling unit (the transect segment as compared to the pixel). In spite of this difference, it is interesting to notice that models built with micronekton provided higher explained deviances (see above), and higher predicted densities: Mannocci and colleagues predicted a maximum density of 1.3 and 0.1 individuals/km² for *Delphininae* in the SWIO and FP, 0.6 and 0.1 for *Globicephalinae* in the SWIO and FP, and 0.025 and 0.017 for sperm and beaked whales in SWIO and FP.

Moreover, the 2 studies yielded similar prediction maps overall, although Mannocci and colleagues provided predictions in a smaller region defined by a minimal convex polygon. In spite of the log-scaled colours, prediction maps were similar for *Delphininae* in both the SWIO and FP, with highest predicted densities in the Mozambique Channel and the Seychelles in the SWIO, and around the Marquesas in FP. Both studies predicted very low densities of sperm and beaked whales in the SWIO and FP as compared to the other 2 guilds, with the highest densities on the slope in the SWIO, and around the Marquesas in FP. *Globicephalinae* is the guild for which the 2 studies were the most divergent. Mannocci and colleagues predicted intermediate densities east of Madagascar, while our models predicted very low densities in this area, as compared to the Mozambique Channel.

To date, SEAPODYM has only been used to predict tuna populations dynamics (Lehodey *et al.* 2008, 2010; Senina *et al.* 2008; Sibert *et al.* 2012), albacore tuna catch rates (Briand *et al.* 2011) and habitat preferences of sea turtles (Abecassis *et al.* 2013).Therefore, this study stands out being the first using the simulated distributions of micronekton as predictors of cetaceans distribution. Such predictors provide additional insights into predator distributions, through the integration of the food web, as micronekton is 2 trophic levels closer to predators than primary production. In addition, as depth is a key factor in cetacean foraging strategy, the integration of the vertical dimension in the models through micronekton functional groups should improve cetacean habitat models.

It must be kept in mind that SEAPODYM outputs are simulated data, then including a part of uncertainty. However, since we obtained low uncertainty on model parameters and similar predictions with SEAPODYM and with static and oceanographic covariates, we reasonably think that SEAPODYM is accurate enough to ensure robust predictions at the regional scale. Further, it must be noticed that in areas where some micronekton functional groups are not modelled by SEAPODYM (*i.e.* bathypelagic functional groups in the neritic strata), we were not able to provide predictions of cetacean densities. This may be of importance in the case of *Delphininae*, given that this guild contains several species with extensive coastal populations (Bearzi 2005; Torres and Read 2009).

Marine predator relationships with their prey have already been studied at smaller scale, the prey patch level. Torres and colleagues (2008) demonstrated that dolphin distribution modelling was more successful with environmental variables than with prey distribution. This is explained by habitat heterogeneity at the fine scale, which is coincident with the patchiness of prey distribution. Benoit-Bird and colleagues (2013) also studied the spatial relationships between predator and prey for 2 seabird and 1 seal species. The authors demonstrated the importance of prey patch characteristics, but found no direct spatial relationship between predators and their prey.

These studies indicate that, at small-scale, the prey patch characteristics (physical habitat inducing aggregation of prey) are more important for predator distributions than the overall distribution of prey biomass. However, processes highlighted at such small spatial scale are probably not relevant at the broader scale studied here.

4.3. Costs of living induce habitat selection

Delphininae are the most energetically costly of our guilds. The most abundant genera (*Stenella spp* and *Tursiops spp*) are known to largely forage at night, mainly from the surface to 200m, following both vertical and horizontal migration of mesopelagic micronekton (Benoit-Bird and Au 2003; Klatsky *et al.* 2007; Scott and Chivers 2009). These 2 genera also perform regular or more occasional excursions down to 400-500 m, depending on species

(Dolar *et al.* 2003; Klatsky *et al.* 2007). Given these characteristics, *Delphininae* are expected to forage in the epipelagic and mesopelagic layers.

In the SWIO, mean predicted densities showed a 16.2 ratio between sectors, with high densities in high quality habitats. *Delphininae* showed a negative relationship with euphotic depth and a positive relationship with the biomass of mesopelagic micronekton (the 2 most contributory covariates), indicating a clear preference for areas where biomass is the highest and the most accessible.

Delphininae appear to select areas where they can forage at lower cost. In areas of high predicted densities, the mean euphotic depth is of 80m, thus placing the boundary between the epipelagic and the mesopelagic layers at about 120m, and the boundary between the mesopelagic and the bathypelagic layers at 360m. Therefore, their diving abilities should allow *Delphininae* to reach the areas of high mesopelagic biomass to forage.

In contrast, in oligotrophic areas (Mascarene and east of Madagascar), the euphotic depth is deeper with a mean of 100m. Therefore, the boundary between the epipelagic and the mesopelagic layers is at 150m, and the boundary between the mesopelagic and the bathypelagic layers is at 450m. Given these boundaries and the low production and biomass of epipelagic and mesopelagic layers, *Delphininae* may need to forage on the bathypelagic layer to meet their energetic needs. This may induce high costs of foraging since they dive at their maximum abilities.

Therefore, it seems that in the SWIO, *Delphininae* select areas where they can reach high biomasses of mesopelagic micronekton with the lowest effort (where euphotic depth is shallow), in order to optimize their foraging success.

In FP, epipelagic and mesopelagic productions and biomasses are far lower than in the SWIO, while productions and biomasses of the bathypelagic layer are equivalent in both regions. This characteristic may explain the importance of the bathypelagic micronekton in the selected model in FP. In such an oligotrophic region, *Delphininae* may not be able to fulfil their needs by foraging in the epipelagic and mesopelagic layers, and therefore may have to dive deeper to reach the bathypelagic layer. Consequently they remain in the north of the region, where the bathypelagic layer is shallower (about 360m), and thus more accessible. *Delphininae* are nevertheless positively related to the epipelagic micronekton production, and are concentrated around the Marquesas, the only sector where both surface and deep productivity are high.

Globicephalinae present similar patterns to *Delphininae*, but appear to select areas on a different basis. In the SWIO, high densities of *Globicephalinae* are found in areas with intermediate epipelagic micronekton production and low euphotic depth. They seem to select areas where high surface production is the easier to reach. High densities are predicted on the

slope of the Seychelles and southern Madagascar shelves, which is consistent with some previous observations in the tropics (Baumgartner 1997; Baird *et al.* 2011).

In FP, the bathypelagic biomass is the most contributory predictor, with a similar relationship than for *Delphininae*, while the other 3 covariates have low contributions and apparently no effects on density. Therefore, *Globicephalinae* also seem to select this deep layer, where they can sustain their energetic needs. However, in contrast to *Delphininae*, this layer is probably more accessible for *Globicephalinae* which dive deeper: up to 1500 m for the most frequently identified species both in the SWIO and in FP, *Peponocephala electra*, according to its diet (mesopelagic fishes and squids) (Jefferson and Barros 1997), up to 1019 m at dawn/dusk for *Globicephala macrorhynchus* (Aguilar Soto *et al.* 2008) and up to 700 m for *Pseudorca crassidens* (Oleson *et al.* 2010). Contrary to *Delphininae*, our results indicate *Globicephalinae* do not only forage on the highest bathypelagic biomasses, but also on intermediate biomasses. This may be due to their lower energetic costs, allowing them to forage deeper and not only in the highest quality habitats, and be more flexible in oligotrophic regions.

On the one hand, we expected costly predators to preferentially forage on high quality habitats within each region. Our results highlighted similar patterns of distribution for *Delphininae* and *Globicephalinae*, with a sharp preference for areas of high micronekton production and/or biomass, which is in accordance with the hypothesis and previous studies based on primary production (Mannocci *et al.*, 2013; Mannocci *et al.* in revision).

On the other hand, we expected to find important differences between our study regions, given their characteristics. For *Delphininae* and *Globicephalinae*, predicted densities were indeed much higher in the productive SWIO than in the oligotrophic FP.

Patterns differ for sperm and beaked whales which have the lowest cost of living. In the SWIO, they showed a slight preference for areas with high productions. Given the low ratio (2.2) of mean predicted densities between sectors, sperm and beaked whales had similar density irrespective of habitat quality, which could indicate they may accommodate to both productive and oligotrophic areas. In FP, this ratio was higher (11) because densities were higher around the Marquesas compared to other sectors. However, in FP, mean predicted densities were the same as in the SWIO: around 0.04 individuals per km². This similarity between a productive but contrasted region and an oligotrophic one may indicate that sperm and beaked whales can sustain their low energetic needs in both high and low quality habitats.

Beaked whales, the most common genus of this guild in both areas, are known to forage between 460 and 1890m (Baird *et al.* 2006; Tyack *et al.* 2006), while sperm whales forage between 400 and 1300m (Watkins *et al.* 2002; Amano and Yoshioka 2003) and *Kogidae* potentially forage to 1500m, as inferred from their diets (Willis and Baird 1998). These foraging ranges include the 3 layers defined in SEAPODYM; hence the selected covariates

seem consistent with their diving abilities. Sperm whales are known to perform both deep and shallow foraging dives (less than 200m; Watkins *et al.* 2002). As the latter were a commonly observed species in the SWIO (Mannocci *et al.* 2013), this diving pattern could explain the presence of the epipelagic production as a predictor (although the less contributory) in the model for this region.

Due to their lowest relative costs of living, sperm and beaked whales were expected to be less dependent on high quality habitats. Our results seem in accordance with that expectation as predicted densities showed low variations both within and between regions. The mean predicted densities were the same in the SWIO and in FP, and the between-sector ratios were low in the 2 regions (although higher in FP).

4.4. Conclusion

The use of micronekton distribution as predictors in cetacean models provided fairly good results to consider SEAPODYM as a useful tool in cetacean habitat modelling. Indeed, the reasonable deviances, the overall low uncertainty and the consistency between the predictions presented here and the predictions obtained in previous studies (Mannoci *et al.* submitted, 2013) indicate that these results are robust.

This study confirms the results obtained by Mannocci and colleagues about strategies of habitat utilization and costs of living of top predators. *Delphininae* and *Globicephalinae*, with relatively high costs of living, showed a strong dependency to habitat quality. In the productive but contrasted SWIO, they optimized their foraging strategy by selecting areas where they can reach the highest biomass and/or production with lowest effort. In the oligotrophic FP they have to select the bathypelagic layer to sustain their energetic requirements, which may induce greater foraging costs.

For sperm and beaked whales, characterized by the lowest costs of living, the models did not highlight any strong differences within and between regions, indicating they can accommodate of both productive and oligotrophic areas to fulfill their energetic requirements.

Finally, simulated micronekton distributions are useful for providing robust predictions of cetacean distributions for the implementation of Marine Protected Areas, without having to conduct expensive surveys on prey distributions. However, it would be of great help to confront these results with future surveys in the regions of interest to evaluate the performance of the models.

References

Abecassis, M. et al. 2013. A Model of Loggerhead Sea Turtle (Caretta caretta) Habitat and Movement in the Oceanic North Pacific. - PLoS ONE 8: e73274.

Aguilar Soto, N. et al. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). - J. Anim. Ecol. 77: 936–947.

Amano, M. and Yoshioka, M. 2003. Sperm whale diving behavior monitored using a suction-cup-attached TDR tag. - Mar. Ecol. Prog. Ser. 258: 291–295.

Baird, R. W. et al. 2006. Diving behaviour of Cuvier's (Ziphius cavirostris) and Blainville's (Mesoplodon densirostris) beaked whales in Hawai'i. - Can. J. Zool. 84: 1120–1128.

Baird, R. W. et al. 2011. Movements of two satellite-tagged pygmy killer whales (Feresa attenuata) off the island of Hawai 'i. - Mar. Mammal Sci. 27: E332–E337.

Baumgartner, M. F. 1997. The distribution of Risso's dolphin (Grampus griseus) with respect to the physiography of the northern Gulf of Mexico. - Mar. Mammal Sci. 13: 614–638.

Baumgartner, M. F. and Mate, B. R. 2005. Summer and fall habitat of North Atlantic right whales (Eubalaena glacialis) inferred from satellite telemetry. - Can. J. Fish. Aquat. Sci. 62: 527–543.

Bearzi, M. 2005. Dolphin sympatric ecology. - Mar. Biol. Res. 1: 165–175.

Becker, E. A. et al. 2010. Comparing California Current cetacean–habitat models developed using in situ and remotely sensed sea surface temperature data. - Mar. Ecol. Prog. Ser. 413: 163–183.

Benoit-Bird, K. J. and Au, W. W. 2003. Prey dynamics affect foraging by a pelagic predator (Stenella longirostris) over a range of spatial and temporal scales. - Behav. Ecol. Sociobiol. 53: 364–373.

Benoit-Bird, K. J. et al. 2013. Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. - PLoS ONE 8: e53348.

Briand, K. et al. 2011. A study on the variability of albacore (Thunnus alalunga) longline catch rates in the southwest Pacific Ocean. - Fish. Ocean. 20: 517–529.

Brodeur, R. D. et al. 2005. Micronekton–What are they and why are they important. - Pac Mar Sci Org Pices Press 13: 7–11.

Buckland, S. T. et al 2001. Introduction to distance sampling: estimating abundance of biological populations. - Oxford University Press.

Cañadas, A. et al. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. - Aquat. Conserv. Mar. Freshw. Ecosyst. 15: 495–521.

Chambers, J. M. and Hastie, T. 1992. Statistical models in S. - Chapman & Hall London.

De Ruijter, W. P. et al. 2004. Eddies and dipoles around South Madagascar: formation, pathways and large-scale impact. - Deep Sea Res. Part Ocean. Res. Pap. 51: 383–400.

Dolar, M. et al. 2003. Comparative feeding ecology of spinner dolphins (Stenella longirostris) and Fraser's dolphins (Lagenodelphis hosei) in the Sulu Sea. - Mar. Mammal Sci. 19: 1–19.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. - Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

ESRI 2011. ArcGIS Desktop: Release 10. - Environmental Systems Research Institute.

Estes, J. A. et al. 2001. Predators, ecological role of. - Encycl. Biodivers. 4: 857–878.

Ferguson, M. C. et al. 2005. Predicting Cuvier's (Ziphius cavirostris) and Mesoplodon beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean. - J. Cetacean Res. Manag. 7: 287.

Forney, K. A. 2000. Modelos Ambientales de Abundancia de Cetáceos: Reducción de la Incertidumbre en Tendencias Poblacionales. - Conserv. Biol. 14: 1271–1286.

Forney, K. A. et al. 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. - Endanger. Species Res. 16: 113–133.
Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - Ecol. Model. 135: 147–186.
Harrell Jr, F. E. 2013. Hmisc: Harrell Miscellaneous.
Hastie, T. and Tibshirani, R. 1999. Generalized Additive Models. - Chapman & Hall/CRC.
Hedley, S. L. et al. 1999. Spatial modelling from line transect data. - J. Cetacean Res. Manag. 1: 255–264.
Heithaus, M. R. et al. 2008. Predicting ecological consequences of marine top predator declines. - Trends Ecol. Evol. 23: 202–210.
Hidaka, K. et al. 2003. Biomass and taxonomic composition of micronekton in the western tropical–subtropical Pacific. - Fish. Ocean. 12: 112–125.
Jaquet, N. et al. 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. - Mar. Ecol. Prog. Ser. 145: 1–10.
Jefferson, T. and Barros, N. 1997. Peponocephala electra. - Mammalian Species: 1–6.
Kaschner, K. et al. 2012. Global Coverage of Cetacean Line-Transect Surveys: Status Quo, Data Gaps and Future Challenges. - PLoS ONE 7: e44075.
Klatsky, L. J. et al. 2007. Offshore bottlenose dolphins (Tursiops truncatus): movement and dive behavior near the Bermuda pedestal. - J. Mammal. 88: 59–66.
Lehodey, P. et al. 2008. A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. - Prog. Ocean. 78: 304–318.
Lehodey, P. et al. 2010. Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups. - Prog. Ocean. 84: 69–84.
Libralato, S. et al. 2006. A method for identifying keystone species in food web models. - Ecol. Model. 195: 153–171.
Longhurst, A. R. 2007. Ecological geography of the sea. - Academic Press.
MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. - Am. Nat.: 603–609.
Mannocci, L. et al. in revision. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre. - Prog. Ocean.
Mannocci, L. et al. 2013. Predicting top predator habitats in the Southwest Indian Ocean. - Ecography 36: 001–018.
Marques, F. and Buckland, S. T. 2004. Covariate models for the detection function. - In: Advanced Distance Sampling. Oxford University Press, pp. 31–47.
Martinez, E. et al. 2009. Central South Pacific thermocline water circulation from a high-resolution ocean model validated against satellite data: Seasonal variability and El Niño 1997–1998 influence. - J. Geophys. Res. Oceans 114: n/a–n/a.
McCullagh, P. and Nelder, J. A. 1989. Generalized linear models (Monographs on statistics and applied probability 37). - Chapman Hall Lond. in press.
Mills, L. S. et al. 1993. The keystone-species concept in ecology and conservation. - BioScience 43: 219–224.
New, A. L. et al. 2005. Physical and biochemical aspects of the flow across the Mascarene Plateau in the Indian Ocean. - Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 363: 151–168.
Oleson, E. M. et al. 2010. Status review of Hawaiian insular false killer whales (Pseudorca crassidens) under the Endangered Species Act.
Österblom, H. et al. 2008. Junk-food in marine ecosystems. - Oikos 117: 967–977.
R Core Team 2012. R: a language and environment for statistical computing. - R Foundation for Statistical Computing.

Redfern, J. V. et al. 2006. Techniques for cetacean–habitat modeling. in press.
Rougerie, F. and Rancher, J. 1994. The Polynesian south ocean: features and circulation. - Mar. Pollut. Bull. 29: 14–25.
Schipper, J. et al. 2008. The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. - Science 322: 225–230.
Schouten, M. W. et al. 2003. Eddies and variability in the Mozambique Channel. - Deep Sea Res. Part II Top. Stud. Ocean. 50: 1987–2003.
Scott, M. D. and Chivers, S. J. 2009. Movements and diving behavior of pelagic spotted dolphins. - Mar. Mammal Sci. 25: 137–160.
Senina, I. et al. 2008. Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: Application to skipjack tuna. - Prog. Ocean. 78: 319–335.
Sibert, J. et al. 2012. Shifting from marine reserves to maritime zoning for conservation of Pacific bigeye tuna (Thunnus obesus). - Proc. Natl. Acad. Sci. 109: 18221–18225.
Signorini, S. R. et al. 1999. Mixing and phytoplankton bloom in the wake of the Marquesas Islands. - Geophys. Res. Lett. 26: 3121–3124.
Spitz, J. et al. 2012. Cost of Living Dictates what Whales, Dolphins and Porpoises Eat: The Importance of Prey Quality on Predator Foraging Strategies. - PLoS ONE 7: e50096.
Torres, L. G. and Read, A. J. 2009. Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (Tursiops truncatus) in Florida Bay, Florida. - Mar. Mammal Sci. 25: 797–815.
Torres, L. G. et al. 2008. Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity. - Ecol. Appl. 18: 1702–1717.
Tyack, P. L. et al. 2006. Extreme diving of beaked whales. - J. Exp. Biol. 209: 4238–4253.
Watkins, W. A. et al. 2002. Sperm Whale Dives Tracked by Radio Tag Telemetry. - Mar. Mammal Sci. 18: 55–68.
Willis, P. M. and Baird, R. W. 1998. Status of the dwarf sperm whale, Kogia simus, with special reference to Canada. - Can. Field-Nat. 112: 114–125.
Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. - Chapman & Hall/CRC.
Wood, S. 2013. mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation.

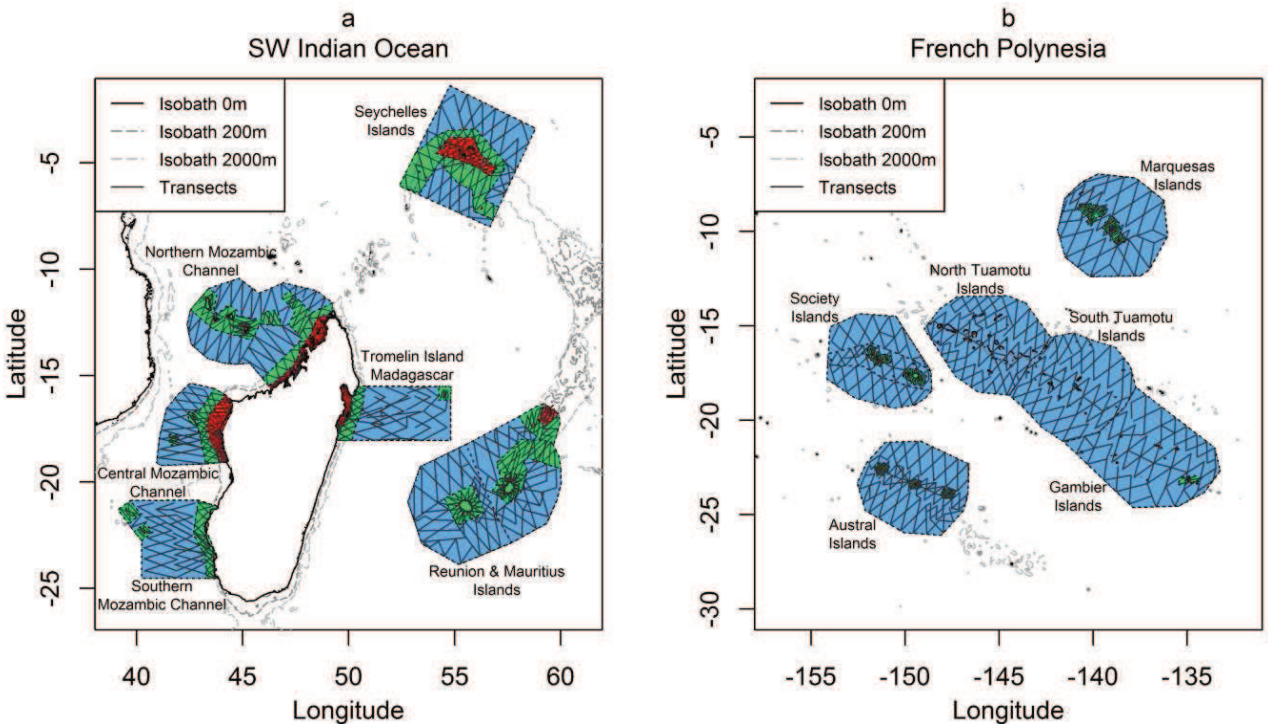


Figure 1. Study regions: Southwest Indian Ocean (a) and French Polynesia (b). Six sectors were sampled in each region. Each sector was subdivided into bathymetric strata: neritic strata (red; absent in French Polynesia), slope strata (green) and oceanic strata (blue). Sampled transect lines are represented by solid lines inside sectors. For details on the sampling design, see Mannocci *et al.* 2013 and Mannocci *et al.* submitted.

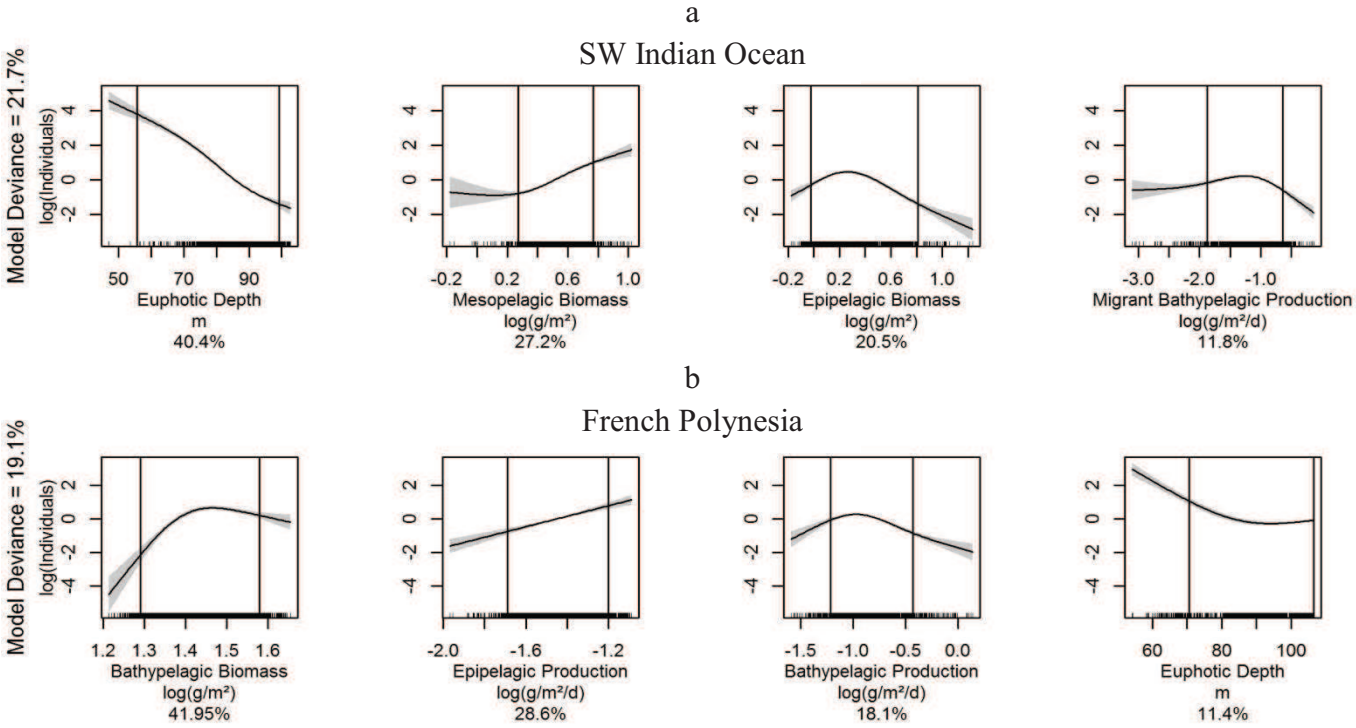


Figure 2. Smoothed functions for the selected covariates for *Delphininae* in the Southwest Indian Ocean (a) and French Polynesia (b). The solid line is the smooth function; shaded regions represent the 95% confidence intervals. The percentage indicated below each graph is the contribution of each covariate in the linear predictor.

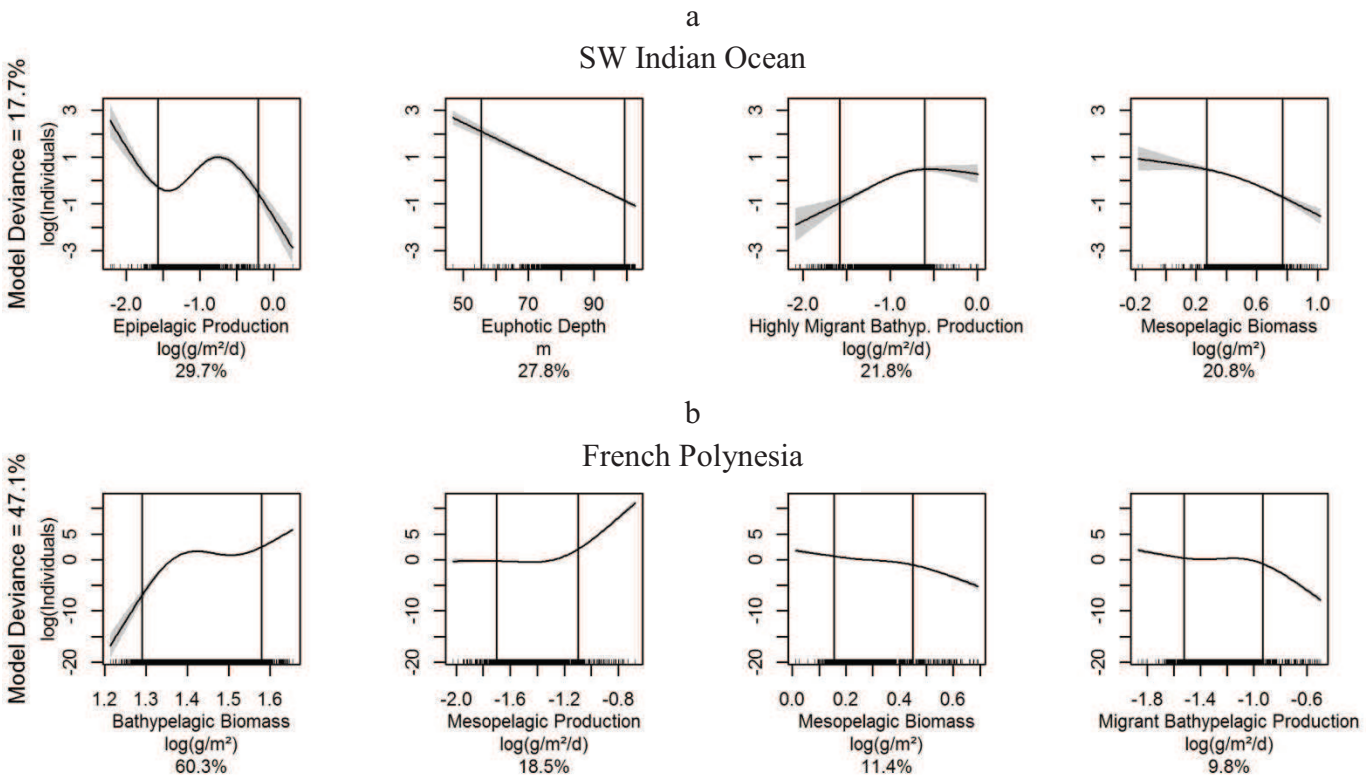


Figure 3. Same Legend as Figure 2 for *Globicephalinae*.

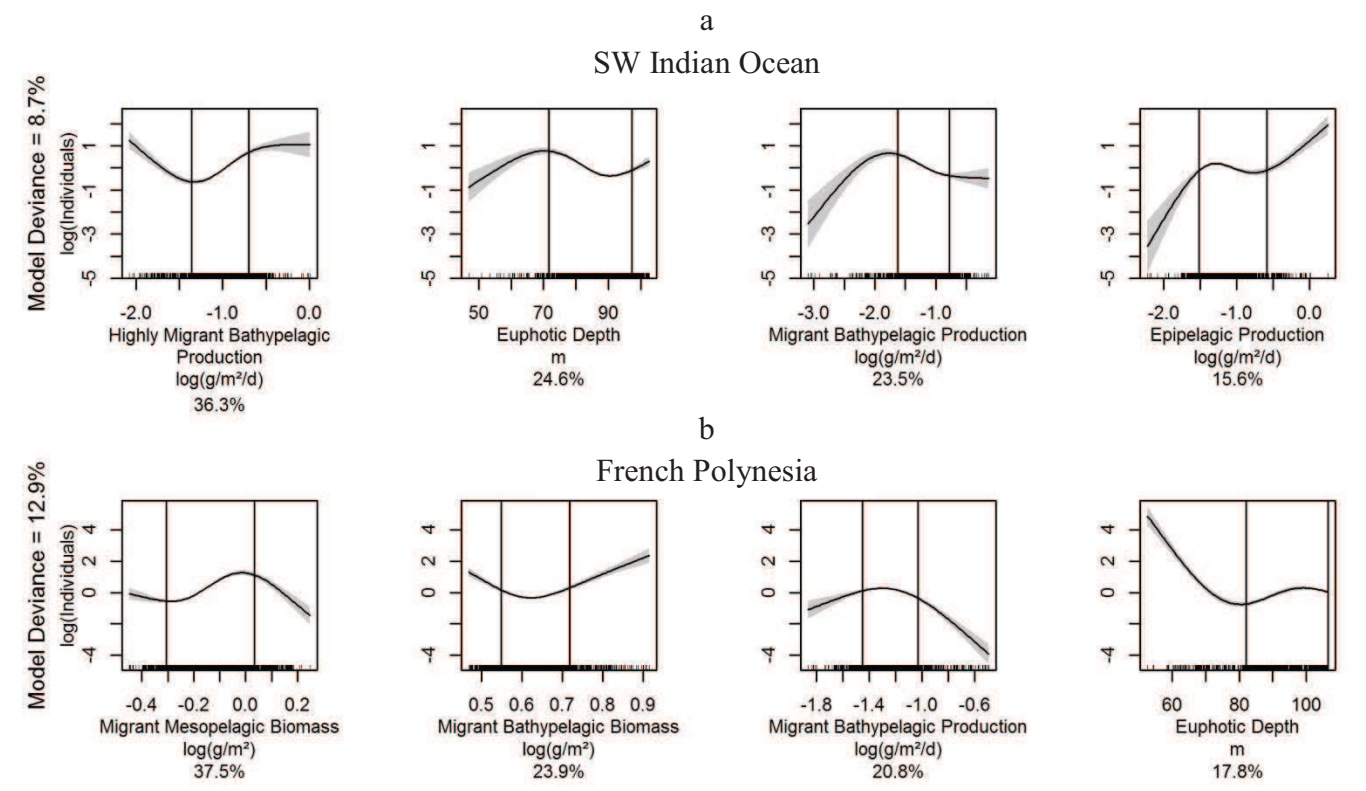


Figure 4. Same Legend as Figure 2 for sperm and beaked whales.

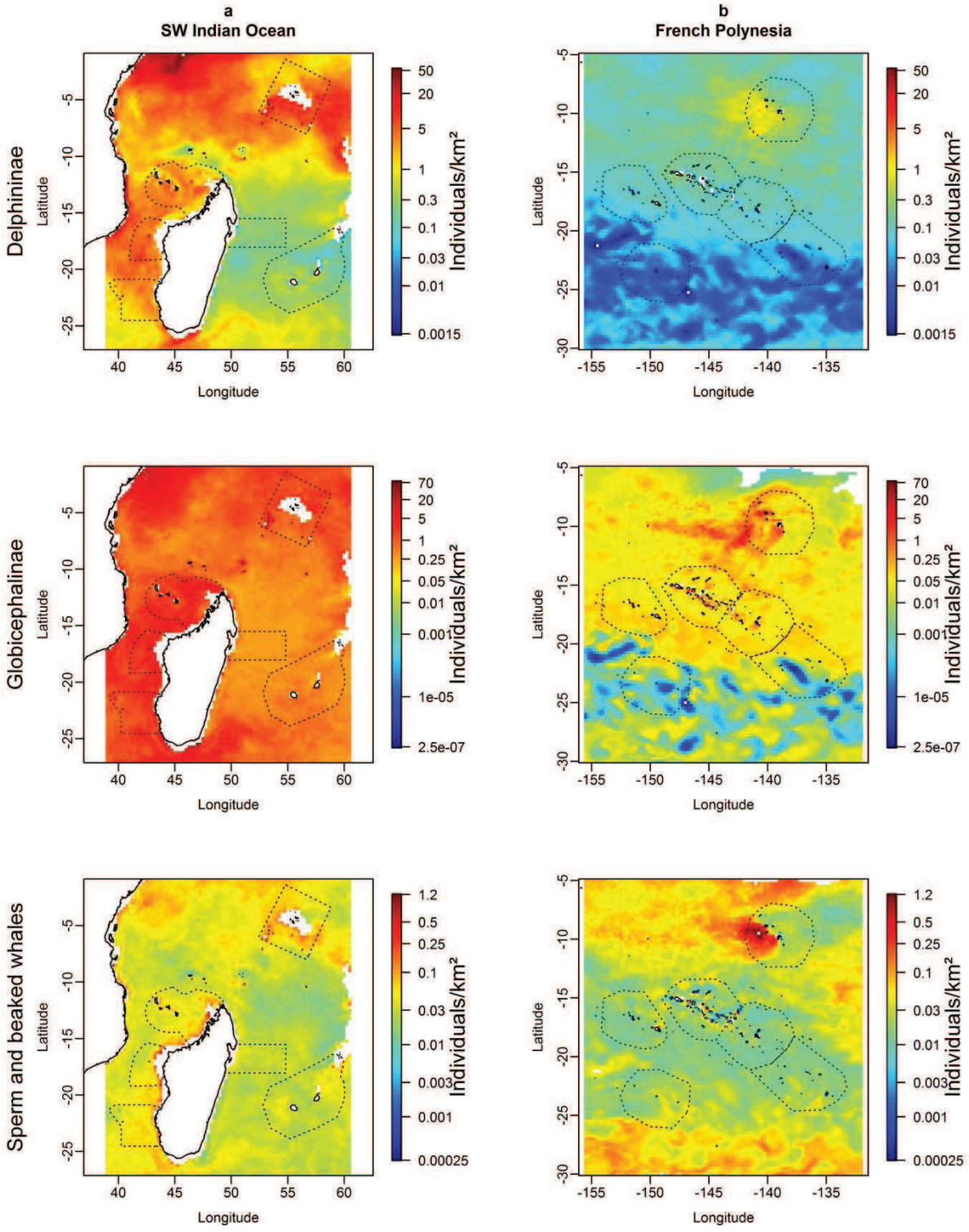


Figure 5. Predicted relative densities (individuals per km²) for the 3 cetacean guilds in the Southwest Indian Ocean (a) and French Polynesia (b). The limitation of predictions inside the range of sampled covariates values resulted in empty pixels in French Polynesia. In the Southwest Indian Ocean empty pixels were due to the absence of SEAPODYM outputs for the bathypelagic micronekton functional groups in the neritic strata (bathymetry < 200m). In order to enhance the contrasts, we used the same colour scale (in log) for each guild in both regions but the colour scale is not comparable between the different guilds.

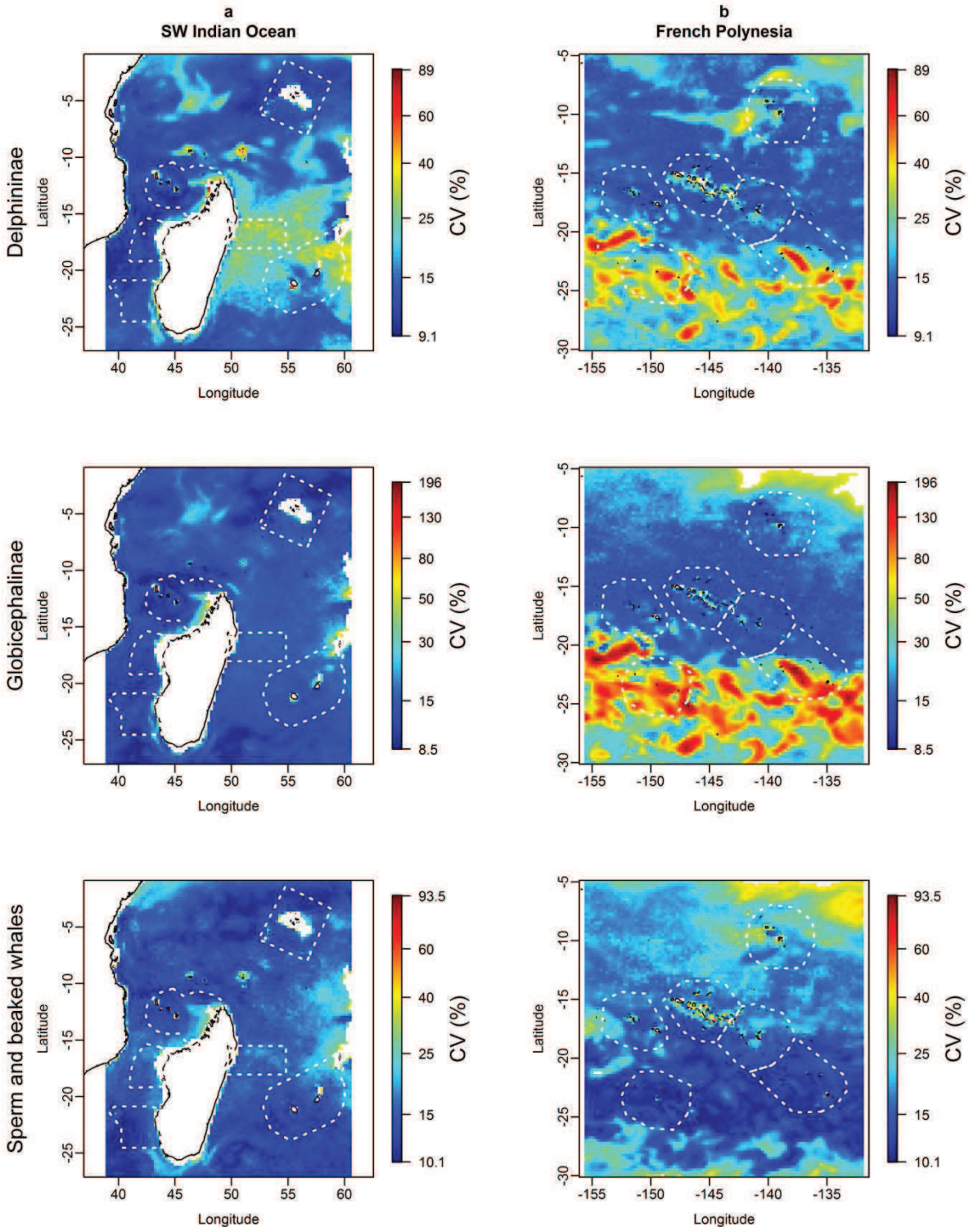


Figure 6. Uncertainty maps associated with the predictions for the 3 cetacean guilds in the Southwest Indian Ocean (a) and French Polynesia (b). The limitation of predictions inside the range of sampled covariates values resulted in empty pixels in French Polynesia. In the Southwest Indian Ocean empty pixels were due to the absence of SEAPODYM outputs for the bathypelagic micronekton functional groups in the neritic strata (bathymetry < 200m). In order to enhance the contrasts, we used the same colour scale (in log) for each guild in both regions but the colour scale is not comparable between the different guilds.

Table 1. Statistics of the predictions for *Delphininae*: mean predicted densities (individuals per km²) and mean uncertainty (CV,%) for each sector and for the whole regions. The ratio between the highest and the lowest density sector is indicated for each region (between-sector ratio). In the SWIO, NMC: northern Mozambique Channel, CMC: central Mozambique Channel, SMC: southern Mozambique Channel, RM: Réunion-Mauritius, SE: Seychelles, TM: Tromelin-Madagascar. In FP, MAR: Marquesas, NTU: North Tuamotu, STU: South Tuamotu, GAM: Gambier, SOC: Society, AUS: Australs.

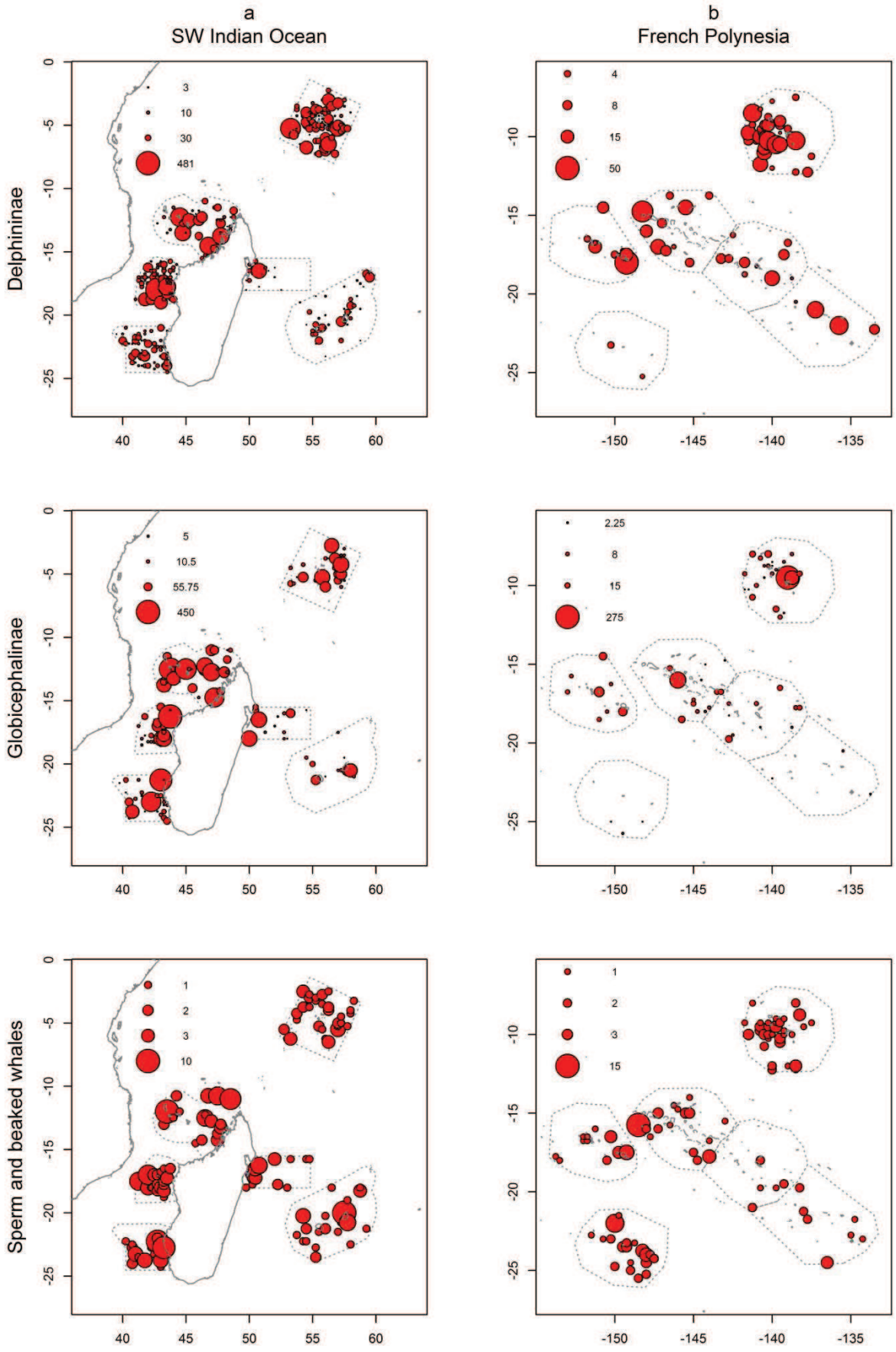
Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	2.8 ± 1.32	14.8 ± 8.3	MAR	0.39 ± 0.31	17.9 ± 5.7
SMC	2.42 ± 0.95	14.2 ± 4.95	NTU	0.13 ± 0.05	15.9 ± 6.22
CMC	4.37 ± 1.29	12.02 ± 3.12	STU	0.096 ± 0.03	15.2 ± 3.5
RM	0.27 ± 0.16	22.2 ± 6.97	GAM	0.04 ± 0.03	24.6 ± 14
SE	4.81 ± 3.11	12.7 ± 2.33	SOC	0.08 ± 0.03	14.6 ± 3.6
TM	0.24 ± 0.08	27.3 ± 3.16	AUS	0.02 ± 0.01	31.4 ± 11.4
Whole region	*2.66 ± 4.13*	*17.8 ± 7.4*	*Whole region*	*0.1 ± 0.12*	*20.4 ± 9.6*
Between-sector ratio	16.2		Between-sector ratio	19.5	

Table 2. Same legend as Table 1 for Globicephalinae

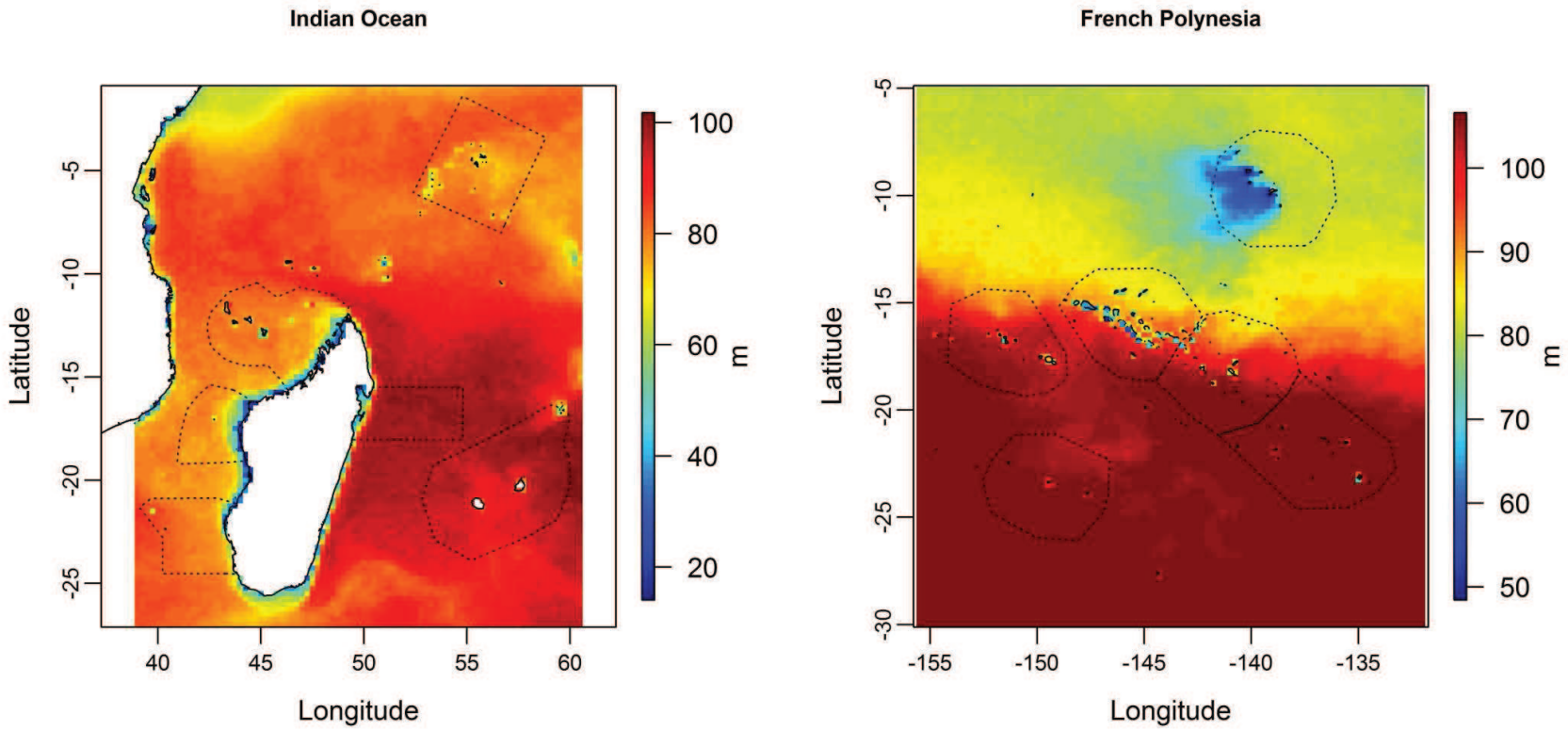
Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	2.85 ± 1.68	14.7 ± 9.41	MAR	0.28 ± 0.5	18.1 ± 3.8
SMC	1.92 ± 1.21	13.13 ± 4.28	NTU	0.14 ± 0.34	15.52 ± 5
CMC	2.91 ± 1.11	13.46 ± 5.42	STU	0.09 ± 0.12	14.12 ± 2.62
RM	0.44 ± 0.16	15.54 ± 4.73	GAM	0.04 ± 0.04	48.1 ± 41.1
SE	1.53 ± 0.99	12.63 ± 3.22	SOC	0.07 ± 0.03	16.3 ± 5.9
TM	0.31 ± 0.24	15.63 ± 1.7	AUS	0.01 ± 0.02	71.84 ± 33.7
Whole region	*1.29 ± 1.83*	*14.01 ± 4.07*	*Whole region*	*0.07 ± 0.2*	*34.6 ± 29.5*
Between-sector ratio	9.4		Between-sector ratio	25.5	

Table 3. Same legend as Table 1 for sperm and beaked whales.

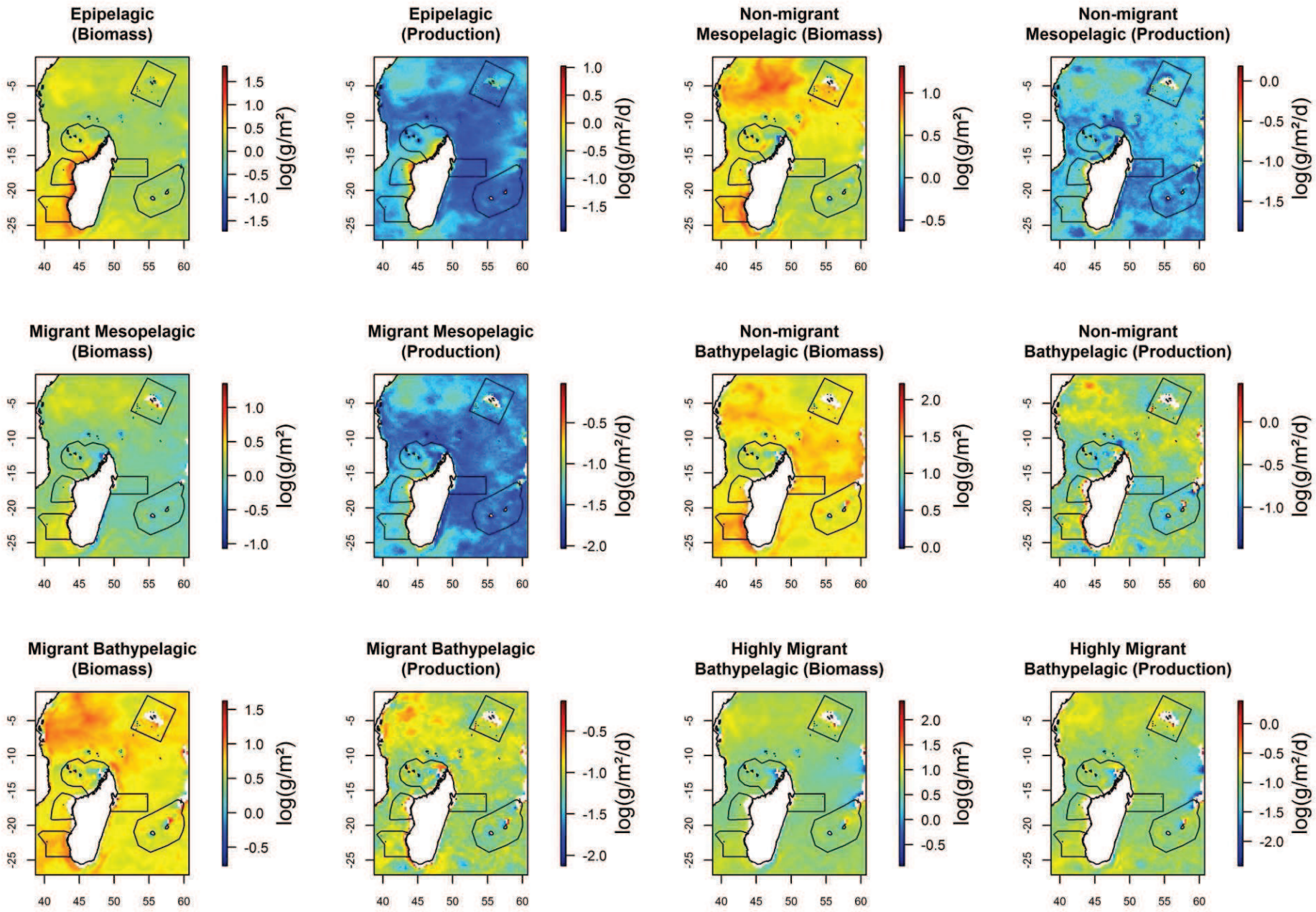
Southwest Indian Ocean			French Polynesia		
Sectors	Mean Prediction	Mean CV	Sectors	Mean Prediction	Mean CV
NMC	0.06 ± 0.04	15.84 ± 5.2	MAR	0.11 ± 0.2	22.2 ± 5
SMC	0.06 ± 0.02	12.99 ± 2.8	NTU	0.02 ± 0.02	19.05 ± 7.9
CMC	0.06 ± 0.05	16.48 ± 2.6	STU	0.01 ± 0.01	16.6 ± 4.9
RM	0.03 ± 0.01	14.82 ± 3.8	GAM	0.02 ± 0.01	12.4 ± 3
SE	0.07 ± 0.03	13.9 ± 3.5	SOC	0.02 ± 0.01	17.76 ± 4.7
TM	0.03 ± 0.01	16.3 ± 2.2	AUS	0.02 ± 0.01	11.9 ± 1.5
Whole region	*0.04 ± 0.02*	*14.9 ± 3.9*	*Whole region*	*0.04 ± 0.05*	*18.4 ± 6.5*
Between-sector ratio	2.2		Between-sector ratio	11	



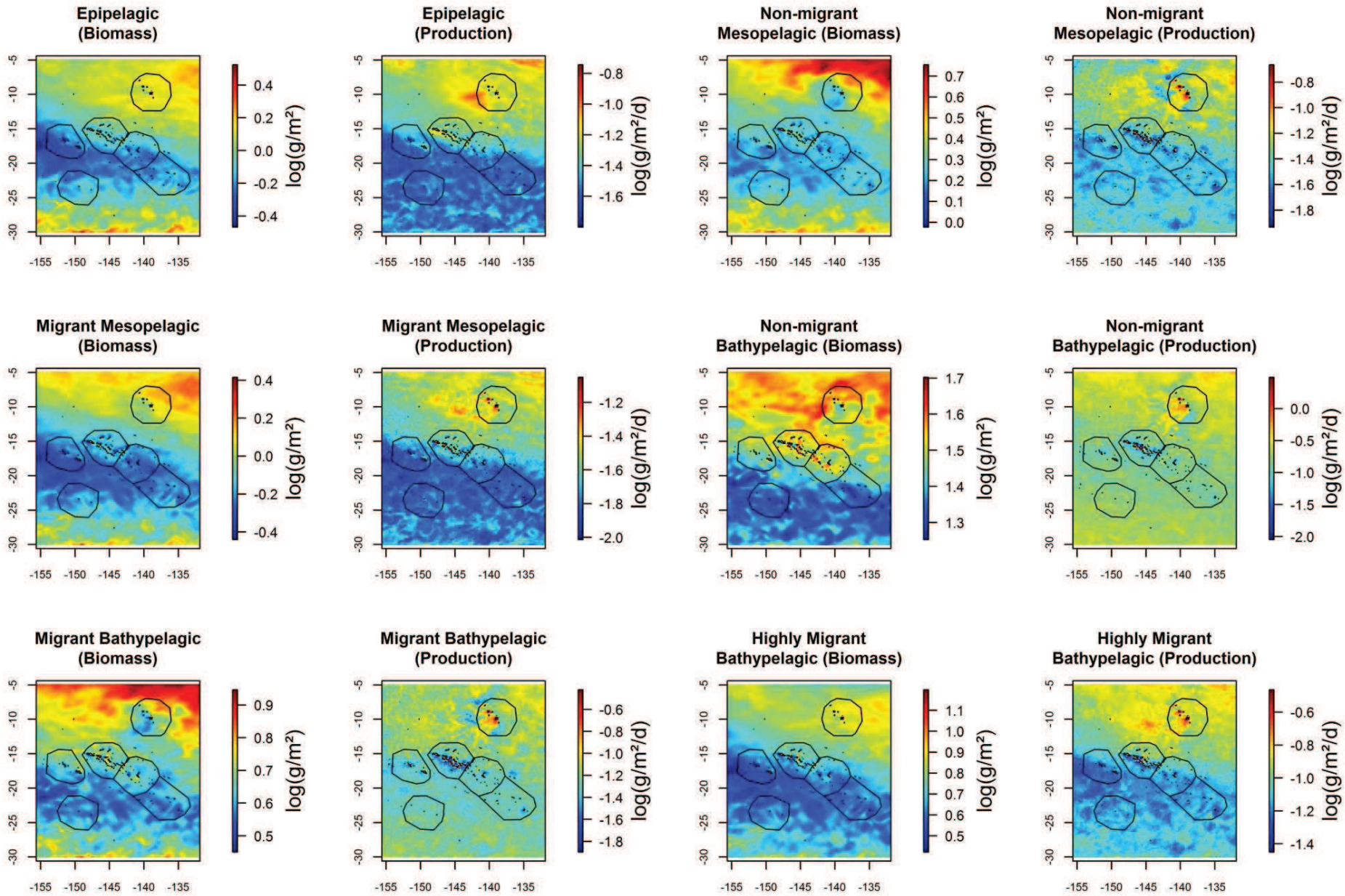
Appendix 1. Numbers of individuals observed per sampled pixel for each cetacean guild in the Southwest Indian Ocean (a) and French Polynesia (b). The 25th, 50th, 75th quartiles and the maximum number of individuals per pixel are indicated at the top left of each map. For details on the sightings see Mannocci *et al.*, 2013 and Mannocci *et al.* in revision.



Appendix 2: Euphotic depth in the Southwest Indian Ocean and French Polynesia. Values were averaged over the survey period of each region.



Appendix 3: SEAPODYM micronekton outputs in the Southwest Indian Ocean. Values were averaged over the survey period for the whole region. Covariates were log-transformed before modelling.



Appendix 4: SEAPODYM micronekton outputs in French Polynesia. Values were averaged over the survey period for the whole region. Covariates were log-transformed before modelling.

Distribution des cétacés et oiseaux marins dans les océans tropicaux: rôles des facteurs physiographiques, océanographiques et biologiques

Résumé

Les prédateurs marins supérieurs, ici les cétacés et les oiseaux marins, doivent développer des stratégies optimales d'utilisation des ressources et des habitats. Notre objectif était d'explorer leurs habitats en fonction de leurs coûts de vie. Nous avons postulé que les prédateurs coûteux étaient contraints d'occuper les habitats de meilleure qualité alors que les prédateurs plus économes pouvaient occuper les habitats de qualité moindre. Nous nous sommes basés sur des guildes de cétacés et oiseaux définies selon leurs coûts de vie et les observations de survols aériens dans trois régions tropicales (l'Atlantique Ouest tropical, le Sud Ouest de l'Océan Indien et la Polynésie française). Nous avons construits des modèles additifs généralisés à partir de variables physiographiques (ex: profondeur), océanographiques (ex: activité tourbillonnaire) et biologiques (ex: chlorophylle et micronecton) pour décrire la qualité des habitats. Nous avons d'abord modélisé les habitats des cétacés et oiseaux à l'échelle régionale. Les cétacés coûteux occupaient les habitats de meilleure qualité alors que les cétacés plus économes occupaient aussi les habitats de qualité moindre. La distribution des oiseaux reflétait principalement celle des colonies et leur dépendance à la qualité de l'habitat semblait moins claire. Nous avons ensuite mis en évidence des propriétés génériques de distribution des cétacés et fourni des prédictions circumtropicales. Cette thèse a donné un nouvel aperçu des stratégies d'utilisation des habitats des prédateurs supérieurs à la lumière de leurs coûts de vie. Ces prédictions spatiales ont des implications majeures pour la gestion de ces espèces et de leurs écosystèmes.

Mots clés : cétacés, oiseaux marins, survols aériens, océans tropicaux, modèles d'habitat, variables environnementales, macroécologie

Distribution of cetaceans and seabirds in tropical oceans: roles of physiographic, oceanographic and biological factors

Abstract

Marine top predators, here cetaceans and seabirds, must develop optimal strategies of resource and habitat utilization. The main goal of this dissertation was to investigate cetacean and seabird strategies of habitat utilization in relation to their energetic costs of living. We hypothesized that predators with high costs of living should be constrained to high quality habitats, whereas less active predators could cope with habitats of lesser quality. We studied the habitats of cetacean and seabird guilds defined according to their likely costs of living. We relied on sightings collected from aerial surveys in three tropical regions (the western tropical Atlantic, the Southwest Indian Ocean and French Polynesia). We built generalized additive models based on a range of physiographic (*e.g.* depth), oceanographic (*e.g.* mesoscale activity) and biological variables (*e.g.* chlorophyll concentration and micronekton) to describe the quality of pelagic habitats. We first modeled cetacean and seabird habitats at the regional scale. Energetically costly cetaceans appeared to be constrained to the highest quality habitats, whereas less active cetaceans exploited habitats of lesser quality. Seabird distributions primarily reflected colony locations and their dependences on habitat quality were less clear. We then highlighted generic properties of cetacean distributions and provided predictions at the circumtropical scale. This dissertation gave new insights on top predator strategies of habitats utilization in light of their costs of living. These spatial predictions have significant implications for the management of these species and of their pelagic ecosystems.

Keywords: cetaceans, seabirds, aerial surveys, tropical oceans, habitat models, environmental variables, macroecology

Laboratoire Littoral Environnement
et SociétéS (LIENSs)
UMR CNRS 7266 / Université de La Rochelle
Bâtiment ILE,
2, rue Olympe de Gouges
17000 LA ROCHELLE ,CEDEX