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Predicting variations in coastal seabird habitats to assess marine protected areas

Auriane Virgili

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AGROCAMPUS OUEST

Centre de Rennes
65 rue de Saint Briec
35042 Rennes Cedex
☎ 02 23 48 50 00
☎ 02 23 48 55 10



Observatoire PELAGIS
Pôle analytique, 5 allées de l'Océan,
17000 La Rochelle
☎ 05 46 44 99 10
☎ 05 46 44 99 45



Université de La Rochelle
23, avenue Albert Einstein
BP 33060 - 17031 La Rochelle -
☎ 05 46 45 91 14
☎ 05 46 44 93 76



**CNRS - Centre national de la
recherche scientifique**

3, rue Michel-Ange
75794 Paris cedex 16 - France
☎ 01 44 96 40 00
☎ 01 44 96 53 90



CEBC - CNRS
Villiers en Bois BP 14
79360 Beauvoir/Niort
☎ 05 49 09 61 11
☎ 05 49 09 65 26

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Predicting variations in coastal seabird habitats to assess marine protected areas

Auriane VIRGILI

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— Synthèse étendue —

Contexte

Les oiseaux marins sont souvent considérés comme des indicateurs de la composition et de la productivité d'un écosystème (Zacharias and Roff, 2001) car ce sont des prédateurs de hauts niveaux trophiques très sensibles aux conditions environnementales (Piatt *et al.*, 2007). En effet, un manque de nourriture, une pollution ou un dysfonctionnement quelconque de l'écosystème se traduit généralement par une diminution de l'abondance des oiseaux et de leur progéniture (Furness and Camphuysen, 1997) par réduction de leur survie ou modification de leur distribution. En outre, leur étude dans leur milieu naturel est relativement aisée car ils sont facilement observables (de visu ou par télémétrie) et s'agrègent naturellement dans les zones de fortes productions marines (Piatt *et al.*, 2007).

Pour se nourrir, les oiseaux de mer sont soumis à de fortes pressions de sélection et doivent donc adapter leurs stratégies d'utilisation de la ressource et des habitats pour maximiser leurs apports nutritionnels et minimiser leurs coûts énergétiques durant leurs périodes d'alimentation (Chaurand and Weimerskirch, 1994). Afin de comprendre comment les oiseaux utilisent leurs habitats, les modèles sont couramment utilisés car ils permettent de corréler la distribution spatiale des oiseaux et les variables environnementales (Vilchis *et al.*, 2006 ; Mannocci, *et al.*, 2014). En outre, ces modèles sont de plus en plus utilisés pour établir des plans de conservation et de gestion des espèces et des écosystèmes car ils permettent de prédire la distribution des espèces et leurs réponses face aux changements environnementaux, qu'ils soient climatiques ou anthropiques (Bailey and Thompson, 2009; Cheung *et al.*, 2009).

La conservation des espèces et le maintien de la diversité biologique est un enjeu majeur pour les états membres de l'Union Européenne. C'est pour cette raison que, dès 1992, le réseau de sites *Natura* 2000 (N2000), basé sur les directives Oiseaux (Parlement Européen, 2009) et Habitats Faune et Flore (Parlement européen, 1992), a été mis en place. Pour répondre aux exigences de ce réseau, la France, à travers l'Agence des Aires Marines Protégées, a mis en place un programme d'acquisition de données sur la mégafaune marine afin de faire un inventaire de la faune présente ainsi qu'une évaluation des sites N2000 et autres sites de conservation établis ou prévus sur les côtes françaises métropolitaines.

Objectifs

Dans cette étude, nous nous sommes concentrés sur certaines espèces emblématiques de côtes françaises telles que les sternes (essentiellement sterne pierregarin *Sterna hirundo*, sterne naine *Sterna albifrons* et sterne caugek *Sterna sandvicensis*), goélands (essentiellement, goéland argenté *Larus argentatus*, goéland leucophée *L. michahellis*, goéland brun *L. fuscus* et goéland marin *L. marinus*), cormorans (grand cormoran *Phalacrocorax carbo* et cormoran huppé *P. aristotelis*). Ces espèces sont qualifiées de côtières car elles ont un lien biologique et physique à la côte qui les oblige à retourner quotidiennement sur la terre ferme, que ce soit pour incuber leurs œufs, nourrir leur progéniture ou bien se reposer. Nous ajoutons à cette première série d'espèces les plongeurs (plongeurs arctique, catmarin et imbrin *Gavia arctica*, *G. stellata*, *G. immer*) et les macreuses (macreuse brune *Melanitta fusca* et macreuse noire *M. nigra*). Dans les deux cas, il s'agit d'espèces principalement hivernantes sur les côtes françaises dont l'habitat est littoral sans pour autant que ces oiseaux reviennent périodiquement à terre. L'étude ne porte pas sur les nombreuses autres espèces encore plus littorales qui utilisent principalement l'estran.

Le but de l'étude était de déterminer, à partir de données d'observation d'oiseaux, les mécanismes qui influencent le plus la distribution des oiseaux marins le long des côtes ouest et nord de la France. En outre, nous avons cherché à déterminer les effets des variations, notamment saisonnières, de ces mécanismes dans le but de proposer une première

évaluation des sites de protection établis ou prévus le long des côtes françaises. Cette évaluation repose sur le critère de la Directive Oiseaux indiquant qu'un site hébergeant au moins 1% de la population 'nationale'¹ d'une espèce devrait être désigné comme Zone de Protection Spéciale (ZPS).

Méthode

Les données que nous avons utilisées pour la modélisation sont issues de deux campagnes d'observation aérienne, dénommées SAMM (Suivi Aérien de la Mégafaune Marine), réalisées durant l'hiver 2011/2012 et l'été 2012 en Manche et dans le Golfe de Gascogne. A partir de ces données, nous avons créé des groupes d'espèces pour faciliter les analyses et pour palier la difficulté d'identification de certaines espèces proches lors des survols.

Pour modéliser les habitats, nous avons utilisé des Modèles Additifs Généralisés (GAMs). Deux types de variables ont été sélectionnées pour les modèles, des variables physiographiques statiques qui reflètent la bathymétrie et la nature du substrat (pente, profondeur, distance à la côte sableuse ou rocheuse et distance à la colonie) et des variables océanographiques dynamiques qui décrivent les masses d'eau (température de surface, anomalie de hauteur d'eau et courants). Pour les variables océanographiques, nous avons utilisé deux résolutions temporelles à 7 jours et 28 jours (moyennées respectivement sur les 6 et 27 jours précédant le jour échantillonné durant la campagne) pour tenir compte de possibles décalages entre une condition océanographique donnée et son effet sur les niveaux trophiques intermédiaires. A partir de ces variables, une fois les valeurs extrêmes et les observations correspondant à de mauvaises conditions d'observation enlevées, nous avons sélectionné le modèle qui expliquait le mieux la distribution des oiseaux [meilleure déviance et plus faible indice de validation croisée généralisée (GCV)].

Par la suite, ce modèle nous a permis de prédire la distribution de chacun des groupes d'espèces étudiés sur une zone plus étendue que notre zone d'étude. Les prédictions ont été faites sur les deux périodes de campagne (hiver 2011/2012 et été 2012) afin de comparer nos sorties de modèles aux observations faites pendant les campagnes.

Pour finir, nous nous sommes servis des prédictions pour fournir, pour chaque aire marine protégée, site du réseau *Natura* 2000 ou non, une mesure de son importance pour la protection de chacune des espèces d'oiseaux de mer côtiers (% de l'abondance prédite dans les limites de l'AMP par rapport à l'abondance prédite dans la superficie totale de la zone d'étude ; Fig.i).

Résultats et discussion

Grâce aux survols aériens, sans prendre en compte les transects parcourus dans de mauvaises conditions de vol, 28 068 km ont été échantillonnés en hiver et 31 427 km en été ce qui représentait un total de 2 459 observations d'oiseaux côtiers en hiver et 3 318 en été, utilisées pour les analyses de ce travail.

Les espèces étudiées ont été rencontrées majoritairement dans les strates côtière et néritique de Manche et d'Atlantique durant les deux saisons mais les macreuses et plongeurs étaient presque uniquement présents en hiver, et sur les côtes de la Manche pour ces derniers.

¹ Il s'agit ici de l'ensemble des individus d'une même espèce présents dans les eaux sous juridiction française. Cette définition ne présage pas des véritables structures de populations qui ne se superposent pas aux limites administratives.

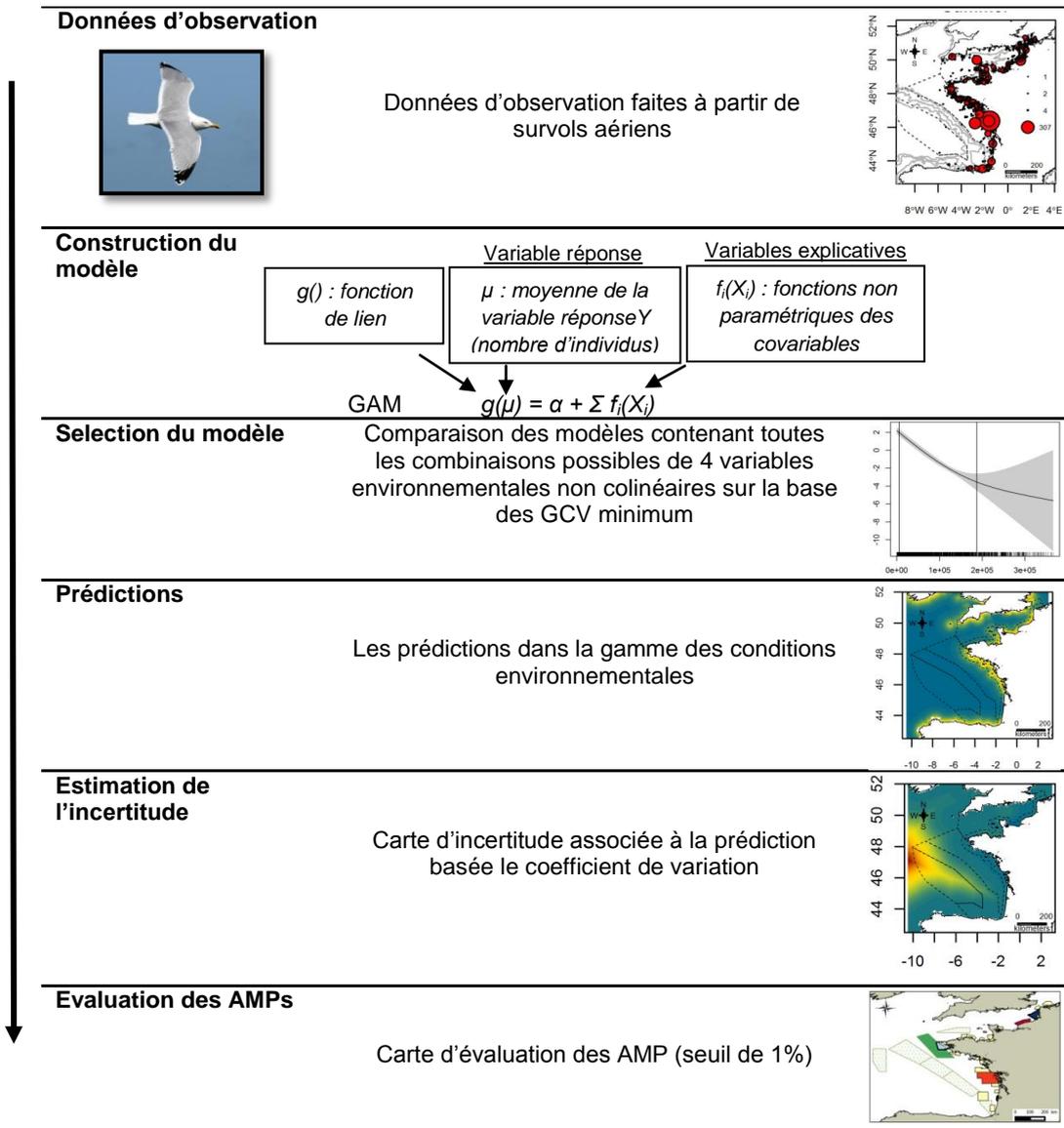


Fig. i. – Schéma explicatif de la démarche expérimentale (exemple du groupe goélands argenté/leucophée en hiver).

Nos modèles d'habitats présentait une déviance comprise entre 24,5 et 62,2%, ce qui indique la relative robustesse de nos modèles. A l'exception des plongeurs, pour lesquels la profondeur représentait le paramètre déterminant le plus leur distribution (à 38,9%), toutes les autres espèces étaient majoritairement influencées par la distance à la côte la plus proche, souvent avec une inversion entre la côte sableuse et la côte rocheuse selon la saison. Par exemple, les densités de sternes étaient négativement corrélées à la côte rocheuse en hiver et à la côte sableuse en été. Cette inversion s'explique majoritairement par la localisation des colonies en été qui, selon les espèces, sont établies soit sur les côtes sableuses (cas des sternes), soit sur les côtes rocheuses (cas des goélands). En plus de la distance à la côte, nous avons déterminé les covariables physiographiques et océanographiques qui influencent dans une moindre part la distribution saisonnière de chaque groupe d'espèce. En hiver par exemple, la distribution des goélands gris (goélands argenté et leucophée) était nettement influencée par la distance à la côte sableuse (à 62,5%), aux courants (à 18,4%), à la température moyenne de surface (à 10,8%) et aux variations de cette température (à 8,4%).

En ce qui concerne les prédictions, les plus fortes densités des espèces étudiées étaient majoritairement concentrées près des côtes notamment autour des îles, dans les estuaires, les baies ou près des colonies. Pour les goélands et les sternes, qui peuvent être observées plus au large, des patrons de distribution étaient observés avec une absence notable des goélands au large des côtes landaises en été et une quasi absence des sternes le long des côtes du Golfe de Gascogne en hiver.

Après évaluation des sites protégés que sont les parcs naturels marins (PNM), les zones de protection spéciales (ZPS) et les propositions de grandes zones pour l'établissement de des futurs sites *Natura 2000* au large, il s'est avéré que ces dernières propositions au large ne concernent pas les espèces côtières. Inversement, il apparaîtrait que les PNM de l'Iroise et des Estuaires Picards et Mer d'Opale soient essentiels à la conservation des espèces côtières, notamment pour les plongeurs qui séjournent pour en grands nombres sur les côtes picardes ; ce n'est pas le cas pour le PNM du Bassin d'Arcachon. Concernant les ZPS établies, en considérant toutes les espèces étudiées, il apparaîtrait que seules 14 ZPS sur 66 soient pertinentes pour la conservation en mer des oiseaux marins côtiers. Ces ZPS sont : "Pertuis Charentais-Rochelaise", "l'Île d'Yeu", "Littoral sein-marin", "Chausey", "Estuaire de la Loire – Baie de Bourgneuf", "Trégor Goëlo", "Estuaires Picards", "Cap Gris-Nez", "Ouessant Molène", "Panache de la Gironde", "Banc des Flandres", "Baie du Mont Saint-Michel", "Mor Braz" et les "Îles d'Houat et d'Hoëdic". Ce constat plaide pour l'établissement de plus grands sites protégés que ceux désignés jusqu'à présents ou de la gestion étroitement coordonnée des sites existants formant alors un réseau.

Conclusion

Dans cette étude, nous avons utilisé des variables physiographiques et océanographiques pour modéliser les habitats d'oiseaux de mer côtiers à partir de données d'observation récoltées durant deux campagnes aériennes réalisées pour la première fois sur les côtes françaises métropolitaines au cours de deux saisons, hiver et été. Nous avons particulièrement mis l'accent sur les oiseaux marins côtiers que nous avons définis comme des espèces qui ont un lien biologique ou écologique quotidien avec la côte afin d'accomplir certaines fonctions biologiques essentielles comme la nidification, l'élevage des jeunes ou tout simplement pour se reposer. Les résultats des modèles montrent clairement ce lien avec la côte au travers des patrons de distribution, mais ne reflètent pas les emplacements particuliers des colonies. Nous avons également été en mesure de prédire si les oiseaux étaient plutôt à la recherche de structures océanographiques stables ou prévisibles dans le temps ou s'ils étaient capables d'ajuster leurs stratégies d'utilisation du milieu aux variations environnementales à court terme.

Grâce à l'étendue spatiale des campagnes d'observation et des données environnementales, ce travail nous a permis de fournir une première évaluation des aires marines protégées établies au sein du réseau *Natura 2000* le long de la Manche et de l'Atlantique Nord-Est. Il s'est avéré que certaines AMPs ne seraient pas pertinentes pour les espèces étudiées, ce qui n'exclut pas qu'elles le soient pour d'autres espèces ou pour ces mêmes espèces dans la partie terrestre de leur budget d'activités. En outre, ce travail devrait être complété par des prévisions à long terme qui pourraient mettre l'accent sur les réponses des oiseaux de mer aux caractéristiques océanographiques variables. Ce travail devrait constituer une base pour aider les gestionnaires à gérer et surveiller les AMP côtières.

— Préambule —

Cette étude sur les variations saisonnières des habitats d'oiseaux marins côtiers s'inscrit dans un travail d'équipe réalisé au sein de l'observatoire *PELAGIS*, à la demande de l'Agence des Aires Marines Protégées dans le cadre du projet SAMM (Suivi Aérien de la Mégafaune Marine) du programme PACOMM (Programme d'Acquisition de Connaissances sur les Oiseaux et les Mammifères Marins). Ce programme vise à recueillir des nouvelles données et compléter les données existantes pour évaluer les sites *Natura 2000* en mer actuels et informer les gestionnaires sur des zones d'intérêt biologique susceptibles de justifier la désignation de nouveaux sites dans la Zone Economique Exclusive (ZEE) française. Par ailleurs, le programme PACOMM permettra, dans le cadre de la DCSMM (Directive Cadre Stratégie pour le Milieu Marin), d'établir une situation de référence sur les distributions et abondance de la mégafaune marine dans les eaux sous juridiction française ainsi de proposer des dispositifs de suivis efficaces de la mégafaune marine à partir de campagnes aériennes, de campagnes d'observations depuis des bateaux et de suivis télémétriques et acoustiques.

L'ensemble de ce travail, réalisé en collaboration avec Léa David (chef de mission), Ghislain Dorémus (formation des observateurs, observateur), Hélène Falchetto (gestion de bases de données), Charlotte Lambert (modélisation d'habitats), Sophie Laran (estimations d'abondance), Emeline Pettex (organisation opérationnelle du projet, estimations d'abondance et analyse des distributions), Amandine Ricart (analyse double-plateforme), Vincent Ridoux (direction scientifique), Eric Stephan (chef de mission) et Olivier Van Canneyt (aide à la conception du projet, formation des observateurs, observateur), donnera lieu à la rédaction d'un rapport d'évaluation de cette mégafaune marine le long des côtes françaises métropolitaines qui sera fourni à l'Agence des Aires Marines Protégées, dont un des chapitres sera consacré aux habitats des oiseaux marins côtiers.

Le rapport de stage présenté ici préfigure le chapitre qui sera consacré aux habitats des oiseaux marins côtiers et l'article à soumettre ultérieurement dans une revue scientifique internationale.

— List of abbreviations —

7d / 28d – 7 days / 28 days

A – Average

D_{colony} – Distance to the nearest colony

D_{coast} – Distance to the nearest coast

D_{SC} – Distance to the nearest sandy coast

D_{RC} – Distance to the nearest rocky coast

CV – Coefficient of variation

EEZ – Exclusive Economic Zone

EU – European Union

GAM – Generalized Additive Model

GLM – Generalized Linear Model

Grad – Gradient

SPA – Special Protected Areas

MS – Member States

MPA – Marine Protected Area

MNP – Marine Nature Parks

N2000 – Natura 2000

NAO – North Atlantic Oscillation

SAMM – Suivi Aérien de la Mégafaune Marine / Aerial Census of Marine Megafauna

SD – Standard Error

SPA – Special Protected Area

SST – Sea Surface Temperature

SSH – Sea Surface Height

V – Variance

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1 Introduction

Seabirds, being animals of high trophic levels, are often considered as indicators of ecosystem composition and productivity (Zacharias and Roff, 2001). Indeed, their high visibility, relative to organisms living permanently under water, their aggregation in productive marine hotspots, their potential for being fitted with telemetry devices and for being observed by using systematic and dedicated methodologies, allow to approach some biological and physical patterns of the marine ecosystems (Piatt *et al.*, 2007). They seem to be good indicators of the ecosystem status, since a decrease in seabird abundance or breeding success or changes in their distribution can indicate pollution, decrease in food availability or more general disorders in ecosystem structure and functioning (Furness and Camphuysen, 1997). For example, a sharp drop in the contribution of Pacific sardines (*Sardinops sagax*) to the diet of Californian seabirds from 1989 onwards was followed by a collapse of landings in 1991 (Velarde *et al.*, 1994; Fig.1). Thus, low seabird density in a particular area could indicate unsuitable habitat and lack of food.

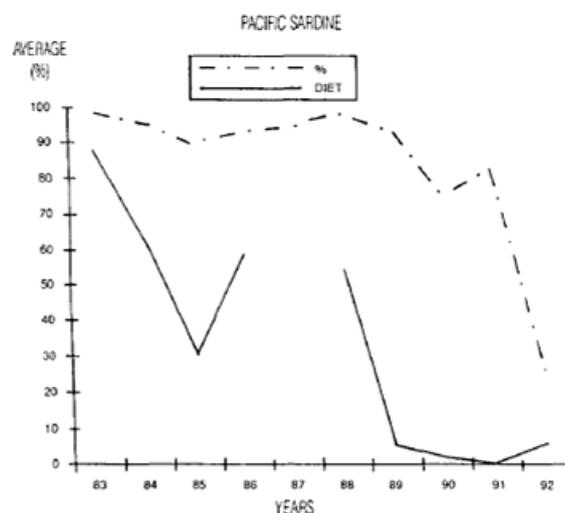


Fig. 1. – Percentage of Pacific sardine in commercial landings and in the diet of seabirds, 1983-92 (Velarde *et al.*, 1994).

Facing generally low predation risks at sea and high selection pressure for food, seabirds may have to modulate their strategies of resource and habitat utilization to maximize food intake and minimize energy costs during foraging. Thus, seabird biological characteristics, in particular all aspects that determine individual's energy requirements, are strong driver of habitat and resource use strategies to optimize foraging success (Chaurand and Weimerskirch, 1994).

Correlating spatial distributions of seabird sightings and environmental variables, both biotic and abiotic, is a common way to quantitatively analyse habitat use by seabirds (Vilchis *et al.*, 2006) and other pelagic megafauna (Becker, *et al.*, 2010; Mannocci, *et al.*, 2013; 2014) through habitat modelling. For instance, biological and physical processes such as distance to the colony, water depth and current speed determine Arctic Tern (*Sterna paradisaea*) and Common Tern (*Sterna hirundo*) distributions (Schwemmer *et al.*, 2009) because these variables affect prey availability close to the water surface for these central place foragers. Hence, densities of foraging birds were negatively correlated with distance to the colony and positively correlated with current speed (Schwemmer *et al.*, 2009).

In addition, habitat models are increasingly used for the management and conservation of species and ecosystems. Indeed, they allow to predict species distribution (Mannocci, *et al.*, 2014), to define areas for species conservation (Bailey and Thompson, 2009), or to predict species responses to environmental change (Cheung *et al.* 2009).

European Union (EU) Member States (MS) are engaged in protecting habitats and species of community interest by setting, managing and monitoring a coherent network of

protected areas, called the *Natura 2000* (N2000) network, under the Birds and the Habitat Directives (Directive 2009/147/CE, Parlement Européen, 2009; Directive 92/43/CEE, Parlement européen, 1992). These two directives have primarily been designed for and implemented in terrestrial and coastal ecosystems but a recent impetus was given to expand the N2000 network at the scale of the Economic Exclusive Zones (EEZ) of all EU MS.

A crucial aspect in designing and monitoring N2000 sites and more generally any spatially defined conservation tool is the availability of relevant scientific data to identify the location of key areas, understand their functioning, notably in relation to existing human activities, and monitor the effect of conservation measures implemented by managers.

In France, most existing marine N2000 sites lie within 12 nautical miles from shore. At the EU biogeographic seminar in Galway (Evans, 2012) it was concluded that the representativeness of the network was inadequate, especially offshore. In parallel to this, for a majority of these sites the management plans have still to be drafted. Hence, the Marine Protected Area Agency set up a knowledge acquisition program on marine birds and mammals in order to assess existing N2000 sites and provide relevant information to the managers as well as make an inventory of species across waters under French jurisdiction (EEZ) to supplement the network, notably offshore (Pettex, et al., 2012).

In addition to N2000 sites, similar considerations also apply to other conservation sites such as Marine Nature Parks, National Parks with marine areas, Marine Nature Reserves, sanctuaries (PELAGOS) that are already established in France and managed by a variety of organisms either at national, regional or local level.

In this study, we focused on coastal seabird species defined as all species that have a strong daily link to the coast for the accomplishment of one or several key biological functions such as breeding or resting and therefore have to commute on a daily basis between the coast and more or less distant foraging habitats at sea. The study area being mostly composed of the French EEZ of the Atlantic and Channel seabords, this definition encompasses terns (mostly *Sterna hirundo*, *Sterna albifrons* and *Sterna sandvicensis*), cormorants (*Phalacrocorax carbo* and *P. aristotelis*) and large gulls (mostly *Larus argentatus*, *L. michahellis*, *L. fuscus* and *L. marinus*). Although, they do not use terrestrial habitat during the non-breeding season, divers (*Gavia spp.*) and scoters (*Melanitta fusca* and *M. nigra*) are also considered here as their foraging and resting habitats are strictly coastal. The study did not deal with the numerous more littoral seabirds species mainly dwelling in the tidal zone. Besides, species that commonly spend long periods at sea without the constraint to commute to the coast on a daily basis (e.g. procellariiforms, awks, gannets *Morus bassanus*, and the more offshore-dwelling gulls) are supposed to respond differently to spatiotemporal patterns of marine habitats and are therefore being considered in a separate work.

The aim of this study was to identify the mechanisms that mostly influence distribution patterns of coastal seabirds and determine the effects of their variations, notably seasonal, on the expected distributions of these species. These mechanisms include *inter alia* tidal currents, sea surface temperature, sea surface height, nature of seabed, nutrient inputs from rivers, nature and state of coastal habitats, distance to coast and depth. The resulting models will be used to examine the relevance of the existing and proposed marine protected areas for coastal seabirds. Relevance was simply assessed by estimating for every species of interest the proportion of its total abundance in French waters predicted to be present within the boundaries of every single MPA (N2000 sites and other categories of MPA).

We collected seabird data from two aerial surveys, named the SAMM surveys (*Suivi Aérien de la Mégafaune Marine*, Aerial Census of Marine Megafauna) that were conducted during the winter 2011/2012 and the summer 2012 in the English Channel, the Bay of Biscay, the Celtic Sea and the Mediterranean Sea, and used a strip transect methodology. For the purpose of this specific work, the latter region will not be considered any further.

The vast extent of the study area encompasses contrasted biological and physical characteristics of coastal and marine habitats that are the main drivers of the observed patterns of habitats use by seabirds. To characterize seabird habitats, we relied on oceanographic and physiographic variables obtained from satellite data and data extracted from models. These physical and biological covariates were used as proxies for prey

abundance and prey availability, which was supposed to be the main source of coastal seabird aggregation at sea (Schwemmer *et al.*, 2009).

In this study we used Generalized Additive Models (GAMs) in order to predict coastal seabird habitats. Then we examined seabird responses to seasonal variations in environmental conditions. Finally, we provided spatial predictions of seabird distribution in the aim of assessing the relevance of the network of coastal marine protected areas for our species of interest.

2 Materials and Methods

2.1 Study area

Our study area was divided in two areas, the English Channel and the eastern North Atlantic Ocean. It covers 376,000 km² and encompasses the Exclusive Economic Zone (EEZ) of mainland France and some adjacent areas, for the sake of maintaining ecological and conservation consistency. The study thus comprised the entire English Channel, including waters under the jurisdiction of the United Kingdom and the Channel Islands and the Bay of Biscay, including some Spanish waters encompassing all the slope and canyon habitats of the southern Bay of Biscay (Fig.3).

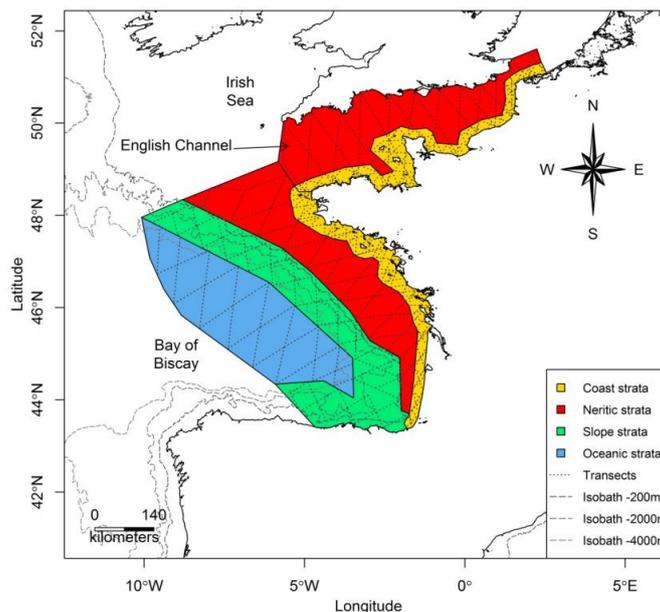


Fig. 3. – The study area covers the entire EEZ of mainland France extended to adjacent areas in the Atlantic and Channel. Surveys were carried out along transects across bathymetric strata represented in colours (coastal, neritic, slope, oceanic).

In accordance with the Large Marine Ecosystems described by Longhurst (2006), we have considered the English Channel and the eastern North Atlantic Ocean as a single entity.

The English Channel, with a size of 92,946 km², stretches between the English and French coasts and from the tip of Brittany (Ushant) to the Dover Strait. In the northeast Atlantic Ocean, our study area covers 282,901 km² and encompasses the Bay of Biscay from the tip of Brittany to the Spanish coast. In its northern part, it extends from the south of the Celtic shelf to the abyssal plain of the Bay of Biscay and then the study area narrows down parallel to the continental slope and includes the canyons of the Basque Country.

The Bay of Biscay is characterized by a weak general oceanic circulation and weak currents and by the presence of eddies (cyclonic and anticyclonic) due to current instability (Koutsikopoulos and Le Cann, 1996). This instability is caused by seasonal variation of current orientation mostly as an effect of wind regime. For example, most of the year, the residual current is oriented to the south-east, whereas in winter, it is oriented to the north-west. Near the coast and in estuaries, the presence of freshwater associated with winds causes the formation of density currents usually oriented to the north (Koutsikopoulos and Le Cann, 1996). Despite this weak general circulation, the Atlantic waters and the Channel waters are linked by a residual circulation mostly driven by tidal currents and prevailing south-westerly winds which brings Atlantic waters to the North Sea (Grioche and Koubbi, 1997). The particularity of this residual circulation is its high monthly variability and its sensitivity to weather conditions (Salomon et al., 1993).

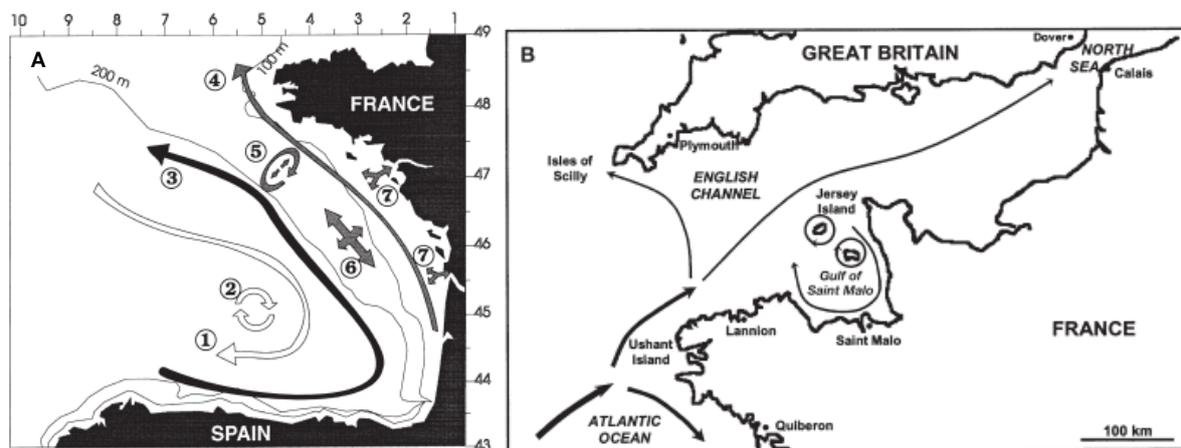


Fig. 4. – A: Circulation and currents in the Bay of Biscay: 1 general oceanic circulation, 2 eddies, 3 slope currents, 4 shelf residual circulation, 5 tidal currents, 6 wind induced currents, 7 density currents (Koutsikopoulos and Le Cann, 1996). B: Long-term, average current trajectories in the English Channel (Billot et al., 2003).

The area is also characterized by the presence of fronts. In the summer, the formation of strong vertical temperature gradients in the Bay of Biscay, (up to 9-10 degrees) is combined with the creation of thermal fronts caused by the interactions between topography and tidal currents (Koutsikopoulos and Le Cann, 1996).

In the English Channel, a frontal zone, whose distance to the coast highly depends on tidal cycles, separates coastal from offshore waters (Grioche and Koubbi, 1997) and tidal cycles induce a destratification of shallow waters by turbulent mixing in areas of low depth and strong currents (Lagadeuc et al., 1997). The coastal area delimited by the above-mentioned fronts in the Channel, is characterized by lower salinity, higher turbidity and higher phytoplanktonic biomass as compared to offshore waters (Grioche and Koubbi, 1997). These fronts themselves can be beneficial to seabirds since they generate passive accumulation of plankton, fish eggs and larvae and consequently predatory fish aggregations as well as optimal growth of some fish species like sardines (*Sardina pilchardus*) or blue whiting (*Micromesistius poutassou*) (Brandt, 1993; Fernandez et al., 1993). Hence, the English Channel and the eastern North Atlantic Ocean appear to represent suitable environments for the recruitment of many species and the establishment of nurseries.

Furthermore, phytoplankton concentration is subject to seasonal variations. Indeed in winter, phytoplankton concentration is low and a sharp bloom of phytoplankton is observed in spring (Aiken et al., 2004). This bloom may be correlated with the North Atlantic Oscillation (NAO) index since warmer conditions produced by a positive NAO may cause an earlier and higher production of phytoplankton (Irigoien et al., 2000). The spring bloom is followed by episodic blooms in summer and autumn and finally phytoplankton concentration declines down to its minimum in winter (Aiken et al., 2004). Thus, for seabirds which feed on benthic preys, shallow waters are targeted whereas high turbidity, high phytoplankton concentration,

currents speed and low salinity in the English Channel are favourable for the aggregation of preys, which constitute the main food source for pelagic seabirds.

2.2 Experimental strategy

As explained above, the operational aim of the study was to assess the value for the conservation at sea of coastal seabirds of marine protected areas (MPAs) established along the French Atlantic and Channel under *Natura* 2000 framework. Seabird observations were collected during aerial surveys, carried out in the winter 2011/2012 and the summer 2012. Survey effort, which is the amount of time or of distance spent in standard observation condition, was deployed along transects, defined as straight lines or narrow sections across study area, along which observations are made or measurements taken. Legs that are parts of transects surveyed under similar observation and meteorological conditions were in turn split into 10km-long segments that constitute the unit of effort for further statistical analyses (see details under 3.2).

From seabird observations, habitats were modelled with Generalized Additive Models (GAMs) using environmental parameters as explanatory variables (3.3 and 3.4) instead of geographic coordinates to explain data variations (Ferguson *et al.*, 2006). Two categories of environmental variables were selected for their potential to be drivers of seabirds prey availability. Seabirds being homeotherms it was assumed that seawater temperature *per se* was less of an issue than drivers of prey availability.

Physiographic variables are static and relate to bathymetry and nature of substrate. Sea bottom slope and depth interact with water circulation to create water movement that determine primary production and availability or aggregation of prey at predictable locations (Lagadeuc *et al.*, 1997). Distance to nearest colony and distance to nearest sandy or rocky coast are of crucial importance for the energy balance of species that commute daily between coastal breeding or roosting sites and at-sea foraging areas.

Oceanographic variables are dynamic and describe water masses. Sea surface temperature (SST), its variability over time and its horizontal gradients reveal front locations and intensities as well other mesoscale activities which are often associated to plankton aggregations (Grioche and Koubbi, 1997). In offshore habitats sea surface height (SSH) and its variability is considered as a proxy of nutrient aggregations and primary production because the flux of nitrate is greatly influenced by eddy activity and a strong eddy activity leads to high standard deviation in the SSH (Oschlies and Garçon, 1998). In inshore habitat strong standard deviation of SSH is related to tidal movements. Currents play an essential role in the distribution of seabird preys because of local water mixing (Grioche and Koubbi, 1997).

For these oceanographic variables, two temporal resolutions were used. At the seven-day resolution, oceanographic conditions were averaged over the six days prior to sampled day, and similarly at the twenty-eight-day resolution. These two resolutions were tested to account for possible time lag between a given oceanographic condition and its effect at intermediate trophic levels.

Once the best model was selected, seabird distributions were predicted across the whole study area. Predictions were made for the two survey periods (*i.e.* winter 2011-12, and summer 2012) to assess validity of the models by comparing with actual sightings. Long-term predictions would also be instructive to managers, as they would inform on the value of each MPA in the long-term in case the survey year was atypical, but such predictions require an extensive work of environmental data acquisition and processing that was out of the present study timeframe.

Finally, predicted distributions were used to provide, for each protected area, a measure of its importance for the protection of every species of coastal seabirds (% of prediction within MPA relative to across total survey area) (Fig.2).

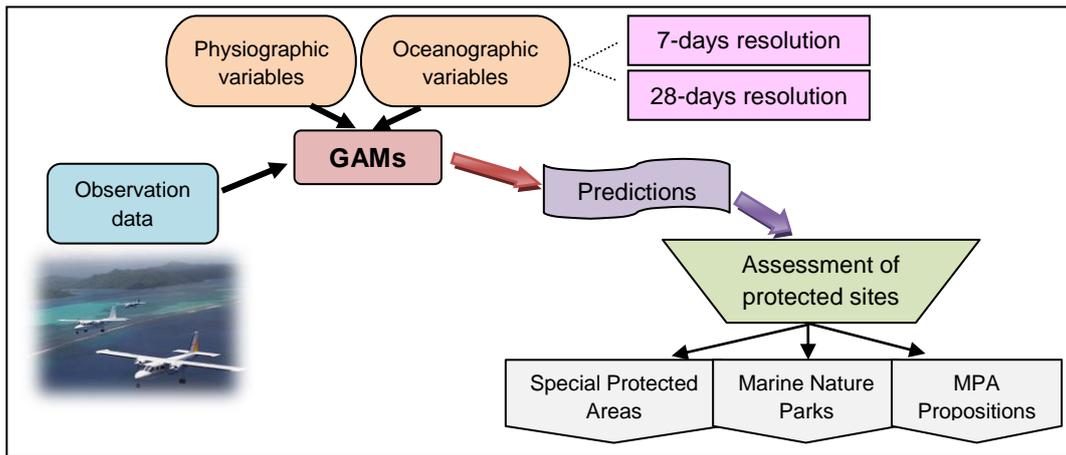


Fig. 2. – Experimental approach of the project (MPA: Marine Protected Areas).

2.3 Data collection

2.3.1 Species of interest

In this study, we focused on the distribution of coastal seabird species, *i.e.* species which have a daily biological or ecological link with the coast to accomplish some key biological functions such as nesting, chick rearing or simply resting. Aquatic species wintering at sea in coastal habitats were also included. Under this definition the coastal species of interest to the present study included members of the gull and tern family Laridae, the cormorant and shag Phalacrocoracidae, the divers Gaviidae and the marine ducks *Melanitta* spp.

Because of the difficulty in identifying several species from the air, some species were pooled into groups sharing common morphological characteristics used as identification criteria when viewed from above (Table 1). This variety of species encompasses sedentary and migratory species (Appendix A showed breeding periods and presence on the French coasts of each species group).

Table 1. – Composition of seabird groups. Taxonomy was extracted from WoRMS (WoRMS Editorial Board, 2014) and pictures were provided by Oiseaux.net (2014).

Family	Group names	Group composition	Pictures
Laridae	Herring gull complex	Herring gull <i>Larus argentatus</i> , Yellow-legged gull <i>Larus michahellis</i>	
	Black-backed gulls	Great black-backed gull <i>Larus marinus</i> , Lesser black-backed gull <i>Larus fuscus</i>	
	Terns	Arctic tern <i>Sterna paradisaea</i> , Common tern <i>Sterna hirundo</i> , Little tern, <i>Sterna albifrons</i> , Sandwich tern, <i>Sterna sandvicensis</i>	
Phalacrocoracidae	Cormorants and Shags	Great cormorant <i>Phalacrocorax carbo</i> , European Shag <i>Phalacrocorax aristotelis</i>	
Gaviidae	Divers	Red-throated diver <i>Gavia stellata</i> , Black-throated diver <i>Gavia arctica</i> , Great Northern Diver <i>Gavia immer</i>	
Anatidae	Scoters	Common scoter <i>Melanitta nigra</i> , Velvet scoter <i>Melanitta fusca</i>	

2.3.2 Aerial survey methods

We collected seabird data during two aerial surveys, namely the SAMM surveys (*Suivi Aérien de la Mégafaune Marine*, Aerial Census of Marine Megafauna) that were aimed at mapping the winter and summer distributions of pelagic megafauna across all French waters in order to inform the N2000 process. These surveys were designed for multiple targets, including marine mammals and birds, sea turtles, large fish and elasmobranchs, as well as macro debris (Pettex et al. 2012). Considering that cetaceans are the least frequent and most elusive of all target species, the general survey methodology was designed as to optimize cetacean sighting conditions. Surveys were conducted in the eastern North Atlantic and the English Channel mostly across waters under French jurisdiction (Fig.3) in winter 2011-2012 (from November to February) and summer 2012 (from May to August). Within each region, a stratification was defined according to bathymetry. The "Coastal" stratum extended from the coast to the limit of 12 nautical miles; the "Neritic" stratum was from the coast (0 m isobaths) to the 200 m isobaths; the "Slope" stratum encompassed the continental slope from 200-2000 m isobaths; and the "Oceanic" stratum included all waters beyond the 2000 m isobaths. Seabird observations were conducted along linear transects using the strip transect methodology which allows to sample sightings in a corridor of 200 m on either side of the track followed by the aircraft. The strip width was marked on each side of the fixed landing gear corresponding to an angle of 42° from the horizon, at 183 m flight elevation. Contrary to the line transect methodology, which takes into account the fraction of individuals missed by observers and the decrease in detection probability with increasing distance from the transect line, the strip transect methodology is based on the assumption that all individuals present in the strip are detected (Fig.5). It has been shown (Certain and Bretagnolle, 2008) that strip transect methodology is well adapted for seabird observations because there is a limited effect of visibility bias and distance bias, provided that strip width is reasonably narrow.

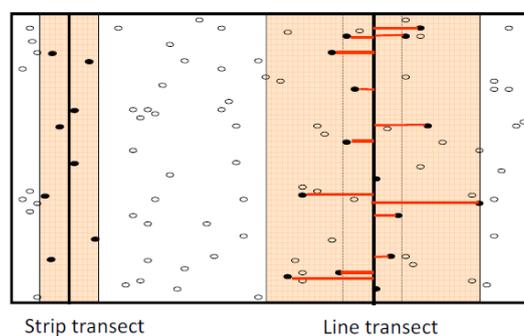


Fig. 5. – Comparison between strip transect and line transect methodologies. In the strip transect method, it is assumed that all objects in a known width strip are seen whereas the line transect method takes into account the proportion of missed observations related to the distance from the transect (Mannocci, 2013).

To carry out the aerial surveys, Britten Norman 2, that are high-wings, double-engine aircrafts equipped with bubble windows, were used; three aircrafts were operated for the winter survey against only two in the summer (Fig.6). Survey transects were flown at a target altitude of 183 m (600 feet) and a speed of 167 km.h⁻¹ (90 knots), following standard methodology for cetacean survey (Hammond et al., 2005). Teams for each flight were composed of one pilot and four observers. At anyone moment of a survey flight, two observers were positioned at the bubble windows on each side of the aircraft, the navigator collected the data on a laptop connected to a GPS, and the fourth observer was off duty. To limit biases due to fatigue, the four observers rotated duties and position in aircraft approximately every two hours of flight. Data were recorded instantly with the VOR 8.6 software developed for cetacean aerial surveys (Hiby and Lovell, 1998; SCANS, 2006). Turbidity, glare severity, cloud coverage, Beaufort Sea state and subjective observation conditions were recorded at the beginning of each transect and when any value changed.



Fig. 6. – (a) Britten Norman 2 aircraft; (b) Bubble window (Pettex et al., 2012).

Transects followed a zigzag pattern as this optimizes the use of available flight time by reducing transit while providing a uniform coverage of the area. Transects were equally distributed and oriented in order to sample the different depths across all bathymetric strata (Fig.7).

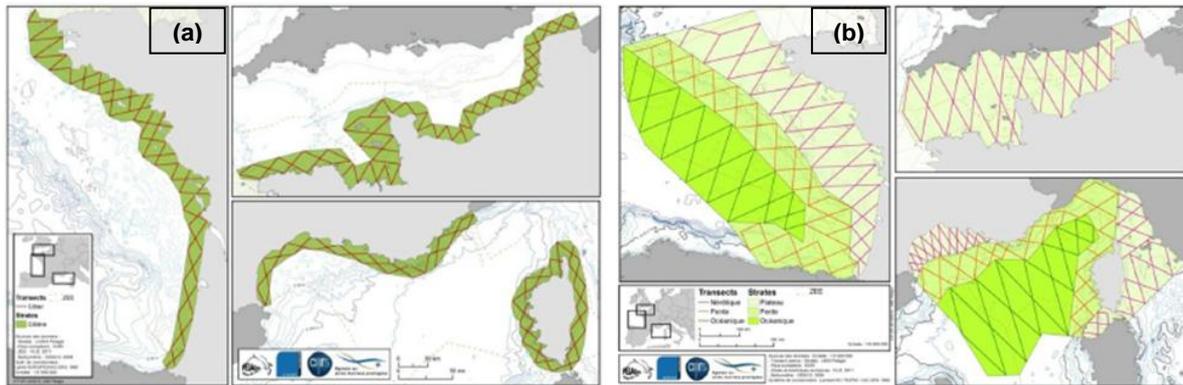


Fig. 7. – Sampling design: transects planned in (a) coastal stratum; (b) neritic, slope and oceanic strata (from light green to dark green) (Pettex et al., 2012). Effort actually flown may differ in some areas because of field conditions, notably wind regime (Appendix B).

2.3.3 Data organization

Transects were organized in legs of identical detection condition and further split into segments of 10 km, to avoid excessive variability in observation conditions (see Appendix B for transects flown per month during the two surveys). Moreover, segments with poor observation conditions, *i.e.* all segments with sea state Beaufort ≥ 4 and poor subjective observation conditions were removed. Finally, the software ArcGis 10 (ESRI, 2011) was used to locate on a map the sightings of each species groups and join observations to segments (Fig.8).

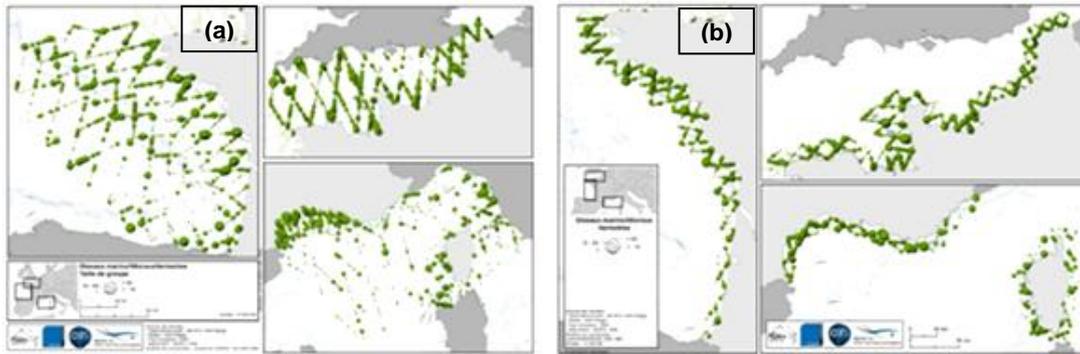


Fig. 8. – Example distribution map of all seabird sightings throughout the study area in summer: (a) neritic, slope and oceanic strata; (b) coastal stratum (Pettex et al., 2012).

2.4 Habitat variables

Oceanographic and physiographic variables were selected to model seabird habitats (Table 2; see also Appendix D for variables which were tested but not included in models).

Table 2. – Environmental variables used to model seabird habitats.

Physiographic Covariates		Sources
Slope	Slope (degree)	GEBCO 2008
Depth	Depth (m)	GEBCO 2008
D_c	Distance to the nearest coast (km)	QGIS 2.2.0
D_{RC}	Distance to the nearest rocky coast (m)	QGIS 2.2.0
D_{sc}	Distance to the nearest sandy coast (m)	QGIS 2.2.0
D_{colony}	Distance to the nearest seabird colony (m)	QGIS 2.2.0
Oceanographic covariates		
SST_M	Average sea surface temperature (K)	ODYSSEA model
SST_V	Variance of sea surface temperature (K)	ODYSSEA model
SST_{grad}	Gradient of sea surface temperature (K)	ODYSSEA model
SSH_M	Average sea surface height (m)	MARS 3D/INGV models
SSH_{sd}	Standard deviation of the sea surface height (m)	MARS 3D/INGV models
Currents	Daily maximum intensity of the currents (m.s ⁻¹)	MARS 2D model

Physiographic variables (slope and depth) were obtained from the GEBCO 30 sec grid (General Physiographic Chart of the Ocean; <http://www.gebco.net/>). This grid was also used in QGIS-2.2.0-Valmiera (QGIS Development Team, 2014), to calculate distance to nearest colony (D_{colony}) and distance to nearest coast (D_{coast}). They represent the shortest distance between midpoint of each segment and the location of a colony or the 0 m isobath. Distance to nearest sandy coast ($D_{sandy\ coast}$) and nearest rocky coast ($D_{rocky\ coast}$) were also calculated thanks to the EuroSION database (Geology, Geomorphology and Erosion Trend; www.eea.europa.eu/data-and-maps/data/shoreline). Distance to colony was included in the models only for the summer season, as it is the breeding season for most seabird species: however breeding seasons (Appendix A) generally do not fully match our summer survey period. Colony locations were summarized from Cadiou *et al.*, (2005) for France, JNCC (Joint Nature Conservation Committee; www.jncc.defra.gov.uk) for United-Kingdom and SEO/BirdLife (www.seo.org) for Spain (Appendix C showed referenced colonies).

Daily sea surface temperatures (SST) were extracted from ODYSSEA model (IFREMER; <http://www.myocean.eu/>) and then, averages and variances were calculated for each sampled days during the surveys with a temporal resolution of 7 and 28 days. We also computed SST gradients as the difference between the minimum and maximum SST values found in the eight pixels surrounding any given pixel (Fig.9); temporal resolutions of 7 and 28 days were used.

$$(SST\ gradient)_i = minimum(SST_{neighbours\ i}) - maximum(SST_{neighbours\ i})$$

Fig. 9. – Calculation of SST gradients.

In addition, we used data extracted from models provided by *Previmer* (www.previmer.org). Thanks to the MARS 3D model (Previmer, 2014), we were able to extract the daily sea surface height (SSH) (0.05° spatial resolution) for the two survey seasons and then calculate its average and standard deviation for the 7 and 28 days prior to sampled day.

Data of MARS 2D model provided by *Previmer* (www.previmer.org), allowed us to extract the hourly speed of tidal currents in the Atlantic Ocean for the survey periods. Thus, we could calculate maximum intensity of tidal currents with a resolution of 7 and 28 days.

Finally, we created a joint between the centre of each segment and habitat variables to assign the values of all variables to the location of each segment and date of the surveys (Appendix E showed average contribution of each environmental covariate).

2.5 Model construction

2.5.1 Model development

To model relationships between seabird distributions and environmental variables and to predict seabird distributions, we used GAMs (Hastie and Tibshirani, 1986) which permit to identify correlations between the number of animals and a variety of habitat parameters. This method takes into account the non-Gaussian distribution of individuals and non-linear dynamics of marine habitats and allows maximizing the quality of inference, description and prediction of habitats.

In the present study, we modelled the response variable Y (number of individuals per segment) with a link function $g()$ which relates the mean of the response variable $\mu = E(Y|X_1, \dots, X_n)$ to the additive predictor $\alpha + \sum f_i(X_i)$ as:

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

where $f_i(X_i)$ are non-parametric smooth functions (splines) of the covariates (Hastie and Tibshirani, 1986). Accounting for non-constant effort, we included an offset which takes into account the variation in the amount of effort per segment and was calculated as segment length multiplied by twice transects width (2*200 m). We tested the effect of oceanographic and physiographic covariates on abundance for each season and each seabird group by using quasi-Poisson distribution with variance proportional to the average to avoid over-dispersion of tail distributions (Hedley *et al.*, 1999). A logarithmic link function was used to relate the average of the response variable and the additive predictor. To avoid over-fitting of the data, which has no ecological averaging (Ferguson *et al.*, 2006), we restricted curve smoothing to three degrees of freedom. GAMs were fitted in R-3.0.1 (R Core Team, 2013) with the *mgcv* package, especially *gam* and *predict.gam* functions (Wood, 2006; 2013).

2.5.2 Model selection and predictions

For model selection, oceanographic and physiographic variables described in 2.3 were used. Correlations between variables were calculated and we excluded pairs of collinear variables (*i.e.* with a Spearman coefficient <-0.7 and >0.7 calculated with `Hmisc` package (Harrel, 2013). For each seabird group, observation outliers and environmental variables outliers were excluded and all models with combinations of 1, 2, 3 or 4 covariates were tested.

The model with the lowest generalized cross-validation (GCV) associated to the highest explained deviance, which evaluate the model's fit to the data, was selected. Following Mannocci et al. (2013), a maximum of four covariates per model was used to avoid excessive complexity of models and difficulty in their interpretation. Finally, from the `predict` function of the `mgcv` package (Wood, 2013), we wrote a script permitting to calculate the contribution of each covariate in the selected model.

For each group of species, the best model and the associated covariates were used to predict relative density of individuals in a generated grid of $0.05^\circ \times 0.05^\circ$ resolution. We first calculated daily predictions for all days of the surveys by using the `predict` function and then we calculated the average prediction over the entire period. We also computed an associated coefficient of variation ($CV=sd/average$) to provide uncertainty maps. Prediction grids include the sampled geographic sectors and extend outside of study area within the range of covariates used in model fitting to avoid extrapolation (Fig.10).

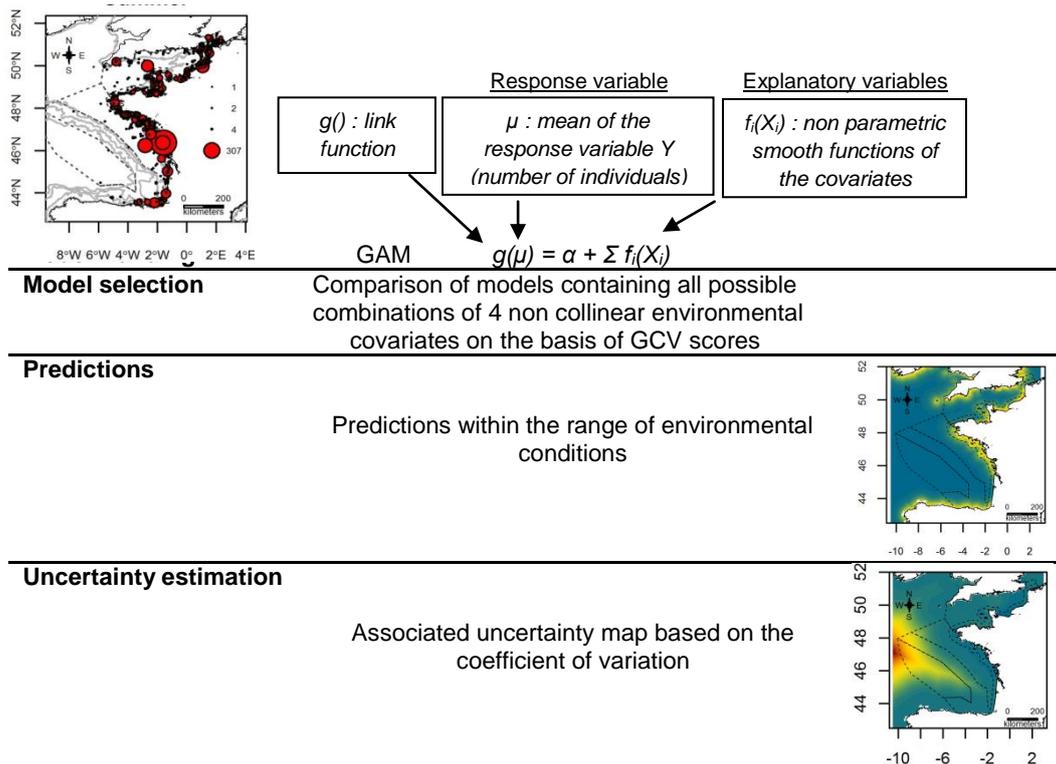


Fig. 10. – Stages of habitat modelling (example of herring gull complex in winter).

2.6 Assessment of marine protected areas

To assess marine protected areas, we calculated a ratio to obtain a percentage of individuals included in the area compared to the total number of individuals predicted across the entire study area. To do this, we used files of all Special Protected Area (SPA) and Marine Nature Park (MNP) delimitations as well as offshore putative limits of proposed MPA (Fig.11). According to the “Birds Directive” (Directive 2009/147/CE, Parlement Européen, 2009), a protected area has to be designated when more than 1% of individuals present in a MS national EEZ are included in the area.

Thanks to the `extract` function from raster package (Hijmans *et al.*, 2014), we extracted predicted densities for every pixel in all MPA and in the whole study area. Then we ranked all MPAs in term of seabird densities and determined the proportion of total abundance that is present in every MPA.

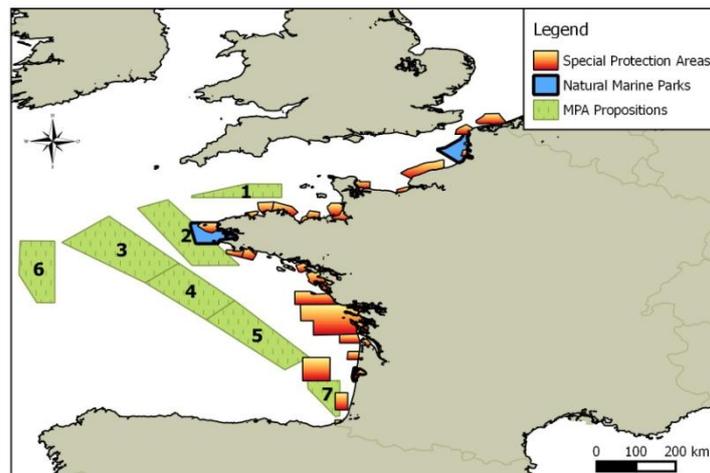


Fig. 11. – Marine Protected Areas used for the assessment (provided by MPA Agency).

3 Results

3.1 Data processing

3.1.1 Detection conditions and survey effort

The aerial survey actually covered 32,445 km of transects in winter and 33,864 km in summer, which represent respectively 8.65% and 9.03% of the surface of the study area, given the 200 m sighting band on each side of the track (English Channel and Bay of Biscay) (Table 3). The focal species were mostly observed in the coastal and shelf strata, which correspond together to 72% of total effort. Detection conditions were very good during the two surveys with 87% of effort in winter and 93% of effort in summer carried out under sea state ≤ 4 and medium to excellent subjective conditions. Overall, detection conditions were a little better in the Bay of Biscay than in the Channel in the summer (94% of effort with sea state ≤ 4 versus 90%); conversely in winter, detection conditions were better in the Channel than in the Bay of Biscay (89% versus 85%).

For habitat analysis, we did not consider poor detection conditions (sea state ≥ 4 and subjective observation conditions poorer than medium) to ensure correct identification of species. Hence, effort considered for analysis spanned 28,068 km of transects in the winter (*i.e.* 7% of the surface of the study area) and 31,427 km in the summer (*i.e.* 8% of the surface of the study area).

Table 3. – Effort by strata performed during the two surveys. This table presents the total effort carried out in the Bay of Biscay and the Channel in winter and summer and the effort used for analysis without taking into account poor observation conditions (Beaufort ≥ 4 and subjective observation (SubjNum) conditions poorer than medium).

Bathymetric strata	Surface area (km ²)	Total survey effort in winter (km)	Survey effort in Beaufort <4 and SubjNum >3 (km & %)	Ratio Effort Beaufort <4 and SubjNum >3/ Area (%)	Total survey effort in summer (km)	Survey effort in Beaufort <4 and SubjNum >3 (km & %)	Ratio Effort Beaufort <4 and SubjNum >3/ Area (%)		
Bay of Biscay									
Coastal	27 293	4 459	3 816	86%	14%	4 336	4 004	92%	15%
Shelf	103 374	7 345	6 329	86%	6%	7 135	6 500	91%	6%
Slope	87 584	6 411	5 185	81%	6%	6 419	6 340	99%	7%
Oceanic	91 183	2 599	2 365	91%	3%	5 087	4 831	95%	5%
Total	282 141	20 814	17 695	85%	6%	22 977	21 675	94%	8%
English Channel									
Coastal	26 682	4 467	4 079	91%	15%	4 410	4 065	92%	15%
Shelf	92 875	7 162	6 292	88%	7%	6 477	5 687	88%	6%
Total	92 875	11 629	10 371	89%	11%	10 887	9 752	90%	11%
Grand total	375 016	32 443	28 066	87%	7%	33 864	31 427	93%	8%

3.1.2 Seabird sightings

In the whole study area, a total of 18,155 sightings of seabirds were collected in winter and 8,439 in the summer (Appendix F). Among these sightings, our groups of coastal species represented 2,459 sightings in winter and 3,318 sightings in summer (Table 4, Appendix F). Irrespective of the season, black-backed gulls and herring gull complex were the most frequently encountered taxa whereas the least observed seabirds were terns in the winter and scoters in the summer (see Appendix F for seabird sightings during the two seasons).

Most of studied species were observed in coastal and neritic strata but in varying proportions (see Appendix G for sighting maps of each group). Individuals of the herring gull complex were more common in the summer than in winter in Channel/Bay of Biscay, with an encounter rate of 4.57 against 2.75 sightings.100km⁻¹. Conversely, black-backed gulls were slightly more common in winter than in summer (2.70 sightings.100km⁻¹ and 2.41 sightings.100km⁻¹ respectively). Terns were much less frequently observed in winter (0.27 sightings.100km⁻¹) than in summer (2.16 sightings.100km⁻¹). Conversely, cormorants and shags were more observed in winter (0.77 sightings.100km⁻¹) than in summer (0.58 sightings.100km⁻¹). Divers were mainly observed in the Channel (99% of sightings) and only in winter with an encounter rate of 0.66 sightings.100km⁻¹). Finally, scoters were hardly observed in summer (0.07 sightings.100km⁻¹) and more frequent in winter (0.42 sightings.100km⁻¹).

Table 4. – Number of sightings and individuals (Ind nb) in each group by sector and season.

Groups	English Channel / Bay of Biscay			
	Winter		Summer	
	Sightings	Ind nb	Sightings	Ind nb
herring gull complex	892	3133	1549	3367
black-backed gulls	877	2079	816	1420
terns	88	203	731	1437
cormorants and shags	250	555	198	493
divers	215	846		
scoters	137	2086	24	94

Because of the absence of some species or of the small number of sightings combined with poor observation conditions, some habitat models were not feasible. Hence, models for divers and scoters in summer have not been fitted in the following section.

3.2 Habitat modelling

3.2.1 Model selection

For all models, explained deviance varied between 24.5% (herring gull complex in winter) and 62.2% (divers) and in most cases, the number of individuals was mostly influenced by the distance to nearest coast (sandy or rocky coast) (Fig.12).

Whatever the season, the number of individuals of the herring gull complex was mostly influenced by the distance to the nearest coast, with a link to sandy coast (62.5%) in winter and rocky coast (72.9%) in the summer. In winter, the number of individuals was negatively correlated to distance to nearest sandy coast (D_{SC}), maximum 28-days currents (Currents 28d), average 7-days sea surface temperature (SST_M 7d; with a minimum of individuals at 14°C), and positively correlated to variance of 7-day SST (SST_V 7d). In contrast, in the summer, the number of individuals was negatively correlated to distance to nearest rocky coast (D_{RC}) and maximum 28-days currents (Currents 28d) and positively correlated to 28-days standard error of sea surface height (SSH_{sd} 28d), with two slight inflections at 1.2 and 1.8 m, as well as with 7-days average SSH (SSH_M 7d), with a maximum at 0.2 m.

Similarly to the herring gull complex, the number of black-backed gulls was mostly negatively influenced by the distance to the nearest sandy coast (65%) in winter and the nearest rocky coast (75.8%) in the summer. In winter, we observed a maximum of individuals at a 28-days average temperature of 11°C and a 28-days variance temperature of 0.3°C and an increasing number of individuals with an increasing 28-days variance of SSH. In the summer, the maximum number of individuals was reached for a short D_{RC} , a 28-days maximum current speed of $0.5 \text{ m}\cdot\text{s}^{-1}$, a low 28-days variance of SST and a 7-days average of SSH of 0.2 m. For higher values, the number of individuals decreased to zero.

For divers, which were observed only in winter, the number of individuals was negatively correlated to depth (38.9%). Divers showed an optimal distance of 20 km from nearest rocky coast, as well as a preference for strong variations of SSH and average current speeds (around $1 \text{ m}\cdot\text{s}^{-1}$).

In contrast to gulls, the number of terns was mostly influenced by the distance to, the nearest rocky coast in winter (60%) and the nearest sandy coast in the summer (48.3%) with higher concentrations at short distance from shore. The maximum of individuals in winter was observed for short distance to rocky coast, strong gradients of 28-days SST, weak 7-days current speed ($0.4 \text{ m}\cdot\text{s}^{-1}$) and a 28-days average SST around 12°C . In contrast, in the summer, in addition to D_{SC} , terns showed a maximum of individuals for short distance to sandy coast, strong 28-days standard error of SSH, low 7-days average SSH (around -0.2 m) and low 28-days current speed (around $0.4 \text{ m}\cdot\text{s}^{-1}$).

The number of cormorants and shags was strongly correlated to distance to the nearest coast (74.6% in winter and 83.3% in the summer), with higher values for short distances. In winter, altimetry played a role in individual distributions with a higher number of individuals for a high 28-days standard error of SSH, a low 28-days average SSH (around 0.1 m) and low 7-days average of SST. In contrast, in summer, temperature was more important with highest values of individuals for weak distance to sandy coast, high current speed, 7-days average SST around 16°C and weak 28-days variance SST (around 1°C).

Finally, like all other studied species, scoters were also negatively correlated to distance to nearest coast (69.3%), particularly sandy coast, but were also correlated to 7-days standard error of SSH (positively), 7-days current speed (negatively) and 28-days variance of SST (mode at around 0.7°C).

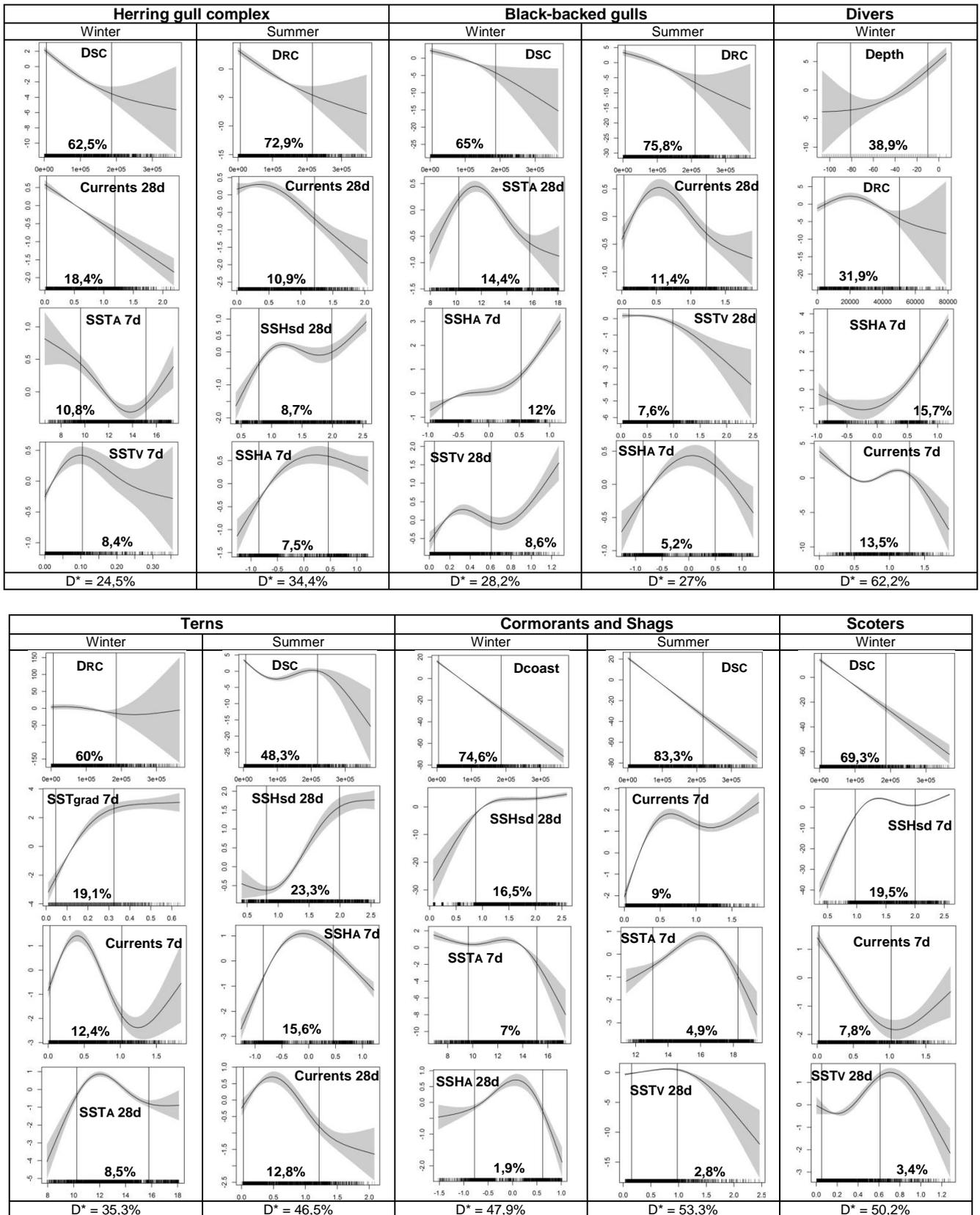


Fig. 12. – Forms of smooth functions for the selected covariates for each group of species. The solid line in each plot is the smooth function estimate and shaded regions represent approximate 95% confidence intervals. The percentage in each plot represents the proportion of the covariate in the model. The y-axis indicates the number of individuals in log and zero indicates no effect of the covariate. D^* represent the explained deviance of each model. Best model fits are between the vertical lines indicating the 10th and 90th quantiles of the data. 7d and 28d mean respectively 7-days temporal resolution and 28-days temporal resolution.

3.2.2 Predictions

As we focus on coastal seabird habitats, we presented our predictions in two coastal subregions, the Bay of Biscay and the Channel, to better visualize the prediction maps (Fig.13; see Appendix H for general maps of the whole study area).

Predicted seabird distributions revealed a strong link to the coast with highest predicted distributions near the coast whatever the group or the season. Overall, highest predicted densities were observed in bays (Bay of Somme, Mont Saint-Michel Bay...), while waters off northern coast of Brittany and Aquitaine coast were less densely populated.

The distribution of herring gull complex varied little between seasons but densities were higher in the summer (Fig.13a). In winter, they were present along the coasts of the whole study area whereas in the summer they were almost absent off the coast of Aquitaine.

For black-backed gulls, highest densities were predicted in winter around the Bay of Somme and lower densities were found elsewhere in the coastal part of the continental shelf. In the summer, similarly to the herring gull complex, black-backed gulls were absent from off the Aquitaine coast (Fig.13b).

Densities of terns were mostly predicted inshore with low predicted densities in winter and higher densities in the summer (Fig.13c). In summer, highest densities were predicted in bays, near estuaries and colonies (Appendix C).

For cormorants and shags, predicted densities were strictly coastal with low seasonal variations in distribution patterns. Highest densities were predicted around islands, near estuaries and near colonies (Appendix C; Fig.13d).

Divers were only present in winter in the Channel, highest densities being predicted around the Bay of Somme, the Bay of the Seine and the Gulf of Saint Malo (Fig.13e).

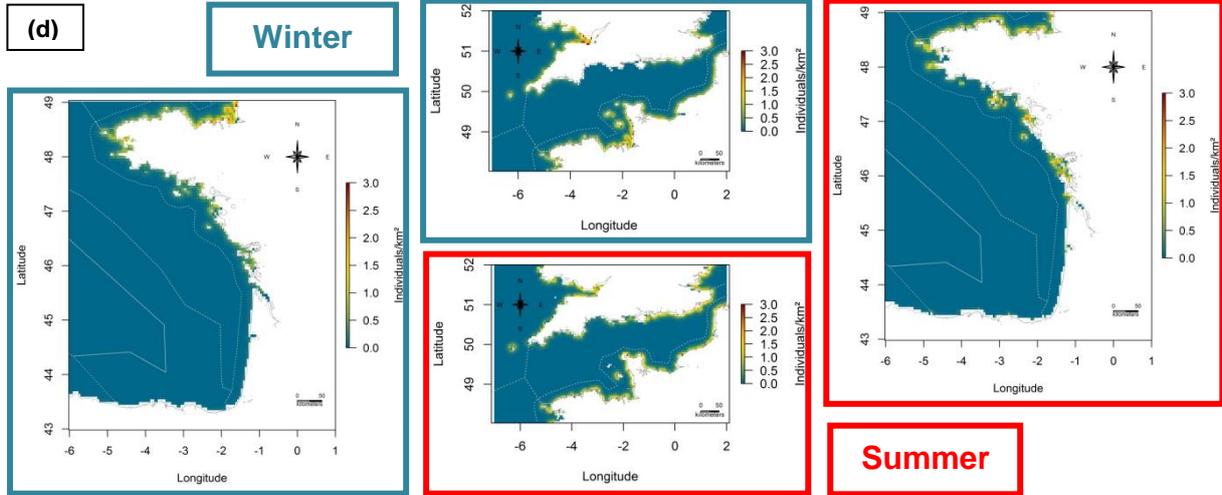
For scoters, densities were only predicted in winter and were the highest in the Mont Saint-Michel Bay, the Iroise Sea area, the *Pertuis Charentais* and the Loire estuary (Fig.13f).

Finally, prediction maps agreed with observed distributions of seabirds (Appendix F). Besides, uncertainty maps (Appendix I) showed that higher predicted densities were associated with lower uncertainties (low coefficient of variation), whereas lower predicted densities were associated with higher uncertainties (high coefficient of variation). Particularly, densities predicted far from the coasts corresponded with the highest uncertainties.

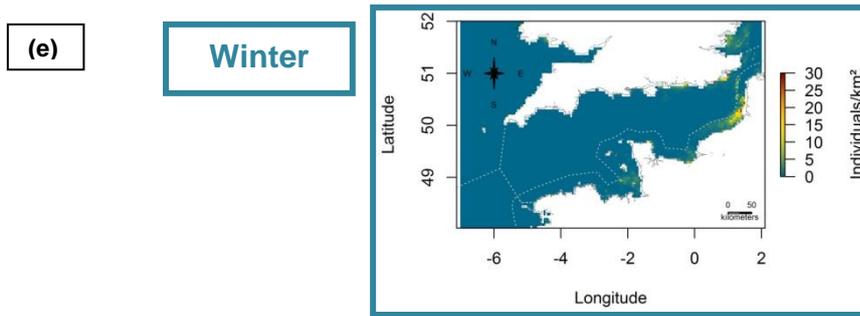
3.3 Assessment of marine protected areas

The relevance of protected areas depended on the species or group of species considered. Following the “Birds Directive”, we considered that a protected area is required to allow the conservation of a species when at least 1% of the ‘national population’ was included in it (Appendix J showed ratios of seabirds groups in all protected areas). In this context ‘national population’ has a strictly administrative meaning with no prejudice of actual population structure.

Cormorants and Shags



Divers



Scoters

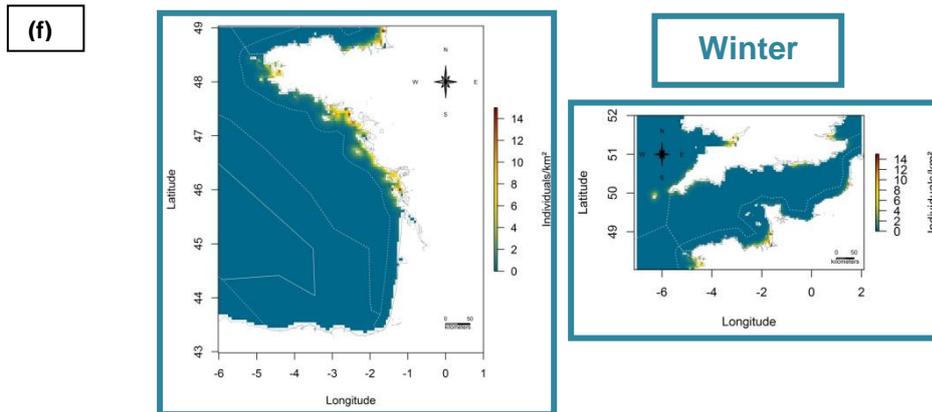


Fig. 13. – Predicted relative density (number of individuals per km²) for each group of seabirds. Predictions encompassed the surveyed sectors but in these figures we highlighted coastal areas (see general predictions in Appendix G). White areas indicate the absence prediction due to the lack of environmental data or environmental data beyond the range of environmental covariates sampled in the surveys.

For the herring gull complex, whatever the season, only three Special Protected Areas (SPA), ("*Pertuis Charentais Rochebonne*", "*Littoral seino-marin*" and "*Ile d'Yeu*") gathered more than 1% of the 'national populations' (Fig.14a). Regarding Marine Nature Parks (MNP), two of them, the MNPs of "*Iroise*" and of "*Estuaires Picards et Mer d'Opale*", appeared to represent more than 1% of 'national population'.

For black-backed gulls, results were contrasted between seasons and sites (Fig.14b). The area "*Pertuis Charentais*" reached the threshold of 1% for the two seasons but the "*Littoral Seino-Marin*" SPA presented the highest value in winter and had a ratio < 1% in the summer. The reverse was true for the "*Ile d'Yeu*" SPA. In both seasons, the two MNPs of the Channel appeared to be relevant for this species group; higher concentrations were shown in winter in the "*Estuaires Picards et Mer d'Opale*" MNP.

For terns, concerning MNPs, results were identical to those of other Laridae (Fig.14c). For the conservation of terns, the SPA "*Pertuis Charentais*" appeared to be the only one being relevant at the two seasons. In addition, "*Estuaire de la Loire - Baie de Bourgneuf*", "*Ile d'Yeu*" and "*Panache de la Gironde*" SPAs appeared to be relevant in winter and "*Littoral seino-marin*", "*Chausey*", "*Baie du Mont Saint Michel*" and "*Banc des Flandres*" SPAs seemed to be relevant in the summer.

For cormorants and shags, the two MNPs located in the English Channel appeared to be above the 1% criterion (Fig.14d). In addition, the SPAs "*Pertuis Charentais*", "*Chausey*", "*Ouessant Molène*", "*Estuaire de la Loire- Baie de Bourgneuf*", "*Littoral seino-marin*" and "*Tregor Goëlo*" all reached values higher than the threshold for the two seasons.

For divers, as we fitted a model only on the English Channel, we considered only this area for the assessment of protected areas (Fig.14e). The MNP "*Estuaires Picards et Mer d'Opale*" appeared to be extremely relevant for the protection of this group since as much as 21.25% of 'national population' appeared to overwinter within the limits of this MPA. The SPAs "*Estuaires Picards*", "*Littoral seino-marin*" and "*Chausey*" were home to over 1% of 'national population' in each site.

Finally, the two MNPs of the Channel were above the 1% criterion for the scoters, as were the SPAs "*Pertuis Charentais*", "*Chausey*", "*Baie du Mont Saint-Michel*", "*Île d'Yeu*", "*Estuaire de la Loire - Baie de Bourgneuf*", "*Mor Braz*" and "*Île d'Houat Hoëdic*" (Fig.14f).

Quite logically, all proposed offshore Marine Protected Areas (MPA) appeared to be irrelevant for any coastal seabird.

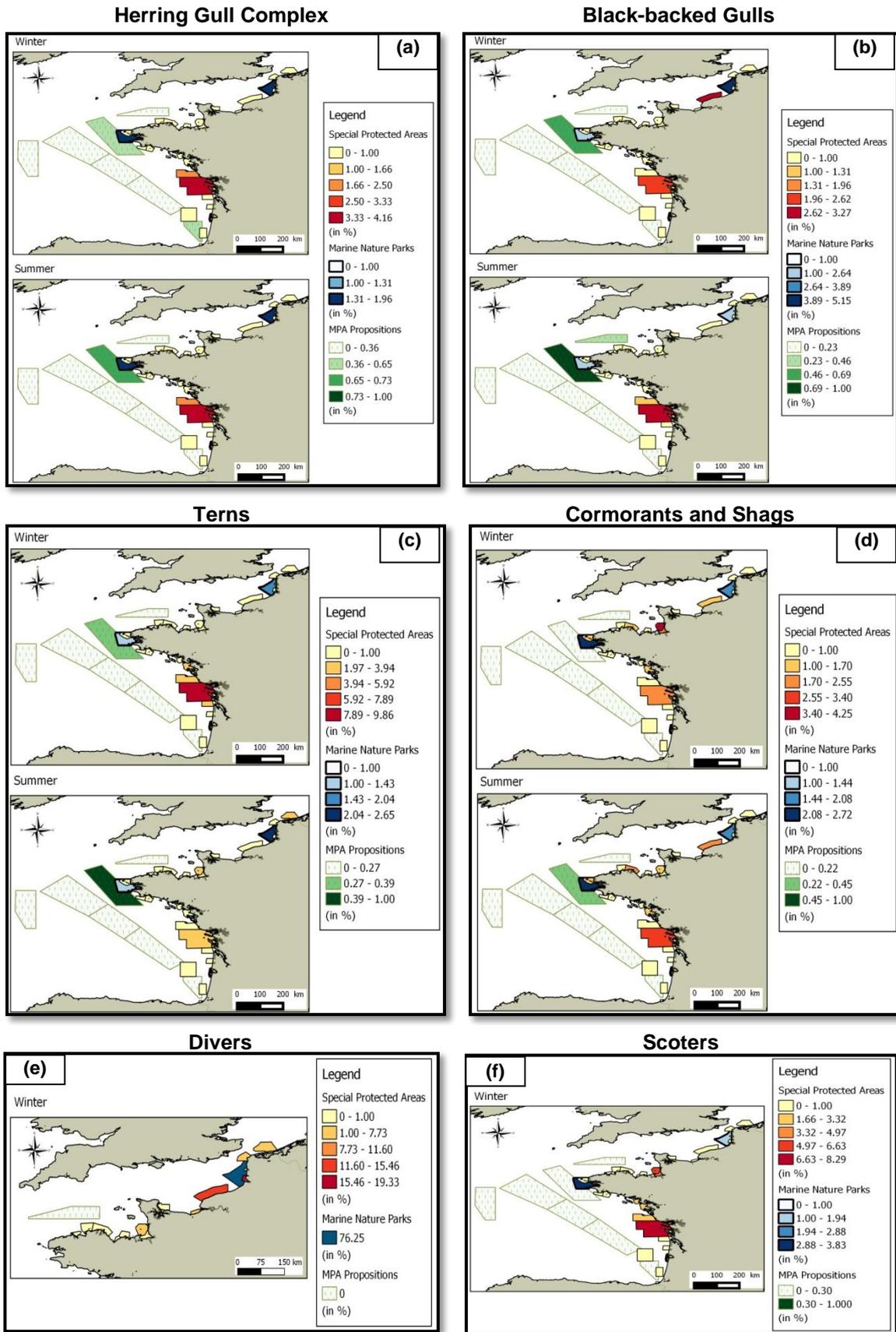


Fig. 14. – Assessment of Special Protected Areas, Marine Nature Parks and Marine Protected areas (MPA) propositions on the French coasts. Classes represented the percentage of individuals in each protected area relative to total number of individuals of each group present in French EEZ. A 1% threshold is prescribed by the Birds Directive for the designation of SPA.

4 Discussion

4.1 Methodological considerations

This study provided for the first time a synoptic view of the distribution of coastal seabirds along the Atlantic and Channel coasts of France, and its seasonal variations, allowing existing and proposed MPAs of different categories to be compared as to their relevance for the conservation at sea of these species. It followed on similar studies conducted in French over-seas Territories' waters of the Caribbean, the southwest Indian and the central South Pacific (Mannocci *et al.* 2012; 2013; 2014) and was based on the same study protocols applied in a distinct region with a distinct species assemblage.

Aerial surveys are increasingly used to determine distribution and abundance of seabirds and other pelagic megafauna, because they have the potential to cover extended areas in a relatively short period of time and at comparatively lower costs than by using dedicated vessels. However, two sources of limitations are generally recognised to be associated with such surveys. Firstly, weather conditions affect seabird detection as a result of sun glare or poor sea state, introducing a negative bias that likely increases with distance from the track line. However, according to Certain and Bretagnolle (2008), visibility bias have a limited effect on pelagic aerial surveys for most seabird species provided that strip width is kept within a few hundred meters. Here, observation strip was limited to 200m on each side of the aircraft, restricting potential source of bias. Overall, with the strip transect methodology, we assumed that all individuals were detected within the strip (Tasker, *et al.*, 1984). Nevertheless, some seabirds were missed during flights, therefore densities were biased low in most cases. The other source of error relates to the difficulty to identify seabirds from the air. Indeed, during flights, species with common morphology, like European shags and great cormorants, the different terns, or the variety of medium-sized gulls, were difficult to tell apart; that is why they were pooled into groups.

In this study, GAMs were used to model seabird habitats following Vilchis *et al.* (2006), Ferguson *et al.* (2006), and Mannocci *et al.* (2013, 2014). Indeed, compared to GLMs (General Linear Models), GAMs are non-parametric models which allow not to constrain predictor variables and, thanks to non-parametric smooth functions, are more flexible than GLMs. They also fit better to the data and provide non-linear relationships between densities of individuals and environmental covariates (Becker *et al.*, 2010). Though, they are data-intensive, *i.e.* they needed a lot of sightings to work well (Ferguson *et al.*, 2006) and thus, model for scoters in summer did not work. Finally, to avoid over-fitting and following Ferguson *et al.* (2006), degree of freedom were restricted to 3 for each smooth function.

In addition, trying to compensate the large number of zero, inherent to the method of data counting, we have attempted to model habitats using zero-inflated models. This method combines two models, one which reports the number of individuals once they are detected and the other explains the probability of non observation (*i.e.* zeros) generally with a Logit function (Wenger and Freeman, 2008). This method is appropriate for describing the spatial distribution of rare species such as marine mammals, but seabirds have a higher probability of detection and present higher densities so this method was not necessary. Indeed, modelling with zero-inflated models, we have hardly noticed any difference between the predictions maps from GAMS and zero-inflated models, so we chose to stick to this methodology the relevance of which has been proven repeatedly (Becker, *et al.*, 2010; Mannocci, *et al.*, 2014; Vilchis, *et al.*, 2006).

Regarding environmental data, using indirect or distal oceanographic covariates, instead of more causal or proximal ones, such as prey abundance or availability, could cause a mis-

explanation of seabird distributions (Austin, 2002). However, the fairly high explained deviances obtained for most models showed their relative effectiveness. The absence of some variables in selected models such as distance to nearest colony could be explained by the interaction between other covariates. Distance to nearest colony was often correlated to distance to nearest coast because of the high number of colonies located along the coastline (see appendix C for colony locations). Also, since not all individuals of a population are involved in the breeding at the same time, distance to nearest colony may not be as relevant as distance to coast; this would be particularly the case in species known to have a poorly synchronized breeding season such as the great cormorant for instance. Finally, we tested some descriptors of seabed substrate as environmental variables but none was ever selected although several species of interest are notorious epibenthic feeders (cormorant and shag, divers, scoters). This may be due to the inadequate resolution of these data (too coarse) or to the fact that this information is already expressed by more distal information such as current speed for instance.

Finally, the geographical scale used for fitting the models and predicting distributions (the Atlantic and Channel waters) could be considered too large and the spatial resolution (generally 0.05° spatial resolution, *i.e.* about 5 km) too coarse given the focus of the present work on coastal species. Indeed, predicting on smaller areas would allow the use of some variables at finer resolution, possibly informing the manager at the scale of local processes that are important for a particular MPA of interest. Conversely the temporal scale of the predictions, restricted here to the seasons of the survey, could be considered too short for managers that would endeavour to design MPAs and their management plans for the long term, *i.e.* where and when most animals are present year after year. However, the aim of the study was not to inform the manager of every single MPA about the best management plan to be implemented. Instead, the aim of the study was to determine coastal seabird distribution at a large scale in English Channel and eastern North Atlantic in order to make an overall assessment of N2000 sites and offshore MPA proposals. In this point of view, we made the assumption that the year of the survey was representative of seabird distribution in the long term. We were reinforced in this choice by the fact that physiographic covariates, that are static by definition, contributed to over 60% of the explained variance in all cases but two (terns in the summer and divers). Additionally, the rest of the explained variance was partly explained by current speed and SSH, two oceanographic covariates strongly driven by tide and physiography, and therefore not subject to major year-to-year changes. However, a next refinement would be to make predictions over a period of 10 years to assess year-to-year variability in coastal seabird distribution. This would require extensive and time-consuming work of environmental variable downloading and processing, which was not considered an immediate priority.

4.2 Seabird response to the variability of oceanographic conditions and link with strategies of habitat use

Thanks to GAMs, we could model and predict coastal seabird distributions in the English Channel and the eastern North Atlantic during two seasons (winter 2011-12 and summer 2012). For the herring gull complex and black-backed gulls, we noticed a significant effect of the nearest sandy coast in winter and the nearest rocky coast in the summer. This difference could be explained by the settlement of most colonies on rocky coasts in the summer and the necessity for adults to commute back and forth between colonies and foraging habitats to share incubation duties and feed the chicks, whereas in winter, birds extensively use sand banks and beaches as roosting sites (Cadiou *et al.*, 2005). This would also explain the marked predicted absence of these two groups off the Aquitaine coasts in the summer (Fig.13).

Besides, the seasonal distribution of the herring gull complex is clearly influenced by currents, SST in winter and altimetry (SSH) in summer with a preference for comparatively weaker temperatures in winter and higher variations of altimetry in the summer, this latter features being likely associated to tides. This in line with gulls expanding their distribution very close to the coast in winter, whereas in the summer, tidal front driven phytoplankton production and therefore prey aggregations would influence their foraging activity (Oschlies and Garçon, 1998). Additionally, the 28-day resolution of currents and SSH variation indicated a constant preference for lower current speed and higher SSH variations. In contrast, the 7-day resolution of SST and SSH suggested weekly or even daily adjustments of foraging grounds according to temperature and altimetry patterns, in particular in the summer.

Contrary to the herring gull complex, SST and SSH influence black-backed gull distributions irrespective of the season with a preference for cooler SST and high variations of SSH and SST in winter, suggesting the preferential use of areas with stronger tides in large embayments. In contrast, in summer they would prefer weaker currents, and lower SSH and SST variations, more likely associated with areas of weaker tidal currents (Koutsikopoulos and Le Cann, 1996). Overall, black-backed gulls responded better to 28-day than to 7-day temporal resolutions, indicating that they would feed at places that are recurrently favourable irrespective of the situation of the exact day.

Regarding terns, we predicted much lower densities in winter and an influence of the nearest sandy coast in the summer (Fig.13). These species mostly breed on shallow coasts, including sand banks, shallow islets and salt-pans, and generally migrate at lower latitude in winter (BirdLife International, 2014). In addition to nearest coast, terns were clearly influenced by fronts, low speed currents and low average SST in winter, which suggest that they would forage on more productive zones. In the summer, higher densities were influenced by stronger SSH variations which cause nutrients mixing and therefore prey aggregations (Grioche and Koubbi, 1997), confirming Schwemmer, *et al.* (2009)'s work. In winter, terns responded better to 7-day resolution variables whereas in the summer they responded better to 28-day resolution variables, suggesting a less opportunistic foraging strategy, based on the knowledge of recurrently favorable foraging sites as a response to the addition energy costs incurred by adults rearing their chicks.

Irrespective of the season, cormorants and shags were strongly linked to the coast as they feed within a 35 km radius from the colony where they incubate the eggs and rear their chicks in the summer, and resting on roosting sites when non breeding (BirdLife International, 2014). This relationship is clearly shown by the GAMs (Fig.12). In addition to the distance from the coast, in winter, high bird densities were mainly associated to high SSH variations, suggesting that cormorants and shags would be sensitive to prey aggregations near the coasts or to areas with extensive tidal movements. In the summer, densities were higher for weaker currents, higher SST and weaker SST variations, typical characteristics of productive shallow waters (Koutsikopoulos and Le Cann, 1996). All these results were compatible with the strictly coastal distributions observed on predictions maps for both seasons (Fig.13). Cormorant and shag distributions were more associated with variables at 28-day resolution in winter whereas in the summer they better responded to currents and SST at a 7-day resolution.

Divers were mostly present in the study area in winter. They were sensitive to depth, highest densities being generally recorded in waters shallower than 20 m (BirdLife International, 2014), which was confirmed by the GAMs (Fig.12). They mostly lived in bays and estuaries where food is abundant, altimetry is weak and tidal currents relatively high (BirdLife International, 2014). Predictions maps clearly showed divers concentration in bays and estuaries (Bay of Somme, Mont Saint-Michel Bay...). Divers only responded to static

covariates and 7-day resolution oceanographic variables suggesting that they would adapt their foraging strategies to short-term variations of SSH and currents.

Scoters were mostly dwelling near the coasts where currents and SST variations were weak and SSH variations high (Fig.12), *i.e.* they preferred shallow waters with extensive tidal movements and high accessibility to their benthic prey, quite in line with the literature (BirdLife International, 2014) and predictions maps which showed a strictly coastal distribution (Fig.13). Scoters generally responded to oceanographic variables at 7-day resolution, again suggesting some degree of short term adjustment of habitat use according to SSH variations and currents.

4.3 Relevance of marine protected areas

Through this study, we aimed to assess marine protected areas along the English Channel and eastern North Atlantic coasts. The Special Protection Areas (SPAs) were created under the Birds Directive (Directive 2009/147/CE, Parlement Européen, 2009) relative to the conservation of wild birds. All Special Areas of Conservation (SACs), designated under the Habitats Directive for non-bird features (species and habitats), and SPAs constitute the *Natura 2000* network, which aims to contribute to the conservation of biological diversity in the EU.

To make our assessment, we considered the 1% level (1% of 'national population' live at least seasonally in the MPA) as the target threshold for establishing an SPA, as prescribed by the Birds Directive. Here, we determined if every MPA, either existing, proposed or only being considered, would reach this threshold by using the predicted densities integrated within each MPA compared to estimated densities integrated across the whole study area. The same assessment was conducted for all existing SPAs, for the three Marine Nature Parks (MNP) established to date and for a number of areas that are currently being discussed for the designation of new N2000 sites. A site will be considered relevant for coastal bird conservation if it is predicted to reach the 1% threshold, and otherwise irrelevant.

Concerning MNP, the MNP "*Baie d'Arcachon*" is assessed irrelevant for coastal bird conservation at sea as none of the species of interest was present at the 1% threshold. This does not preclude that this MNP can offer an efficient protection for coastal seabirds on their terrestrial habitat; hence, this MNP shelters a large Tern colony on the Banc d'Arguin sand bank (Cadiou, *et al.*, 2005), but it appears that most of these birds forage out of the limits of the park. The other two MNP, the "*Iroise*" and "*Estuaires Picards et Mer d'Opale*" parks were assessed relevant for coastal bird conservation at sea, as, thanks to their large surface areas, almost all species group of coastal seabirds reached the 1% threshold; in addition, a special case must be made about the high value of the "*Estuaires Picards et Mer d'Opale*" MNP which is home to a fifth of the diver populations wintering in French waters (Fig.14).

Regarding offshore areas currently being discussed for the future designation of N2000 sites, none is of any relevance for coastal seabirds, quite expectedly. Given the great distance to shore of most of these sites none reached the 1% threshold despite of their generally large to very large surface areas.

For existing SPAs, when one considers all studied species for the two seasons, it appeared that only 14 out of 66 SPAs designated along the Channel and eastern North Atlantic French coasts were relevant for the conservation at sea of at least one of these groups. These areas were: "*Pertuis Charentais-Rochelaise*", "*Ile d'Yeu*", "*Littoral seino-marin*", "*Chausey*", "*Estuaire de la Loire – Baie de Bourgneuf*", "*Tregor Goëlo*", "*Estuaires Picards*", "*Cap Gris-Nez*", "*Ouessant Molène*", "*Panache de la Gironde*", "*Banc des Flandres*", "*Baie du Mont Saint-Michel*", "*Mor Braz*" and "*Iles d'Houat and d'Hoëdic*". There are two main reasons behind this assessment. Firstly, some covariates are not available for the most coastal pixels of the study area, precluding any prediction to be made (see "*Baie du Morbihan*" and "*Estuaire de la Gironde*" sites). Secondly, many N2000 sites, even when they

shelter significant coastal seabird colonies or winter roosting sites are not selected because their extension at sea is too limited. This is a clear case in favour of larger MPAs for these coastal species, when conservation issues are based on processes that take place at sea. Alternatively, a network approach to the management of sites that share common features, here coastal seabird species, would appear as the only way by which most of these small SPAs could play a role in the conservation at sea of these features. Indeed, when one sums up the fraction of the 'national population' that use habitats present within the complete network of SPAs, it can be estimated that from 12.4-33.6% according to species groups is under N2000 protection (Appendix J). It is therefore crucial that the many authorities involved in the development and implementation of all the site-specific management plans act in close co-operation.

This evaluation should contribute to the scientific basis to be used by AAMP in its negotiations for the improvement of the current MPA network with other actors involved in the N2000 process, such as managers and fisheries.

5 Conclusion and prospects

This study was part of a larger project aiming at using static physiographic and dynamic oceanographic variables to model pelagic megafauna habitats from sightings collected during aerials surveys that were carried out for the first time across French metropolitan waters in winter 2011-12 and summer 2012. Here, we particularly focused on coastal seabirds, defined as species that have a daily environmental or ecological link with the coast to accomplish some key biological functions such as nesting, chick rearing or simply resting. The GAMs and the predicted distributions clearly showed this link with the coast, but without specifically reflecting the locations of colonies as these colonies are fairly regularly spread along the coastline, and for several species partial mismatch between breeding season and survey period, as well as poorly synchronized breeding, result in an extensive fraction of the population being unrelated to colonies during part of the summer. We were also able to predict how some seabirds responded better to stable long-term structures while others were able to adjust their foraging strategies to shorter-term environmental variations.

Thanks to the large spatial coverage of the study, this work allowed us to provide a first synoptic assessment of marine protected areas established, proposed or being considered along the Channel and eastern North Atlantic French coasts under the N2000 network and other national conservation tools. It appeared that less than a quarter of existing SPAs reached the 1% threshold prescribed by the Birds Directive. Developing larger protected areas and ensuring tightly co-ordinated management of the existing ones are the two avenues proposed for improving the relevance of the French N2000 network for the conservation at sea of coastal seabirds.

This work has to be complemented with long-term predictions that could highlight the responses of seabird to year-to-year variations of oceanographic variables and thus contribute to refine the predictions made here. Similar works are being conducted for all the other components of pelagic megafauna (pelagic seabirds, cetaceans, sea turtles...) in French metropolitan waters. They should ultimately provide a reference for the conservation and monitoring of these species in fulfilment of the EU Birds Directive, Habitats Directive and Marine Strategy Framework Directive.

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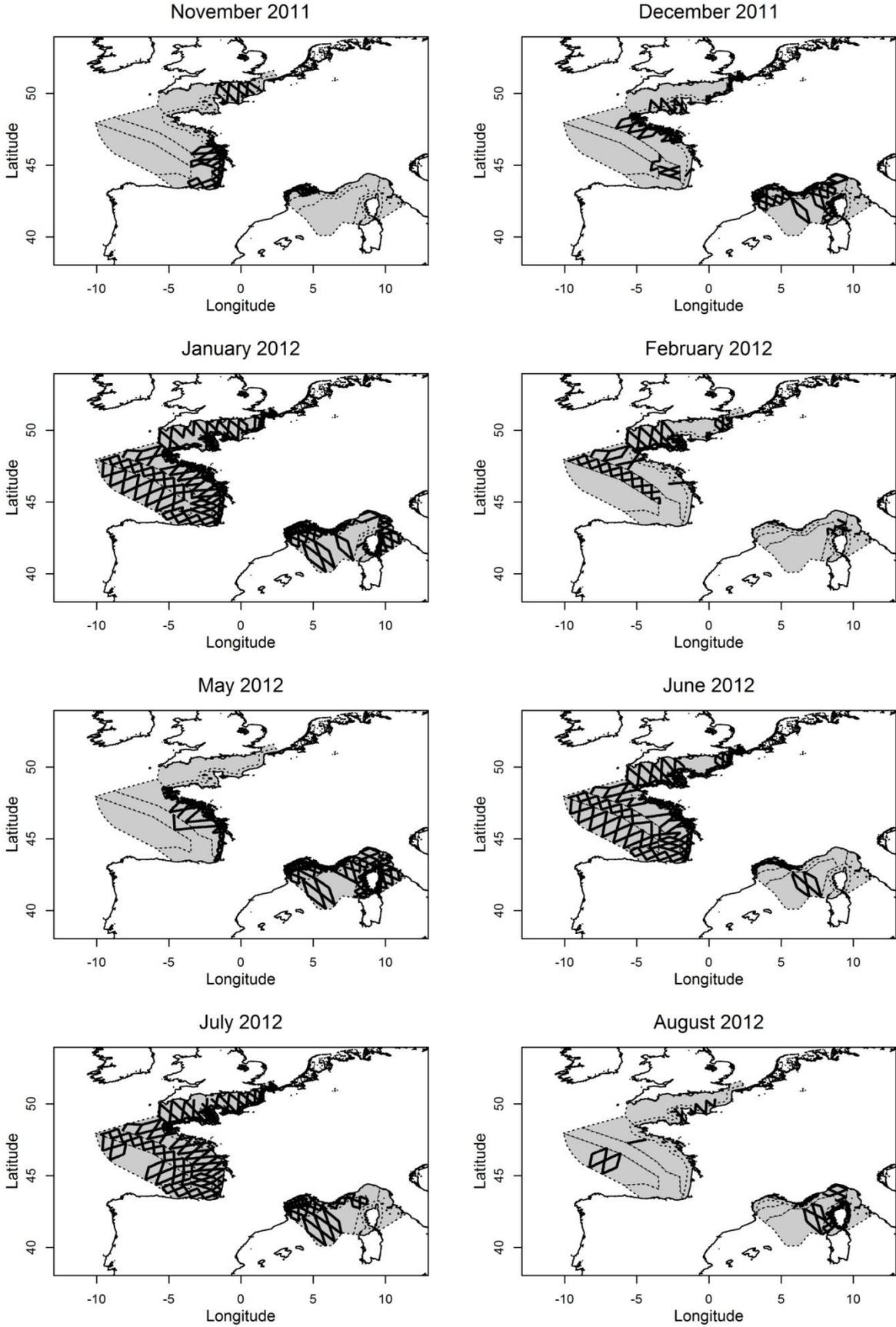
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Appendices

Appendix A: Presence on the French coasts and breeding periods of each studied species. (Sources: Cadiou *et al.*, 2005; Muséum National d'Histoire Naturelle, 2013)

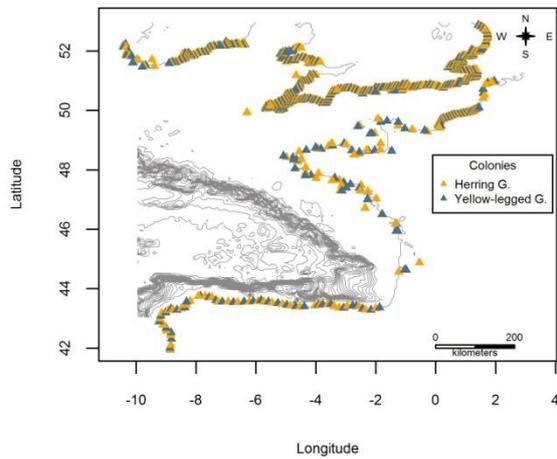
Group names	Common Name	Scientific Name	Breeding Period	Presence on the French coasts
herring gulls complex	Herring gull	<i>Larus argentatus</i>	December to July	All the year
	Yellow-legged gull	<i>Larus michahellis</i>	September to mid-June	All the year
Black-backed gulls	Great black-backed gull	<i>Larus marinus</i>	December to June	All the year
	Lesser black-backed gull	<i>Larus fuscus</i>	End-January to June	All the year
Terns	Arctic tern	<i>Sterna paradisaea</i>	May-June	Marginal
	Common tern	<i>Sterna hirundo</i>	March to August	March to August
	Little tern	<i>Sterna albifrons</i>	April to August	April to August
	Sandwich tern	<i>Thalasseus sandvicensis</i>	March to August	All the year
Cormorants and Shags	Great cormorant	<i>Phalacrocorax carbo</i>	December to August	All the year
	European shag	<i>Phalacrocorax aristotelis</i>	December to end-July in northern Atlantic coast October to July in Corsica	All the year
Divers	Divers	<i>Gavia spp</i>	April to September	October to April
Scoters	Common scoter	<i>Melanitta nigra</i>	May to July	July to April
	Velvet scoter	<i>Melanitta fusca</i>	May to August	October to March

Appendix B: Monthly effort realised during the two aerial surveys SAMM.

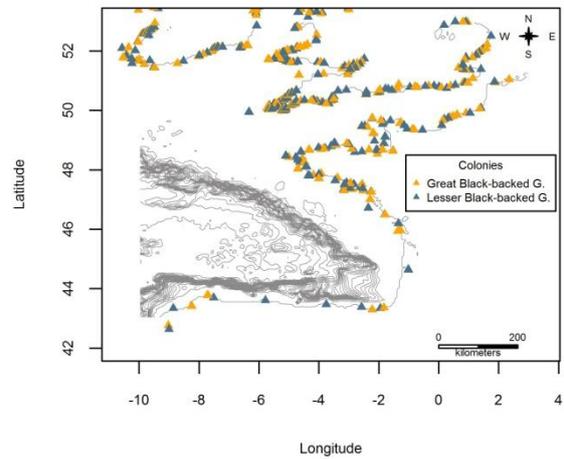


Appendix C: Colonies relevant to the study area. (Summarized from: Cadiou *et al.*, 2005; JNCC (Joint Nature Conservation Committee; www.jncc.defra.gov.uk); SEO/BirdLife (www.seo.org)). Since 2005, it is possible that some colonies have disappeared and others have emerged in France but no census of breeding seabirds has been done since.

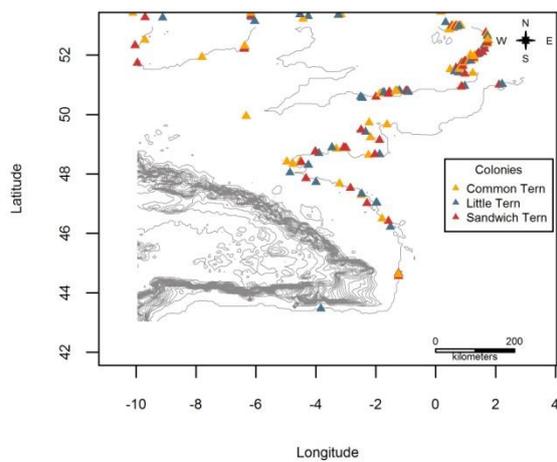
Herring Gull Complex



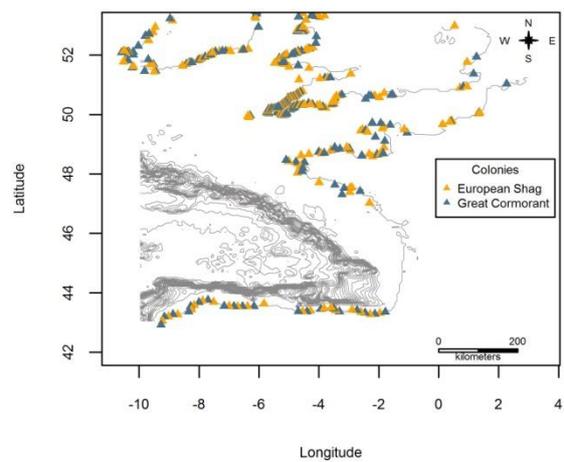
Black-backed Gulls



Terns



Cormorants and Shags



Appendix D: Environmental variables tested but not included in models.

- The nature of the seabed has been tested for coastal models based on maps provided by the MPA Agency for Channel and Bay of Biscay areas. The classification has been simplified into 5 classes: Sands, Muds, Rock or biogenic reef, Coarse or mixed sediments and Seagrass meadows to facilitate the analysis. Because of the interaction with other variables like currents and the nature of the variable (qualitative variable), we chose not to include it in models.

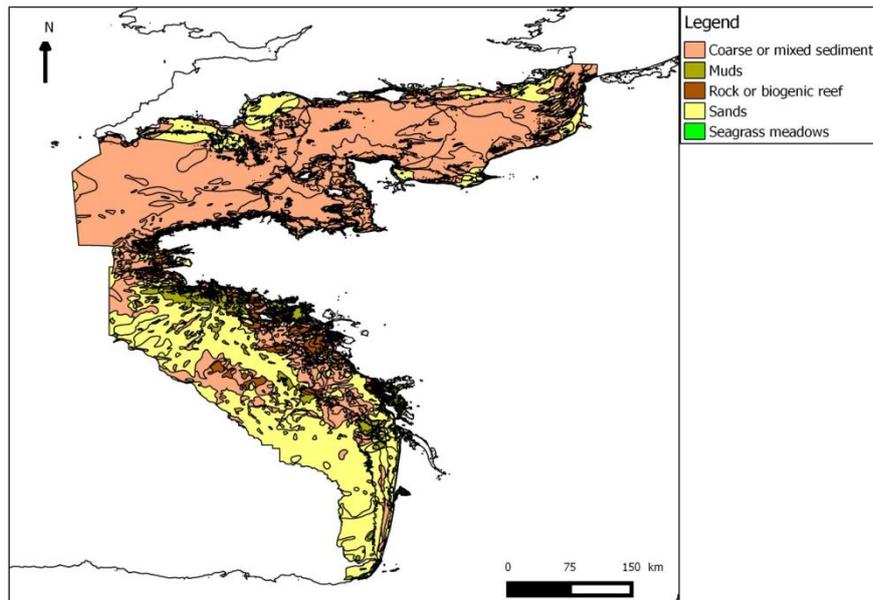


Fig. Nature of the seabed in Channel/ Bay of Biscay.

- We also extracted the sea surface salinity (SSS) from MARS 3D models like SST (2.4) and we calculated the average, the variance and the gradient over the two periods. However, because of the weak variations of the values except in estuaries, this variable distorted the models and induced huge confidence intervals, that is why we did not include the variable and in models.

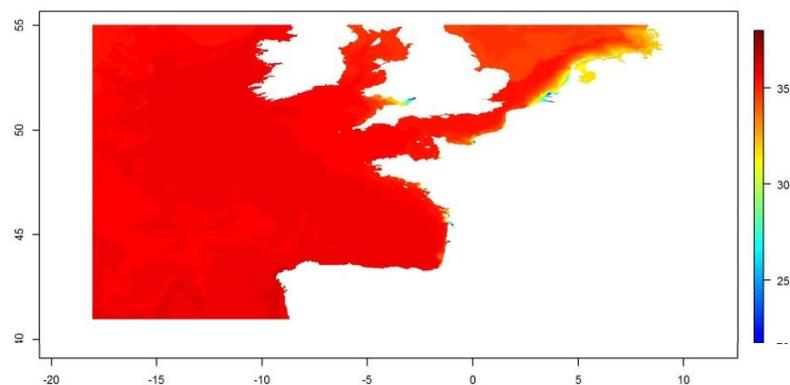
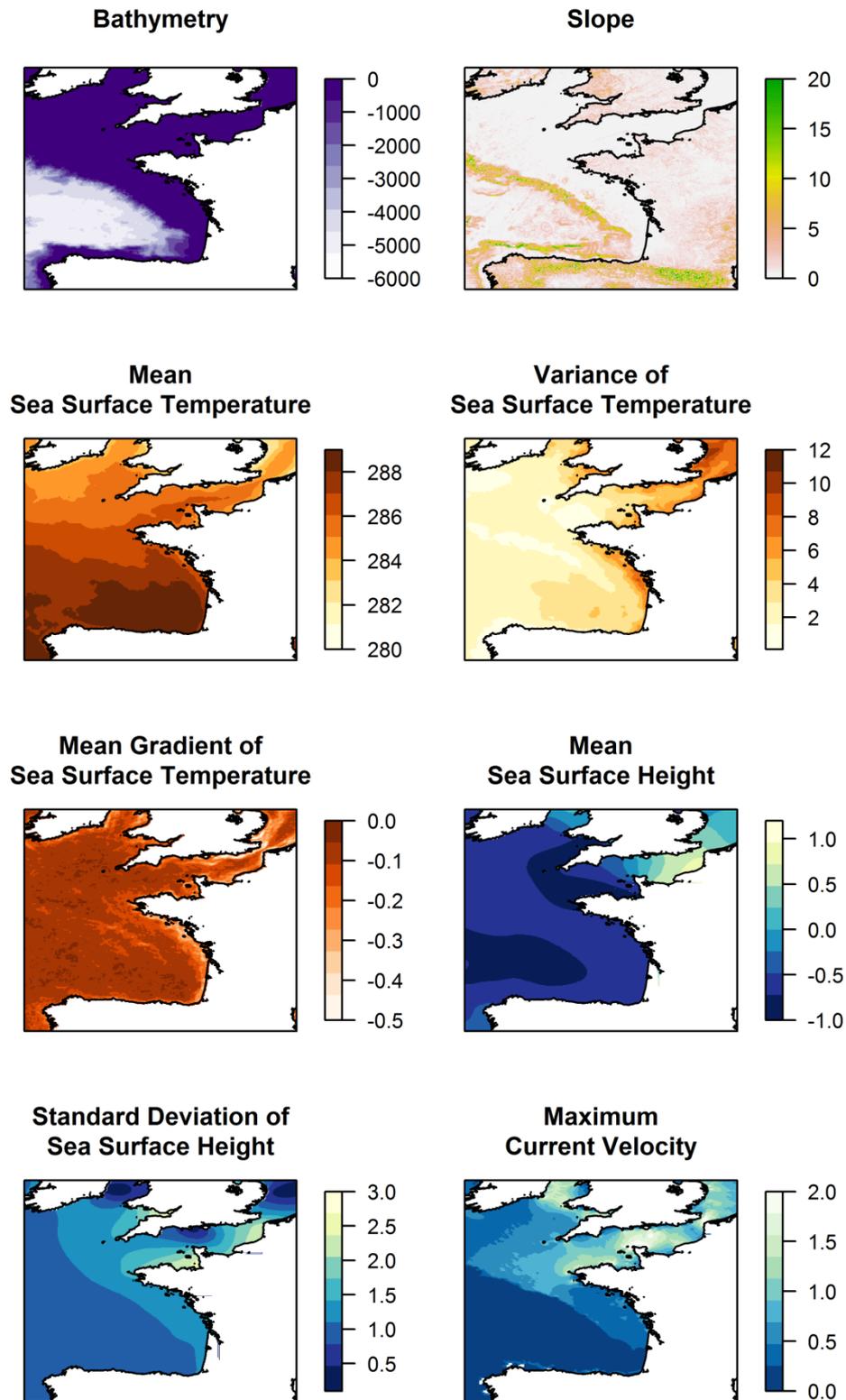


Fig. SSS recorded for the 19/11/2011 (Source: MARS3D model)

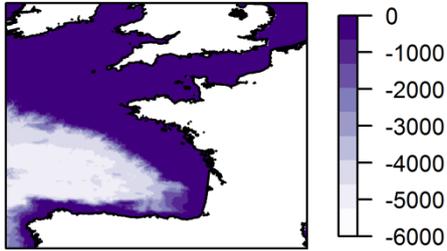
Appendix E: Averaged maps of covariates over the two seasons.

WINTER

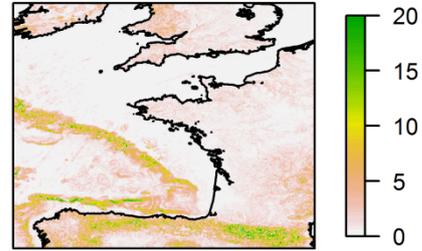


SUMMER

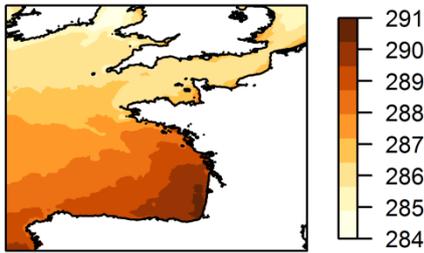
Bathymetry



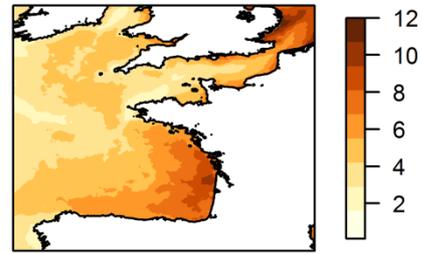
Slope



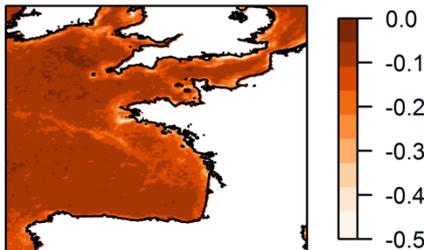
Mean Sea Surface Temperature



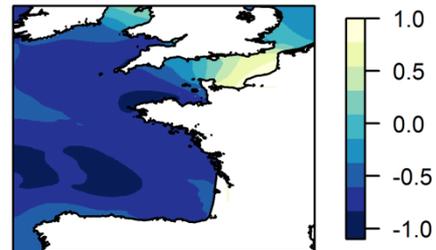
Variance of Sea Surface Temperature



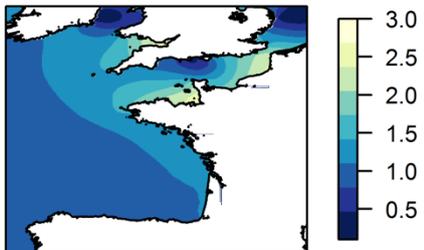
Mean Gradient of Sea Surface Temperature



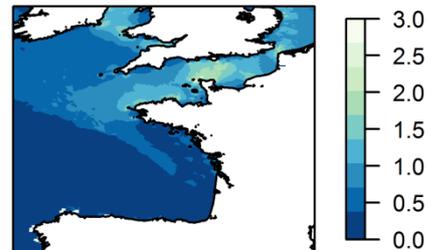
Mean Sea Surface Height



Standard Deviation of Sea Surface Height



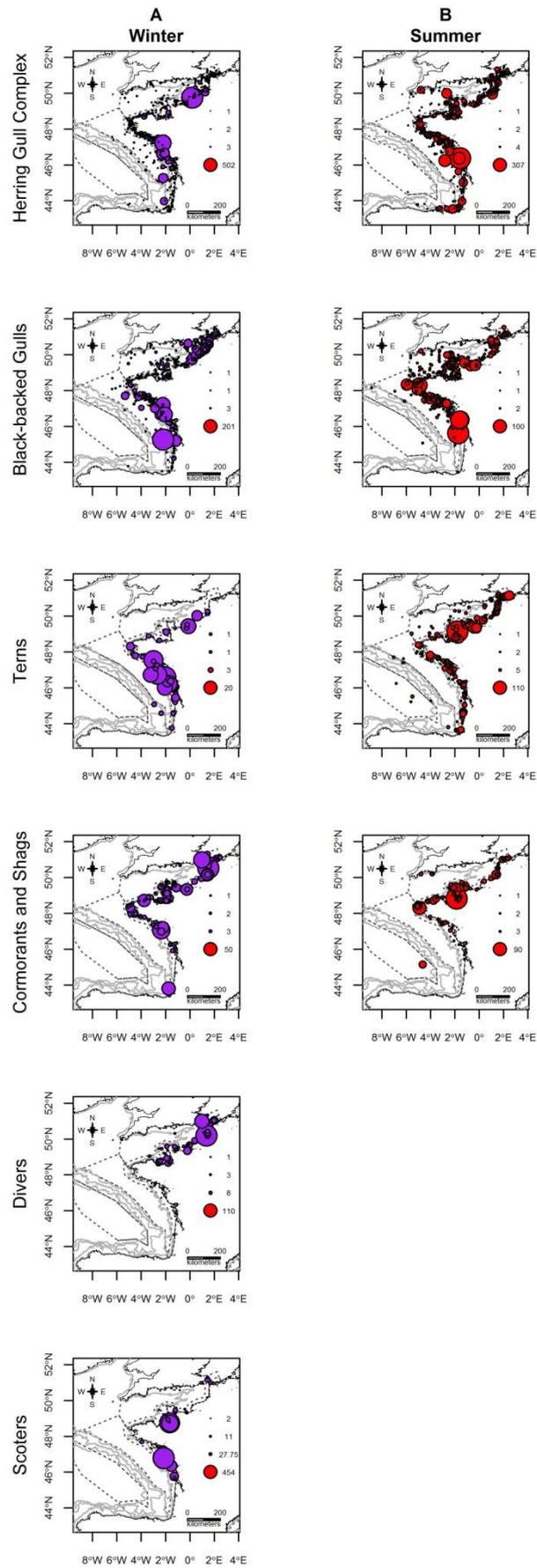
Maximum Current Velocity



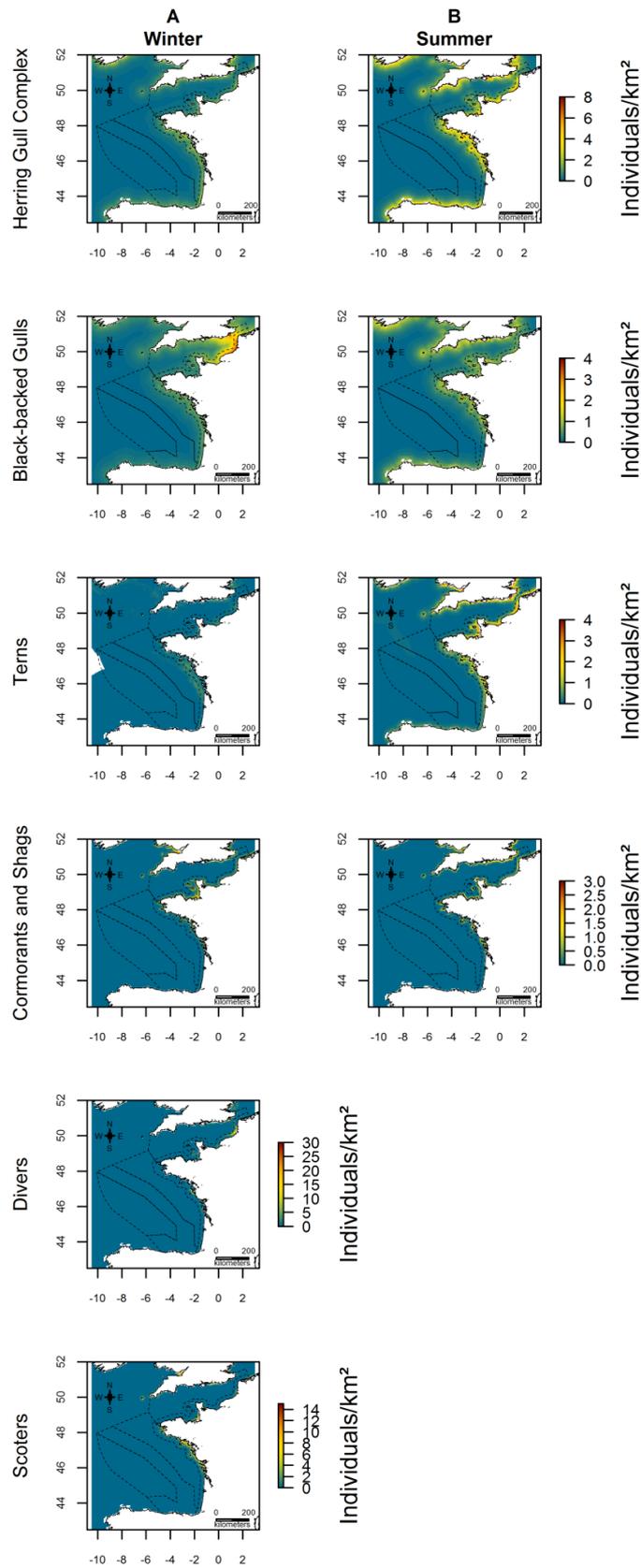
Appendix F: Seabird species, number of sightings and number of individuals (in parenthesis) observed during the two surveys

Common Name	Classification	English Channel		Bay of Biscay	
		Winter	Summer	Winter	Summer
Auks <i>spp</i>	<i>Alcidae spp</i>	0 (0)	0 (0)	6 (7)	1 (2)
Guillemot / Penguin	<i>Alca / Uria spp</i>	3785 (12133)	135 (327)	2430 (4701)	104 (201)
Northern Gannet	<i>Morus bassanus</i>	1914 (5336)	1457 (2415)	1783 (5787)	1083 (1795)
Northern Fulmar	<i>Fulmarus glacialis</i>	226 (499)	95 (108)	120 (241)	100 (175)
Mediterranean shearwater	<i>Calonectris diomedea</i>	0 (0)	0 (0)	0 (0)	110 (324)
Small Shearwater	<i>P. yelkouan/ puffinus/ mauretanicus</i>	3 (13)	97 (464)	13 (18)	82 (306)
Puffin <i>spp</i>	<i>Puffinus sp / Calonectris spp</i>	3 (3)	1 (1)	2 (4)	5 (8)
Large Shearwater	<i>Calonectris/ P. gravis /griseus</i>	0 (0)	0 (0)	0 (0)	118 (567)
Petrel ind.	<i>Hydrobatidae/Oceanites/ Oceanodroma</i>	5 (10)	66 (89)	152 (296)	482 (629)
Common Gull	<i>Larus canus/audouinii</i>	95 (117)	2 (2)	14 (14)	0 (0)
Herring Gull Complex	<i>Larus argentatus / michahellis</i>	394 (1234)	891 (1549)	498 (1899)	658 (1818)
Black-backed Gull	<i>Larus marinus/ Larus fuscus</i>	509 (961)	207 (308)	256 (975)	124 (245)
Lesser black-backed Gull	<i>Larus fuscus</i>	4 (4)	128 (185)	17 (24)	260 (508)
Great black-backed Gull	<i>Larus marinus</i>	78 (102)	43 (62)	13 (13)	54 (112)
Large Gulls <i>spp</i>	<i>Larus fuscus/argentatus...</i>	253 (2999)	192 (1175)	138 (1695)	230 (2076)
Little Gull	<i>Larus minutus</i>	95 (227)	3 (22)	44 (51)	3 (4)
Black-headed Gull	<i>Larus ridibundus</i>	36 (72)	30 (38)	32 (52)	8 (11)
Mediterranean Gull	<i>Larus melanocephalus</i>	10 (14)	0 (0)	6 (7)	3 (4)
Black-legged Kittiwake	<i>Rissa tridactyla</i>	1172 (1571)	39 (49)	1083 (1662)	34 (44)
Small Gulls ind.	<i>Larus ridibundus / melanocephalus...</i>	876 (2370)	235 (415)	723 (1375)	109 (198)
Sandwich Tern	<i>Sterna sandvicensis</i>	1 (1)	115 (172)	10 (25)	96 (147)
Common/Arctic Tern	<i>Sterna hirundo / paradisaea</i>	0 (0)	293 (666)	10 (35)	111 (185)
Little Tern	<i>Sterna albifrons</i>	0 (0)	6 (13)	0 (0)	0 (0)
Terns <i>spp</i>	<i>Sterna spp</i>	11 (24)	62 (173)	56 (118)	48 (81)
Laridae <i>spp</i>	<i>Laridae spp</i>	243 (2585)	47 (361)	56 (1245)	34 (902)
Great Skua	<i>Catharacta skua</i>	50 (52)	21 (22)	141 (156)	46 (53)
Arctic/ Pomarine Skua	<i>Stercorarius parasiticus / pomarinus</i>	4 (4)	0 (0)	0 (0)	5 (5)
Great Cormorant	<i>Phalacrocorax carbo</i>	0 (0)	11 (16)	37 (103)	15 (18)
European Shag	<i>Phalacrocorax aristotelis</i>	0 (0)	3 (3)	7 (13)	5 (27)
Cormorants and Shags	<i>Phalacrocorax spp</i>	191 (415)	142 (360)	15 (24)	22 (69)
Divers <i>spp</i>	<i>Gavia spp</i>	212 (843)	0 (0)	3 (3)	0 (0)
Velvet Scoter	<i>Melanitta fusca</i>	3 (17)	0 (0)	0 (0)	1 (1)
Common Scoter	<i>Melanitta nigra</i>	16 (209)	1 (5)	20 (680)	0 (0)
Scoters <i>spp</i>	<i>Melanitta spp</i>	67 (833)	22 (88)	31 (347)	0 (0)
Brant Goose	<i>Branta bernicla</i>	50 (221)	0 (0)	11 (909)	0 (0)
Common Shelduck	<i>Tadorna tadorna</i>	0 (0)	1 (1)	4 (145)	4 (59)
Grebes <i>spp</i>	<i>Podiceps spp</i>	5 (5)	0 (0)	10 (11)	0 (0)
Other Birds	<i>aves</i>	47 (1635)	50 (194)	56 (593)	89 (312)
Total	Sightings Individuals	10358 34509	4395 9283	7797 23228	4044 10886

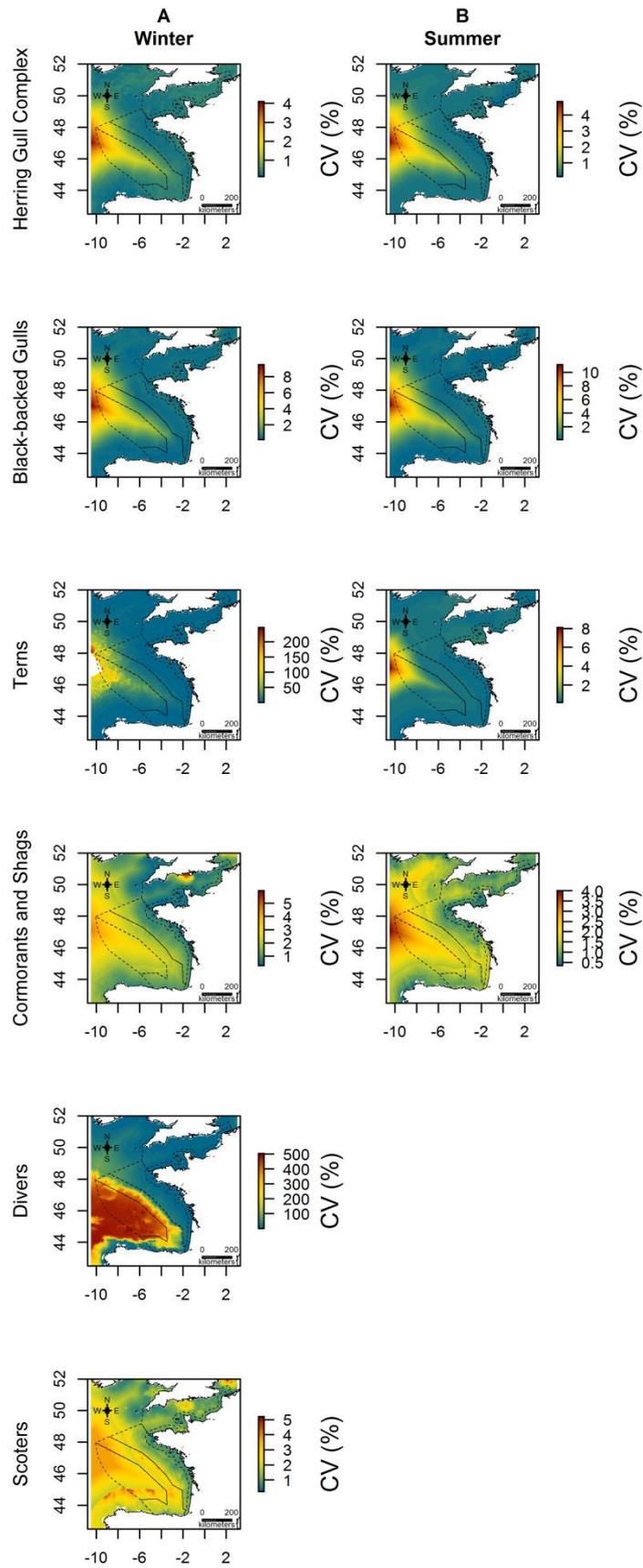
Appendix G: Distribution maps of seabird sightings for each group.



Appendix H: Predicted relative density (number of individuals per km²) for each group of seabirds on the whole prediction area. The scale in common to both seasons for each group, in order to allow comparisons



Appendix I: Uncertainty maps associated to predictive relative density of each group. (CV: coefficient of variation in %)



Appendix J: Ratio of individuals presented in each protected area. Identification Numbers of MPA propositions correspond to those showed on Figure 11 (MPA: Marine Protected Areas; Win: winter; Sum: summer). The absence of number indicated the inability to assess the SPA because of the absence of prediction (absence of values of environmental variables). Highlight sites indicated threshold $\geq 1\%$ for at least one species group. TOTAL indicated the proportion of each group included in the full N2000 Network.

SITCODE	SITENAME	herring gull complex		black-backed gulls		terns		cormorants and shags		divers	scoters
		Win	Sum	Win	Sum	Win	Sum	Win	Sum	Win	Win
FR2210068	ESTUAIRES PICARDS BAIE DE SOMME ET D AUTHIE	0.18	0.15	0.30	0.06	0.07	0.37	0.27	0.18	5.39	0.69
FR2310044	ESTUAIRE ET MARAIS DE LA BASSE SEINE	0	0	0.31	0	0	0	0.02	0	0	0
FR2310045	LITTORAL SEINO-MARIN	0.90	1.00	3.27	0.86	0.56	0.96	1.53	1.93	3.57	0.08
FR2510037	CHAUSEY	0.70	0.92	0.24	0.67	0.91	2.01	4.25	1.13	2.03	6.42
FR2510046	BASSES VALLEES DU COTENTIN ET BAIE DES VEYS	0.03	0.11	0.02	0.02	0.01	0.29	0.11	0.08	0.02	0.08
FR2510047	BAIE DE SEINE OCCIDENTALE	0.34	0.59	0.38	0.53	0.26	0.77	0.80	0.84	0.20	0.21
FR2510048	BAIE DU MONT SAINT MICHEL	0.25	0.34	0.08	0.18	0.35	0.97	1.81	0.39	0.21	4.62
FR2510059	ESTUAIRE DE L ORNE										
FR2510099	FALAISE DU BESSIN OCCIDENTAL	0	0.03	0	0	0	0.05	0	0	0	0
FR2512001	LITTORAL AUGERON	0.22	0.29	0.23	0.14	0.29	0.55	0.41	0.18	0.55	0.04
FR2512002	LANDES ET DUNES DE LA HAGUE	0	0.01	0	0	0	0.01	0	0	0.01	0
FR2512003	HAVRE DE LA SIENNE	0	0	0	0	0	0	0	0	0	0
FR3110038	ESTUAIRE DE LA CANCHE	0.02	0.03	0.11	0.01	0.02	0.04	0.11	0.06	0.20	0.01
FR3110039	PLATIER D OYE										
FR3110085	CAP GRIS NEZ	0.16	0.23	0.96	0.27	0.05	0.41	0.56	0.63	0.72	0.01
FR3112006	BANCS DES FLANDRES	0.65	0.27	0.98	0.45	0.35	1.86	0.80	0.72	0.39	0.67
FR5210090	MARAIS SALANTS DE GUERANDE TRACTS DU CROISIC DUNES DE PEN BRON	0	0	0	0	0	0	0	0	0	0
FR5210103	ESTUAIRE DE LA LOIRE	0	0	0	0	0	0	0	0	0	0
FR5212007	MARAIS DU MES BAIE ET DUNES DE PONT MAHE ETANG DU PONT DE FER ILE DUMET										
FR5212009	MARAIS BRETON BAIE DE BOURGNEUF ILE DE NOIRMOUTIER ET FORET DE MONTS	0.04	0.07	0.10	0.04	0.05	0.14	0.12	0.12		0
FR5212013	MOR BRAZ	0.45	0.46	0.17	0.27	0.42	0.35	0.41	0.28		2.47
FR5212014	ESTUAIRE DE LA LOIRE BAIE DE BOURGNEUF	0.69	0.79	0.38	0.67	1.12	0.87	1.24	1.58		2.72
FR5212015	SECTEUR MARIN DE L ILE D YEU JUSQU AU CONTINENT	1.94	2.06	0.84	1.31	3.19	0.94	0.60	0.37		2.86
FR5310011	COTE DE GRANIT ROSE SEPT ILES	0.20	0.10	0.18	0.24	0.24	0.10	0.82	0.63	0.01	0.01
FR5310050	BAIE DE SAINT BRIEUC EST	0.10	0.14	0.04	0.10	0.03	0.28	0.54	0.20	0.12	0.25
FR5310052	ILES DE LA COLOMBIERE DE LA NELLIERE ET DES HACHES	0.03	0.03	0.01	0.02	0.03	0.07	0.16	0.06	0.02	0.20
FR5310054	ILOT DU TREVORS	0.01	0.01	0.01	0.02	0	0.01	0.05	0.06	0.01	0
FR5310055	CAP SIZUN										
FR5310056	BAIE D AUDIERNE	0	0	0.01	0	0	0	0.03	0		0
FR5310057	ARCHIPEL DE GLENAN	0.62	0.68	0.29	0.43	0.65	0.41	0.29	0.33		0.39
FR5310070	TREGOR GOELO	0.47	0.25	0.27	0.38	0.32	0.39	1.26	2.22	0.23	0.09
FR5310071	RADE DE BREST BAIE DE DAOULAS ANSE DE POULMIC	0.03	0.04	0.01	0.02	0	0.06	0.08	0.05		0.09
FR5310072	OUESSANT MOLENE	0.31	0.28	0.28	0.47	0.33	0.28	1.57	1.32		0.45
FR5310073	BAIE DE MORLAIX	0.11	0.07	0.07	0.11	0.11	0.10	0.54	0.43	0.11	0.01
FR5310074	BAIE DE VILAINE	0.04	0.06	0.04	0.03	0.01	0.07	0.27	0.03		0.54

	FR5310086	GOLFE DU MORBIHAN	0	0	0.01	0	0	0	0.07	0	0	
	FR5310092	RIVIERE DE PENERF	0.07	0.07	0.03	0.05	0.03	0.10	0.04	0.06	0.08	
	FR5310093	BAIE DE QUIBERON	0.03	0	0	0	0.02	0	0	0.16	0	
	FR5310094	RADE DE LORIENT ETANGS KERVRAN ET KERZINE ANSES GAVRES ET PEN MANE	0	0	0	0	0	0	0	0	0	
	FR5310095	CAP D ERQUY CAP FREHEL	0.28	0.25	0.12	0.27	0.23	0.41	0.92	0.73	0.07	0.26
	FR5312003	BAIE DE GOULVEN	0	0.01	0	0	0	0.01	0	0	0.52	0
	FR5312004	CAMARET										
	FR5312005	RIVIERES DE PONT L ABBE ET DE L ODET	0	0	0	0	0	0	0	0	0	0
	FR5312009	ROCHES DE PENMARCH	0.40	0.49	0.19	0.33	0.38	0.27	0.17	0.18		0.18
	FR5312010	DUNES ET COTES DE TREVIGNON	0.12	0.12	0.07	0.05	0.05	0.06	0.17	0.04		0.17
	FR5312011	ILES HOUAT HOEDIC	0.22	0.24	0.09	0.20	0.20	0.22	0.30	0.63		1.09
	FR5410012	ANSE DU FIER D ARS EN RE	0.10	0	0	0	0.03	0	0	0.18		0
	FR5410013	ANSE DE FOURAS BAIE D YVES MARAIS DE ROCHEFORT	0.03	0	0	0	0.01	0	0	0.02		0
	FR5410028	MARAI DE BROUAGE ILE D OLERON	0.05	0.07	0.04	0.06	0.02	0.11	0.10	0.24		0.22
	FR5410100	MARAI POITEVIN	0.05	0	0	0	0	0	0	0		0
	FR5412011	ESTUAIRE DE LA GIRONDE MARAIS DE LA RIVE NORD	0	0	0	0	0	0	0	0		0
	FR5412012	BONNE ANSE MARAIS DE BREJAT ET DE SAINT AUGUSTIN	0	0	0	0	0	0	0	0		0
	FR5412020	MARAI ET ESTUAIRE DE LA SEUDRE ILE D OLERON	0	0	0	0	0	0	0	0		0
	FR5412025	ESTUAIRE ET BASSE VALLEE DE LA CHARENTE	0.02	0.03	0.03	0.03	0.02	0.05	0.06	0.12		0.14
	FR5412026	PERTUIS CHARENTAIS ROCHEBONNE	4.16	3.93	2.11	3.26	9.86	2.60	2.19	2.80		8.29
	FR7210030	COTE MEDOCAINE DUNES BOISEES ET DEPRESSION HUMIDES	0	0	0	0	0	0	0	0		0
	FR7210031	COURANT D HUCHET										
	FR7210065	MARAI DU NORD MEDOC	0.02	0.09	0.01	0.03	0.00	0.15	0.01	0.02		0.00
	FR7212002	ROCHERS DE BIARRITZ LE BOUCCALOT ET LA ROCHE RONDE										
	FR7212013	ESTUAIRE DE LA BIDASSOA ET BAIE DE FONTARABIE	0	0.03	0	0	0	0.01	0	0		0
	FR7212014	ESTUAIRE DE LA GIRONDE MARAIS DU BLAYAIS	0	0.00	0	0	0	0	0	0		0
	FR7212016	PANACHE DE LA GIRONDE	0.62	0.59	0.36	0.55	2.23	0.47	0.13	0.35		0.20
	FR7212017	AU DROIT DE L ETANG D HOURTIN CARCANS	0.39	0.09	0.17	0.09	0.49	0.26	0.07	0.05		0.07
	FR7212018	BASSIN D ARCACHON ET BANC D ARGUIN	0.09	0	0.05	0.01	0.10	0.08	0.01	0.12		0.01
	FR7212019	TETE DE CANYON DU CAP FERRET	0.31	0.04	0.17	0.03	0	0.02	0	0		0
	FR7212020	PLATEAU AQUITAIN ET LANDAIS	0.92	0.24	0.31	0.19	0.30	0.19	0.02	0.01		0.03
		TOTAL	16.3	15.3	13.3	12.4	23.4	17.4	22.9	19.5	14.4	33.6
Marine Nature Parks	FR9100001	IROISE	1.65	1.70	1.18	2.29	1.27	1.17	2.55	2.72		3.83
	FR9100005	ESTUAIRES PICARDS ET MER D OPALE	1.56	1.96	5.15	1.14	2.00	2.65	1.52	2.00	21.25	1.41
	FR9100006	BASSIN D ARCACHON	0.25	0.01	0.12	0.02	0.13	0.20	0.04	0.16		0.04
MPA Propositions	1		0.13	0.11	0.18	0.28	0.15	0.02	0	0	0	0
	2		0.65	0.73	0.49	0.92	0.39	0.27	0.22	0.45		0.30
	3		0.03	0.02	0.03	0.04	0	0.06	0	0		0
	4		0.04	0.03	0.04	0.05	0	0.03	0	0		0
	5		0.04	0.02	0.02	0.01	0	0.05	0	0		0
	6		0	0	0	0	0	0	0	0		0
	7		0.54	0.28	0.21	0.20	0.16	0.08	0.01	0		0.01



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Enseignant référent : Olivier LE PAPE

Auteur : **Auriane VIRGILI**

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Pôle analytique,
5 allées de l'Océan, 17000 La Rochelle

Maître de stage : **Vincent RIDOUX**

Titre français: Prédire les variations d'habitats des oiseaux marins côtiers pour évaluer les aires marines protégées.

Résumé :

Les oiseaux, comme tout prédateur, doivent maximiser leurs apports nutritionnels et minimiser leurs dépenses énergétiques lors de leurs périodes d'alimentation et ainsi optimiser leurs stratégies d'utilisation des ressources et des habitats. Ces stratégies dépendent essentiellement des conditions environnementales, déterminantes pour la disponibilité des ressources, et peuvent être décrites grâce à des modèles d'habitat adaptés à la mise en place de plans de conservations des espèces et des écosystèmes. Les objectifs de cette étude étaient : (1) déterminer les mécanismes qui influencent le plus la distribution des oiseaux marins le long des côtes Françaises ; (2) déterminer les effets des variations saisonnières de ces mécanismes; (3) proposer une évaluation des sites de conservation établis ou prévus le long de ces côtes et dans les eaux de la Manche et de l'Atlantique sous juridiction française. Nous avons recueilli des données d'observations d'oiseaux marins côtiers issues de campagnes aériennes réalisées en Manche et dans l'Atlantique Nord-est en hiver et en été. Nous avons classé les oiseaux en groupes morphologiques et décrit leurs habitats en utilisant des variables physiographiques et océanographiques à l'aide de modèles additifs généralisés (GAM). Pour finir, nous avons fourni, pour chaque site de conservation, une mesure de son importance pour la protection des espèces étudiées. Il apparaîtrait que la distribution des oiseaux marins côtiers soit essentiellement déterminée par la distance à la côte et que les plus fortes densités soient prédites près des côtes avec d'éventuelles variations selon la saison. Enfin, il semblerait qu'une majorité des sites de protection établis sur les côtes françaises ne soient pas pertinents pour la conservation des espèces étudiées.

Mots-clés : Manche · Atlantique Nord-est · France · Oiseaux de mer côtiers · Goélands · Sternes · Cormorans · Plongeurs · Macreuses · Campagnes aériennes · Modélisation d'habitat · Distribution · Modèles Additifs Généralisés · Aires Marines Protégées · Zones de conservation

Title: Predicting variations in coastal seabird habitats to assess marine protected areas.

Abstract :

Seabirds, like other predators, need to maximize their nutritional intakes and minimize their energy costs during foraging periods and thereby optimize their strategies of resources and habitats utilization. These strategies mainly depend on environmental conditions and can be described through habitat models for the implementation of conservation plans of species and ecosystems. The objectives of this study were: (1) to determine the mechanisms that mostly influence the distribution of seabirds along the French coasts; (2) to determine the effects of seasonal variations of these mechanisms; (3) to provide an assessment of all conservation sites established or proposed along these coasts and in Channel and Atlantic waters under French jurisdiction. We collected data of coastal seabird sightings from aerial surveys carried out in the English Channel and the eastern North Atlantic in winter and summer. We classified seabirds into morphological groups and described their habitats by using physiographic and oceanographic variables in generalized additive models (GAM). Finally, we provided, for each conservation site, a measure of its importance for the protection of the studied species. It would appear that distribution of coastal seabirds was essentially determined by distance to the coast, highest densities being predicted near the coast, with possible variations depending on the season. Finally, it appears that a majority of protected sites established along the French coasts would not be relevant to the conservation at sea of the studied species.

Key Words: English Channel · eastern North Atlantic · France · Coastal seabirds · Gulls · Terns · Cormorants and Shags · Divers · Scoters · Aerial surveys · Habitat modelling · Seabird distribution · Generalized Additive Models · Marine Protected Areas · Conservation areas