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UNIVERSITÉ DE LA ROCHELLE

ÉCOLE DOCTORALE GAY LUSSAC

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**Top predators in marine ecosystem
their response to ocean spatio-temporal variability**

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1. **Lambert C.**, Authier M., Doray M., Dorémus G., Spitz J. and Ridoux V. (in prep) "A story of size and depth: the predator association to prey biomass within the Bay of Biscay". To be submitted to Progress in Oceanography special issue on PELGAS surveys.
2. **Lambert C.** and Ridoux V. (in prep) "Are static MPAs relevant for the protection of highly mobile marine top predators ? The case of the Bay of Biscay". To be submitted to Biological Conservation.
3. **Lambert C.**, Authier M., Doray M., Dorémus G., Spitz J. and Ridoux V. (in prep) "Ocean inter-annual variability impacts the stability of highly mobile top predators habitat preferences". To be submitted to Marine Ecology Progress Series.
4. **Lambert C.**, Pettex E., Virgili A., Delavenne J., Toison V., Blanck A., Ridoux V (in revision) "Habitat modelling predictions reveal seasonal relevance of MPAs for marine megafauna". Deep Sea Research II, topical issue "European marine megafauna".
5. **Lambert C.**, Pettex E., Doremus G., Laran S., Stephan E., van Canneyt O., Ridoux V. (in press) "How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: the Eastern North-Atlantic". Deep Sea Research II, topical issue "European marine megafauna". doi: 10.1016/j.dsr2.2016.06.011.
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7. **Lambert C.**, Mannocci L., Lehodey P., Ridoux V. (2014) "Predicting Cetacean Habitats from Their Energetic Needs and the Distribution of Their Prey in Two Contrasted Tropical Regions". PLoS ONE 9(8): e105958. doi:10.1371/journal.pone.0105958.

Other

8. Pettex E., **Lambert C.** and Ridoux V. (in prep) "Seasonal distribution of juveniles and immatures Northern Gannets reveals avoidance of intra-specific competition with breeding adults". To be submitted to Ecology Letters.
9. Virgili A., **Lambert C.**, Doremus G., Pettex E., van Canneyt O., Ridoux V. (in revision) "Predicting seasonal variations in coastal seabird habitats in the English Channel and the Bay of Biscay". Deep Sea Research II, topical issue "European marine megafauna".
10. Pettex E., Laran S., Authier M., Blanck A., Dorémus G., Falchetto H., **Lambert C.**, Monestiez P., Stéfan E., Van Canneyt O., Ridoux V. (in revision) "Using large scale survey to investigate seasonal variations in seabird distribution and abundance. Part II: the Bay of Biscay and the English Channel". Deep Sea Research II, topical issue "European marine megafauna".
11. Delavenne J., Lepareur F., Witté I., Touroult J., **Lambert C.**, Pettex E., Virgili A., Siblet J-P. (in revision) "Spatial conservation prioritization for mobile top predators in French waters: comparing observation rates and predicted densities as input". Deep Sea Research II, topical issue "European marine megafauna".

CONFERENCE PAPERS

Poster presentations

1. **Lambert C.**, Virgili A., Pettex E., Delavenne J., Toison V., Blanck A., Ridoux V. (2016) "Habitat modelling predictions highlight seasonal relevance of Marine Protected Areas for cetaceans". In Annual Conference of the ECS, Funchal, Madeira. doi: 10.13140/RG.2.1.1500.3288
2. **Lambert C.**, Pettex E., Laran S., David L., Doremus G., Stephan E., van Canneyt O., Ridoux V. (2015) "Cetaceans ecological preferences in response to ocean seasonality". In Annual Conference of the ECS, St Julian, Malta. doi: 10.13140/RG.2.1.2295.7525
3. **Lambert C.**, Mannocci L., Lehodey P., Ridoux V. (2014) "Predicting cetacean habitats from the distribution of their prey in two contrasted tropical regions". In IMBER Conference, Bergen, Norway. doi: 10.13140/RG.2.1.1771.4647

Oral presentations

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3. Pettex E., **Lambert C.**, Laran S., Ricart A., Virgili A., Falchetto H., Authier M., Monestiez P., Van Canneyt O., Doremus G., Blanck A., Toison V., Ridoux V. (2014) "Patrons saisonniers de la distribution des prédateurs supérieurs dans les eaux métropolitaines françaises - Apports pour la désignation des aires marines protégées". In Séminaire FREDD, La Rochelle.

SCIENTIFIC REPORTS

1. Pettex E., Martinez L., **Lambert C.**, Ricard A. (2016) R&D RESPECT – WP2 Rapport Final, Mammifères marins et bruits : vers la quantification des risques. ULR Valor.
2. Ricart A., Pettex E., **Lambert C.**, Falchetto H., Laran S., Blanck A., Ridoux V (2015) "Suivi Aérien de la Mégafaune Marine en Manche Est (SAMM-ME, Hiver 2014)". Technical Report, University of La Rochelle–CNRS UMS 3462, 87 pp. doi: 10.13140/RG.2.1.4871.3121
3. Pettex E., **Lambert C.**, Laran S., Ricart A., Auriane V., Falchetto H., et al (2014) "Suivi Aérien de la Mégafaune Marine en France métropolitaine - Rapport Final". Technical Report, University of La Rochelle–CNRS UMS 3462, 169 pp. doi: 10.13140/2.1.2698.5287

Abbreviations

AAMP	Agence des Aires Marines Protégées
ARS	Area-Restricted Search
BoB	Bay of Biscay
CART	Classification and regression trees
CHL	Chlorophyll a concentration
CS	Celtic Sea
CTD	Conductivity Temperature Depth
CUFES	Continuous Underwater Fish Egg Sampler
CV	Coefficient of Variation
EC	English Channel
ENA	Eastern North-Atlantic
ENM	Ecological Niche Model
ESW	Effective Strip Width
GAM	Generalised Additive Model
GCV	Generalised Cross-Validation
GEBCO	General Bathymetric Chart of the Oceans
GLM	Generalised Linear Model
IFREMER	Institut Français de Recherche pour l'Exploitation de la MER
MLD	Mixed Layer Depth
MODIS	Moderate Resolution Imaging Spectroradiometer
MPA	Marine Protected Area
NPP	Net Primary Production
NWMS	North-Western Mediterranean Sea
OFT	Optimal Foraging Theory
PCA	Principal Component Analysis
PELGAS	PELagiques GAScogne
SAMM	Suivi Aérien de la Mégafaune Marine
SBT	Sea Bottom Temperature
SDM	Species Distribution Model
SSH	Sea Surface Height
SSS	Sea Surface Salinity
SST	Sea Surface Temperature
Zeu	Euphotic Depth

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Introduction

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THE introduction presents the ecological framework of this doctoral work. In particular, the ecological niche concept and the specific characteristics of pelagic ecosystems that have shaped the ecology of marine megafauna are presented. In addition, the consequences of these particularities for such marine species, and in particular for top predators¹, are detailed. Finally, the main questions handled during this thesis and the outline of the dissertation are introduced.

¹Top predators (or apex predator) are the species occupying the higher trophic levels of a given trophic network. In the pelagic ecosystem, these predators are cetaceans, seabirds, large teleosts, sharks, turtles.

1.1 THE ECOLOGICAL NICHE CONCEPT

1.1.1 What is the ecological niche?

"By ecology, we mean the whole science of the relations of the organism to the environment, in the broad sense, all the conditions of existence. These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil, etc."

Generelle Morphologie der Organismen, Ernst Haeckel, 1866

ONE hundred and fifty years ago, Ernst Haeckel crafted the word ecology from the greek words *oikos* (household, habitat) and *logis* (science, knowledge), as the science of the condition of existence, that is of the interactions among organisms and with their environment (the abiotic conditions, Haeckel 1866). Within this rather recent science, the ecological niche is a central concept, of which no domain of ecology is independent. Fundamentally, the niche of a species expresses the relationship between organisms and all aspects of their environment. However, this concept has been given several meanings by successive authors, leading to some confusion in terminology and as to what exactly refers the word "niche". For Grinnell (1917), the niche was the habitats and habits of a species; for Elton (1927), the niche was a species' place and role in the environment, including both positive and negative interactions; for Hutchinson (1957) the niche referred to the range of activities of a species along every dimension of its environment (the n-dimensional hypervolume). Resulting from all these different acceptances of the concept, one of the most frequent confusion in terminology referring to the niche concept is the shortcut by which the niche would equate the habitat of a species.

Actually, the ecological niche is clearly wider than the sole habitat of a species. The niche can be defined as the set of environmental (abiotic and biotic) conditions necessary to the species to sustain a positive growth rate within an ecosystem (its habitat) and the set of positive and negative interactions of the species with its abiotic (feedback effects of the species on its environment, such as soil acidification by pine trees) and biotic environment (*e.g.* competition, commensalism, mutualism, symbiosis, parasitism, prey-predator relationships) as well as the intra-specific interactions (*e.g.* density-dependence; Figure 1.1). Environmental variables defining the habitat, on which the species has no feedback effect of any kind, are the conditions. In contrast, the variables with which a species interact in either positive or negative ways are the resources, either biotic or abiotic. Therefore, abiotic and biotic environments are composed of both conditions and resources (Figure 1.1, McInerny & Etienne 2012c).

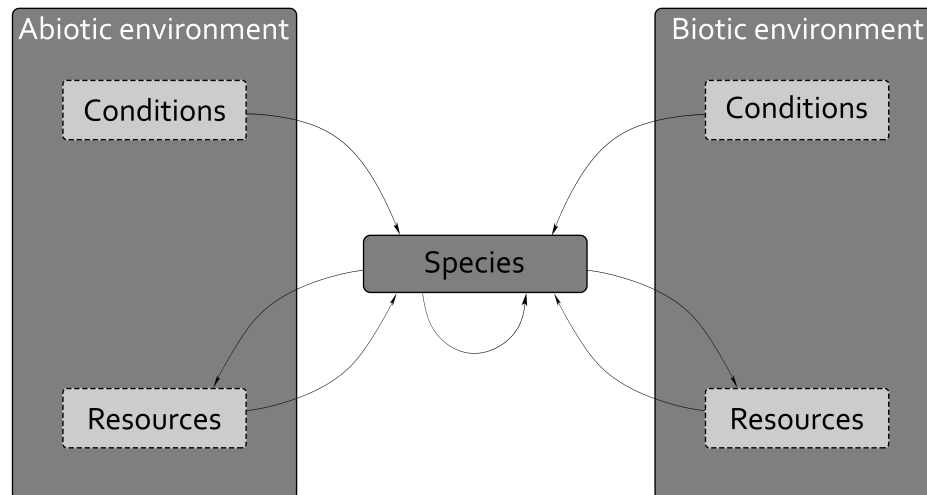


Figure 1.1 – The ecological niche concept, which is also a conceptual representation of Ecology. Redrawn from McNerny & Etienne (2012c).

1.1.2 The temporal dimension of the ecological niche

The ecological niche is a species's space-time of activity, gathering all the activities or vital functions an individual can be involved in throughout its life cycle, such as foraging, breeding, resting, migrating etc. (Fuller 2012). We can therefore consider the overall niche of a species as a juxtaposition of particular niches dedicated to particular activities (foraging niche, breeding niche) since favourable habitats as well as biotic and abiotic interactions can differ depending on the activity.

These activity niches might be more or less overlapping depending on species, with some predators having life stages separated into discrete areas potentially exhibiting separated activity niches. For example, in the case of seabirds, the environmental conditions and interactions encountered by breeding individuals at the colony are fundamentally different from those encountered while foraging at sea: the breeding and foraging activities occur in very different environmental spaces, so that they could represent distinct sub-niches. In the same way, baleen whales often exhibit different niches while breeding *versus* foraging, as the environmental conditions encountered in the geographical areas of each activity, which can be thousands of kilometres away (*e.g.* humpback whales, Clapham et al. 1999), are very different. Therefore, a species' niche could be defined as a sum of different sub-units corresponding to particular activities, but could also be expected to change according to individual experience.

In addition to variations linked to species activity requirements, the ecological niche of an individual species could also vary as a response to variations of its environment. Indeed, in the case of an environment with strong spatio-temporal heterogeneity and variability, the ecological niche of a species might vary depending on the conditions actually encountered during each phase of its life, *i.e.* the species have to be flexible. This flexibility could lead species to use varying sub-units of their niches depending on the conditions encountered (winter *vs* summer; unfavourable

vs favourable years). A particular example of such highly dynamic and variable environment in both space and time is the ocean, and particularly pelagic ecosystems, implying particular consequences for marine top predators.

1.2 THE PELAGIC ECOSYSTEM AND ITS SPATIO-TEMPORAL HETEROGENEITY

1.2.1 Definition and environmental features of the pelagic ecosystem

The pelagic ecosystem is the most widespread ecosystem type on Earth, as it encompasses the whole water column of all oceans and seas across the world. Pelagic habitats within this ecosystem are known to be highly variable, due to complex physical processes interacting with biological ones, that lead to the establishment of heterogeneous and dynamic structures at many scales in space and time (Barry & Dayton 1991). These physical processes are linked to water mass dynamics, originating in structural differences between the various layers of the water column.

The water column exhibits a strong vertical and horizontal variability related to water density, incident light intensity, nutrient concentrations, all these parameters determining biological developments. This structural variability leads to water column stratification, with the least dense layers at the surface (Longhurst 2007). Water stratification conditions the spatio-temporal variability of primary productivity, which mostly occurs in the euphotic zone where light intensity is sufficient (Sverdrup 1953). Nutrients are limiting in this layer and primary productivity remains poor in the absence of nutrient replenishment. Therefore, all physical processes that facilitate inputs of nutrients into the surface layer often induce an increase in primary production.

The various physical processes that induce the phytoplankton blooms occur at various spatial and temporal scales, from local (waves; less than a minute) to global scales (climatic conditions or global circulation; from decades to centuries). The predictability of these processes often depends on their scale, larger processes being often more predictable than smaller ones (Hunt & Schneider 1987). The high spatio-temporal heterogeneity of the ocean originates from this multi-scale structuring, further conditioning the structuring of primary production and associated higher trophic levels, for which patchiness is a key feature (Longhurst 2007).

Pelagic ecosystems are often divided into two main types: the neritic domain, that extends from the coastline to the continental shelf edge (around 200 m deep in general), and the oceanic one outward. Due to the proximity to the land, the main difference between these two domains arises from suspended material and nutrient inputs, which are far greater over the shelf since most of nutrient and suspended material loads in the ocean originates from river discharges. Hence, neritic waters often exhibit higher turbidity and are more productive than oceanic waters. Pelagic ecosystems

can be further partitioned into several oceanographic regimes, especially over the shelf, depending on the locally dominant physical processes (Figure 1.2).

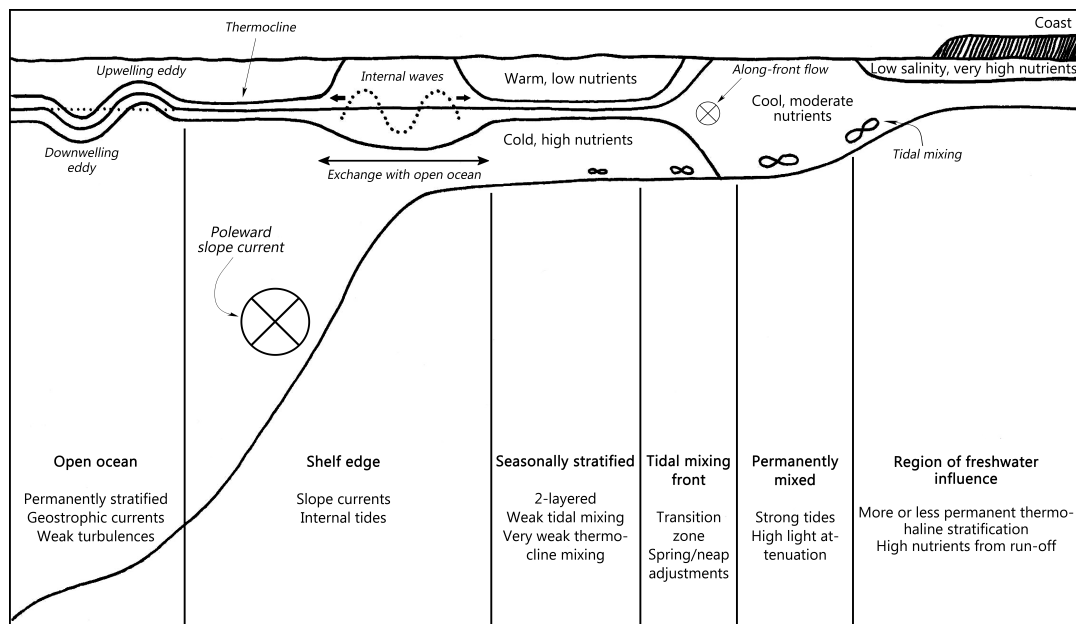


Figure 1.2 – Schematic view of the partitioning of the pelagic ecosystem, with the oceanographic regimes and the corresponding physical processes. Redrawn from Simpson & Sharples (2012), with elements from Hill et al. (2008), Huthnance et al. (2009). These 6 compartments are typical of the western European waters. From shallow waters to open ocean: region of freshwater influence; shallow coastal waters mixed by strong tides and wind; tidal fronts; deeper shelf waters thermally stratified in summer; shelf edge and open ocean (Huthnance et al. 2009). The slope current and along-flow jets flow poleward in the western European waters.

1.2.2 Physical controls driving spatio-temporal variability of the pelagic ecosystems

In temperate ecosystems, in winter, the water column is mixed by turbulences occurring both at the surface, as a result of wind action, and at depth, through the tides (over the shelves). In spring, the heating of the surface layer leads to the formation of a thermocline separating the upper warmer layer from deeper cooler waters: this is the thermal stratification (Figure 1.2, seasonally stratified regime; Longhurst 2007). As it retains phytoplankton at the surface within favourable conditions of temperature and light intensity, the stratification is favourable to phytoplankton growth and lead to the development of blooms, until nutrients are depleted (Sverdrup 1953, Diehl 2002). Nutrient depletion is the main limitation of this summer productivity in temperate ecosystems (Kaiser & Attrill 2011).

In some area however, this depletion is prevented through the stratification break down. The establishment of stratification depends on the equilibrium between surface heating intensity and mixing which redistributes heat through the water column. Several processes can prevent stratification to establish by ensuring a more or less important mixing of the water column.

1.2.2.1 Tides

Over the shelf, the tides stirring the deeper layer and the winds stirring the surface layer can break down the water density gradient and ensure mixing of the water column. In regions where tides are important relative to water depth, mixing by tidal currents prevents the establishment of a summer stratification (Pingree & Griffiths 1978, Simpson et al. 1981). This process ensure the advection of nutrients to the surface layer at the limit between stratified and mixed waters, the tidal front. This advection occurs through four mechanisms: gradual increase of vertical mixing through the front, variability of front localisation thanks to the spring-neap tide cycle, transfers through eddies and friction (Kaiser & Attrill 2011).

These spatially and temporally highly dynamic fronts are easily predictable due to the repeatability of tide cycles (Figure 1.2, tidal mixing front and permanently mixed regimes). In addition to enhancing productivity through nutrient transfers, tidal fronts also aggregate prey, and are easily perceptible. If horizontal tidal currents are the strongest near the coasts, internal tides can have strong effect on the water column at the shelf edge (Green et al. 2008, Huthnance et al. 2009). Internal tide waves interact with the pycnocline and can cause turbulences resulting in a vertical mixing along the slope, enhancing primary production (Figure 1.2, shelf edge regime).

1.2.2.2 Winds

During spring and summer, winds are generally weaker compared to winter, but in specific situations, they can still prevent stratification. In coastal areas, upwellings of deep waters can occur when strong offshore winds blow continuously over several days, ensuring the pumping of deeper water nutrients into the surface layer, thus leading to enhanced productivity. More generally, winds can generate both vertical and horizontal motion of water masses. At small scale, winds are responsible for the poorly predictable short-term Langmuir circulation (Brown et al. 2004). Steady winds over calm waters generate vertical vortices at the surface inducing the alternating of divergence and convergence. However, these movements are not important enough to induce any transfer between waters layers and are restricted to the surface layer.

At large scale, oceanic circulation is strongly linked to the atmospheric circulation, especially through the surface currents. Due to the Coriolis force, wind-driven deviation of water masses occur at 90° from wind direction, generating a motion to the right in the northern hemisphere, and to the left in the southern one. Due to variations in density and friction between water layers, each layer respond differently to the wind and this process generates a spiral of water in motion, potentially of hundreds of meters deep. This process is known as the Ekman's transport (Brown et al. 2004). This transport is the origin of large scale upwellings that develop along the eastern margins of ocean gyres, called the eastern boundary currents, such as the Canaries, Benguela, Humboldt and California currents. These structures of enhanced primary productivity are very stable over both space and time and thus are highly predictable (*e.g.* Carr & Kearns 2003, Chavez & Messié 2009).

1.2.2.3 Geostrophic currents

The instability of large-scale general circulation can generate meso-scale processes, such as meanders and eddies. These structures can last several months, and can be hundreds of kilometres wide (Figure 1.2, open ocean regime; Lévy 2008). Eddies have several origins, of which depends their lifespan. The instability of western boundary currents of ocean gyres (*e.g.* the Gulf Stream rings), the isopycnals movements, or the interaction between currents and topography (*e.g.* between the poleward slope current and the southern Bay of Biscay canyons) can all result in the formation of eddies. Eddies are one of the major processes enhancing primary productivity of the ocean, by pumping deep water up to the surface layer (Oschlies & Garçon 1998, Williams & Follows 1998, Lee & Williams 2000).

However, only cyclonic eddies can uplift deep, nutrient-rich waters into the euphotic zone. In contrast, anticyclonic eddies downwell warm, nutrient-poor waters from the euphotic zone to deep waters. Nevertheless, some nutrient injection and biological enhancement, less important than for cyclonic eddies, can still occur at their margins thanks to layers mixing. Eddies can be fairly predictable, depending on their origin (Bakun 2006, Sabarros et al. 2009): if eddies are temporary oceanographic features, the conditions of their formation are more stable and result in the repeated development of eddies in specific regions.

Between interacting eddies, smaller submesoscale structures, known as filaments, are ejected from eddy systems (Lévy 2008). These structures can be about hundred kilometres in length, but only about ten kilometres large. Filaments are areas of very important nutrients enhancement (Mahadevan & Archer 2000), sometimes more important than the associated eddies. These structures are very important for primary productivity and are prey-rich areas, but have a shorter life-span and hence are less predictable than eddies.

1.2.2.4 River discharges

Thermohaline stratification is also of great importance over the shelf, where river run-offs are responsible for discharge of suspended material and nutrients along with freshwater inputs (Simpson 1997). These river plumes form stratification since the low salinity water spreads over sea water (Figure 1.2, region of freshwater influence regime). Thanks to high nutrient concentration and retention of phytoplankton at the surface, river plumes are often characterised by high productivity (Kaiser & Attrill 2011). The associated salinity gradient requires a high amount of energy to be broken, but its extent and intensity completely depend on rainfall within drainage basins.

Table 1.1 – *Spatial and temporal scales of main oceanographic processes, their effects on primary production (PP), secondary production (SP), biomass aggregation (AG) and areas in which they occur. Process tends to increase (↑), decrease (↓) or have both effects (↕) on production; (?) effect on production unknown; (✓) under the column AG indicates that the process tends to cause physical aggregation of biomass. Modified from Wakefield et al. (2009).*

Processes	Scale		Effects			Areas, examples
	Horizontal (km)	Temporal	PP	SP	AG	
Turbulences						
Langmuir convection cell	0.005–0.5	min–h	?	?	✓	All
Changes in mixed layer depth due to wind, insolation, freshwater, currents, tides, upwelling, internal waves, fronts, etc.	10–1,000	h–w	↕	↕	✓	All. Spring and autumn blooms in temperate latitudes (especially in North Atlantic)
Sub-mesoscale eddies	0.01–20	d–wk	?	?	✓	All
Meanders, eddies	20–300	wk–yr	↑	↑	✓	Margins of major ocean currents
Fronts						
Freshwater plumes; plume fronts	0.005–100	h–mo	↑	↑	✓	Coastal waters
Shelf sea fronts caused by tidally induced mixing	2–10–100	d–mo	↑	↑	✓	Neritic waters
Coastal upwelling due to Ekman transport	10–100–1,000	5 d–yr	↑	↑	✓	Eastern margins of ocean basins
Shelf break fronts	10–500	wk–mo	↑	↑	✓	All shelf breaks
Circulation						
Water masses	100–15,000	mo–dec	–	–		Antarctic surface waters, Subantarctic surface water, subtropical surface water
Climatic fluctuations						
El-Niño - Southern Oscillation	15,000–40,000	4–7 y	↕	↕		Eastern Pacific and worldwide
Other climatic oscillations and regime shifts	15,000–40,000	10–100 yr	↕	↕		Antarctic oscillation; Pacific decadal oscillation
North Atlantic Oscillation						
Medium/long-term climate fluctuations	40,000	> 100 yr	↕	↕		All

1.3 CONSEQUENCES FOR TOP PREDATORS

1.3.1 Environmental heterogeneity: a key feature of top predator ecology

The physical processes described above control primary production intensity within the upper layer of the ocean, through the induction of phytoplankton growth or its retention within the photic zone. Spatio-temporal variability of these processes occur at several nested scales, the temporal persistence of these features increasing with their spatial scales (Hunt & Schneider 1987). Hence, these processes drive the heterogeneity in distribution and structure of biological production across the oceans, from fine (less than a kilometre), coarse (1–100 km), meso (100–1,000 km), to large scales (> 1,000 km) and finally to the Earth's scale marine biomes (Hunt & Schneider 1987, Longhurst 2007).

As a consequence of these physical forcing and plankton aggregating behaviours (shoaling, swarming, vertical and horizontal migrations; Folt & Burns 1999), the biological production of the pelagic ecosystems is characterised by a hierarchical patch system, with high-density small-scale patches nested within low density and larger scale patches (Hunt & Schneider 1987, Kotliar & Wiens 1990, Fauchald 1999). This patchiness induce the aggregation of upper trophic levels within structures that enhance biological production. Therefore most of the physical structures defined above are synonym of higher trophic level prey aggregation (Table 1.1) and act as oases in a desert (Godø et al. 2012), sustaining both increased primary production and rich ecological communities (e.g. Worm et al. 2003; 2005, Sabarros et al. 2009, Tew-Kai & Marsac 2010). This patchiness is essential to the marine ecosystem functioning, since if producers and consumers were homogeneously distributed, the ecosystem would soon be depleted (Brentnall et al. 2003, Mitchell et al. 2008). With such a structure, ocean spatio-temporal heterogeneity shaped the life history of all pelagic organisms.

The life history traits of a species are the biological characteristics that affect its reproduction and survival rates, and therefore its fitness (Stearns 1992). These traits can either be morphological, physiological or behavioural and include *inter-alia* growth and survival rates, number of offspring, age at sexual maturity and first reproduction, as well as parental investment. To fuel these milestones of their life, individuals require energy, which will be further allocated between maintenance, growth and reproduction. The allocation between these three compartments depends on a compromise depending on the activity and status of individuals, as well as the environmental conditions encountered, and it determines the fitness of an individual. To ensure necessary energy intake, and hence fitness (through the quantity of energy allocated to each compartments), foraging strategies exhibited by species have to be optimised (Optimum Foraging Theory; Pyke 1984, Boggs 1992) by maximising energy gains (prey quantity or quality) while minimising energy expenditure of foraging (depends on travel distance, flight or swimming efficiency).

Consequently, in such a spatio-temporally heterogeneous and patchy environment as the oceans,

resource acquisition strategies are under major selection pressure toward high efficiency due to their strong impact on the fitness of individuals (Boggs 1992). Hence, top predators developed particular foraging strategies to cope with this heterogeneity, which are one of the main drivers of their habitat selection and fine-to-large scale distribution patterns. Although the optimisation of foraging strategies depends on the species specific characteristics, such as travel cost (flight or swimming efficiency) or prey capture efficiency, rather similar general strategies are observed across taxa.

Actually, most top predators exhibit multi-scale foraging strategies, characterised by scale-dependant searching behaviours (Fauchald 1999, Weimerskirch 2007, Hays et al. 2016) as a result of foraging in a hierarchical patch system. At large scale, searching behaviour is optimised towards areas of highest prey densities (Figure 1.3), these foraging areas being often associated to predictable features with enhanced primary production and prey aggregation (*e.g.* upwellings, eddies, fronts). Social learning and memory are important elements to find these large-scale predictable features for such long lived and social species. Once over such features, predators start actively searching for prey patches using specific type of movement and behaviour adapted to the structure of prey patches encountered within the environment (Fauchald 1999, Sims et al. 2008): they reduce travel rates and increase turning rate, reducing the searching area (the so-called *Area-Restricted Search* behaviour, hereafter ARS; Figure 1.3). Since at fine scale prey patch localisation is highly ephemeral and unpredictable, the use of other cues than memory is needed to detect these prey patches: a combination of visual cues, such as sub-surface predator (tunas, dolphins) or seabird aggregations (local enhancement; Harrison et al. 1991, Silverman et al. 2004), as well as olfactory (Nevitt & Bonadonna 2005, Nevitt 2008) and acoustic cues (Richardson et al. 1995) has been demonstrated.

This hierarchical searching strategy is the process driving habitat selection at the individual level, with consequences at the population and species scales. When considering all individuals of a population, each scale of these hierarchical strategies can be related to particular ecological processes (Figure 1.3). At the larger scale, the biogeography of a species considers the whole environment where a species can occur, irrespective of its activity or density. However, at meso and coarse scales the searching strategy results in strong differences in densities between habitats, with habitats where density of a given species is disproportionately high compared to their availability (*i.e.* the species habitat preferences). Indeed, increased searching time over particular habitat at the individual level results in higher predator densities at the population level (darker area, Figure 1.3). Such habitats are expected to be predictable oceanographic features associated to prey patch aggregation. At a finer scale (Figure 1.3), the association between individuals and prey patches is looser at the population level since exact prey patch locations are barely predictable, as seen earlier. These finer scales relate to the predator-prey relationships.

1.3.2 The case of seabirds

Seabird evolution has been shaped by strong pressures, leading to the so-called seabird syndrome, corresponding to a range of shared characteristics among all taxa (Gaston 2004). Reduced clutch

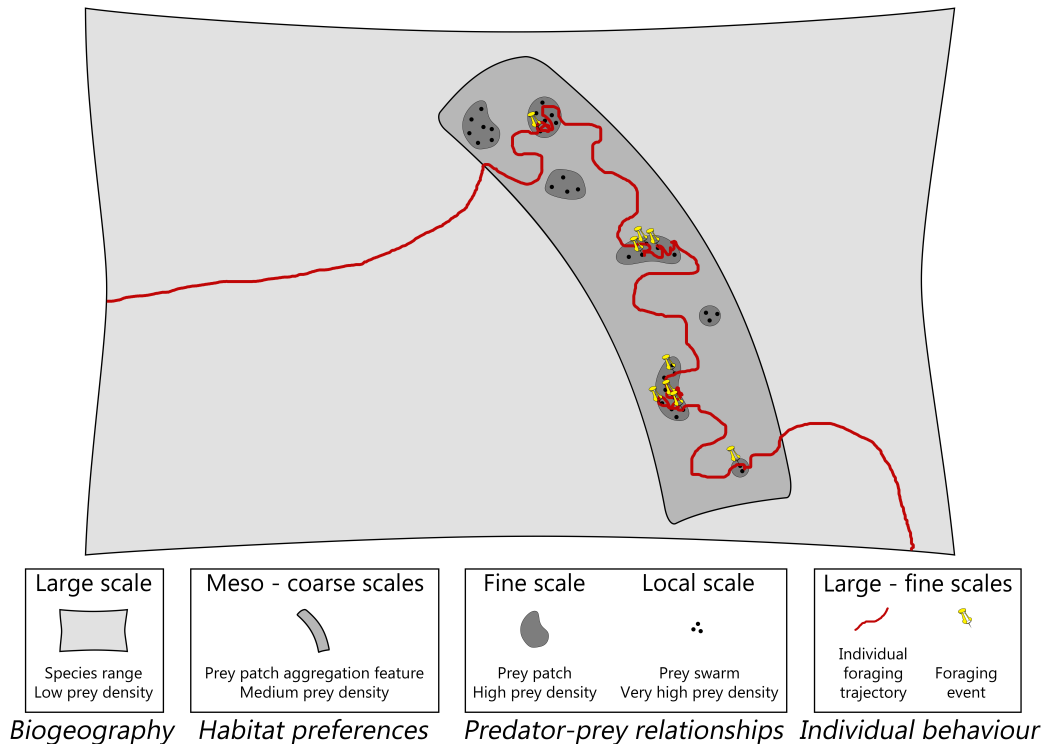


Figure 1.3 – Hierarchical patch system with high-density prey patches (dark grey) nested within lower-density meso or coarse-scale patches (predictable oceanographic aggregation feature, medium grey) within the overall low-density species range (light grey). Red line is the search pattern of a forager, using a nested area-restricted search once within the aggregation feature. The ecological processes corresponding to these various scales are indicated.

size, sexual monomorphism (driven by shared parental care), colonial breeding, late sexual maturity and long-life span are traits shared by most seabird taxa. These characteristics are thought to have been driven by the interaction between bird intrinsic constraints and the heterogeneous marine environment they evolved in (Gaston 2004). Especially, since seabirds have to breed on land, commuting between discrete foraging areas and the colony (central-place foraging) represents an increase in the energy cost of foraging (Pyke 1984).

Given these characteristics, seabirds have to optimise their resource acquisition strategy. Quite in line with this, multi-scale foraging strategies with a strong link to predictable features have been shown for most seabird species (*e.g.* Pinaud & Weimerskirch 2005; 2007), despite some variations between taxa, from mainly coastal (*e.g.* cormorants) to truly oceanic species (*e.g.* Procellariidae), between populations of the same species, depending on the distance separating foraging sites and colonies, between individuals of different age, maturity and reproductive status, and potentially different conditions and personalities (*i.e.* bold *vs* shy).

In particular, seabirds were shown to target discrete and predictable large-scale foraging areas during both breeding and wintering seasons (for many species the targeted areas differ between the two seasons). Site fidelity has also been demonstrated at meso and coarse scales (Weimerskirch

2007). At these scales, site fidelity depends on the habitat considered: it is often stronger for physiography-related forcing features such as shelf edge and tidal fronts, which are more spatially and temporally predictable than oceanographic features. Hence many species target meso-scale features linked to seamounts, shelf edges (Catry et al. 2011, Hedd et al. 2012, Guilford et al. 2012), tidal fronts (Decker & Hunt 1996, Durazo et al. 1998, Jahncke et al. 2005, Schwemmer et al. 2009), sea ice edges (Hunt 1990, Ainley et al. 1993) or eastern boundary currents (González-Solís et al. 2007, Shaffer et al. 2009, Catry et al. 2011, Fort et al. 2012, Péron & Grémillet 2013, Sabarros et al. 2014), while other species target meso-scale oceanic eddies (e.g. in the Mozambic channel (Tew-Kai et al. 2009) or Agulhas Return Current (Abrams 1985, Nel et al. 2001)), or the frontal areas between water masses, such as polar or sub-tropical fronts (Nel et al. 2001, Shaffer et al. 2006, Bost et al. 2009).

1.3.3 The case of cetaceans

Unlike seabirds and pinnipeds, cetaceans are released from any terrestrial reproduction constraints. As free-ranging predators, the range of life history strategies exhibited by cetaceans is wide and diversified (Perrin et al. 2009). All cetaceans are long-lived species with a single, large and precocial young per reproductive cycle. Other parameters as age at sexual maturity and age at first reproduction vary among species, especially between the two suborders of cetaceans, the mysticetes and odontocetes. For baleen whales, the strategies vary less between species than for odontocetes, and most species share the long-range annual migration pattern between foraging in temperate or polar waters and breeding grounds in warmer waters (Chivers 2009), despite an important variability exists across and within species.

The wide range of size within odontocetes reflects the range of successful strategies, from the small-bodied species with comparatively shorter life span (harbour porpoises, \simeq 20 years and about 150 cm long) to large-bodied long-lived species (sperm whales, $>$ 70 years and about 16 m long). These variations combine with the wide range of habitat colonised by cetaceans, from polar to tropical marine biomes, from the oceanic domain to continental freshwaters, and from the surface to thousands of meters deep (Ballance 2009). In addition to this wide range of habitat, foraging characteristics of cetaceans also reflects the diversity of their life history strategies. Indeed, cetaceans can forage on several kinds of prey, such as small-sized schooling species at shallow depth (euphausiids, anchovies, sardine etc.; foraged by baleen whales), larger schooling fishes or squids at shallow depth (hake, myctophids, *Loligo spp*; foraged by many dolphin species), large squids in deep waters (foraged by sperm, pygmy sperm and beaked whales), or finally other top predators (large fishes, marine mammals; foraged by killer, false killer and pilot whales). As a consequence of this diversity of prey, cetaceans also exhibit very diversified foraging behaviour and prey capture techniques, specific to each target prey (Heithaus & Dill 2009).

Despite many different strategies to balance their energy budgets and fulfil their requirements for maintenance, reproduction and growth, odontocetes and mysticetes species present similarities in their resource acquisition strategies. Especially, foraging is not random and many examples show that cetaceans target and track discrete areas or habitats to forage (Stevick et al. 2002), as shown by

ARS behaviour (*e.g.* Bailey & Thompson 2006, Bailey et al. 2009, Garrigue et al. 2015). Many species indeed target highly predictable features in both space and time, such as topographic features. For examples, seamounts and oceanic islands have been shown to attract many cetacean species within all oceans (Kaschner 2008), especially in tropical waters (*e.g.* humpback whales (Garrigue et al. 2015) or beaked whales (Johnston et al. 2008, Roberts et al. 2016)). Shelf edges are also often targeted by offshore cetacean species, where individuals can rely on predictable resources with low temporal variability (Baumgartner et al. 2001, Cañadas et al. 2002, Friedlaender et al. 2006, Azzelino et al. 2008, Roberts et al. 2016). However, cetaceans also rely on more dynamic meso-scale oceanographic features, as eddies or oceanographic fronts (Baumgartner et al. 2001, Bluhm et al. 2007, Cotté et al. 2009; 2011, Woodworth et al. 2012), or at a coarser scale as on tidal fronts or coastal upwellings near seashores (Johnston et al. 2005, Skov & Thomsen 2008). Cetaceans with high energy requirement, *e.g.* small delphinids, tend to respond sharply to primary production and associated prey density, whereas taxa with lower energy requirement relative to their body mass would be more uniformly distributed (Mannocci et al. 2014a;b).

1.4 OBJECTIVES AND OUTLINE OF THE THESIS DISSERTATION

1.4.1 General objectives and hypotheses

As seen above, pelagic ecosystems are good examples of spatio-temporally highly variable environment. This patchy environment have shaped marine predator species leading to congruent general patterns in terms of foraging behaviour and habitat selection, despite difference in life histories. These differences can be expected to condition the response of species to ocean temporal variability, and to lead to various shape and breadth of ecological niches of top predators, including temporally varying sub-niches.

Pelagic ecosystems can be challenging to survey, especially when it comes to determining the distribution and ecological niche of highly mobile species over wide areas. Due to these inherent difficulties, a large amount of studies on pelagic marine top predators dealt with species, or population, that were easily accessible from land. That is typically the case of seabirds and pinnipeds, which have to return to land to breed or moult and hence are fairly easily accessible to either fit geolocation devices or collect various biological samples (biopsies, blood samples, stomach contents, etc.). In contrast, cetaceans are free ranging and far less accessible. If some coastal residential populations are well documented, the offshore at-sea distribution and ecological preferences of most species remain not-so-well known at the population level. However, during the last decades, the development of large-scale at-sea surveys, either ship-borne or aerial, has allowed to gather invaluable knowledge on species that remained poorly known so far. If the effort implemented toward such at-sea surveys is constantly increasing, the knowledge of at-sea distributions, and hence ecological preferences, of many species are still to be improved in vast areas.

The objective of the thesis was thus to describe the at-sea distribution of top predators species, but also to explore how the spatio-temporal variability of the pelagic ecosystems affects two facets of their ecological niches (Figure 1.4). This work focused on the habitat component of the niche (the conditions) and predators association with prey (the resources) for a range of cetacean and seabird species.

The habitat of top predators

The habitat (the conditions) is a central element of the ecological niche of a species, and, by extension, of its ecology. Hence, species-habitat relationships are the basis to clarify marine top predators ecology and further determine their role in communities. As stated above, the knowledge of top predator marine habitats remains to be addressed for many species, and a large part of this thesis is dedicated to highlighting habitat preferences for a set of 14 top predator species.

A species might use different habitats for different purposes, depending on the activity it is involved in: migrating, resting or breeding. These habitats can be defined by both physical or biological characteristics. Since both activities and environmental conditions vary with time, I expected to find varying habitat preferences depending on the considered time scales. Here, I defined habitat preference as a positive association to specific environmental conditions, resulting in a distribution diverging from random. I did not attempt to relate observed habitats with associated activities (habitat use) since this information is most of the time not accessible to survey observers. Habitat preferences are known to be different depending on species traits, and I expected to find different answers to the different levels of spatio-temporal variability of the ocean for species with contrasting life histories. Within this thesis, I focused on the response of predators to seasonal variability of pelagic ecosystems, between winter and summer, and also their response to interannual variability, at a decadal scale.

The impact of age and experience

If the ecological niche is a species space-time of activity, we might expect it to vary according to the age, and hence experience, of individuals. The studied predators are long-lived species with advanced cognitive capacities and characterised by delayed breeding, for which acquisition of foraging efficiency through learning and experience is crucial to ensure a good fitness (Gaston 2004). For such species, theory expects younger individuals to be less efficient than adults, potentially leading to competitive exclusion, and to exhibit different response to environmental variability than adults due to their more limited experience. I explored this hypothesis in the northern gannet, since this species is the most abundant pelagic seabird species in the study area, and juvenile or immature can easily be told apart from adult birds by visual observers.

The biotic resources

Finally, I explored the trophic dimension of top predator ecological niches, focusing on the link from prey to predators, without considering the opposite effect (Figure 1.4). Recent studies showed that the predator association with prey patch depends mostly on patch characteristics, rather than on the biomass or abundance of prey within it (Benoit-Bird et al. 2013). Indeed, the

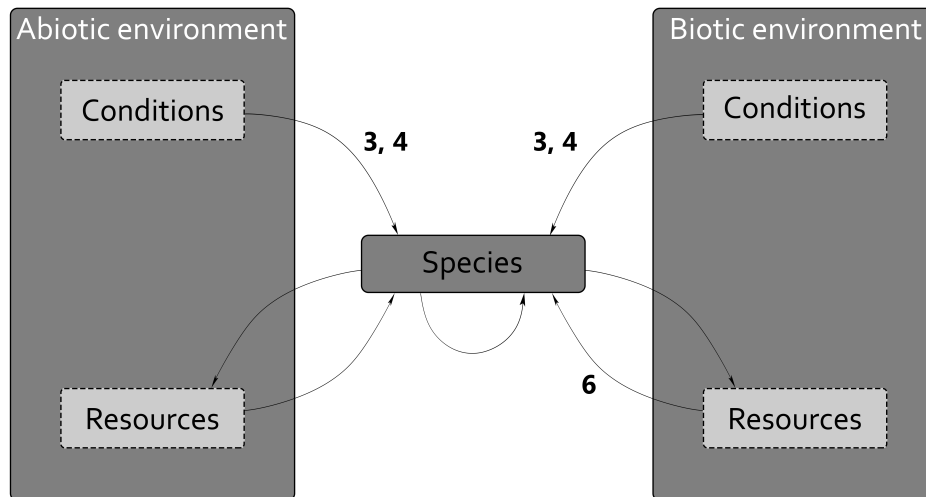


Figure 1.4 – The ecological niche, contrasting species relationships with abiotic and biotic conditions and resources. The different chapters of the thesis are indicated over the corresponding elements of the niche. Redrawn and modified from McNerny & Etienne (2012c).

availability of prey to predators depends on several factors, as the horizontal and vertical accessibility of the patch, or the size of prey. Therefore, here, I explored the association of predators to biomass of small pelagic fishes pooled into four prey size bins and two depth layers.

1.4.2 Outline of the dissertation

The present thesis is divided into four main substantive sections. Based on at-sea survey data, I explored the three facets of the ecological niche presented above for a wide range of cetacean and seabird species (Figure 1.4), in the temperate eastern North-Atlantic and north-western Mediterranean Sea. I chose to present my thesis dissertation as a synthesis, and these substantive chapters are syntheses of results presented in several papers, either published, submitted or in preparation. These publications can be found *in-extenso* within the Appendix volume provided electronically with this thesis dissertation. Links between chapters, papers and appendices are provided in the Table 1.2.

In **Chapters 1 and 2** of the thesis, I explored how the spatio-temporal variability of both biotic and abiotic environmental conditions of the pelagic ecosystems impact habitat preferences exhibited by six cetacean and eight seabird taxa, representing a range of different life histories. In **Chapter 3** (Figure 1.4, 3), I explored how top predators cope with the seasonal variability of pelagic ecosystems given their intrinsic biological constraints within the English Channel, the Bay of Biscay and the north-western Mediterranean Sea. In **Chapter 4** (Figure 1.4, 4), I examined how these predators modulate their habitat preferences as a response to interannual variations of available habitats within the Bay of Biscay, over a 10 years-long study period.

Chapter 3 relies on two papers currently in press, presenting habitat models for cetaceans and

seabirds in the north-western Mediterranean and the eastern North Atlantic, respectively. These papers are given in Appendices B and C, along with the distance sampling analyses on which habitat models are based (Table 1.2). Chapter 4 is related to a paper in preparation. This draft paper is shown in Appendix D, as well as the associated distance sampling analyses (Table 1.2).

In **Chapter 5**, by using the same approach as for Chapter 3, I explored how northern gannet habitat preferences change with age, by comparing adult and young (juvenile and immature) birds. This Chapter relies on a paper to be submitted for publication (Appendix E, Table 1.2).

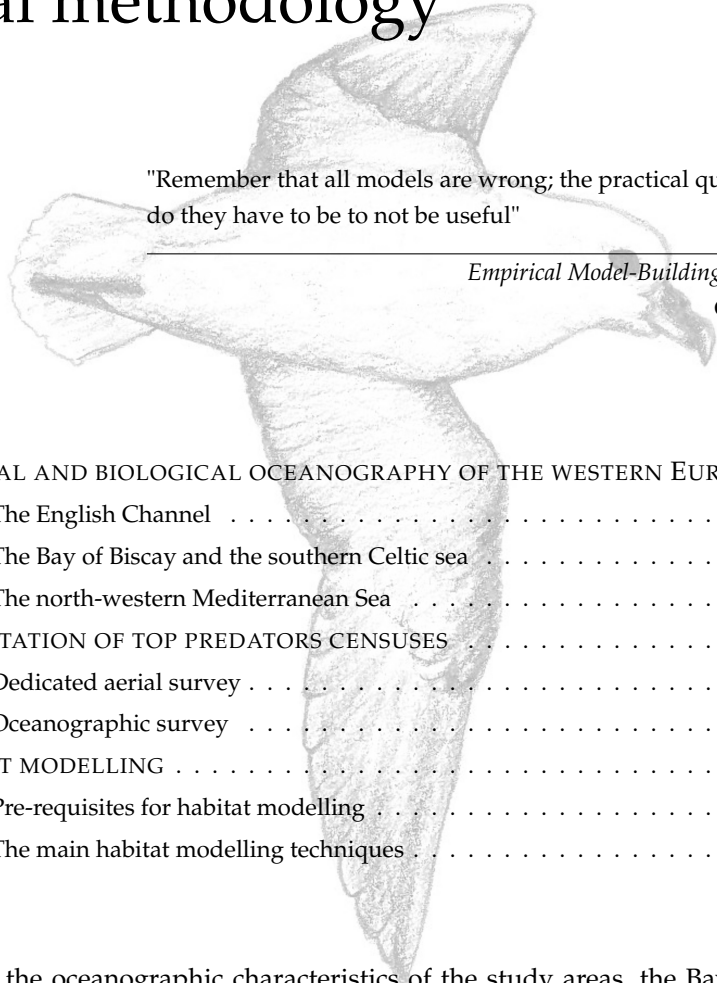
In **Chapter 6**, I explored the link between predators and prey at the individual level, thanks to oceanographic vessel surveys that have sampled concurrently predator and small pelagic fish distributions (Figure 1.4, 6). At the time of preparing the dissertation manuscript, the article derived from Chapter 6 was too preliminary and could not be included as such. As a consequence, results are presented within the chapter itself, and additional informations are provided in Appendix F (Table 1.2).

In the general discussion (**Chapter 7**), I deepen the theoretical framework of this thesis, and in particular the theoretical aspects of the relationship between the ecological niche of a species and its distribution. In a second part, I try to draw a general pattern of the effect of ocean variability on the ecological niche of predators. In particular, I explore whether this variability implies the use of distinct sub-niches depending on the encountered conditions at a particular time scale.

Table 1.2 – Summary of the chapters presented within this thesis dissertation. The ecological processes and related scales handled by each chapter are presented, as well as surveys on which analyses were based, the number of corresponding publication as referenced within the section "Scientific productions", and the associated appendices.

Chapter	Scale of ecological process	Ecological process	Survey	Publication reference	Appendix
2		Methods			A
3	Coarse	Seasonal habitat preferences	SAMM	5, 6	B & C
4	Meso	Decadal habitat preferences	PELGAS	3	D
5	Coarse	Impact of age and experience on the seasonal habitat preferences	SAMM	8	E
6	Fine, local	Predators association with prey	PELGAS	1	F

General methodology



"Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful"

Empirical Model-Building and Response Surfaces
George E. P. Box, 1987

CONTENTS

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IN this chapter the oceanographic characteristics of the study areas, the Bay of Biscay, the English Channel and the north-western Mediterranean Sea, are presented first. Secondly, the two surveys used within this thesis are described, with details about their protocols as well as the observation datasets and associated effort. Finally, methods used to infer the habitat component of species ecological niche based on distribution data are introduced.

2.1 PHYSICAL AND BIOLOGICAL OCEANOGRAPHY OF THE WESTERN EUROPEAN WATERS

THE work presented in this thesis focused on metropolitan French and adjacent waters, thus considering three sectors: the English Channel, the Bay of Biscay and the Celtic Sea, the north-western Mediterranean Sea. The first two sectors belong to the same oceanographic macro-region (the north-east Atlantic margin), but the third stand out, justifying the separation of the two basins (Atlantic *vs* Mediterranean).

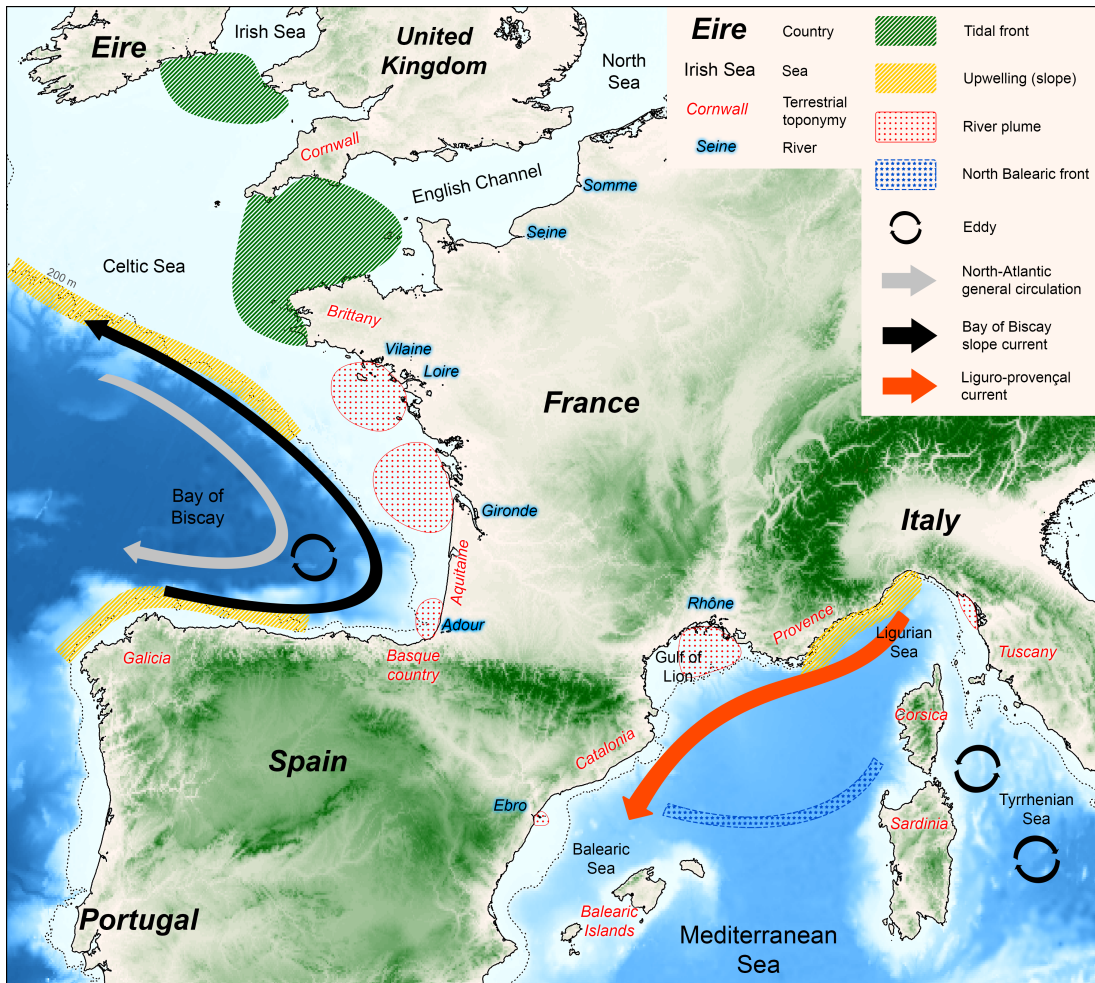


Figure 2.1 – Main oceanographic features of the western European waters, centred over France.

2.1.1 The English Channel

The English Channel (EC) is an epicontinental sea of shallow depth (maximum 172 m in the Hurd Deep, Smith et al. 1975) characterised by a mega-tidal regime. The sea floor is mainly composed of coarse sediments, rocks and sands. The strongest tides in Europe, with largest tidal ranges and

more efficient vertical mixing are found along the French coast of the EC (Brylinski & Lagadeuc 1990). The general circulation within the Channel is mainly from the Atlantic to the North Sea.

Seasonality is well marked, with winter vertically mixed waters and summer stratified waters. However, tidal currents and winds prevent stratification locally or temporally, in particular along the coasts of the eastern EC. In summer, between the stratified Celtic Sea waters and the homogenised cold waters of the eastern EC occurs a sharp tidal front, usually between the tip of Brittany and south-western England. The precise location of this front vary with the intensity of tidal currents, being situated around Channel Island during low coefficients, but farther west during strong tides, which results in a variation of around 200 km (Figure 2.1). This front is of crucial importance in the area, since it aggregates plankton in high densities, and is known to be actively frequented by northern gannets, auks, and small cetaceans.

The Channel being the southern limit of the cold temperate biogeographic region, it is characterised by the presence of several species of northern affinities and the southernmost colonies northern gannets, northern fulmars, black-legged kittiwakes and auks.

2.1.2 The Bay of Biscay and the southern Celtic sea

The Bay of Biscay (BoB) is characterised by a broad continental shelf, from 180 km in the northern BoB, to 20 km in the south (Capbreton Canyon), and around 30–40 km wide along the Iberian coasts (Koutsikopoulos & Le Cann 1996). The oceanic part of the BoB is 2,000–5,000 m deep. Currents in the area are fairly complex (Figure 2.1). The general circulation, originating from the north-Atlantic gyre, is weak and flows from north to south (Koutsikopoulos & Le Cann 1996, Pingree & Garcia-Soto 2014), while the slope current is strong and flows from the Iberian Peninsula to the northern BoB along the shelf break. In the southern BoB, the interaction between these two opposite circulations frequently results in meso-scale eddies that are relatively persistent in time (Pingree & Le Cann 1992, Caballero et al. 2014). Over the shelf, currents are mainly driven by winds, tides or freshwater inputs, depending on the area. Tidal currents are predominating in shallower areas, mostly in the northern BoB, while wind driven currents predominate elsewhere, generating an important spatio-temporal variability of local currents (Koutsikopoulos & Le Cann 1996).

The sediments over the plateau are mainly composed of sands and muds, with two large mudflats: the "great mudflat" located in the northern BoB at about 100 to 150 m deep, and the Landes mudflat located off the Aquitaine coast in the southern BoB. These mudflats are known as nurseries for juveniles of several fish species.

Seasonality is well marked, with a thermal stratification establishing during spring from south to north. In French coastal waters however, this summer stratification is prevented by tidal forcing in the north and wind-driven coastal upwelling in the south (Koutsikopoulos & Le Cann 1996). A second major summer structure occurs when the tidal waves interact with the continental margin, inducing colder and nutrient-rich waters to reach the surface, mostly around 47°N (Green et al.

2008). This structure is marked by strong productivity. Upwellings also occurs along the western Iberian margin. In autumn, stratification breaks down first in the northern BoB, and the whole shelf is vertically mixed in winter, although some thermohaline stratification is maintained in large river plumes (Loire and Gironde estuaries; Jegou & Lazure 1995). In terms of productivity, the phytoplankton blooms occur in spring, then productivity lowers down in summer as a result of nutrients depletion, and a secondary bloom appears in autumn, mostly in coastal waters (Pinnegre & Garcia-Soto 2014). Some blooms can also occur in river plumes during winter, if sufficient radiance.

The BoB is an interesting area due to its location at the intersection of the cold temperate and the warm temperate biogeographic regions. The top predator community is hence very diversified, with the occurrence of species of warm as well as cold affinities.

2.1.3 The north-western Mediterranean Sea

Although long considered as an oligotrophic sea (Margalef 1985), the north-western Mediterranean basin (NWMS) is now known as being strongly heterogeneous. The eastern basin is oligotrophic, but the north-western basin exhibits the highest productivity of the whole Mediterranean, and shows similarities with the eastern North Atlantic for its marked seasonality (D'ortenzio & Ribera d'Alcalá 2009).

The NWMS is characterised by a complex topography, with large continental shelves in the Gulf of Lion and the Tyrrhenian Sea and steep slopes indented by numerous canyons elsewhere. The general circulation is dominated by deep Atlantic originating waters entering the area from the eastern Mediterranean through the Tyrrhenian Sea, and flowing across the Ligurian to the Balearic Sea, along the continental slope (Figure 2.1). This current is known as the Liguro-Provençal or Northern Current (Millot 1999). Wind regime, topography and general circulation generate two permanent fronts: the Ligurian Front along the steep slopes of the Ligurian Sea, and the North-Balearic Front (Sournia et al. 1990). The Gulf of Lion remains a particular area within NWMS, being the only wide neritic plateau in the area (up to 40 miles wide), with sand and mud sediments. The combined effect of winds and river discharge, mainly from the Rhône river, generates high productivity throughout the year (Morel & André 1991). The Rhône river plume spreads out to hundred kilometres from the river delta (Morel et al. 1990, Sournia et al. 1990).

Seasonality (D'ortenzio & Ribera d'Alcalá 2009) is characterised by a strong summer stratification limiting phytoplankton growth and overall biological production, whereas water mixing during winter due to the combination of low surface temperatures and strong winds results in the breakdown of water stratification and in nutrients being upwelled to the surface layer. This enrichment of the euphotic layer allows phytoplankton bloom and mesotrophic conditions to develop in the NWMS from late winter to spring (Auger 2011, Morel & André 1991, Sournia 1973, Bosc et al. 2004). Three main regions of productivity can be identified: the Ligurian Sea characterised by its richness in euphausiids and cephalopods; the Rhône river plume where low salinity and high

nutrients concentration induce strong planktonic productivity; and the Gulf of Lion with high densities of small pelagic fish.

2.2 PRESENTATION OF TOP PREDATORS CENSUSES

2.2.1 Dedicated aerial survey

2.2.1.1 Protocol and survey design

The SAMM aerial surveys (*Suivi Aérien de la Mégafaune Marine*, Aerial Census of Marine Megafauna) were conducted in the winter 2011-2012 (November 17 to February 12) and the summer 2012 (May 16 to August 08) by the Observatoire PELAGIS for the French Agency for Marine Protected Areas (*Agence des Aires Marines Protégées*; AAMP). Sampled transects followed a zig-zag layout, and were designed manually to both maximise the use of flight time and coherently cover the variety of marine habitats surveyed, while ensuring an equal coverage probability within each stratum (Figure 2.2). To do so, the survey area was split into three main strata: neritic, slope and oceanic strata. A coastal stratum was overlaid to the neritic one to increase survey effort within coastal waters. These strata were organised in the three main sectors described above: BoB, EC and NWMS. All transects were flown at least once. In winter, a total of 46,205 km of transect was sampled, against 52,315 km in summer (Table 2.1). Effort was distributed across a total surface area of 556,393 km² (282,141 km² in BoB, 92,875 km² in EC and 181,377 km² in the NWMS; Table 2.1 and see Appendix A).

Table 2.1 – *The repartition of effort across the three main sectors: Bay of Biscay, English Channel and Mediterranean Sea. Are presented the total surface of each sector, the total survey effort flown and the effort flown in good conditions (i.e. in Beaufort sea-state < 4 and subjective conditions > medium).*

		Surface area	Survey effort	Effort in good conditions	
		km ²	km	km	% of total effort
Bay of Biscay	Winter	282,141	20,814	17,695	85%
	Summer		22,977	21,675	94%
English Channel	Winter	92,875	11,629	10,371	89%
	Summer		10,887	9,752	90%
Mediterranean Sea	Winter	181,377	13,762	13,133	95%
	Summer		18,451	17,218	93%

Survey platforms were high-wing double-engine aircrafts, with bubble windows allowing observers to scan right under the plane. The two trained observers recorded sightings and group size, as well as observation conditions (Beaufort sea-state, glare severity, turbidity, and cloud coverage) at the start of each transect, and whenever the detection conditions changed. Sightings

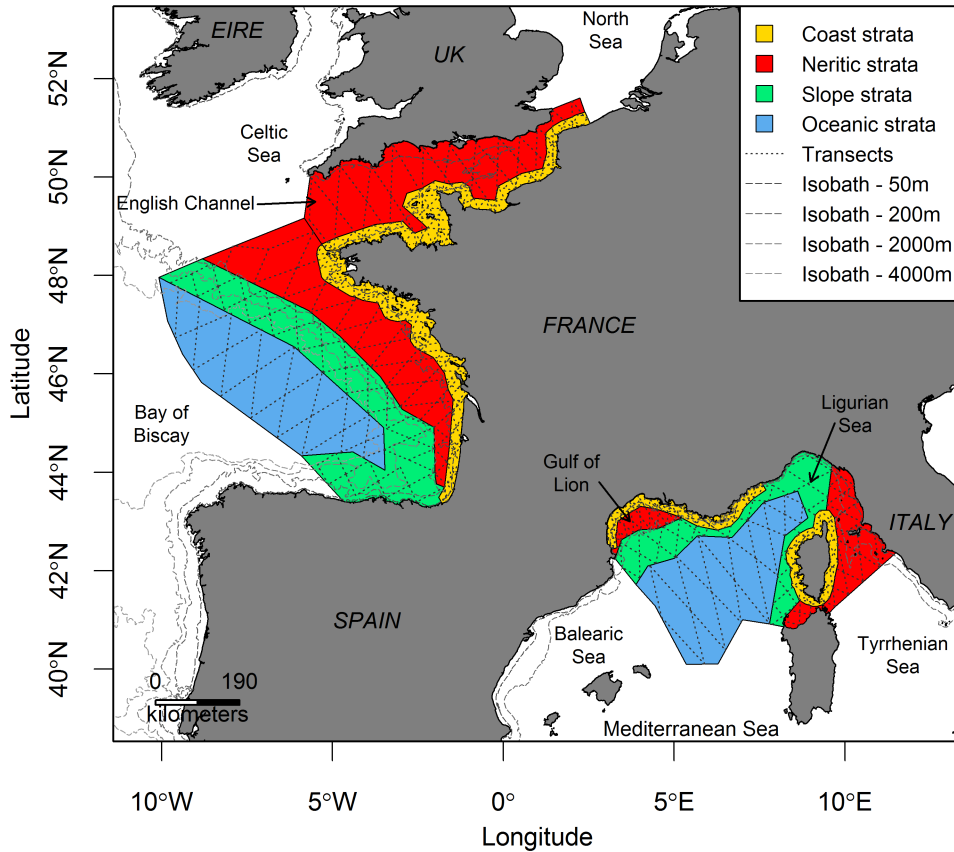


Figure 2.2 – Sampling design of SMM survey, with the four strata.

were recorded at the lowest taxonomic level possible, but groupings were done when species could not be identified with certainty. SMM survey provided a census of all megafauna, including turtles, sharks, large fishes, cetaceans and seabirds, but in this study, I focused only on the latter two taxa.

Observations were collected following standardised protocol designed for aerial surveys, based on line-transect methodology for cetaceans (Buckland et al. 2001), and strip-transect methodology for seabirds (Certain & Bretagnolle 2008). In the first case, all sightings of cetaceans were recorded along with the corresponding angle to the track line. For a fixed flight altitude of 182 m, this angle allowed to determine the Effective Strip Width (ESW) sampled on each side of the plane through distance sampling analysis. In the second case, seabirds were recorded within a band of 200 m on each side of the transect, under a perfect detection assumption. Transects were sampled at a ground speed of 167 km/h.

2.2.1.2 Sightings

As said above, the identification of species from the air can lead to difficulties telling apart some morphologically similar species. Hence, some groupings were necessary. The observed distributions of these groups, along with the corresponding encounter rates, defined as the number

of sightings per unit distance flown in effort, are presented in Appendix A (Figure A2–5, Table A1). These distributions and encounter rates were based on all sightings, in either good or poor observation conditions.

Five groups of cetacean species were studied: harbour porpoise, small-sized delphinids, bottlenose dolphin, Globicephalinae and fin whale. Harbour porpoise (*Phocoena phocoena*), identified at the species levels with no ambiguity, was only present in the ENA. Small-sized delphinids gathered both common (*Delphinus delphis*) and striped dolphins (*Stenella coeruleoalba*), which can hardly be differentiated from the air. In the ENA, both species can be encountered, but in the NWMS, the group was probably mostly composed of striped dolphins since the common dolphin has become a rare species in the area. Bottlenose dolphin (*Tursiops truncatus*) was identified at the species level in both ENA and NWMS. Long-finned pilot whale (*Globicephala melas*) and Risso's dolphin (*Grampus griseus*) were both identified at the species level, since the species are easily identifiable, but given the low number of sightings for each species separately, they were gathered for the habitat modelling study. Finally, fin whale (*Balaenoptera physalus*) was identified at the species level without ambiguity. The species was only studied in the NWMS, since it was too scarce in the ENA. All sightings unidentified with certainty within one of these groups were left apart.

Seven groups of pelagic seabirds species were studied: northern fulmar, small-sized shearwaters, large-sized shearwaters, storm petrels, northern gannet, auks and black-legged kittiwake. Northern fulmar (*Fulmarus glacialis*) was only sighted within the ENA. The small-sized shearwaters group was composed of yelkouan and Balearic shearwaters (*Puffinus yelkouan* and *P. mauretanicus*) in the NWMS, but of Manx (*Puffinus puffinus*) and Balearic shearwaters in the ENA, where the sightings were scarce in winter. Large-sized shearwaters were only composed of Cory's shearwater (*Calonectris diomedea*) in the NWMS, but in the ENA the group might also include great and sooty shearwaters (*Puffinus gravis* and *P. griseus*), two migrating species passing by in summer. The group was absent from all survey regions in winter. Storm petrels gathered different species depending on the basin. In the ENA, it grouped European (*Hydrobates pelagicus*), Wilson's (*Oceanites oceanicus*) and Leach's (*Oceanodroma leucorhoa*) storm petrels, while in the NWMS it was only composed of European storm petrel (*Hydrobates pelagicus melitensis*), where it was almost absent in winter.

Northern gannet (*Morus bassanus*) is the largest seabird of European waters and is identifiable at the species level with no ambiguity from a plane. The species mostly occurred in the ENA, but a few sightings were also made in the NWMS, where a few pairs are known to attempt breeding in summer and some individuals to spend winter. Auks were composed of common guillemot and razorbill (*Uria aalge* and *Alca torda*). Some sightings of auks were also made in the Gulf of Lion, but as for gannets, these sightings in the NWMS were not considered during the thesis, since they represent marginal individuals. Black-legged kittiwake (*Rissa tridactyla*) was the only Laridae species studied here. As for cetaceans, all sightings not identified with certainty within one of these seabird groups were left apart.

2.2.2 Oceanographic survey

2.2.2.1 Halieutic survey

Protocol Contrary to the SAMM surveys, exclusively dedicated to top predators observation, top predator observations on-board oceanographic cruises have developed from a pre-existing vessel survey whose primary objective was to provide annual estimates of small pelagic fish stock sizes. These cruises are the PELGAS surveys, that have been conducted by IFREMER on-board the R/V *Thalassa* since 2000, although it is only since 2003 that top predator observers joined the program (Doray et al. 2014).

The survey design is optimised for acoustic sampling of pelagic fish. It is typically composed of a series of transects perpendicular to the coast covering the shelf, from Spain to northern French coast (Figure 2.3). The transects are regularly spaced every 12 nautical miles, and cover a linear distance of about 6,500 nautical miles (depending on the years); they are sampled at a speed of 10 kn, allowing the survey to be completed in about 30 days.

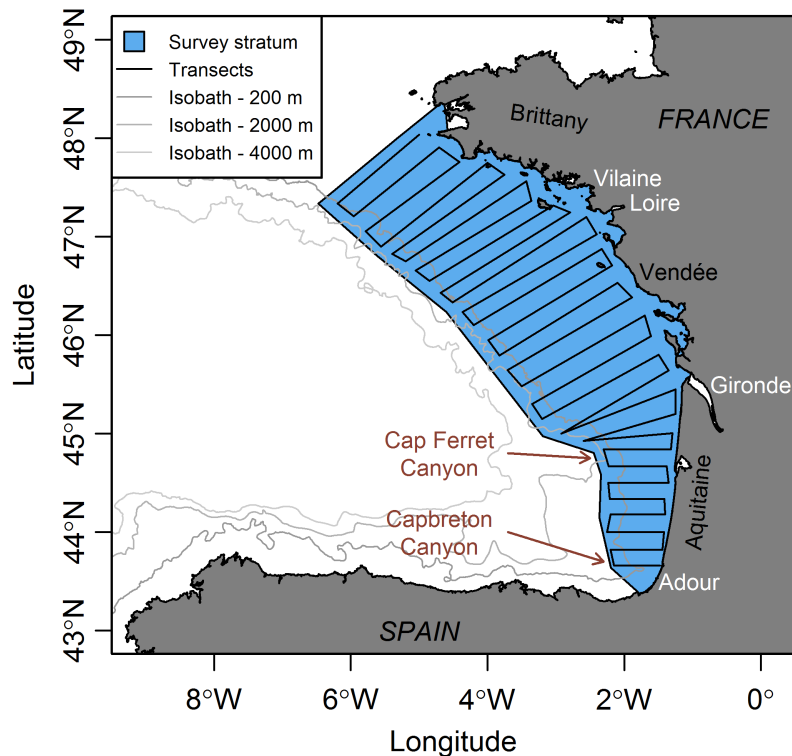


Figure 2.3 – Survey area and theoretical sampling design of PELGAS survey. The four main estuaries are indicated.

When sampling these transects, acoustic detection is carried on continuously by echosounders (Doray et al. 2014). When significant patches of echotraces are detected on the echosounder, the acoustic sampling effort is interrupted and trawl hauls are made in the patch to check species and size composition, age classes and biomass in order to improve the assignment of echotraces to par-

ticular fish species. Once processed, acoustic data allow biomass, abundance, mean body length and mean weight of target species to be estimated per sampled nautical mile. These informations are further split into two layers: a surface layer from 10 to 30 m deep (there is an acoustically blind zone from 0 to 10 m), and a deep layer from 30 m onward. However, for depth shallower than 50 m, the two layers cannot be disentangled and the acoustic data are aggregated over the whole water column.

In parallel to the acoustic survey, hydro-biological sampling is also done to study the distribution of eggs of small pelagic fishes, zooplankton, chlorophyll *a* concentration and various physical parameters measured *in-situ* (oxygen concentration, etc.; Doray et al. 2014). During day-time and acoustic sampling, sardine and anchovy eggs are counted every three nautical miles thanks to a Continuous Underwater Fish Egg Sampler (CUFES). During night-time, the hydro-biological sampling is complemented by hydrology stations matching the transect sampled during the day. Conductivity Temperature Depth (CTD) profiles are performed over stations from the surface to 1–2 meters above the sea floor, and sea water samples are collected at the seabed, the pycnocline, the chlorophyll *a* maximum and at the surface to measure bio-physical environmental parameters of the water column. Plankton net tows are also performed to assess mesozooplankton (200 μm – 2 mm) species composition and biomass. All along the vessel track sea surface temperature and salinity are also recorded.

The total survey effort varied each year depending on the annual duration of the survey and at-sea conditions (Figure 2.4). Additional transects were sampled during some years (*i.e.* 2010), sometimes extending off the shelf and out of the usual PELGAS survey stratum (Figure 2.4). For further analysis, I only considered effort realised within the usual stratum, for the period 2004–2014, when the top predator protocol was fully implemented.

Prey data from acoustic survey The main species detected during the PELGAS survey are Atlantic herring (*Clupeus harengus*), anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), Atlantic mackerel (*Scomber scombus*), Pacific Mackerel (*Scromber japonicus*), Atlantic horse mackerel (*Trachurus trachurus*), Mediterranean horse mackerel (*Trachurus mediterraneus*), sprat (*Sprattus sprattus*) and blue whiting (*Micromesistius poutassou*). These species occurred in the area during the whole study period. Anchovy, sardine and sprat accounted for the higher biomass over the decade with fairly limited variation between surface and bottom layers (Figure 2.5; Appendix A, Figures A6–12).

2.2.2.2 Predator survey

Protocol Top predator observations were conducted by using a line transect methodology. Predator observation effort spanned from sunrise to sunset whenever the vessel was moving at 10 kn, either in a transect or between two transects. Sighting effort stopped when trawling. The main observation platform was the upper deck of the R/V *Thalassa* (16 m above sea level), but when weather deteriorated (strong wind or rain) observation platform switched to the bridge (14

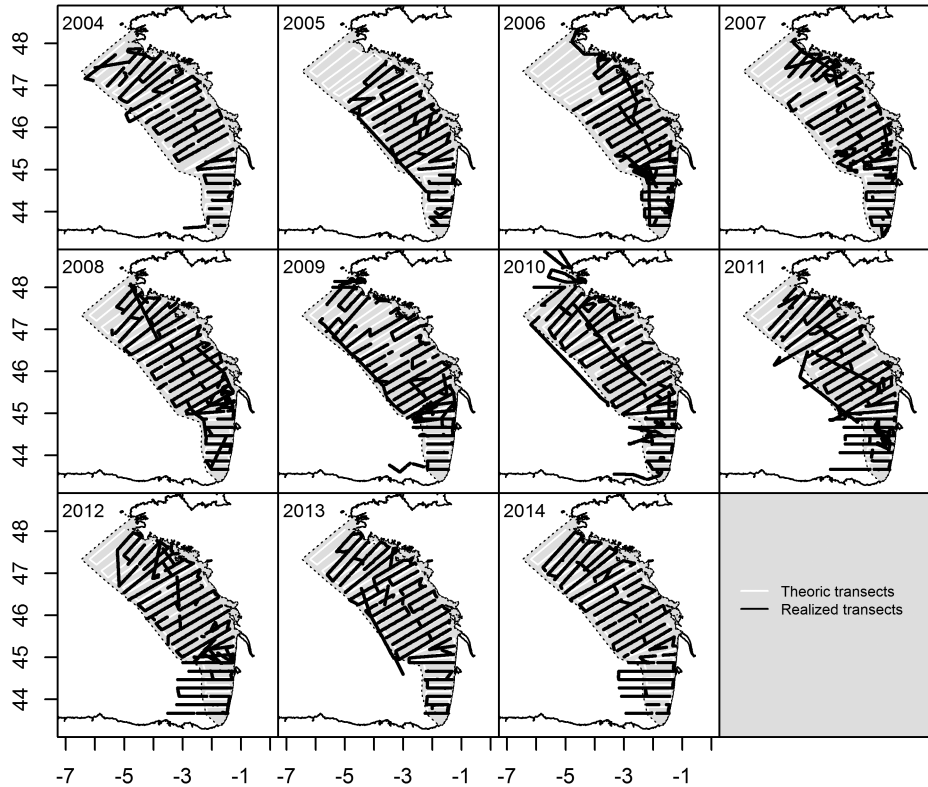


Figure 2.4 – Realized PELGAS route from 2004 to 2014, including inter-transect routes. 2004: 3723.3 km; 2005: 3714.6 km; 2006: 4914.2 km; 2007: 4429.5 km; 2008: 5108.6 km; 2009: 5942.3 km; 2010: 6799.5 km; 2011: 6067.5 km; 2012: 5511.3 km; 2013: 4502.6 km; 2014: 4406.403 km.

m above sea level).

Two trained observers scanned with naked eyes the 180° ahead of the bow, each observers scanning their respective 90° on each side of the vessel. Three observers were on-board, two of them being on-duty at any time while the other was off-duty. Typically the observation session for each observer was two hours long, with a side switch every hour; hence, observation bouts durations were of one hour maximum. Observation conditions (Beaufort sea-state, swell, glare, cloud cover, platform) were recorded at each observer switch, or whenever observation conditions changed. Observation effort was set on the GPS track of the research vessels.

For each sightings the species composition (with binoculars checking if necessary), number of individuals, behaviour, time of the observation were recorded. Distance and angle to the boat (estimated by eye after calibration with a Heinemann's stick for distance and with an angle board for the angle) were also recorded in order to compute the perpendicular distance of a sighting to the track line. Attention was paid not to record seabirds attending the vessels (called "followers") by ignoring all individuals coming from behind the boat. When considering the behaviour of species at detection, attention was paid to assess whether the species was attracted to or avoided the vessel, and which activity individuals were engaged in (travelling, foraging, feeding etc.). For

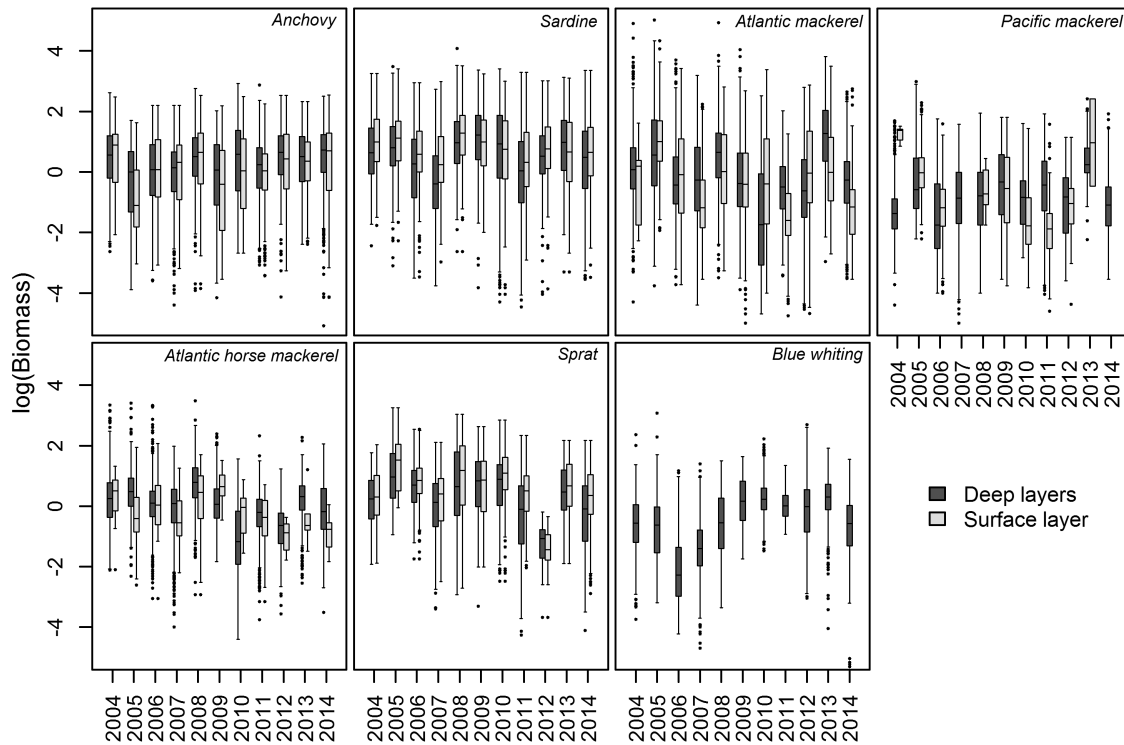


Figure 2.5 – Annual biomasses (in logarithm) for deep (dark grey) and surface (light grey) layers assessed through acoustic detection within the Bay of Biscay from 2004 to 2014 for anchovy, sardine, Atlantic mackerel, Pacific mackerel, Atlantic horse mackerel, sprat and blue whiting.

some species, as for northern gannet and black-legged kittiwake, individual age classes were also recorded.

Predators sightings In the analyses based on the PELGAS surveys, I focused on only five predator taxa: northern fulmar, northern gannet, auks, common and bottlenose dolphins (see Appendix A for raw distributions (Figures A13–17) and annual encounter rates (Table A2)). The advantage of the boat-based surveys is that most sightings can be identified at species level. However, for some species for which a species identification might be difficult even after binocular checking, or for which the number of unidentified individuals remains high, I used the same grouping as for the SAMM surveys. Thus, auks were composed of common guillemots and razorbills.

2.3 HABITAT MODELLING

2.3.1 Pre-requisites for habitat modelling

The ecological niche concept allows to determine which ecological processes drive habitat preferences of a species, based on its distribution. This conceptual framework is essential to build an ecologically relevant habitat model, and drive ecologically relevant conclusions from its results. Indeed, this step allows one to test hypotheses regarding the type and shape of the relationships

between a species and its environment, and will condition the type of model and the environmental variables (biotic, abiotic conditions) that will be used. Habitat modelling, if performed in the niche concept framework, therefore necessitate some basic *a priori* knowledge about the studied species (Guisan & Zimmermann 2000).

The various types of model available for such a purpose will be presented in the following section. Concerning the variables to be used, they can be divided into two categories: proximal *versus* distal variables. The first are the conditions (or resources) to which the species react directly, while the latter are indirect variables, related to resources or regulators of the species distributions (Guisan & Zimmermann 2000). If the first are ideal predictors, they are rarely available at the spatial and temporal extents and resolutions needed for modelling. In contrast, distal variables are often more largely available and thus most habitat models rely on their utilisation. However, in the case of such indirect variables, the model cannot be extrapolated beyond the range of sampled conditions (Elith & Leathwick 2009, Franklin 2010, Peterson 2011, Mannocci et al. 2015), nor be transferred from a geographical area to another one (geographical extrapolation). Indeed, there is no assumptions that the observed shape of relationship in a particular area would be conserved at another one. The particular pre-requisites needed if a model is aimed to be used to conduct geographical extrapolation (prediction to an independent area) will not be detailed here (see for example Guisan & Zimmermann 2000, Elith & Leathwick 2009, Peterson 2011). My goal was explanatory rather than predictive, and I only performed some careful interpolation in predictions (prediction within the range of sampled conditions and within sampled areas).

The quality of sampling is crucial regarding the expectation and outcome of models (Figure 2.6): if sampled conditions are not representative of the actual habitat of a species, then the prediction will not be representative either (Pearson 2010). The conceptual framework is also of importance, especially regarding suitable habitats that are not occupied: if the limitation comes from dispersal abilities, it might be wise to incorporate this factor within the model. One could argue that habitat models infer habitat suitability of a species, giving rise to predicted habitats that are in fact unoccupied due to dispersal limitations or negative biotic interactions (Figure 2.6). However, in the case of source-sink populations, for example, the sampled, and thus predicted, habitats might not be all suitable. The distinction between habitat occupancy and habitat suitability is therefore important.

In fact, several terms are used regarding habitat, and particularly outputs of habitat models: habitat suitability, habitat use (probability), habitat preferences. These terms actually refer to precise definitions (Fuller 2012). The habitat suitability (or quality) refers to the fitness value of a habitat to a particular species. When incorporating population dynamic parameters, it can be called realised habitat quality. Thus, habitat suitability *sensu-stricto* is not reachable by habitat models: the predicted habitat can either be suitable or not. Habitat use corresponds to the activity individuals are involved in a particular habitat, so it implies knowing the activity of every sighted individuals. Such habitat characteristics can be inferred through habitat modelling, but only if the activity of observed individuals is known. Finally, habitat preference refers to a positive association to particular habitat resulting in higher densities in this habitat regarding the whole species

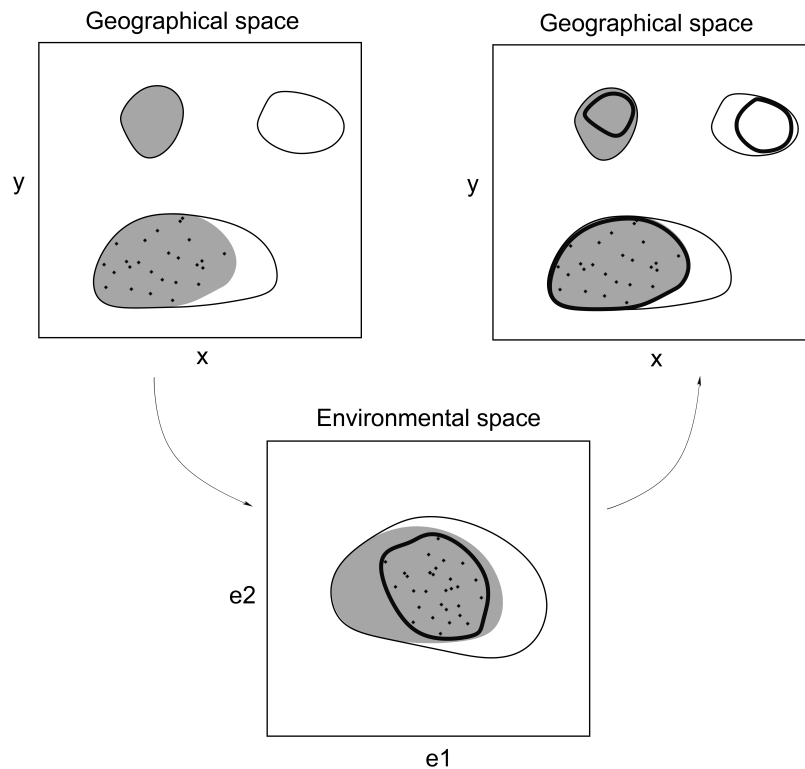


Figure 2.6 – Illustration of the relationship between a hypothetical species' distribution in geographical space and environmental space. Geographical space refers to spatial location as commonly referenced using x and y coordinates. Environmental space refers to Hutchinson's n -dimensional niche, illustrated here for simplicity in only two dimensions (defined by two environmental factors, $e1$ and $e2$). Black dots represent observed species occurrence records. Grey shading in geographical space represents the species' actual distribution (i.e. those areas that are truly occupied by the species). Notice that some areas of actual distribution may be unknown (e.g. grey area with no observations). The grey area in environmental space represents that part of the habitat that is occupied by the species. Again, notice that the observed occurrence records may not identify the full extent of the occupied habitat. The thin solid line in environmental space depicts the habitats suitable for the species, which represents the full range of conditions within which the species is viable. In the geographical space, the thin solid lines depict areas with corresponding suitable conditions; this is the species' potential distribution. Some regions of these suitable habitat and potential distribution may not be inhabited by the species due to biotic interactions or dispersal limitations (e.g. the blank areas). The bold ellipses illustrate how a hypothetical species' distribution model may be fitted to observed species occurrence records. The species' habitat is characterised in the environmental space by relating observed occurrence localities to a suite of environmental variables. Notice that, in environmental space, the model will only identify the part of the habitat defined by the observed records. When projected back into geographical space, the model will predict distribution of the species outside the sampled area. These distributions could either be non-sampled area were the species indeed occur, or areas were the conditions are suitable but the species cannot established due to geographical or biotic constraints (potential distribution). In both cases, the sampled distribution results in partial assessment of the species habitat in the environmental space, leading to partial prediction of species distributional area. Figure redrawn from Pearson (2010).

distribution. Such preference can be either expressed as a probability (of presence), or as a density of individuals. This term is related to those of habitat occupancy (relative occurrence within a particular habitat) and habitat association (can be positive, negative or neutral). See Fuller (2012) for an extensive review of habitat categories.

Two important pre-requisites to habitat modelling are the following: (i) habitat models assume that environmental processes dominate the species distributions, so that these environmental conditions would explain most of the spatial structure of the species distribution (Guisan & Zimmermann 2000, Elith & Leathwick 2009), (ii) they assume that the species is at equilibrium with its environment (Barry & Elith 2006). This assumption is particularly important when aiming at performing some extrapolation.

2.3.2 The main habitat modelling techniques

There is a broad range of available techniques to model species distributions (for extensive reviews, see Guisan & Zimmermann 2000, Redfern et al. 2006, Franklin 2010, Peterson 2011). A variety of techniques rely on different types of data: presence-absence data, presence-only data, presence with pseudo-absence data. Here, I quickly describe the main techniques used to model marine species habitat based on presence-absence data, which are the type of data at the basis of the present work.

2.3.2.1 Ordination methods

Ordination methods are descriptive techniques belonging to the family of multivariate analyses. The main goal of these techniques is to summarise environmental gradients into a reduced number of dimensions that are easier to interpret than the original dataset (Jongman et al. 1995). As habitat modelling techniques, they can be used to explore the arrangement of species along habitat gradients. The aim of these techniques is to partition the variance of the dataset over several orthogonal and independent axes, which are linear combinations of environmental variables describing the species environment, capturing the patterns of the original dataset.

These ordination techniques are mostly used in community ecology to partition the habitat used by several species (*i.e.* Atlantic spotted dolphins and bottlenose dolphins in Mexico (Griffin & Griffin 2003), or seabirds in the eastern tropical Pacific (Ballance et al. 2006)). The assumptions regarding the relationships between species and their environment vary for each ordination technique, some methods assuming linear (principal component analysis, redundancy analysis) or unimodal relationships (correspondence and canonical correspondence analyses).

2.3.2.2 Classification and regression trees

Classification and regression trees (CART) are non parametric methods, unlike the other techniques presented here (Guisan & Zimmermann 2000, Redfern et al. 2006). When the response variable is categorical, classification trees are used, while regression trees are used when response

variables are numerical. These decision trees aim at dividing the data into successive homogeneous subgroups through recursive partitioning method. At each step (split), two daughter nodes are generated on the basis of the predictor variables allowing to obtain the most homogeneous subsets of data.

Decision trees are not the commonest techniques used to infer relationships between cetaceans or seabirds and their habitats, but some applications have been attempted. For example, MacLeod et al. (2007) used CART to explore habitat preferences of cetaceans occurring in western Scotland; MacLeod et al. (2008) used CART to highlight habitat partitioning between two dolphins species based on temperature; while Monsarrat et al. (2015) used regression trees to infer the historical distributions of right whales. However, based on literature, Franklin (2010) showed that decision trees performed poorly compared to other techniques.

2.3.2.3 Regression models

Regression models are clearly the commonest methods used to perform habitat modelling (Redfern et al. 2006). The aim of regression is to model the relationship between species abundance or occurrence (response variable) and single or combinations of environmental variables (explanatory variables). These variables can either be raw variables, or summarised environmental gradients derived from ordination techniques. The use of such gradients avoids multicollinearity in models, but this could also be achieved by not including dependent variables within models (Guisan & Zimmermann 2000, Redfern et al. 2006). All these regression techniques assume observations are independent (no spatial nor temporal autocorrelation).

Simple regressions are a linear functions of the predictors and assume response variables are normally distributed (Gaussian distribution), with constant variance (Guisan & Zimmermann 2000). However, such assumptions can hardly be met in natural systems.

Generalised Linear Models (GLM) overtake this problem by sustaining other distributions of the response variables, as well as non-constant variance (Guisan & Zimmermann 2000). This is achieved by relating the response variable to explanatory variables through a link function, which depends on the assumed distribution of data (Gaussian, Poisson, Binomial, Gamma). Doing so, the linearity and normality assumptions are conserved between the link function and the explanatory variables. If such a link function still is not sufficient to get a linear relationship between response and predictors, a transformed term can be imposed on predictors, leading to polynomial regressions.

Generalised Additive Models (GAMs) are one of the most widely used techniques in habitat models (Guisan & Zimmermann 2000, Redfern et al. 2006). GAMs are extension of GLMs, with which they share the use of a link function and several distributions of response variables. However, unlike GLMs, GAMs allow non-linear relationships to be modelled thanks to the use of non-parametric smoothing functions. Given these characteristics, GAMs model relationships that are often considered as more ecologically relevant than GLMs. This relevance is conditioned to

a good control over these smoothers to avoid over-fitting of the data, through the selection of an appropriate degree of smoothness (*i.e.* degrees of freedom) to be applied to modelled predictors. In addition, this technique provides useful visualisation of response curves as well as robust predictions when the model is well constructed (especially when not over-fitted; Franklin 2010).

In the following Chapters (3–5), the relationships of predators to their habitat were modelled through GAMs. I mostly used distal variables (temperature, salinity, currents etc.), which in most cases were abiotic, although chlorophyll *a* and net primary production were also used in some cases. The smoothers were constrained to 3 degrees of freedom, in order not to overfit the data since I expected the species not to exhibit more than 3 inflexion points in their relationship with their environment (1 degree of freedom would be for linear relationship, 2 for unimodal curve).

The effect of ocean seasonality

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As seen earlier, seasonality is one of the major components of temporal heterogeneity in pelagic ecosystems. The aim of this chapter was to study how top predators cope with this seasonal variability depending on their intrinsic biological constraints, with a particular focus on habitats (Figure 1.4, 3). Since environmental seasonality occurs at a similar temporal scales than phenological cycles of many marine predators, we expected a range of accommodation strongly tighten to the intrinsic characteristics of the different species, notably with an important effect of alternating breeding and non-breeding periods. Therefore, we explored habitat preferences of several cetacean and seabird taxa with varying life history traits in winter and summer, through habitat modelling based on the SAMM surveys, across the English Channel and Bay of Biscay as well as the north-western Mediterranean Sea.

3.1 WHY SHOULD A SPECIES SEASONALLY ADJUST ITS HABITAT PREFERENCES?

3.1.1 Seabirds

COMPARED to inshore seabirds, pelagic seabirds¹ exhibit a particularly acute seabird syndrome, due to the necessity to forage into a patchy environment and, during the breeding season, to commute between foraging and nesting sites (the central-place foraging constraint; Gaston 2004). These sometimes large-scale foraging trips (hundreds to thousands of kilometres; Magalhães et al. 2008) are required during the breeding season to fulfil the adults' energetic requirements and those of their growing chick. These needs can be fairly different, thus leading to additional constraints for adults which may have to forage on different prey and habitats to provision their chick. Food provisioning is therefore critical to secure a good fitness by ensuring both adult survival and the production of high quality offspring. In addition to be a keystone feature of the breeding success, food provisioning is also the most energetically demanding activity during this period. Therefore, the fitness of a pelagic seabird is directly linked to food abundance and accessibility, as well as to the foraging ability of individuals. Hence, the constraints over pelagic seabirds regarding the exploitation of favourable habitats can be high.

Since all energy expenses engaged during breeding period would condition adult survival and further reproductive success, the energy budget has to be optimised by maximising energy intakes while minimising energy expenditures. During the breeding period, adults can achieve this through the optimisation of the trade-off between habitat profitability and distance to the nest. Adults should favour most favourable habitats as close as possible to the colony, to feed their chicks with highest quality prey and high provision rate. This constraint can be relaxed for species with enhanced flight abilities which can travel long distances at lower cost, if their offspring can survive longer provisioning intervals (*e.g.* Procellariidae).

When the chick-rearing period is over, costs of living do not necessarily drop. This is particularly the case at higher latitudes, where unfavourable environmental conditions during the wintering season can be particularly costly for seabirds. However, during this period, individuals are free-ranging and so can target any favourable habitats, with the possibility to overwinter in a different region from where they breed. Therefore, some seabird species would perform winter migrations to areas with more favourable and less costly environmental conditions, while other species would remain within the same area and would compensate the degradation of environmental conditions by adjusting their foraging behaviour (*e.g.* increasing foraging effort; Fort et al. 2013). The conditions for a species to migrate would be that energy gains available at remote foraging grounds would overtake energy expenses incurred while travelling to that ground. Therefore, species with energetically inexpensive flights could perform basin-scale migrations to overwinter

¹Here, "pelagic seabirds" refer to seabirds which only return to the coast to nest but forage on oceanic offshore waters, as opposed to inshore/coastal seabirds which rely on coastal waters to both reproduce and forage.

in high quality and energetically more favourable regions.

As a consequence of these life styles, we expected variations of habitat preferences between the breeding and wintering periods for most pelagic seabird species.

3.1.2 Cetaceans

Contrary to seabirds, most cetaceans are not constrained by local and discrete breeding grounds, especially odontocetes. Apart from a few well-studied resident populations that use restricted home ranges, they are free-ranging year-round and could therefore switch between optimum habitats depending on seasons, or even track a particular habitat year-round. However, cetaceans are characterised by diversified life styles and foraging strategies with varying associated energy costs depending on species, especially according to their diving abilities. These diving abilities determine prey accessibility for a particular cetacean species. If, contrary to seabirds, the horizontal dimension is not constraining their foraging strategies very much, this is not the case of the vertical dimension and commuting from the surface where they breath to the depth where they forage is recognised as a specific case of central-place foraging behaviour (Friedlaender et al. 2016). For example, delphinids or the smaller baleen whales (shallow divers) have costly foraging strategies and have to target highest quality prey (*e.g.* lipid-rich krill or small fishes), while less energetically costly species, such as deep divers, can forage on lower quality prey as squids (Spitz et al. 2012). These variations in costs of living have been shown to drive cetaceans habitat preferences (Mannocci 2013), since habitat preferences would mirror, at least in part, prey quality preferences.

Therefore, we expected to find fairly different habitat preferences between species, with some species relying on high quality habitats while others might be less demanding. We also expected various types of response to ocean seasonality, according to the intrinsic characteristics of each cetacean species. Nevertheless, we overall expected a lower impact of seasonality on cetaceans than on seabirds, resulting in less contrasted habitat preferences between seasons.

3.2 OCEAN SEASONALITY DRIVES TOP PREDATOR HABITAT PREFERENCES

3.2.1 Specific methodology

We performed habitat modelling on winter and summer cetacean and seabird sightings obtained from the SAMM surveys. Transects were subdivided into 10 km long segments of homogeneous conditions. Habitat modelling was then performed on best quality data (Beaufort sea-state from 0 to 3 and subjective conditions from medium to excellent). The effort flown in good conditions represented 87% of total survey effort in winter, 93% in summer in the Eastern North Atlantic (ENA), but accounted for 95% and 93 % of total survey effort in the North-Western Mediterranean Sea

(NWMS, Table 2.1). Habitat modelling, model selection and predictions were conducted by using Generalised Additive Models (GAMs; Hastie & Tibshirani 1990, Wood 2006) with quasi-Poisson distribution, log-link function and sampled area as an offset. The sampled area associated to each segment was the segment length multiplied by twice the corresponding ESW for cetaceans (see Appendices B and C), or by twice 200 m for seabirds.

We included four physiographic variables: depth, slope for cetaceans and seabirds, as well as distance to closest coast and distance to closest colony for seabirds only. Colony locations were compiled from several sources, and geolocated (see Appendices B and C). In addition, we included eight oceanographic variables in the NWMS, six in the ENA: mean sea surface temperature (SST), its variance (SST_{var}) and its gradient (SST_{grad}), mean sea surface height (SSH) and its standard deviation (SSH_{SD}) in both regions; surface chlorophyll *a* concentration (Chl), surface net primary production (NPP) and mean euphotic depth (Zeu) in the NWMS; and maximum tidal velocity (max. velocity) in the ENA. Chlorophyll *a*, NPP and Zeu were not included in the ENA due to an almost permanent cloud coverage over the EC in winter resulting in the absence of data for this period. Regarding tidal current velocity, it was only included for the ENA, since tides are very limited in the NWMS. All oceanographic variables were included at two temporal resolutions: summarised situation over 7 and 28 days prior to each sample day.

We implemented a selection procedure which tested models with at least one and up to four covariates (including variables at both temporal resolution) and excluded all combinations of covariates with absolute value of correlation higher than 0.7 (correlation matrices are presented in supplementary materials of Appendices B and C). The selection procedure was based on the Generalised Cross-Validation criterion (GCV, the lower the better). Once a model was selected, we extracted the contribution of each covariates in the linear predictor by segments, then mapped those contributions allowing the exploration of spatial variations in habitat preferences.

Predictions and their coefficients of variation were then produced for each day of the survey periods, and averaged over seasons. Variance around those overall predictions were computed as the sum of variance around mean prediction and mean of daily variances, then the coefficient of variation was calculated as $CV = \sqrt{seasonal\ variance} / seasonal\ mean$. All analyses were done in R 2.15.3 (R Core Team 2013).

Based on these habitat models and resulting predictions, we explored the variations of habitat preferences for cetacean and seabird species between the winter 2011/2012 and summer 2012. Method, results and discussions for NWMS and ENA are detailed within Appendices B and C. In the NWMS, habitat models were computed for small-sized delphinids, bottlenose dolphins, Globicephalinae and fin whales among cetaceans; and for small-sized shearwaters, large-sized shearwaters and storm petrels among seabirds. For the latter two groups, models were only fitted for the summer season since the number of sightings were too low in winter. Northern gannet, auks and black-legged kittiwake sightings were too anecdotal in both winter and summer to perform any habitat modelling in the NWMS. In the ENA, analyses were conducted for harbour porpoises, small-sized delphinids, bottlenose dolphins and Globicephalinae among cetaceans (not enough

sightings for fin whales); and for northern fulmars, small-sized shearwaters in summer only (too scarce in winter), large-sized shearwaters in summer only (no sightings in winter), storm petrels, northern gannets, auks and black-legged kittiwakes among seabirds. However, we failed to fit any model consistent with data for storm petrels and large-sized shearwaters in the ENA, hence no results are presented for these two groups in the area.

3.2.2 North-Western Mediterranean Sea

Small-sized shearwaters, Globicephalinae, small-sized delphinids and fin whales showed consistent habitat preferences from one season to the next (Table 3.1). Small-sized shearwaters responded to environmental seasonality by targeting areas exhibiting reduced seasonality. They occurred over coastal year-round productive habitats in both winter and summer (Figure 3.2). Doing so, they exploited a habitat which can sustain their energetic requirements throughout the year, during the non-reproductive period as well as during the energetically costly incubating and chick-rearing periods.

The overall seasonality of NWMS seemed to have limited impact on Globicephalinae habitat preferences (Figure 3.1), as they were able to switch between habitats with enhanced productivity from one season to the next (Appendix B). This might be explained by their reduced energetic needs per unit body mass associated to their deep-diving capabilities, that would allow them to explore water layers that are less submitted to surface seasonality. Interestingly, the species were more related to dynamic, yet predictable, oceanographic features (e.g. the Liguro-Provençal Current; Appendix B) than supposed from previous studies, which relied mostly on physiographic variables (Cañadas et al. 2002, Praca & Gannier 2008).

For fin whales and small-sized delphinids, habitat preferences did not vary between seasons, but part of these populations seemed to migrate out of the area during winter. Indeed, these taxa had lower abundance in winter compared to summer in the area (Laran et al. in revision), although their habitat preferences remained similar at both seasons (Figure 3.1). For example, small-sized delphinids exhibited a clear preference for deep oligotrophic oceanic waters at both seasons (consistent with the habitat of their forage species, Würtz & Marralle 1993) but their overall densities were clearly lower in winter. In the case of fin whales, the present results showed a strong preference for the Liguro-Provençal Front, where *Meganyctiphanes norvegica*, the fin whale main prey in the NWMS, is known to aggregate (Astruc et al. 2005), especially in summer. This marked preference was highly consistent with the known ecology of fin whales in the area, and with previous study at the same period (Laran & Gannier 2008, Panigada et al. 2008). In winter, the species is known to perform migration to other parts of the Mediterranean Sea, such as the central Mediterranean, potentially due to variations in resource availability (Aissi et al. 2008). The lower density of fin whales found in winter compared to summer was in accordance with this migration pattern. However, the results showed that a sizeable proportion of fin whales actually remains within the NWMS in winter, where they still target the same habitat than in summer. For these two groups, then, the habitat preferences remained the same throughout the year but part

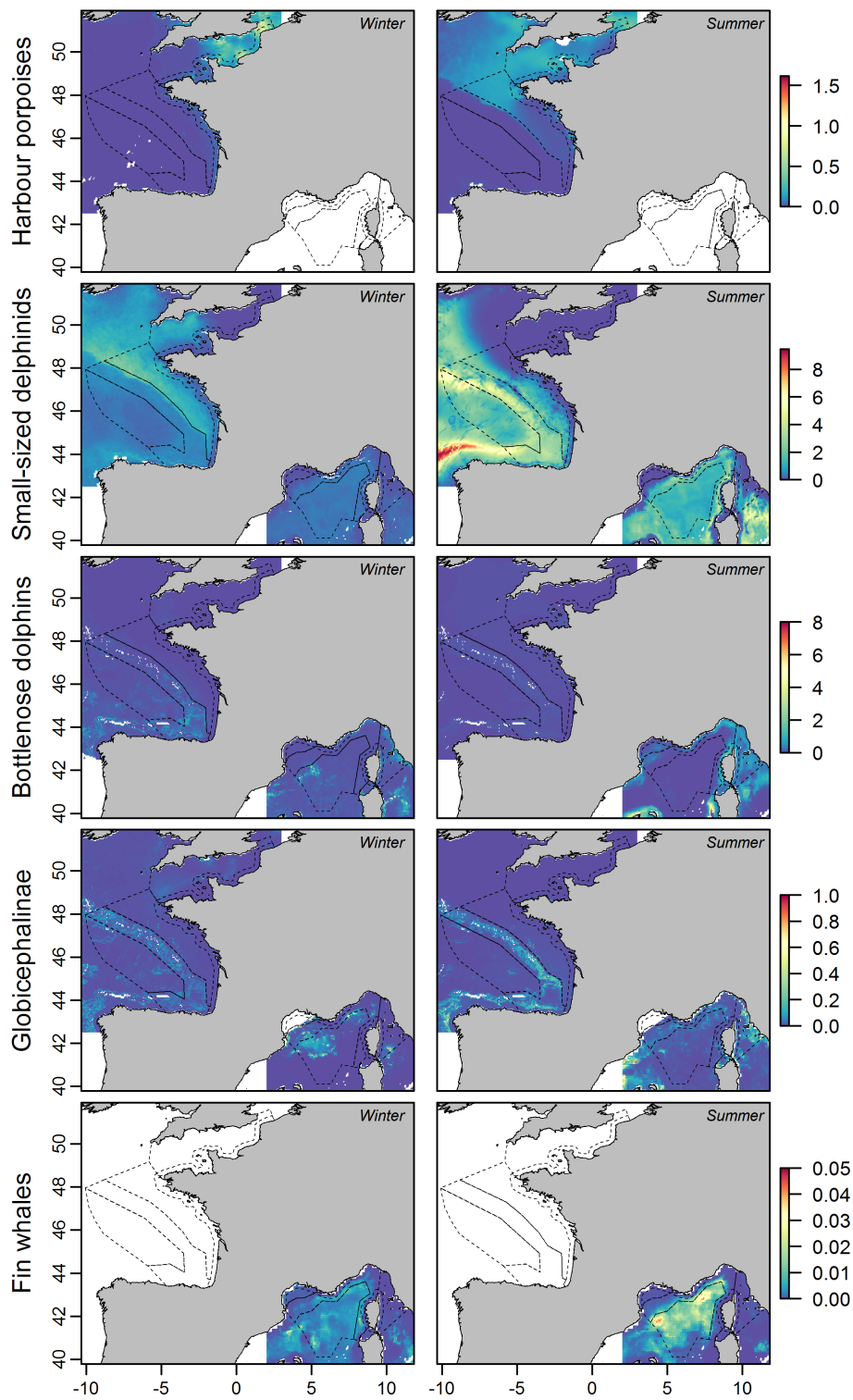


Figure 3.1 – Habitat models prediction for the five studied cetacean species, in individuals per km^2 . Habitat models were performed for each basins separately, and predictions are daily predictions averaged over winter (left) and summer (right). For detailed results and predictions by basin, see Appendices B and C.

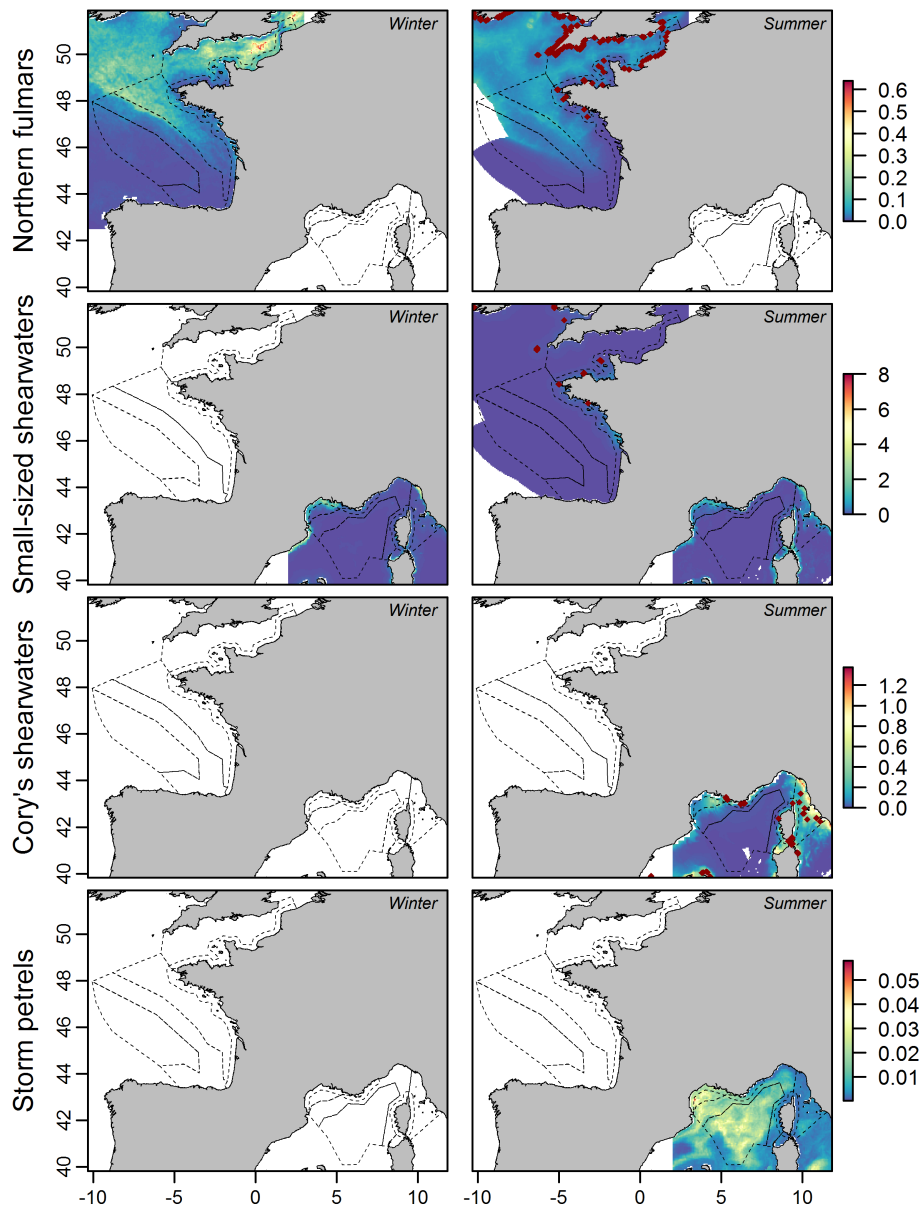


Figure 3.2 – Habitat models prediction for the four studied Procellariiform groups of species, in individuals per km². Habitat models were performed for each basins separately, and predictions are daily predictions averaged over winter (left) and summer (right). Red dots are colony locations, indicated when distance to the closest colony was a selected variable in the model. For detailed results and predictions by basin, see Appendices B and C.

of the population moved out of the NWMS.

In contrast to the above groups, large-sized shearwaters (*i.e.* Cory's shearwaters, in the NWMS), storm petrels and bottlenose dolphins switched habitats between seasons rather than accommodating the same habitat year-round (Table 3.1). The bottlenose dolphins exhibited the widest seasonal shift in habitat preferences among all cetaceans studied here. Our results showed an inversion of habitat preferences, from oceanic waters in winter to comparatively warmer inshore

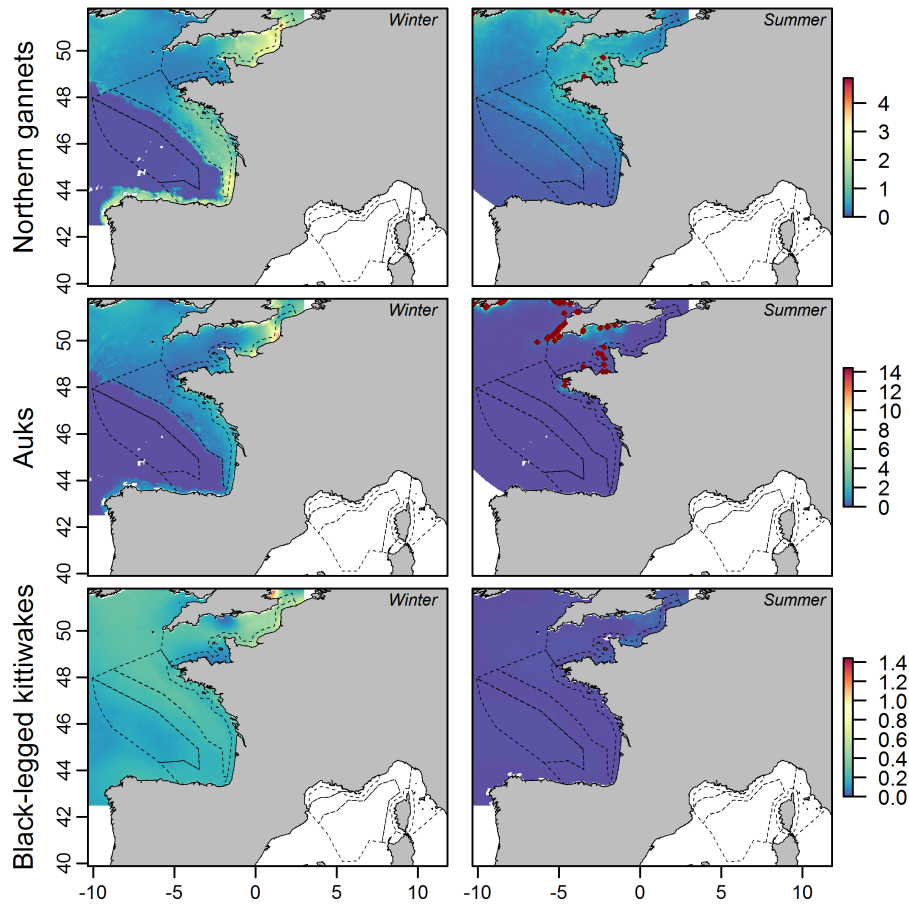


Figure 3.3 – Habitat models prediction for the three remaining studied seabird species (northern gannets, auks and black-legged kittiwakes), in individuals per km². Habitat models were performed for each basins separately, and predictions are daily predictions averaged over winter (left) and summer (right). Red dots are colony locations, indicated when distance to the closest colony was a selected variable in the model. For detailed results and predictions by basin, see Appendices B and C.

waters in summer (Figure 3.1). We hypothesised this movement might be linked to phenological constraints, as the optimisation of calf survival, since the species preferentially used coastal habitats (probably as shelter; Shane et al. 1986, Blanco et al. 2001) during the calving and nursing period and only moved to oceanic waters when calves could follow the adults. Bottlenose dolphins is a well-known flexible species, especially concerning its diet, and thus can easily switch between habitats and prey to sustain such a compromise.

Cory's shearwaters and storm petrels on the other hand, responded to seasonality by migrating out of the study region in winter (Table 3.1). Our results showed storm petrels exhibited a clearly oceanic distribution in summer, and almost completely disappeared from the NWMS in winter (Figure 3.2). According to our results, in summer, Cory's shearwaters targeted warm productive waters close to their colonies, where they could have easy access to reliable resources while breeding (Figure 3.2). Doing so, they targeted a habitat similar to the one exhibited by small-sized shearwaters. But, unlike these latter, they completely left the Mediterranean Sea in winter, which is

Table 3.1 – Summary of habitat modelling results for cetacean and seabird groups in the NWMS and ENA. Is indicated whether the seasonality induces no variation in habitat preferences between winter and summer, any variations in habitat preferences or whether the group was absent from the study region during one season.

		No variations of habitat preferences	Variations of habitat preferences	Absence during a season
Harbour porpoises	ENA		✓	
Small-sized delphinids	ENA		✓	
	NWMS	✓		
Bottlenose dolphins	ENA		✓	
	NWMS		✓	
Globicephalinae	ENA	✓		
	NWMS	✓		
Fin whales	NWMS	✓		
Northern fulmars	ENA		✓	
Small-sized shearwaters	ENA			✓
	NMWS	✓		
Large-sized shearwaters	NWMS			✓
	Storm petrels	NWMS		✓
Northern gannets	ENA		✓	
Auks	ENA		✓	
Black-legged kittiwakes	ENA		✓	

consistent with results from recent telemetry studies on this population (Péron & Grémillet 2013). We cannot simply infer from this migration that the species changed its habitat preferences, since we could expect individuals to leave out of the region to search elsewhere a habitat similar to the one targeted in summer. In fact, Cory's shearwaters seem to track the most productive systems throughout the year: during the breeding season, we showed they would forage on the most productive areas close to the coastline, and during the migration and wintering period similar patterns has been demonstrated by using a telemetry approach (Péron & Grémillet (2013), compare Figure 3.4 with Figure 3.2). Indeed, Cory's shearwaters leave the Mediterranean in October to winter in highly productive large-scale ecosystems, such as the Canary and Benguela Currents (Ramos et al. 2009, Péron & Grémillet 2013). Thanks to their energetically inexpensive flight, Cory's shearwaters can travel very long distances to forage over these highly favourable areas during winter. This pattern would allow birds to optimise their survival since they could forage in optimal grounds when released from reproductive duty and central-place foraging constraints to replenish their reserves before the next reproductive period.

3.2.3 Eastern North-Atlantic

In the ENA, among ten cetacean or seabird taxa, only the Globicephalinae exhibited similar habitat preferences between seasons (Table 3.1). This taxon was shown to be associated with the shelf break throughout the year (Figure 3.1 and Appendix C), as previously described in the area (Kiszka et al. 2007, Certain et al. 2011). This habitat might remain favourable even during winter since, as in the NWMS, they probably exploit deeper layers barely affected by surface layer seasonality. However, in addition to this sharp preference for the shelf edge, Globicephalinae were

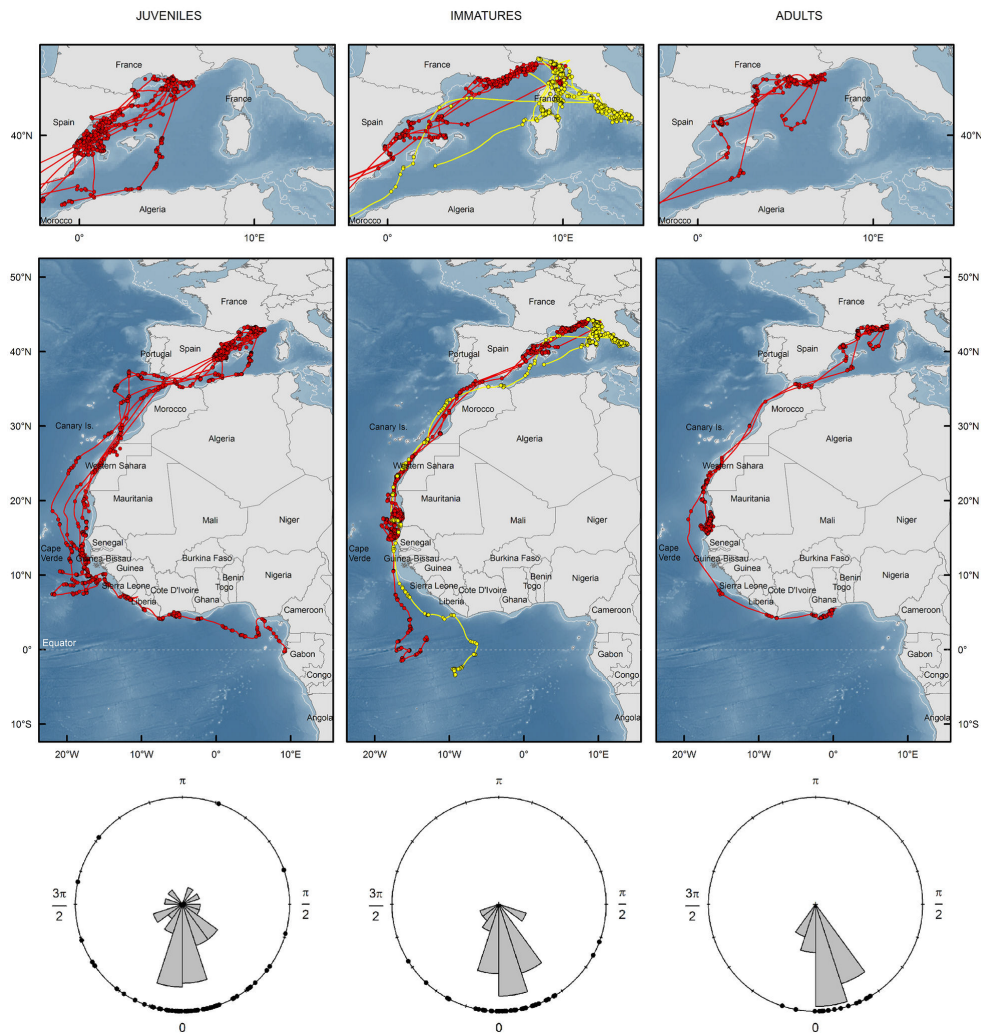


Figure 3.4 – Comparison of juvenile ($n=10$), immature ($n=7$) and post-breeding adult ($n=3$) Cory's shearwaters migratory routes. Upper panel: start of autumn migration/post-fledging departure in the Mediterranean Sea. Middle panel: entire autumn migration/post-fledging departure and arrival at wintering areas. Birds were fitted with PTTs on the Marseille islands (red) and Lavezzi Island, Corsica (yellow). Locations are Argos locations filtered with a speed filter and paths are "reconstructed" tracks using a state-space model. Bathymetry is shown as a blue scale. Lower panel: rose diagrams of turning angles distribution drawn for each life stage highlight inter-stage differences in sinuosity of migratory routes. From Péron & Grémillet (2013), figure doi: 10.1371/journal.pone.0072713.g002.

also shown to performed some incursions into coastal waters during summer, as demonstrated by previous studies and diet analyses (Kiszka et al. 2004, Spitz et al. 2011).

Seasonal variations in habitat preferences of the other cetacean taxa in the ENA (Table 3.1) seemed to result from various processes. The variations observed for harbour porpoises and small-sized delphinids could be related to variations in prey distribution or availability, while for bottlenose dolphins, seasonal variations of habitat preferences might be related to calving and nursing. Indeed, bottlenose dolphins in the ENA exhibited a similar pattern as in the NWMS, with part of the population moving inshore during the calving period (in summer, Figure 3.1; see Appendices

B and C). A large proportion of the population nevertheless remained strongly linked to the shelf edge and associated to predictable aggregative structures (eddies, canyons) even in summer, in agreement with previous studies (Certain et al. 2008; 2011).

Harbour porpoises exhibited an important spatial shift between winter and summer (Figure 3.1), but according to habitat models these distributions were driven by a strong relationship to tides in both cases. In winter, the species preferred shallow dynamic waters, where strong tides interact with seabed topography. These interactions result in highly predictable aggregation features in both space and time, and the association of harbour porpoises to these features was consistent with previous studies in European waters (Goodwin 2008, Pierpoint 2008, Skov & Thomsen 2008). In summer, porpoises moved to the western EC and the CS in areas where spring tide currents can break down water column stratification and ensure trophic web enhancements. Such seasonal large-scale movements have already been shown for harbour porpoises elsewhere in the species range, but without clear explanations: these variations could be linked to sea-ice, prey availability or movement to calving grounds (Neave & Wright 1968, Read & Westgate 1997, Johnston et al. 2005, Sveegaard et al. 2012, Benke et al. 2014).

Small-sized delphinids (common and striped dolphins) underlying habitat preferences also varied between seasons, and so did their distribution (Figure 3.1). In summer, during the calving period (from April to September; Murphy et al. 2013), they were shown to be strongly linked to oceanic waters and especially to the shelf edge, while in winter they were more widely distributed over the shelf up to the western EC. These preferences were consistent with previous knowledge about the two species (Kiszka et al. 2007, MacLeod et al. 2009, Cañadas et al. 2009), and could be linked to foraging optimisation since small pelagic fishes, on which small-sized delphinids generally forage, also move from the shelf edge in summer to the inner shelf in winter (Pusineri et al. 2007, Meynier et al. 2008).

Among seabirds, northern gannets, auks, northern fulmars and black-legged kittiwakes all exhibited seasonal variations in their habitat preferences (Table 3.1), mostly linked to the change from a central-place foraging strategy during breeding period to a free-ranging foraging strategy in winter. More specifically, these seabirds engaged in migrations of various extents as they moved from breeding to wintering grounds. Additionally, individuals present in winter in the study region did not necessarily belong to the same population as those present in summer. It was notably the case for northern gannets, auks and black-legged kittiwakes, for example, since most individuals present in winter in the EC and BoB would actually breed in northern Europe in summer, as France represents their southern breeding range limit and, except for northern gannets, the local colonies only account for a tiny fraction of the populations present in winter. This pattern explains the higher densities encountered in winter compared to summer for these groups (Pettex et al. in revision).

The effect of alternating between central-place and free-ranging foraging strategies was particularly visible for northern gannets, as it resulted in an important variation in habitat preferences between seasons (Figure 3.3). In winter, the species was associated to two main wintering grounds,

in the eastern EC and the southern BoB shelf, driven by different preferences depending on the local oceanographic processes: shallow depth combined with high SSH in the eastern EC against shallow and warmer waters combined with low tidal currents in the southern BoB. This discrepancy illustrates the flexibility of northern gannets, as they can forage on a wide range of prey, and so exploit diverse habitats (Nelson 2002). This could suggest that different combinations of habitat characteristics can provide similar foraging opportunities to a given predator. This flexibility was also clearly visible in the different habitat preferences of northern gannets during the breeding season, as compared to the inter-breeding season. During the breeding season, most individuals were shown to occur within 250 km from the colonies, matching the known mean foraging range around European colonies (Wakefield et al. 2013). Consistently with previous studies based on telemetry (Grémillet et al. 2006, Pettex et al. 2010, Scales et al. 2014), our results confirmed that within this range the northern gannets mainly targeted persistent thermal fronts associated to coastal and central EC tidal fronts.

As for northern gannets, auks exhibited different habitat preferences between breeding and non-breeding periods (Figure 3.3). In winter, a similar pattern to northern gannets was found, although the bimodality was less marked with much higher densities in the eastern EC. During summer, the distribution of auks sharply contracted around colonies, consistently with the known strong tie of the species to their colonies while breeding. Here, most individuals occurred within 50 km around colonies (del Hoyo et al. 2010, Wright & Begg 1997), in line with their flight capacities that are much more limited than most other seabirds.

Black-legged kittiwakes are also known to concentrate around colonies during the breeding period, but European populations widely disperse across the whole north Atlantic in winter (Frederiksen et al. 2012). French colonies are marginal as they are at the southern border of the species range, and densities observed in French waters represent only a low proportion of the European kittiwake population during the breeding period (Cadiou et al. 2004). Indeed, a large difference in densities was found between the two seasons (Figure 3.3), with low densities concentrated around colonies in summer but higher densities widely dispersed over the whole study area in winter, from the shallow eastern EC to deeper waters of the BoB.

Among these pelagic seabirds, the northern fulmar showed the most persistent habitat preferences between seasons (Figure 3.2). As for black-legged kittiwakes, the study area represents the southern limit of the species range within European waters. This limit was clearly visible in the prediction, around 45°N, and corresponded to SST *c.* 12°C in winter and 16°C in summer. In both seasons the species avoided coastal areas, but remained over the continental shelf. Consistently with previous studies (Weimerskirch et al. 2001, Mallory 2006, Edwards et al. 2013), during the breeding season northern fulmars occurred beyond 50 km from the coast, but mostly remained within 100 km from their colony.

Finally, small-sized shearwaters was the only group in the ENA to perform migration during the post-breeding period (Table 3.1), with only a few individuals remaining within the study area in winter. While breeding, they remained in coastal waters, but could range up to 250 km from their

colonies (Figure 3.2). Despite the link to colony of Manx shearwaters highlighted by the results, it cannot be excluded that a sizeable proportion of sighted individuals were Balearic shearwaters, since the species is known to winter in the same areas where Manx shearwaters breed from April to September (Guilford et al. 2012). The absence of sightings during winter is in line with the known long-range transequatorial migration of Manx shearwaters down to the southern Atlantic, before returning to western Europe for breeding (Guilford et al. 2009). Balearic shearwaters also return from migration to NWMS for breeding from September to November (Guilford et al. 2012), thus only a few small-sized shearwaters would remain within the ENA in winter.

3.3 ACCOMMODATING SEASONAL VARIATIONS: A SUMMARY

For seabirds, the main constraint regarding seasonality is undoubtedly central-place foraging during breeding season. Seasonal variations in habitat preferences would be mainly driven by a drastic seasonal change relative to this constraint. Hence, seabirds would have to cope with ocean seasonality within the range of possibilities left available under this constraint. This would explain that a majority of the studied seabird species exhibited some migration between overwintering and breeding grounds. The extent of variations in habitat characteristics between these grounds depends on the plasticity of the considered species.

Procellariidae are characterised by some extreme life history traits among seabirds (Pennycuik et al. 1984). Interestingly, in the present results, these species (northern fulmars, small and large-sized shearwaters) are the seabird species with the less varying habitat preferences between seasons. Thanks to particularly efficient flight abilities allowing them to travel over very large distances at low energy expenditure, we could expect these species to target the most favourable habitats throughout the year. The results seemed to be consistent with this hypothesis. Indeed, Cory's shearwaters habitat preferences exhibited within the NWMS were congruent with the environmental conditions encountered by migrating individuals from NWMS colonies to western Africa, the species targeting inshore productive waters rather than poorer oceanic waters. Small-sized shearwaters exhibited a similar pattern, both in the case of migrating shearwaters in the ENA and resident birds in the NWMS. Finally, northern fulmars have one of the most flexible foraging behaviour among Procellariidae (del Hoyo et al. 2010), and, consistently, the results presented here indicated they were less specialised than shearwaters in terms of habitat, but with lower variations between seasons than most other pelagic seabirds examined in this work.

The other seabird groups exhibited wider variations in habitat preferences between seasons. They also have higher costs of living and lower flight abilities than Procellariidae, so they have to cope with available wintering habitats within a narrower range (which is nevertheless at a basin-scale). As the regions where northern gannets, auks and black-legged kittiwakes breed in northern Europe are harsh during the wintering season, these species would either disperse west or southward to more favourable habitats (which was the case here), or would compensate the poorer environmental conditions by increasing foraging effort (as resident auks in the Arctic; Fort

et al. 2013).

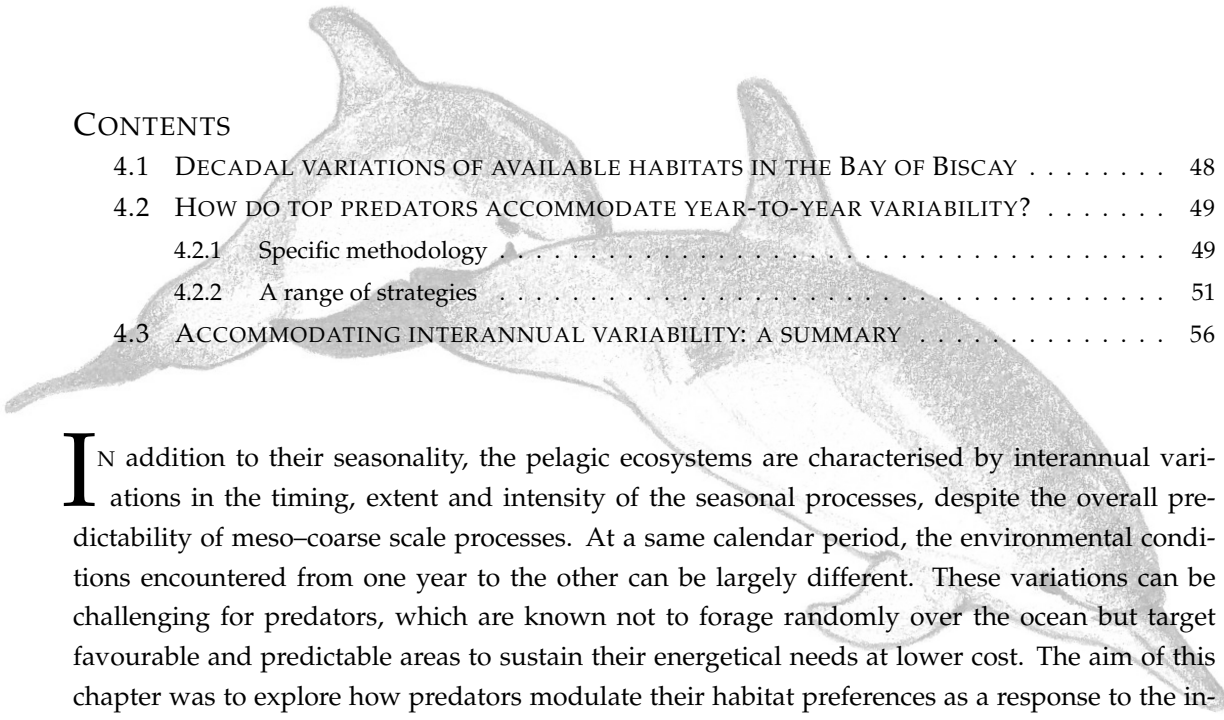
Despite results indicating that both northern gannets and black-legged kittiwakes would adjust their habitat preferences between seasons, computing the same exercise at the European populations scale would be interesting to ensure that the observed differences do not result from population-specific strategies. Gannets have for example been shown to exhibit colony-specific foraging tactics depending on the encountered oceanographic conditions and prey fields (Garthe et al. 2007a), and since they exhibit orientated chain migration (Fort et al. 2012), northern gannets can be expected to have colony-specific wintering habitat preferences.

Given that cetaceans are free-ranging foragers, they can respond more directly to the seasonality of their environment. This may explain the wider range of strategies exhibited by the studied species (Table 3.1): from the preference for habitats with low seasonality, to the preference for a same habitat year-round despite being of lower quality in winter, through the complete shift in habitat preferences between seasons. As expected, most cetacean species had rather similar habitat preferences between winter and summer, although these preferences can lead to different distributions. Interestingly, it is worth noting that both Globicephalinae and bottlenose dolphins, the two taxa found in both basins, exhibited similar response to seasonality between the two basins (Table 3.1). In the case of bottlenose dolphins, the similarity between NWMS and ENA seems in line with the body of evidence supporting the hypothesis of an Atlantic pelagic ecotype origin of the NWMS population (Louis et al. 2014b). Such consistency between basins was not observed for small-sized delphinids, but the species composition of this group differs between the NWMS (striped dolphins only) and the ENA (both striped and common dolphins) so we cannot conclude whether the difference between the two basins arose from their different oceanographic characteristics or to any difference between the two species.

The effect of interannual variability

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IN addition to their seasonality, the pelagic ecosystems are characterised by interannual variations in the timing, extent and intensity of the seasonal processes, despite the overall predictability of meso–coarse scale processes. At a same calendar period, the environmental conditions encountered from one year to the other can be largely different. These variations can be challenging for predators, which are known not to forage randomly over the ocean but target favourable and predictable areas to sustain their energetical needs at lower cost. The aim of this chapter was to explore how predators modulate their habitat preferences as a response to the interannual variations of available habitats within the Bay of Biscay (Figure 1.4, 4), and whether the strategies of predators regarding this interannual variability depends on their intrinsic characteristic as do their response to seasonality (Chapter 3). In the previous chapter, we saw that some species were more flexible than others when facing seasonally varying environmental conditions, therefore we expected to find two kinds of response: (i) species with similar habitat preferences among years, *versus* (ii) species exhibiting important variability in their habitat preferences. This study was based on the analysis of the spring-time PELGAS oceanographic cruises data, from 2004 to 2013.

4.1 DECADAL VARIATIONS OF AVAILABLE HABITATS IN THE BAY OF BISCAY

THE purpose of this study was to explore to what extent habitat preferences exhibited by five mobile top predators species within the Bay of Biscay (BoB) varied during an entire decade (2004–2013). To do so, we first described the habitats available within the PELGAS stratum thanks to a Principal Component Analysis (PCA), which is a conventional method to describe and highlight relationships between a set of variables, here the environmental conditions (Husson et al. 2016). These environmental conditions were described through variables of different origins. First, we used variables collected *in-situ* during the survey: sea surface temperature (SST), sea bottom temperature (SBT), mixed layer depth (MLD) and sea surface salinity (SSS). From SST was computed SST gradient. We also incorporated bathymetry and slope aspect from the GEBCO database. *In-situ* surface chlorophyll *a* concentration and net primary productivity were not available throughout the study period so, instead, we used MODIS monthly composites surface chlorophyll *a* (CHL) concentration and Eppley-VGPM net primary productivity (NPP), for the month of May. A hierarchical cluster analysis was further conducted over the PCA result to segregate the different habitats available in the BoB. The PCA was done in R version 3.2.3 (R Core Team 2015), and detailed method and results are presented in Appendix D.

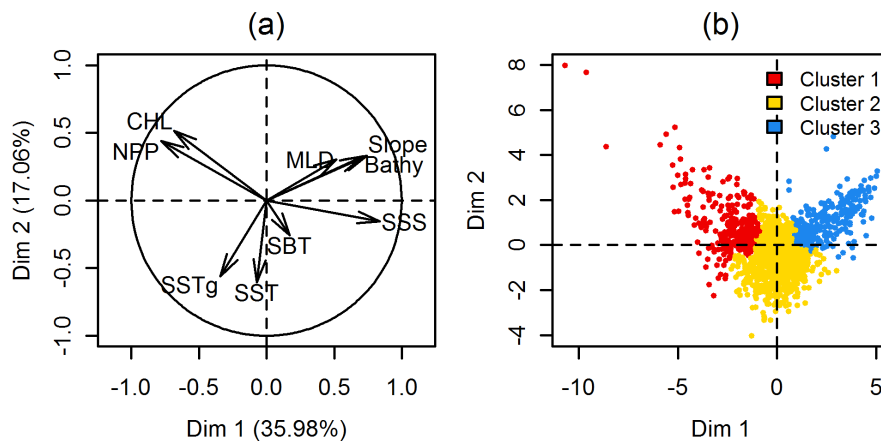


Figure 4.1 – (a) PCA correlation circle and (b) the three clusters defined through the hierarchical clustering, for the first and second dimensions. See text for abbreviation meanings.

The PCA resulted in three main dimensions that explained 68.7% of the variance, with the first dimension explaining 36.0% of the variance, the second 17.1% and the third 15.7% (Figure 4.1a). The first dimension clearly segregated two habitats (Figure 4.1b): the river plumes characterised by high values of CHL/NPP and low SSS at one end (cluster 1, in red), were separated from the shelf edge characterised by high depth, steep slopes and high SSS at the other end (cluster 3, in blue). The second dimension however highlighted a gradient independent from the first dimension, mainly driven by SST. This gradient did not segregate between the first two habitats, both characterised by cold waters, but segregated a third habitat from the other two, corresponding to

the central shelf, otherwise characterised by intermediate values on the first dimension (cluster 2, in yellow). The spatial extent of these habitats varied among years, due to variations in rainfalls and wind patterns. For example, the habitat 1 was almost absent in 2011, due to severe rainfall shortage in April, while in 2009 strong winds extended the river plumes offshore (Figure 4.2).

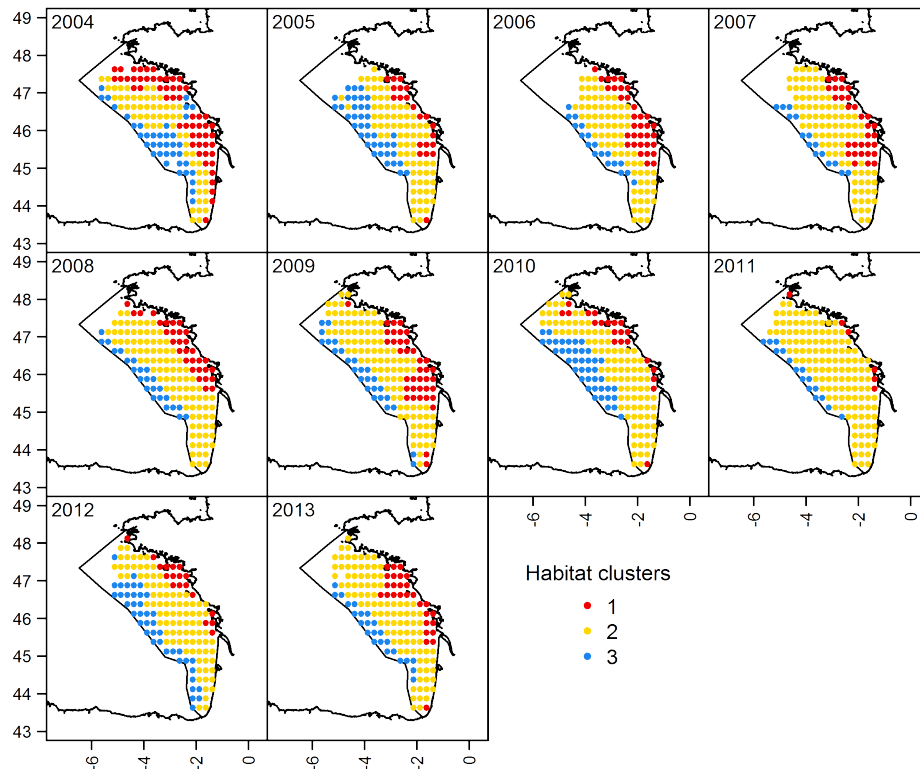


Figure 4.2 – Yearly variations in spatial extent of the three habitats available over the BoB from 2004 to 2013.

4.2 HOW DO TOP PREDATORS ACCOMMODATE YEAR-TO-YEAR VARIABILITY?

4.2.1 Specific methodology

Here, we explored the change of habitat preferences and distributions of five groups of species across years. The taxa of interest were the northern fulmar (*Fulmarus glacialis*), the northern gannet (*Morus bassanus*), auks (common guillemot *Uria aalge* and razorbill *Alca torda*), the common dolphin (*Delphinus delphis*) and the bottlenose dolphin (*Tursiops truncatus*).

Based on the previous PCA, northern fulmars appeared to distribute across habitat clusters 2 and 3, and to avoid habitat cluster 1, corresponding to river plumes (Figure 4.3). Conversely, auks spread out across habitat clusters 1 and 2, and avoided cluster 3 corresponding to the shelf edge,

while northern gannets spread almost equally over all three habitat clusters. Common dolphins were recorded in all three habitat clusters, with no clear preference. Finally, bottlenose dolphins were mostly associated to habitat cluster 3, with some sightings also in habitat cluster 2.

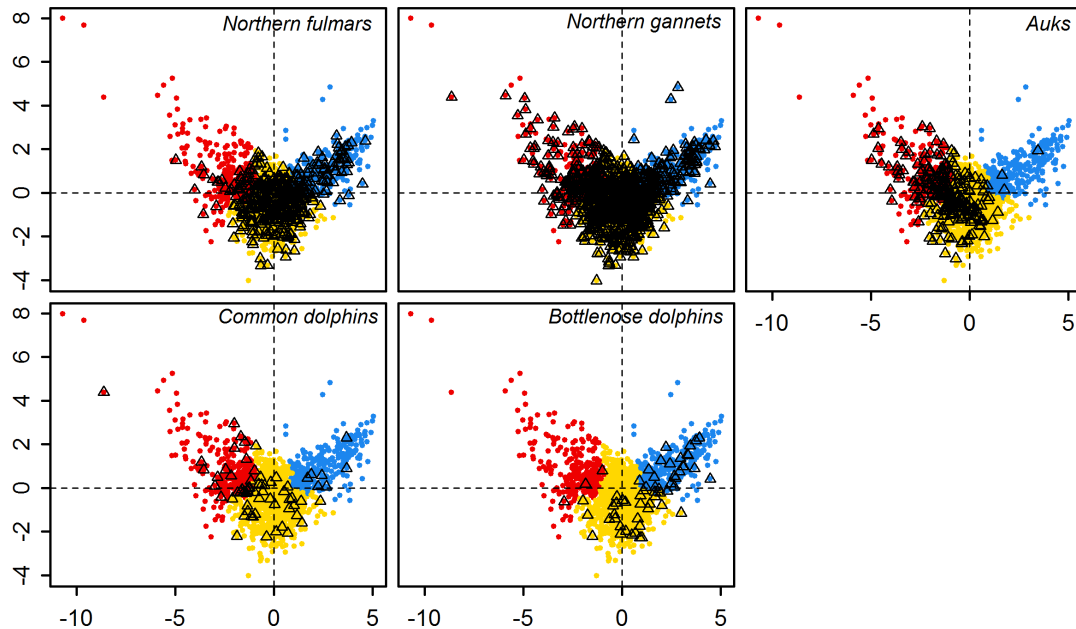


Figure 4.3 – The three clusters defined by the hierarchical cluster analysis (see Figure 4.1). The cells where species were sighted were identified by the black triangles for the five studied species: northern fulmars, northern gannets, auks, common dolphins and bottlenose dolphins.

These projections of cells with sightings over the multivariate space of the PCA provided interesting information on the overall preferences, but they do not allow exploring spatial variations of these preferences. This can be achieved through habitat modelling which allows to spatialise these preferences as well as to explore whether they varied from year to year.

Habitat modelling was conducted by using data sampled within the usual PELGAS study area, with Beaufort sea-state lower than 4 and subjective conditions excellent to medium. All sightings of individuals recorded as attracted to or repelled from the boat were removed, as well as individuals coming to the bow, scavenging behind fishing vessels or coming from the back of the observation platform. To match the format of the covariates, which were available at a 0.25° resolution, we summed the numbers of observed individuals per cell relative to the sampled area by cell. This sampled area was calculated by multiplying the lengths of all segments falling within that cell by twice the ESW of each species so that the effort associated to observations varied according to species (see Appendix D for distance sampling analysis). To explore annual variations in species-specific relationships with pelagic habitat descriptors, here the PCA dimensions, we computed and compared GAMs with and without the year as interaction term. These models linked the number of individuals (response variable) to predictors through a logarithmic link function with a Tweedie error distribution, and with sampled area as an offset. The predictors

were the PCA dimensions as well as the distance to the closest colony for seabirds.

The interest of a PCA is the reduction of dimensions describing the dataset, by summarising all environmental variables (here, nine) into a reduced number of dimensions (here, three). In addition to this reduction, the PCA dimensions also consider the combinations of variables occurring within the dataset. Hence, using the PCA dimensions in place of the raw environmental variables for the habitat modelling has several advantages. Firstly, result interpretations are facilitated by the lower number of covariates included within the model, and secondly, the models consider both the effect of variables and the potential effect of combinations of these variables rather than their simple additive effects.

Predictions were made for the ten years with both models (with *vs* without years as an interaction term), and compared to assess the deviation in spatial distribution resulting from yearly variations in habitat preferences. Finally, the relative predicted densities within each habitats available in the BoB were extracted to explore whether species exhibited any habitat fidelity over the decade. Model fitting and predictions were done in R 3.2.3 (R Core Team 2015), while prediction differences and density extraction within available habitats were done in R 2.15.3. Detailed habitat modelling methods and results are given in Appendix D.

4.2.2 A range of strategies

Our goal was to provide elements to explore predator strategies regarding interannual variability. All predators do not exhibit the same constraints and some are more flexible regarding their foraging habitat than others, since they are able to forage on a wider range of prey for example (*e.g.* northern gannet, dolphins; Nelson 2002), while some species mostly rely on a few high quality prey species, and thus are highly tight to a particular habitat, sometimes leading to collapse in population when perturbations are introduced in the system (*e.g.* auks in the North Sea; Wanless *et al.* 2005).

Depending on species individual characteristics, we expected two cases with different levels of variation in the preferred habitats: (i) some species would use the same habitat year after year, hence spatial variations in the predator distribution would express spatial variation in habitat, leading to the absence of the species in case of habitat absence; (ii) other species would exhibit greater variability in habitat preferences among years, either because they would use all available habitats or remain within the same area irrespective of whether the corresponding habitats changed.

However, the results showed a range of responses to year-to-year variability across species, with some species exhibiting wide habitat preferences, while other had narrower preferences. Interestingly, species showing narrower habitat preferences exhibited stronger stability in these preferences among years while species with looser preferences exhibited higher year-to-year variability (flexible habitat preferences).

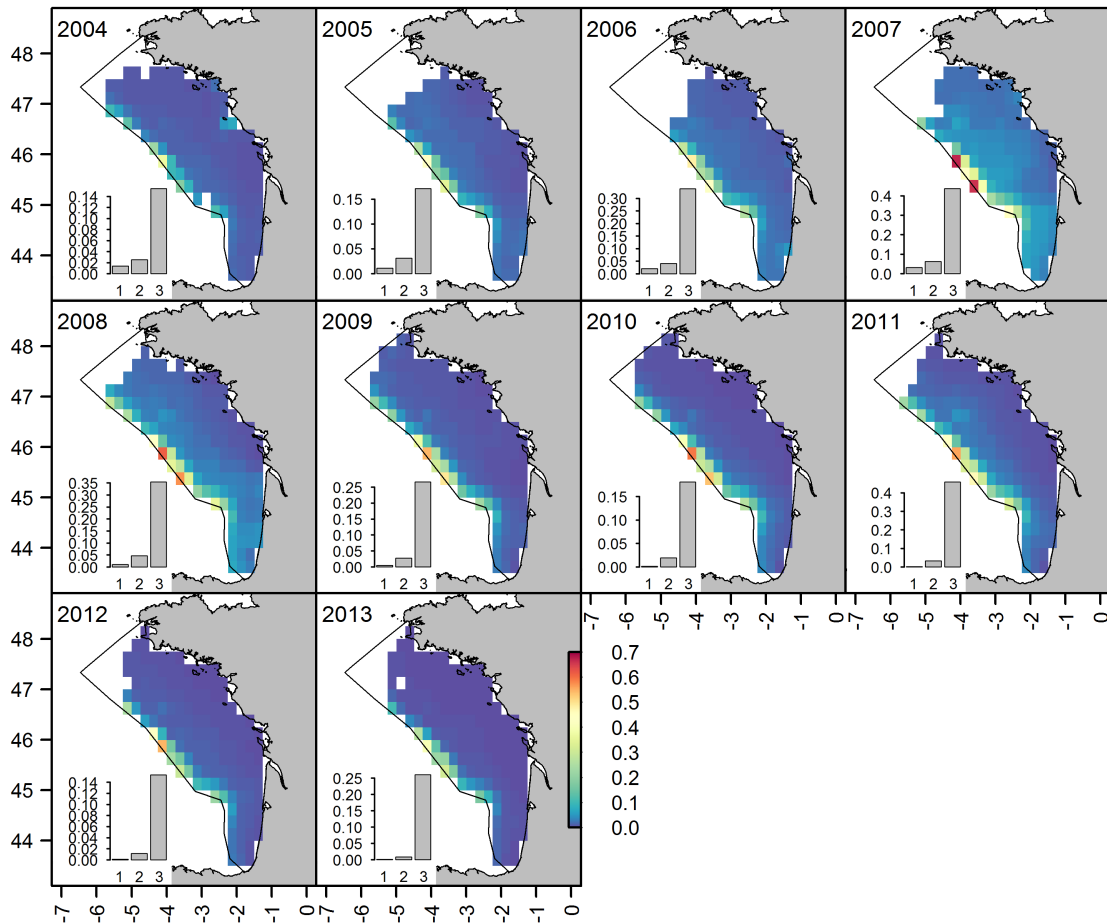


Figure 4.4 – Annual predicted densities from the interaction model for bottlenose dolphins, with the corresponding predicted densities by habitat clusters inserted as barplot, in individuals per km².

The most extreme case was for the bottlenose dolphin, since no difference occurred between the models with and without the year as an interaction term (Figure 4.4). Bottlenose dolphins were confined to the shelf edge during the whole decade, with densities one order of magnitude higher within habitat cluster 3 compared to the other two habitats. This preference was in line with the known ecology of the species in the area, either from large-scale surveys (as in Chapter 3) or from diet analyses (e.g., in BoB, Spitz et al. 2012), in spite of the fact the PELGAS survey was constrained to the shelf and only marginally encompassed the upper shelf break. Nevertheless, the model predicted some bottlenose dolphin intrusions within the shelf, especially in 2005–2008. This preference for the shelf edge was also consistent with the known ecotype of bottlenose dolphin individuals within the BoB, which have been genetically identified as pelagic (Louis et al. 2014b).

The auks also exhibited a sharp preference for one particular habitat, the habitat cluster 1, corresponding to river plumes. However, unlike bottlenose dolphins, differences occurred among years (Figure 4.5). Although these differences were mostly related to the increasing overall abundance of auks over the decade, they also exhibited some spatial differences in the use of river plumes among years, with some plumes preferentially used compared to others. Despite these

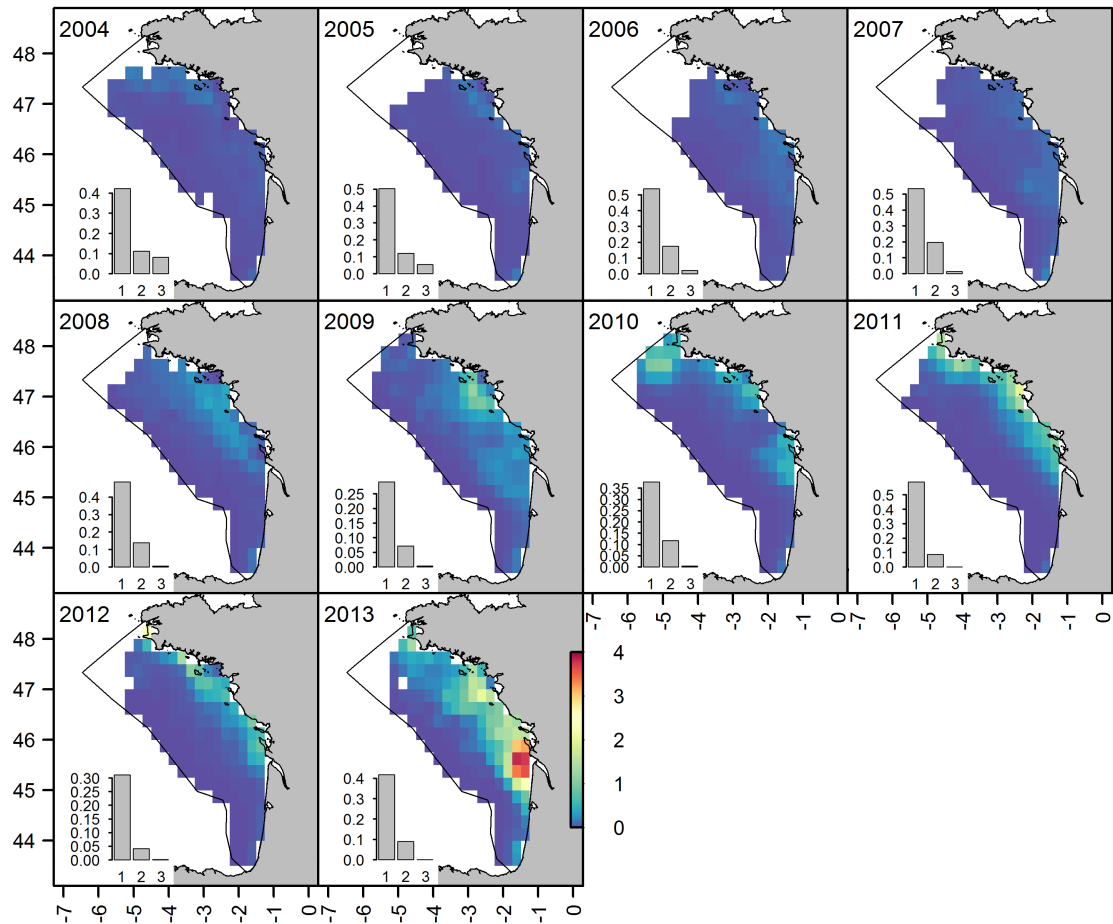


Figure 4.5 – Annual predicted densities from the interaction model for auks, with the corresponding predicted densities by habitat clusters inserted as barplot, in individuals per km².

small variations, the distribution of auks was mostly linked to spatial variations of habitat cluster 1, but when this habitat was reduced or particularly contracted, as in 2010–2012, the species occurred over surrounding habitat 2 as well.

The number of breeding pairs of auks in western Brittany colonies is known to be very low, with only 14 pairs on average between 2000 and 2011 (Cadiou 2014). From these numbers, we supposed that most auks recorded within the BoB during the survey period were non-breeding individuals. We nevertheless included the distance to closest colony within the models, but this variable was poorly relevant. Given auks are known to be tightly linked to their colony during the breeding season (del Hoyo et al. 2010, Wright & Begg 1997), this loose link was consistent with the hypothesis of sightings being mainly composed of non-breeders.

Northern fulmars showed a clear preference for habitat cluster 3. They were present in all three habitat clusters, but at increasing densities from cluster 1 to 3 (Figure 4.6). However, this preference varied spatially among years, the species being more or less widespread over the shelf compared to the shelf edge, especially toward the south. Nevertheless, northern fulmars avoided

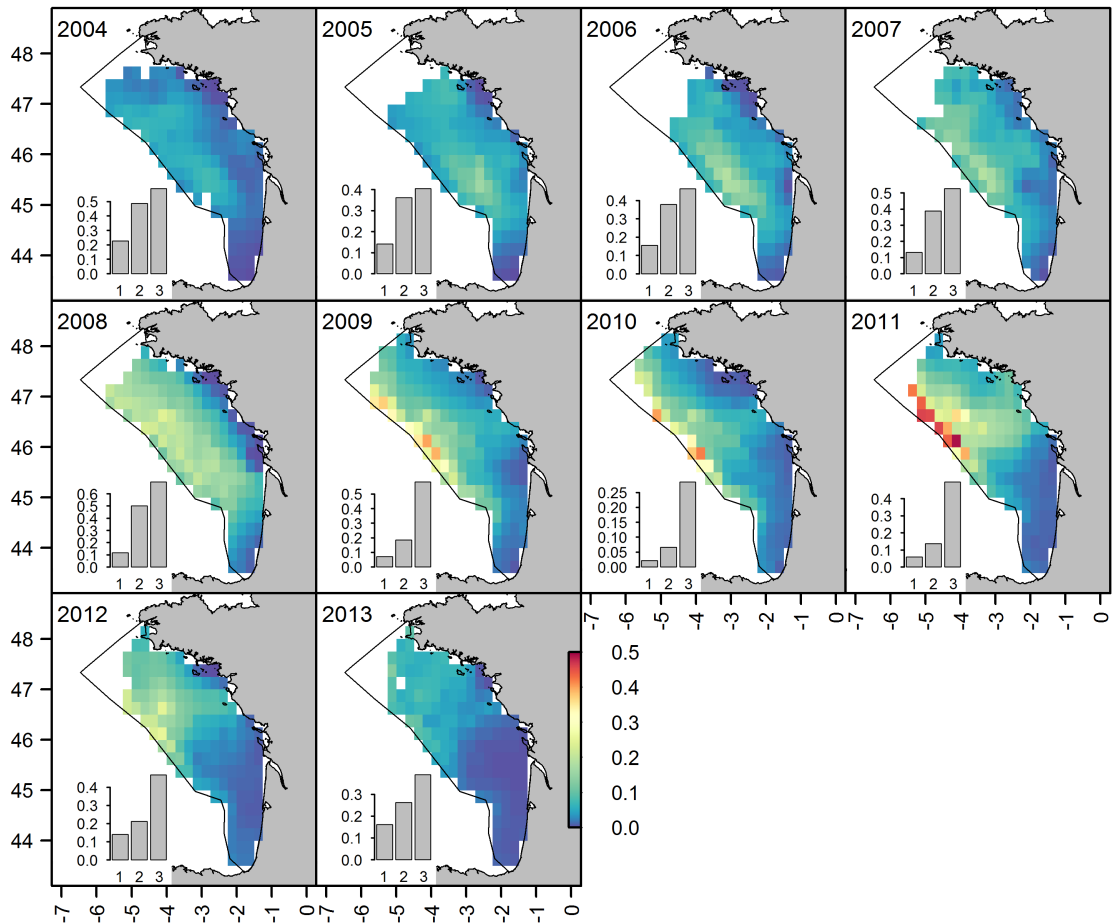


Figure 4.6 – Annual predicted densities from the interaction model for northern fulmars, with the corresponding predicted densities by habitat clusters inserted as barplot, in individuals per km².

coastal waters over the whole decade, quite in line with the known ecology of the species during its breeding season (Mallory 2006, Edwards et al. 2013, Lambert et al. in press). The results suggested that fulmars were able to perform longer trips further south compared to the results obtained from the summer SAMM survey (Chapter 3), possibly as a response to prey availability in spring.

Finally, gannets were clearly flexible in their habitat preferences, with fairly extensive yearly variations (Figure 4.7). This result was consistent with their known plasticity and flexibility in time (Nelson 2002). Overall, a gradient of preference from habitat clusters 1 to 3 appeared, but the amplitude between predicted densities varied substantially among years, with no differences between the three habitats in some years. Despite these variations, a distribution with higher densities in the northern BoB was a recurring pattern, with some occurrence along the shelf edge during some years.

As seen in Chapter 3, gannets breeding in the Channel and the Irish Sea, where are found the breeding colonies closest to the BoB, target discrete predictable and favourable features, notably

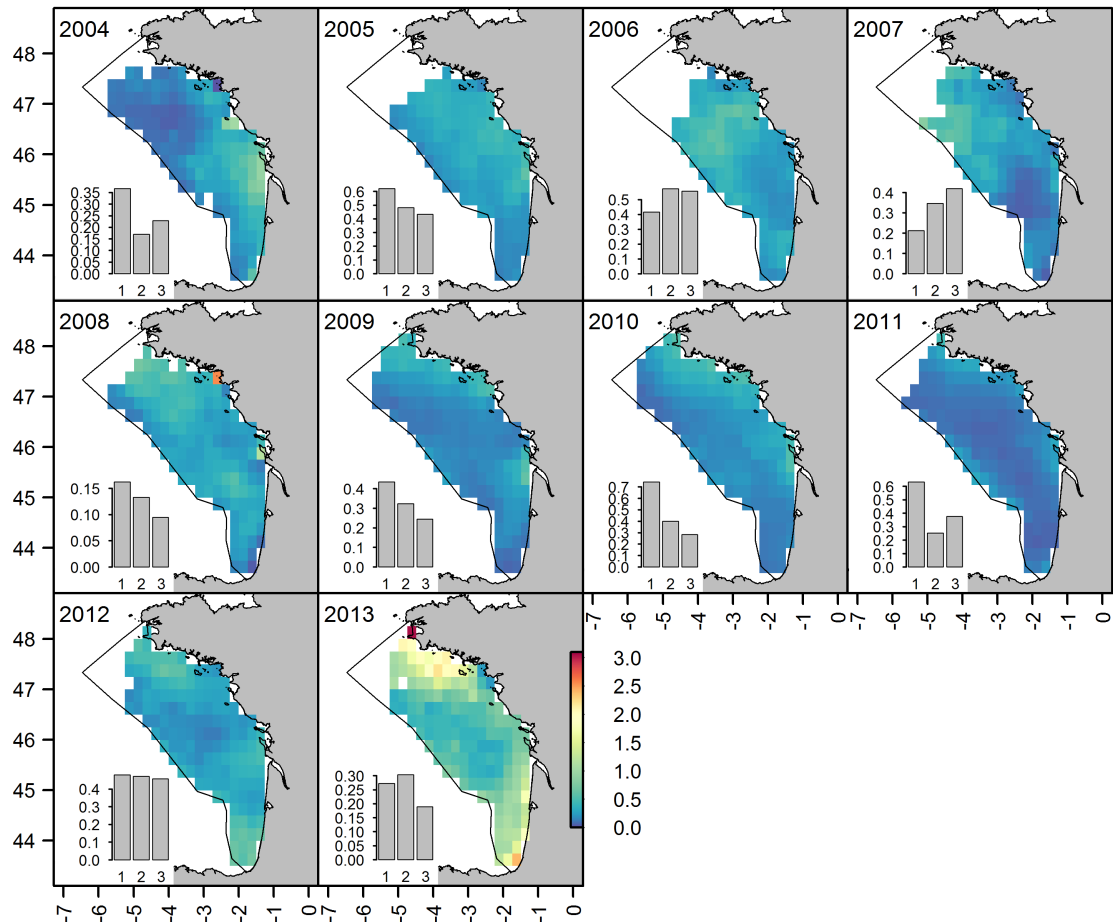


Figure 4.7 – Annual predicted densities from the interaction model for northern gannets, with the corresponding predicted densities by habitat clusters inserted as barplot, in individuals per km².

tidal fronts (Pettex et al. 2010, Scales et al. 2014, Lambert et al. in press). The consistency of such a result between studies from different colonies, different years and different methodologies (telemetry and aerial survey) suggested a low interannual variability in habitat preference of breeding gannets in the Channel and the Irish Sea. Yet, here, northern gannets exhibited looser preferences and an important variability among years.

The higher variability exhibited by gannets in BoB during the PELGAS survey compared to literature might originate from their reproductive status. Indeed, we assumed that most sighted gannets were non-breeders since (i) breeding gannets are known to remain within the Channel and the Irish Sea (Pettex et al. 2010, Wakefield et al. 2013, Scales et al. 2014), and (ii) within the PELGAS data immature or juvenile birds were more numerous than of adults. Since non-breeders are less energy-demanding, individuals might be more flexible in their foraging habitat compared to breeding gannets, thus explaining the higher variability shown here compared to habitat preferences of breeding adult gannets within the Channel and Irish Sea. This higher interannual variability in habitat preferences for non-breeders compared to breeders is consistent with the known ecology of the species, which is particularly plastic once released from reproductive duty

(Nelson 2002).

For the common dolphin, models failed to capture the observed variations in distribution for this species, and none of the PCA dimensions were significant. The variables used within the PCA thus revealed to be uninformative regarding the common dolphin distribution, which might probably be driven by other parameters than those used in this study.

4.3 ACCOMMODATING INTERANNUAL VARIABILITY: A SUMMARY

There was no relationship between the type of preferred habitat and the stability of predator preferences since the two species with the most stable and narrow preference targeted opposite habitats, *i.e.* the river plumes for auks *versus* the shelf edge for bottlenose dolphins. However, both species targeted two spatially stable habitats, particularly the bottlenose dolphin which was always found over the greatest depths of the study area. The shelf edge is less productive on average than river plumes, but remains a favourable habitats with fairly high levels of productivity, especially when associated to slope upwelling in the northern BoB or to canyons in the south. Thus bottlenose dolphins targeted the more predictable habitat in the area, as it is linked to topographic features. Since the species is rather flexible in terms of diet and foraging strategies, and is able to shift between prey and increase foraging effort when necessary, the bottlenose dolphin could easily compensate reduced prey quality or quantity in any poor years.

As seen in Chapter 3, seabirds have more constraining ways of life due to terrestrial breeding. The PELGAS surveys are conducted in spring, a season corresponding to the breeding period for the three seabird species studied here. Only comparatively small seabird colonies are present within the BoB for fulmars and auks, representing marginal numbers of breeding pairs compared to European colonies (Cadiou et al. 2004), while the closer northern gannet colony was in the western EC. Therefore, seabirds sighted during the PELGAS surveys should mostly be non-breeders. For this reason, the results presented here improved our understanding of the ecology of non-breeding individuals, which are inaccessible to other seabird at-sea investigation methods such as telemetry, bio-logging or isotopic analyses. In Chapter 3, we saw that auks and gannets had rather similar habitat preferences during the wintering period, but exhibited fairly different patterns during the breeding season. Interestingly, this difference during the breeding season was also observed for non-breeding individuals, and the two species exhibited rather different responses to interannual habitat variability within the BoB.

Auks are more demanding than gannets, with a lower flexibility in terms of foraging prey, thus explaining the limited interannual variability of their preference for the most productive habitat. They remained within their most favourable habitats, matching its spatial variations. This suggests that rather than switching habitats during poor years, they would modulate foraging effort to compensate for variations in prey availability, as previously shown in wintering individuals (Fort et al. 2013), and as suspected for bottlenose dolphins. On the contrary, gannets are known to

be flexible, especially during the wintering period (Nelson 2002). As shown in Chapter 3, during the breeding period the increase in energy demand induces a focus on specific productive habitats within reach from colonies. Thanks to the results presented here and in Chapter 3, we have a broader image of the impact of breeding constraint over gannets: in summer, the non-breeders frequent a wide range of habitats and exhibit an important interannual variability in this pattern while breeders are constrained to discrete foraging habitats around their colonies, especially tidal fronts in the study area, with limited variations among years. Non-breeders would thus probably be less impacted by poor years, since they could switch between available habitats or even migrate to more favourable areas.

Age-dependent response to ocean variability in a long-lived seabird

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IN previous chapters, we explored the response of top predators to two different levels of temporal variability in the pelagic ecosystems, seasons and years. We considered predator populations as homogeneous for the considered areas and periods of time. However, these populations are actually composed of several age or maturity categories. In the case of marine top predators with high cognitive capacities, learning is crucial to become a successful predator within a patchy and variable environment as pelagic ecosystems. It is also one of the main characteristics of long-lived species. Younger individuals would be less efficient in their foraging than adults as they are less experienced (e.g. Fayet et al. 2015), while adults are submitted to different constraints, particularly during the breeding season. Such variations in individuals characteristics are expected to result in differences in their use of the environment and their responses to its variability (Lack et al. 1954). The aim of this study was to explore whether the response to seasonal variability was different depending on the age or maturity stage of individuals. To answer this question, the study was based on northern gannets, the most abundant seabird species in our datasets and one of the seabird species for which age categories can easily be identified from plumage patterns.

5.1 WHY SHOULD SEASONAL HABITAT PREFERENCES VARY WITH AGE?

CHAPTER 3 demonstrated the crucial importance of the central-place foraging constraints for seasonal habitat preferences in northern gannets (Figure 3.3). In particular, gannets targeted persistent thermal fronts within 250 km from their colonies in the western English Channel (EC) and Irish Sea during the summer season, while in winter gannets wintering in the eastern North-Atlantic (ENA) targeted either the southern Bay of Biscay (BoB) or the eastern EC.

We have seen that these variations were strongly linked to the necessity for seabirds to optimise their energy budget, especially during the breeding period when adults have to produce more effort to sustain both their own energetic needs and that of their chicks. We demonstrated that these constraints led to the pattern observed during summer, with gannets targeting favourable habitats located as close as possible to the colony. We assumed that the majority of individuals recorded during the SAMM survey were breeding adults, but, within the gannet population of the ENA, a fraction of the population is actually not breeding. These individuals can either be breeding adults that failed earlier in their reproduction or non-breeding adults, juvenile or immature individuals. Since these individuals are released from the central-place foraging constraints associated to incubation and chick-rearing, they can be expected to exhibit distinct habitat preferences to breeding adults since they can freely target favourable habitats away from the colonies, as shown in Chapter 4. Nevertheless, we did not expect a complete absence of link to the colony since young gannets are also known to visit colonies before sexual maturity (Nelson 2002, Votier et al. 2011). The frequency of these visits increase with age, and 4th year gannets almost behave as adults although they do not actually reproduce.

In this study, we compared adult and young gannets, and proposed to test the hypothesis that the two age categories should display similar habitat preferences out of the breeding season, when they are all free-ranging foragers and when the competition for resources is supposed to be reduced. During the breeding season, we hypothesised that breeding adults should outcompete and spatially exclude the other categories thanks to greater experience, since the competition for resources would be higher around breeding colonies (Lewis et al. 2001, Wakefield et al. 2013). Yet, whether such a spatial segregation would lead to diverging habitat preferences is to be explored.

5.2 SEASONAL HABITAT PREFERENCES AND AGE IN NORTHERN GANNETS

5.2.1 Specific methodology and raw data

The methodology used for this analysis was described in Chapter 3, separating sightings of adults northern gannets from immature and juvenile individuals (hereafter "youngsters"). Detailed methods

and results are presented in Appendix E. Juvenile gannets (first year gannets) are recognisable from their completely brown plumage. Through subsequent moults, white plumage develops, from the belly frontward to the head, then gradually on the back and wings (Nelson 2002). By their 4th year, immature gannets mostly wear the adult plumage, but still display some black feathers among the secondaries and in the tail. Therefore, within the data of the SAMM survey, 4th year gannets have probably been assigned to the adult category since these erratic black feathers are hardly noticeable from the air.

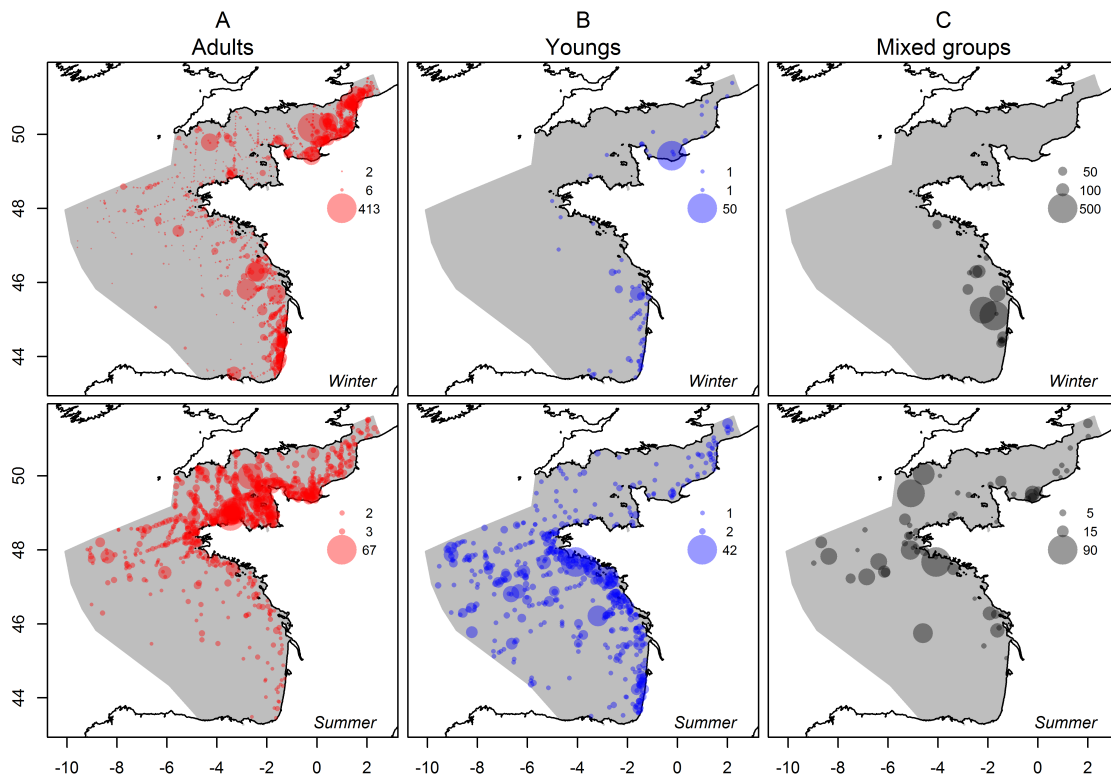


Figure 5.1 – Sightings of adults (A), immatures (B) and mixed groups (C) northern gannets in winter (upper panel) and summer (lower panel). Legends are 50, 75 and 100 percentiles of sighting flock sizes.

Sightings of adult birds were more numerous than of young ones, especially in winter (see Appendix E for details). In winter, adults were more concentrated in the southern BoB and eastern EC, while in summer they were mostly concentrated around colonies of *Rouzig* and *Les Etacs* in the western EC (Figure 5.1A). Young birds were scarcer in winter, but had an overall distribution restricted to the southern BoB and eastern EC, quite similarly to adults (Figure 5.1B). In summer, they were mostly encountered within the BoB, especially along the coast and the shelf edge. Interestingly, most sightings of young gannets were of immature birds rather than juveniles, which are known to mostly spend their first year in remote areas as off western Africa (Nelson 2002). Sightings of mixed groups (adults mixed with youngs) were scarce in winter, with only 15 sightings in the southern BoB (Figure 5.1C). In summer, they were more numerous, spread over the Chan-

nel and northern BoB. Given we had no estimation of the proportion of adult and young gannets within these mixed flocks, these sightings were left apart for the habitat modelling.

5.2.2 Habitat preferences of adult birds

In winter, two wintering areas stood out (Figure 5.2A, and Appendix E for detailed results) in the southern BoB and the eastern EC, with the same driving habitat preferences as shown in Chapter 3. In summer, adults exhibited a preference for thermal fronts within 250 km from the closest colony, matching the known mean foraging range for European colonies (Grecian et al. 2012) and preferences from previous studies (Grémillet et al. 2006, Pettex et al. 2010, Scales et al. 2014) and from Chapter 3. The prediction around colonies matched particularly well the shape of foraging ranges identified in Wakefield et al. (2013) (Figure 5.3).

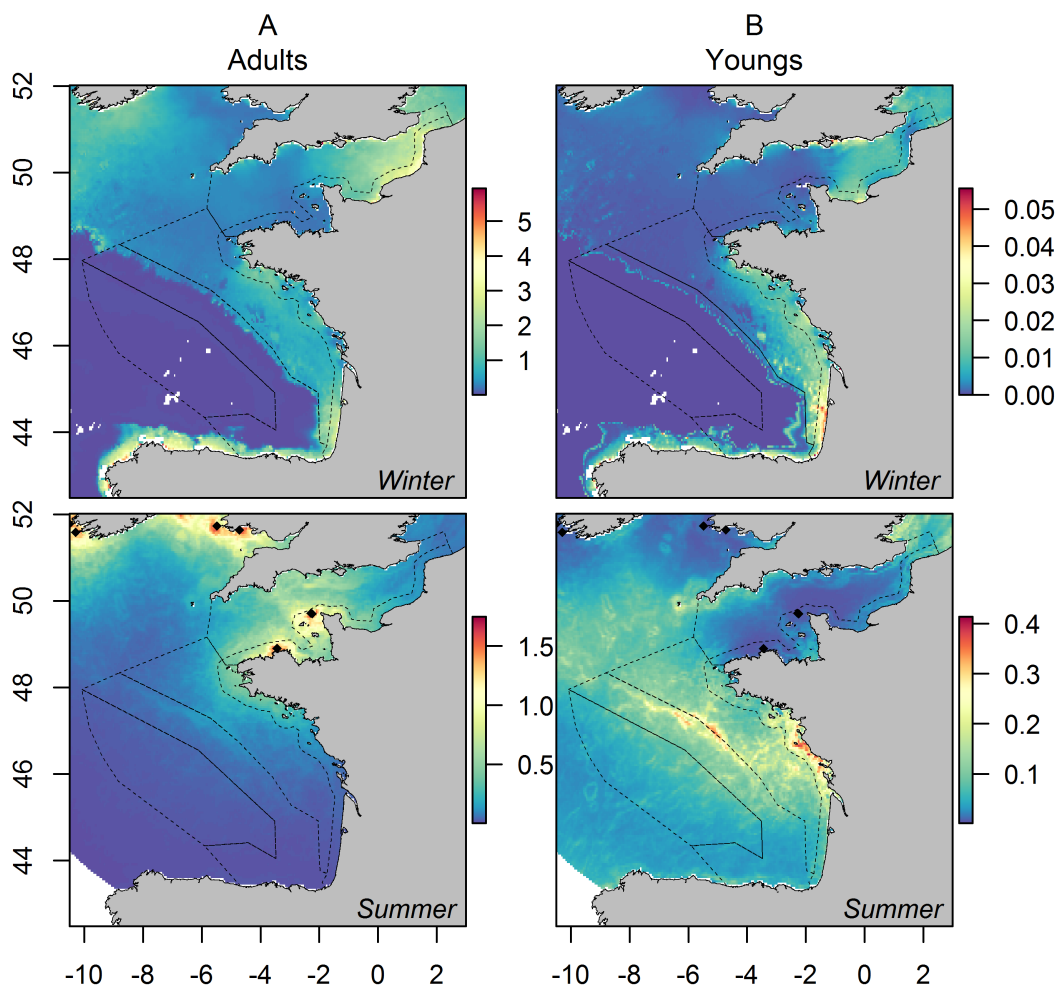


Figure 5.2 – Habitat predictions in individuals per km² for adult (A) and immature (B) northern gannets in winter (upper panel) and summer (lower panel). Black dots are the colony locations.

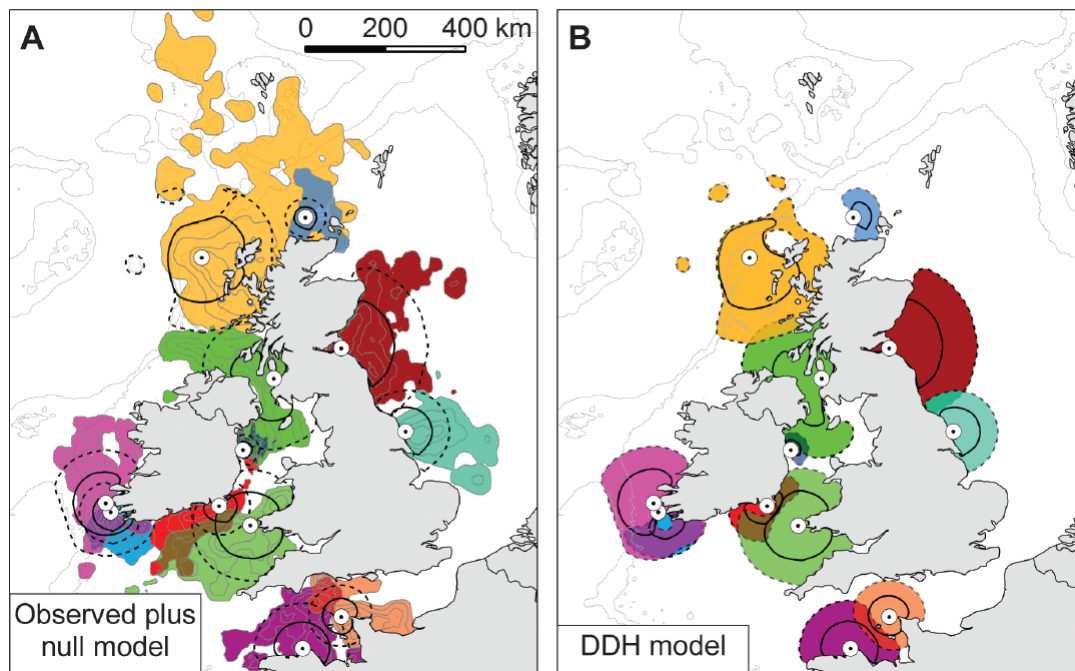


Figure 5.3 – Density-dependent competition and colony segregation. Density-dependent competition within and between colonies explains large-scale among colony segregation. (A) Observed colony utilization distributions (coloured polygons plus 95, 75, 50, and 25% UD contours) are largely mutually exclusive. This is at odds with the null model (predicted 75 and 95% UD, solid and dashed lines), which assumes density-dependent competition only within colonies, predicting broad overlap between some UD. (B) The density-dependent hinterland (DDH) model additionally assumes competition between colonies, providing a better fit to the tracking data. From Wakefield et al. (2013).

5.2.3 Habitat preferences of young birds

In winter, young gannets exhibited distribution and habitat preferences similar to those of adults, with two main wintering areas in the southern BoB and eastern EC (Figure 5.2B). However, they were predicted to be present in the Celtic Sea at lower densities than adults. During the breeding period, the distribution pattern exhibited by young gannets was overall the opposite of the adult one, despite similar oceanographic habitat preferences. Young birds clearly avoided areas located within a 200 km radius from the colonies, but outside this range they targeted predictable thermal fronts, similarly to adults. Their density dropped for distances larger than 400 km from colonies. Therefore, because they are not constrained to commute back and forth from the colonies, they were mostly associated to predictable and productive fronts due to coastal and slope upwellings in the BoB.

5.3 AGE-DEPENDENT INTRA-SPECIFIC INTERACTIONS

Because gannets form large to very large colonies (several hundreds to tens of thousand breeding pairs), breeders are subject to high levels of intra-specific competition, as a large amount of birds have to forage upon the same resources in the same area (Lewis et al. 2001). This supposedly strong competition for food resources have been shown to shape foraging trip distances and dura-

tions in gannets, leading to mean foraging range around colonies to be proportional to colony size (Wakefield et al. 2013). Hence, as the number of gannets increases in a colony, individuals have to forage farther from the colony to find enough food (Lewis et al. 2001). Such a pattern would be due to competition resulting prey depletion around the colony. Density-dependent competition was also shown to shape foraging range of neighbouring colonies (Wakefield et al. 2013): birds from smaller colonies would be constrained to shorter ranges and excluded by birds from larger neighbouring colonies where foraging ranges overlap (Figure 5.3). In such a competitive environment, experience is a major determinant of foraging efficiency, as recently shown in shearwaters (Fayet et al. 2015), and age becomes a crucial determinant of spatial segregation of seabirds during the breeding season.

Our results confirmed that young gannets generally behave as adults in their habitat preferences, but avoid areas close to colonies where adults forage extensively (Figure 5.2). This mechanism results in an avoidance of areas of most intense competition for food around colonies during the breeding period (Nelson 2002, Wakefield et al. 2013). Since adults would be more experienced and efficient predators, such competition would be in their favour, leading to potentially severe reduction of foraging efficiency for young birds, and consequently of condition and survival as well. By exploiting favourable areas farther from the colony, leading to spatial segregation from adults, young birds could avoid this competition while remaining close enough to gain experience for further reproduction and foraging in the same kind of habitats. In addition, it is worth noting that there is some overlap between both distributions, with young gannet density increasing slowly as adult gannet density decreases while going farther from colonies. These two spatially segregated distributions were perfectly complementary, and when added up, resulted in the same distribution as the one predicted in Chapter 3 for all age categories combined.

In addition to the importance of experience in such a density-dependent competition context, we can suppose that this competition is a strong pressure upon individuals to increase efficiency in their foraging strategies, by targeting highly predictable and favourable features. During the last decade, telemetry studies on chick-rearing gannets in the EC and Irish Sea have shown that breeders indeed preferentially target such predictable features, with a particular preference for tidal fronts (Grémillet et al. 2006, Pettex et al. 2010, Scales et al. 2014). Here, this preference was confirmed at the population scale, as well as the mean foraging range around colonies. Given the consistency of this result with literature for this area, we could suppose that, at the population scale, breeding gannets consistently forage over these highly predictable and favourable structures across years.

In winter, the situation was different, with both groups exhibiting similar preferences and spatial distributions. During this season, gannets are known to spread across the whole species range (Nelson 2002, Kubetzki et al. 2009, Fort et al. 2012) and doing so occur at lower densities. Competition is therefore reduced, so that adult and young birds can share the same habitats and resources. Moreover, young birds would probably benefit from social learning by following adults during the wintering season. This pattern was consistent with previous telemetry studies showing young gannets wintering in areas partially similar to adults (Grémillet et al. 2015).

5.4 AGE-DEPENDENT RESPONSE TO OCEAN VARIABILITY: A SUMMARY

As a conclusion, age and experience of the northern gannet, a long-lived seabird, shaped the response of individuals to ocean variability as expected. Density-dependence has important consequences on distribution of gannets depending on their age and experience during the breeding period, when less experienced young birds could not sustain competition from adults and become spatially segregated from them, despite targeting similar habitats. During the wintering season, as competition decreases with lower density, spatial segregation between adult and young gannets vanishes and youngs and adults exhibited similar habitat preferences and distributions.

A story of size and depth: the predator association with prey

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THE previous chapters explored the impact of ocean temporal variability on habitat preferences of several predator species. However, as seen in the Introduction, the ecological niche of a species is also characterised by the relationships of a species to its resources, including predator-prey interactions. Several studies explored predator-prey associations, but results were highly variables depending on the considered scales and parameters. Indeed, the suitability of a prey to a predator depends not only on its raw biomass or abundance, but also on the prey field structure in the three dimensions of the water column. For example, variables as prey patch depth, inter-patch distance or aggregation were shown to be more relevant than overall biomass and abundance (Benoit-Bird et al. 2013). Finally, the suitability of a prey also depends on its size and its quality, since predators are physically best adapted to forage on particular prey size range and have specific energy requirements per unit body mass. Therefore, in the present chapter, the association between predator occurrence and forage fish biomass has been explored in the Bay of Biscay, taking into account prey size and vertical distribution. This exploration was made possible by simultaneously recording prey biomass and predator occurrence, and spanned from 2004 to 2014.

6.1 PREDATORS ASSOCIATION WITH THEIR PREY

PREVIOUS chapters focused on temporal variations in habitat preferences at the population level. Top predators were shown to respond differently to ocean variability at the meso and coarse scales depending on their intrinsic characteristics. When focusing at a smaller scale however, other ecological processes than habitat selection can be explored, such as predator-prey relationships (Figure 1.3). As seen earlier, the distribution of prey patches is ephemeral and unpredictable. Hence, according to the Optimal Foraging Theory (Pyke 1984, Boggs 1992), predators have to develop strategies to forage efficiently in this environment, and target predictable features they know are associated to prey patch aggregation (Figure 1.3). As a consequence, if optimising their foraging success was the main driver of their distribution, marine top predators would be expected to be positively associated to prey concentration.

Although many studies attempted to correlate the distributions of predators and prey, the predator-prey relationship was often found to be weak, with disparate results obtained at different scales. However, most of these studies relied on non-simultaneous sampling of predator and prey distributions (Garthe et al. 2007b, Torres et al. 2008, Hazen et al. 2009, Montevecchi et al. 2009, Lambert et al. 2014, Friedlaender et al. 2016), or only consider total biomass or abundance of prey (Ainley et al. 2009, Hazen & Johnston 2010, Hazen et al. 2011, Benoit-Bird et al. 2011, Cox et al. 2013). Yet, the Optimal Foraging Theory predicts that efficient foraging also depends on the vertical dimension. A prey patch would be available, for example, not only if it is located close to a colony, but would also need to be accessible to predators, especially in terms of depth in the case of air-breathing marine predators (MacArthur & Pianka 1966, Pyke 1984).

Therefore, the suitability of a prey for a predator is a function of prey patch size and density, but also of patch accessibility, which varies vertically depending on the predator diving capacities, as well as horizontally, depending on the distance of the patch to a colony for example. This accessibility also depends on the ability of a species to perceive and find the patch. Several studies have shown all these parameters to be crucial in the link between predators and prey (Cairns 1988, Piatt 1990, Garthe et al. 2007a;b, Montevecchi et al. 2009, Benoit-Bird et al. 2011; 2013, Lambert et al. 2014, Boyd et al. 2015, Hazen et al. 2015, Friedlaender et al. 2016). Finally, prey suitability to a predator also relates to prey characteristics, in terms of size (is the predator able to catch them efficiently?) or quality (is the prey energetic contents adequate regarding energetic requirements of the predator? Spitz et al. 2012).

Thus, in contrast with studies that only consider the local biomass and abundance of prey, looking at prey field structure (aggregation of prey, inter-patch interval, depth of patches) was more successful (Benoit-Bird & Au 2003; 2009, Benoit-Bird et al. 2013, Boyd et al. 2015, Hazen et al. 2015). A common finding is that the predator-prey association is stronger when prey are patchily distributed.

6.2 TOP PREDATORS AND SMALL PELAGIC FISHES IN THE BAY OF BISCAY

6.2.1 Hypotheses and predictions

The PELGAS survey provided data sampled simultaneously on both predator distributions and prey fields. This unique opportunity allowed us to explore, at fine scale, the association of predators with their prey. However, as shown above, this relationship depends mostly on the prey suitability to predators, which results from prey accessibility, size and quality. In the Bay of Biscay (BoB), small pelagic fishes studied during the PELGAS survey all share similar high energetic contents, and have been shown to be preferential prey for dolphins (Meynier et al. 2008, Spitz et al. 2010; 2012). Thus, we chose not to contrast species by taxonomy nor quality and to pool all species of small pelagic fishes together (herring *Clupea harengus*, anchovy *Engraulis encrasicolus*, sardine *Sardina pilchardus*, sprat *Sprattus sprattus*, mackerels *Scomber scombrus* and *S. japonicus*, horse mackerels *Trachurus trachurus* and *T. mediterraneus*). Rather than considering the effect of taxonomy on predator-prey association, we explored the association of predators to these high quality prey taxa depending on their mean body size and depth in the water column.

This relationship to prey field was studied for the five most sighted top predator species, with three seabirds and two cetaceans: northern fulmars, northern gannets, auks (mostly common guillemot and a few razorbill), common and bottlenose dolphins. In the BoB, all these species are known to rely, at least partially, on small pelagic fishes, as clupeids or scombrids.

Among the seabirds studied here, there are three different foraging techniques corresponding to different maximum accessible depth. Northern fulmars are surface feeders and only occasionally perform shallow plunges. Northern gannets are accomplished plunge divers and can reach 20 m deep by plunging alone, and up to 30 m when actively swimming after prey. Auks are surface divers, and chase their prey by actively swimming from 10 to 30 m deep, with occasional dives up to 180 m (del Hoyo et al. 2010). Contrary to seabirds, in shelf habitats cetaceans can forage through the whole water column and adjust their strategies depending on the targeted prey.

In parallel to these different feeding techniques, all these predators are also known to rely on different sensory systems to locate prey aggregations. Northern fulmars use visual and olfactory cues (Nevitt & Bonadonna 2005, Nevitt 2008), while northern gannets would mostly be visual; both are attracted by indirect evidence of the presence of their prey using public information such as other birds actively feeding or fishing vessels (Harrison et al. 1991, Silverman et al. 2004). Auks would be mostly visual underwater predators. Finally, dolphins locate their prey both by passive acoustics and echolocation (Richardson et al. 1995).

Given this wide range of foraging techniques and capacities to locate their prey, we expected to find different associations of these predators with the surrounding prey field described as different prey size and depth categories. Overall, we assumed that if a predator targets a particular

prey category, a relationship should be detected; conversely we assumed that the absence of any association with the prey field would suggest the absence of predator-prey interaction.

In order to control for prey field structure, we simulated virtual random distributions for each predators and considered that an observed relationship was relevant if it was diverging from the one observed with a random distribution. Such a divergence would indicate that predators are either positively or negatively associated to the prey field in a way that was not due to chance alone.

6.2.2 Data processing

6.2.2.1 Acoustic data

The eight small pelagic fish taxa detected during the PELGAS surveys were separated into four size classes, based on the mean body length affected to each echotrace: < 10 cm; 10–20 cm; 20–30 cm; > 30 cm. For each of these size classes, the biomass detected by nautical miles was summarised over three depth layers: from 10 to 30 m deep ("surface"), from 30 m to the sea floor ("deep") and for the whole water column ("total"). In waters shallower than 50 m, the surface and deep layers could not be separated, and fish biomasses were included into both layers. Values of fish biomass were log-transformed ($\log(\text{biomass} + 1)$). The distribution of fish detections by size class, year and depth are given in Appendix F1.

6.2.2.2 Predator data

For the analyses, we only considered predator sightings that were sampled under Beaufort sea-state lower than 7 and subjective conditions from medium to excellent. Each sighting was then associated with the closest acoustic nautical mile, and if no acoustic sampling occurred closer than 1 nm from a sighting, this one was discarded. The distribution of the remaining sightings are presented in Appendix F2.

Finally, for each sighting, we computed the residual biomass associated to it within increasing distances, from 0 nautical miles corresponding to the nautical mile matching the sighting, to a maximum of 12 nm around it (the distance between two adjacent transects; Figure 6.1). For each distance i from 0 to 12, the residual biomass ε_x was computed as $\forall i_{0 \rightarrow 12}; \varepsilon_{x_i} = \bar{x}_i - \bar{x}_{12}$. Therefore, by construction, the residual biomass converged to zero for the largest distances. When a sighting occurred close to a transect end in the acoustic sampling, the maximum distance was restricted to the distance from the sighting to this end. For every predator sightings collected from 2004 to 2014, this distance-based residual biomass was computed for the four prey size classes and the three depth layers, and constrained to nautical miles sampled on the same day as the sighting being considered in order to ensure temporal consistency.

The summary statistics by distance for each year were then computed for each predator species, providing annual mean relationships between the residual biomass and the distance for each prey

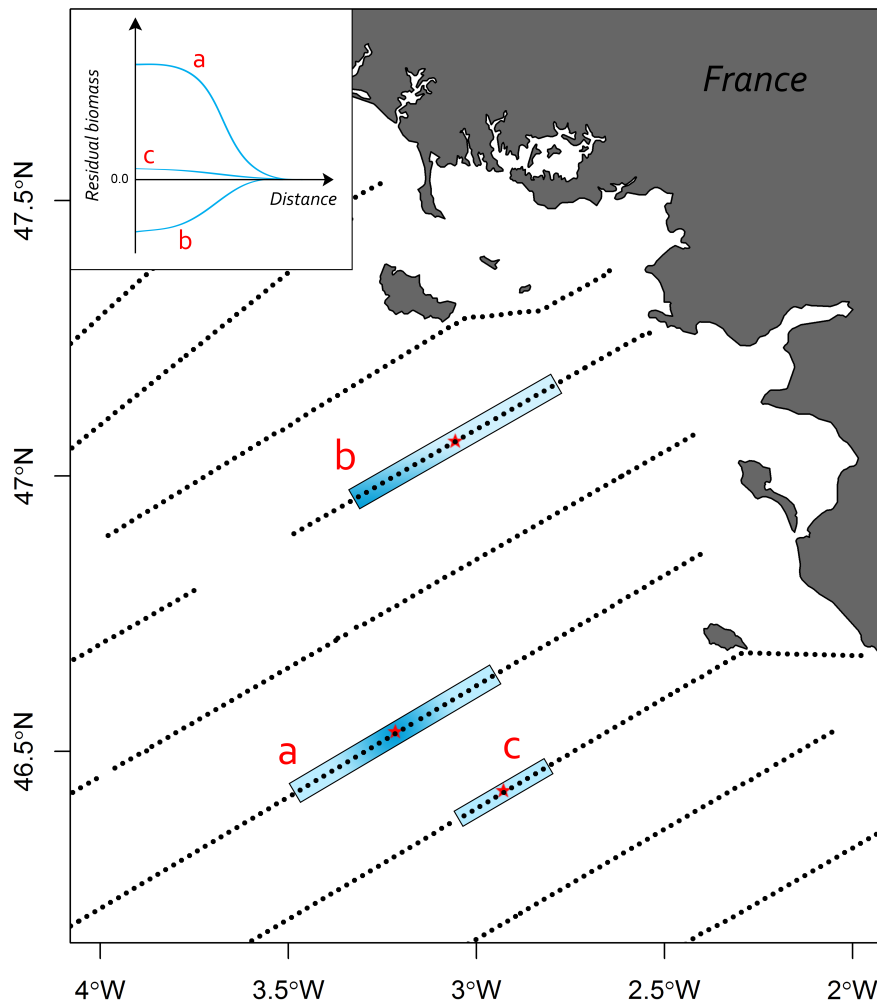


Figure 6.1 – Summary of the method used to compute the residual biomass around predator sightings and expected result. Black dots represent the acoustically sampled nautical miles, and red stars are hypothetical predator sightings. Blue rectangles represent the maximum distance computed around a sighting: the maximum distance was of 12 nautical miles from sightings (a and b), but when arriving at one end of a transect, the maximum distance was limited to the distance from the sighting to the transect end (e.g. five nautical miles in the case c). The blue gradient within rectangles represents the prey biomass distribution. The inset indicates expected relationships between residual biomass and the distance in these three cases: a, sighting positively associated to biomass; b, sighting negatively associated to biomass; c, no pattern.

size and depth layer, weighted by the number of sightings per year. The averaged relationship over the eleven years was fitted over the data thanks to a smoother, using local polynomial regression fitting from package `ggplot2` (Wickham 2009), in R 3.2.3 (R Core Team 2015).

We expected three kinds of relationships with the prey field for increasing distances around sightings (Figure 6.1). If predators were positively associated to prey biomass, that is if the highest biomass they could encounter within this maximum distance of 12 nautical miles around them occurred below or very close to this sighting, residual biomass should be maximum at shorter

distances (case *a*). However, if the maximum biomass was always located away from the sighting, we expected negative residual biomass at shorter distances (case *b*). In the case of a rather uniform prey field around the sighting, we expected a flat relationship (case *c*). Finally, if there was no relationship between predators and prey, we expected the three cases to be equiprobable, and the overall mean to be similar to *c*.

6.2.2.3 Simulated predator data

In order to assess whether the observed relationships diverged from a random situation, we simulated hundred datasets for each predator. These datasets were simulated by generating randomly distributed sightings, with an annual number of sighting equal to the observed situation to ensure the two datasets were constructed with similar stochasticity (stochasticity increases with decreasing sighting number).

As for the observed dataset, we computed for each of these simulated sightings the residual biomass by increasing distance, per prey size category and layer depth. The summary statistics applied to these simulated data were identical to those applied to the predator datasets: annual averaged relationships by simulation (100 simulations \times 11 years) and overall averaged relationships by simulation (100 averaged relationships).

6.2.3 Relationships between predators and forage fishes

6.2.3.1 Overall association between predators and prey biomass

The comparison between the polynomial regressions fitted over observed predator data and the simulated random datasets allowed us to assess whether the relationship between residual biomass and distance diverged from random (Figure 6.2 and Appendix F3–Figure 11). If the observed general average was included within the range of simulated random distributions, we considered there was no particular relationship between predator occurrence and the local biomass of small pelagic fish. In contrast, if the observed averaged relationship diverged from simulations, we considered the link between predators and local prey was not random.

Among the five studied groups of species, fulmars did not exhibit any preferential relationship to prey biomass: their general averages were not diverging from the simulated random distributions for any prey size and depth (Figure 6.2, green; Appendix F3–Figure 11a). In addition, these averages were generally flat (type *c*, Figure 6.1).

In contrast, gannets and auks exhibited a clear preferential association to some categories of prey (type *a* relationship, Figure 6.1). The residual biomasses were higher for the observed predator distribution than for a random distribution for the first two prey size classes, at the three layer depths (Figure 6.2, red and blue; Appendix F3–Figure 11b–c). However, for gannets, the relationships for the first prey size class were only marginally different from a random distribution, as they were at the edge of the range of simulated random distributions (Figure 6.2, blue; Appendix

F3–Figure 11c).

For cetaceans, the situation was different (Figure 6.2, purple and yellow; Appendix F3–Figure 11d–e). The relationships diverged from random for several prey classes, but the residual biomasses at short distances from the sightings were always lower than expected from a random distribution of predators (type *b*, Figure 6.1). This negative relationship was observed for the first and second prey size classes at the three layer depths in common dolphin, but the relationships to total and deep layers for the first size class and to the surface layer of the second class were only marginally different from random. For bottlenose dolphins, a similar negative relationship was observed for the first and second size classes in the total and deep layers, while the relationship to the fourth size class in these layers, as well as for third size class in the deep layer, were marginally different from random.

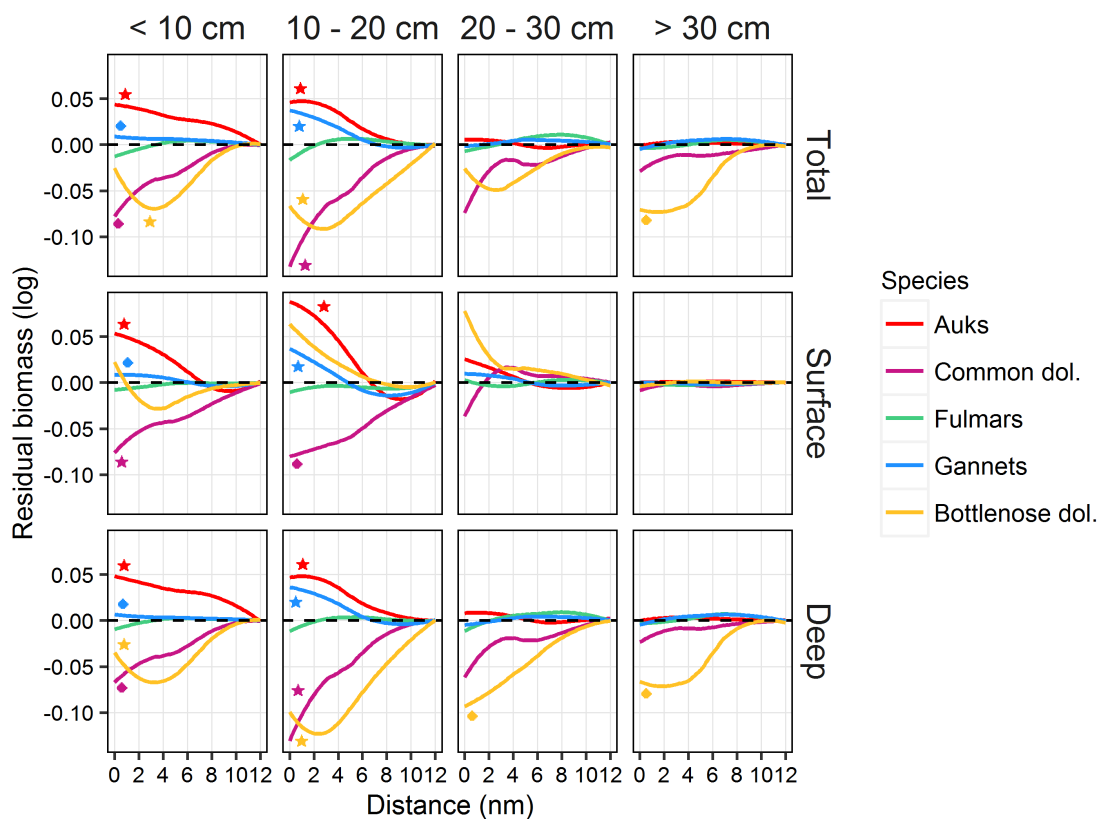


Figure 6.2 – Observed overall averaged relationships between the residual biomass (log) and the distance from the sighting (distance, in nautical miles) for the five studied species, the four prey size classes (columns) and depth layers (rows). The stars indicate relationships clearly diverging from a random distribution (see Appendix F3–Figure 12), the diamonds indicate marginal relationships compared to the random distribution.

6.2.3.2 Inter-annual variability of this association

Interannual variability of observed annually averaged relationships was compared to annual averages from simulated random distributions (Appendix F3–Figure 12). These random distri-

butions varied largely, but overall they were centred on zero with as many years with negative relationships as years with positive ones. For northern fulmars (Appendix F3–Figure 12a), the same pattern was observed, the annual averages being centred on zero. However, for seabird species exhibiting preferential association to the first two prey size classes, gannets and auks, interannual variability was biased towards positive values (Appendix F3–Figure 12b–c). In particular, for gannets, all annual averages were positive despite their variability, with some years higher than the range of random averages, in particular for the second size class (10–20 cm). For auks, the pattern was rather similar for the first prey size class (< 10 cm), but for the second size class, the range of observed annual averages was wider than for gannets, and although most annual averages were positive, some were negative (boxplot’s whiskers, Appendix F3–Figure 12b–c).

For cetaceans, the annual averages were clearly negative for the first two size classes, especially for common dolphin, but their variability was quite large with some positive years (Appendix F3–Figure 12d). For bottlenose dolphins, the pattern was more complicated regarding the four size classes (Appendix F3–Figure 12e). Indeed, despite the majority of annual averages being negative, the range was wide with some positive and negative outliers. However, this amount of variability might originate from the stochasticity induced by the low number of sightings per year.

6.2.4 The effect of size and depth on predators association with prey

6.2.4.1 Seabirds

Our results highlighted three kinds of association of top predators with small pelagic fishes in the BoB. First, northern fulmars were shown to exhibit no relationship to small pelagic fish biomass in the area, regardless of prey size and layer depth. This absence of relationship might be related to the opportunistic diet of the species, which is known to rely extensively on fisheries discards as well as offals (del Hoyo et al. 2010). Therefore, the species might not be particularly preying upon small pelagic fishes.

Contrary to fulmars, auks and gannets were clearly shown to associate with higher local forage fish biomass, as indicated by the strongly positive relationships to higher residual biomasses of 0–20 cm prey, both in the surface and deep layers. These layers were consistent with the known diving abilities of the two groups, since both gannets and auks are known to reach the deeper layer for foraging (del Hoyo et al. 2010). In addition, prey sizes targeted by these species were consistent with their known diet and previous study in this area. By exploring the spatial co-occurrence of predators and prey in the BoB, Certain et al. (2011) showed gannets were associated with Atlantic horse mackerel from 10 to 20 cm long, while common guillemot targeted sardine and sprat of 10–15 cm.

In the case of auks, the results also highlighted a strong variability between years, with some years characterised by negative averages, especially for the second prey size class (10–20 cm). Therefore, despite an overall strong link to small pelagic fishes between 0 and 20 cm long, auks seemed to be

poorly associated with this size class during some years. This variation in the association of auks with small pelagic fishes might be correlated to yearly variations in their diet, since auks are also known to forage on zooplankton (del Hoyo et al. 2010).

For gannets, the variability of their association with fishes were lower than in auks, and the annual averages were clearly biased towards positive residual biomasses for the second size class (10–20 cm). This range of prey size have been shown to be targeted by gannets in several other studies (Hamer et al. 2007, Certain et al. 2011). This prey size range have been shown to be particularly preserved over time (Hamer et al. 2007), unlike the extent of foraging trips and their duration. Indeed, Hamer et al. (2007) demonstrated that chick-rearing gannets were flexible regarding many components of their foraging strategies (prey species, trip durations etc.), but not regarding their target prey size, which was comprised between 7 and 32 cm. In the present study, most gannets were assumed to be non-reproductive individuals (the closest colony being too far away from the Bay of Biscay, in northern Brittany), as discussed in Chapter 4. Our results therefore complement those of Hamer et al. (2007) by showing that gannets target the same prey size range when non-breeding.

6.2.4.2 Cetaceans

Both common and bottlenose dolphins exhibited an association with residual biomass of small pelagic fishes. This association was consistent with the known diet and observed prey size length for both species in the BoB, as assessed from previous studies based on stranded individuals (*e.g.* Meynier et al. (2008) for common dolphins, Spitz et al. (2006) for bottlenose dolphins).

Interestingly, bottlenose dolphin was the only species with a relationship to pelagic fishes diverging from random for the four size classes in the deeper layer. This is consistent with the diving capacities and diet of the species, which is known to forage deeper than common dolphins, and on larger prey. Previous study on bottlenose dolphin diet in the BoB (Spitz et al. 2006) have shown the importance of large demersal fishes and cephalopods, together with some small pelagic fishes. Our results seemed to confirm that the species would forage in the deeper layer, and would substantially rely on small pelagic fishes. Such an association with pelagic fishes was previously identified by Certain et al. (2011) in the area, with an association of bottlenose dolphins with Atlantic horse mackerel and mackerel larger than 20 cm. Yet, the present work suggested the species could in fact have a larger spectrum of prey size than suggested by these previous results. The association of bottlenose dolphins with the whole prey size spectrum identified in this study was consistent with results from stomach contents, since Spitz et al. (2006) identified prey ranging from 0 to 66 cm long within the remains.

Unlike bottlenose dolphins, common dolphins are cooperative pelagic feeders which are known to rely extensively on small pelagic fishes (Meynier et al. 2008). Extensive variation in terms of fish species prevalence was found in the common dolphin diet, provided that about 80% of the diet was made of fat fish (Meynier et al. 2008). In spring, dolphins were described to forage essentially on anchovy and sprat (in term of mass) from 3 to 19 cm of body length (Meynier et al. 2008) which

is consistent with the results presented here, showing an association with small pelagic fishes smaller than 20 cm.

As we know from stomach contents that both dolphin species forage on small pelagic fishes, we expected to find a positive relationship to prey biomass, as for seabirds. Surprisingly, here, cetaceans were in fact negatively correlated to these prey. This negative association might be linked to predator-prey behavioural adjustments, the prey being able to avoid the dolphins, by detecting them either visually or acoustically, or to prey depletion around predators. However, such processes would occur at very local scale (the prey patch, < 1 nm), and could not explain the negative relationship at larger scales, up to 12 nm.

In the case of dolphins, it is known that the aggregative characteristics of the prey play a key role in their prey selection (Benoit-Bird & Au 2003; 2009). Rather than the overall biomass, prey patch size, shape, depth and inter-spacing would be critical for the predator. A patch of aggregated prey will be favoured to loose patch, even if it represents a lower biomass. Unfortunately, in the data used here, the precise structuring of the prey field across the water column was not yet accessible. Yet, the consideration of depth and size of prey was a first approximation of this prey field structuring, which turned out to be relevant. However, the importance of prey patch characteristics might not be the explanation for this negative relationship: if the simple biomass was not the determining factor of predator association with prey, the relationship would be flat rather than negative.

Another explanation might be that dolphins would mostly forage at dawn or dusk as many other pelagic predators, while sightings were mostly recorded during day-time. Given the size of the study area, dolphins could potentially perform horizontal movements between day-time resting areas and night-time or dusk foraging areas at a daily scale. However, here again, such a pattern would lead to an absence of association with the prey. Yet, here the dolphins were indeed associated with prey sizes and depths completely consistent to their known diet, which makes us confident these relationships were indeed foraging associations.

6.3 PREDATORS ASSOCIATION WITH PREY: A SUMMARY

As expected, the accessibility of prey in terms of depth and size was crucial in determining the association of seabirds and cetaceans with prey biomass. The associations found with particular prey size and depth were highly consistent with the literature, which was mostly based on diet analyses performed on stranded individuals for cetaceans or regurgitates of seabirds at the colonies. Indeed, northern fulmars were shown not to be particularly associated to small pelagic fishes, as they are opportunistic feeders, while gannets and auks were clearly associated to small pelagic fishes from 0 to 20 cm long in body length. Regarding cetaceans, common dolphins were mostly associated to small pelagic fishes from 0 to 10 cm long, while bottlenose dolphins seem to

rely on the four prey size classes within the deeper layer only.

The advantage of the present analysis, compared to methods used in the literature, is that we have a snapshot of the population at large, including the non-breeding segment of populations hardly sampled through traditional methods in the case of seabirds, which are restricted to colonies. In addition, since it was based on the whole population, it would be more representative than stranded individuals (for cetaceans), which might be biased towards poor quality individuals.

Despite the consistency of association with prey size and depth compared to literature, the direction of this association in the case of cetaceans remains puzzling. As this negative association was only observed in cetaceans, it probably originates from processes that discriminate them from seabirds, as acoustic communication or echolocation for example. Is this negative relationship linked to behavioural avoidance of pelagic fishes as a response to echolocation clicks of foraging dolphins? Does it come from a prey depletion around predators? Does it originate in a mismatch between day-time resting areas and night-time foraging ones? Is it generated by the use of prey categories not enough informative regarding the precise structuring of prey patches? In all cases, this result deserves to be deepened by further analyses.

Interestingly, the results describing the year-to-year variability of predator association with prey were consistent with habitat preference stability (Chapter 4). Indeed, we expected the more flexible species, which exhibited the more variable habitat preferences, to be the more stable in their association with prey since they would be able to track best habitats in accordance with the encountered conditions. On the contrary, we could expect species with strong habitat fidelity to have a more variable association with prey, since they use the same habitat even during poor years, when they would face low prey biomass. This expectation was confirmed since gannets, the more flexible species, indeed had the lower variations in their association with prey, this latter being always positive, while species with stable preferences, auks and bottlenose dolphins, indeed had clearly more varying prey association.

General discussion

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THEORETICAL aspects of the relationship between the ecological niche concept and species distribution were examined, and a general picture of the response of top predators to the spatio-temporal variability of pelagic ecosystems was drawn, especially in terms of habitat and association with prey, from the results presented in the previous chapters. In addition, the implications of these varying ecological responses and habitat preferences for a spatially explicit conservation strategy of these mobile species was discussed.

7.1 THE ECOLOGICAL NICHE CONCEPT AND SPECIES DISTRIBUTION MODELLING

7.1.1 Historical developments of the niche concept

THE concept of ecological niche has a rather complex historical development, nested in the development of Ecology in general. The first ecological niche definitions were mostly verbalisms, without any formalisation of the concept by equations. As Ecology expanded, with the development of new ramifications and concepts, the niche concept extended accordingly. However, this growth was not smooth, and each sub-domains of ecology finally developed its own niche concept. Today, we could almost find as many niche concepts as ecological particular cases, and plethora of different terminologies. The niche concept is often used in the context of species distribution modelling (Species Distribution Model, SDM), and the variety of these techniques have led to many attempts to define what SDM actually models of a species ecology (Soberón 2007, Kearney 2006, Pulliam 2000, Holt 2009, McNerny & Etienne 2012a;c;b).

Grinnell (1917) defined the niche as a subdivision of habitat environmental conditions where a species can survive and reproduce, but which are not affected by this species. Elton (1927) extended this definition by emphasising the functional role of the species in its ecosystem, especially regarding fine scale variables that are consumed or modified by the species. Hutchinson (1957) provided the most popular view of the niche, and its concept of the n-dimensional hypervolume is often used in attempts to assess species niche. Hutchinson introduced the distinction between the fundamental, defined as the hypervolume of environmental conditions where a species has a positive growth rate, and the realised niches, defined as the niche of a species once competitive interactions are considered.

Based on Hutchinson's definition, many authors further refined the niche concept. For example, Holt (2009) stated that a species could be absent from suitable habitats (fundamental niche) for historical reasons or dispersal limitations. Pulliam (2000) incorporated concepts from metapopulation into the ecological niche, and showed that a species could occur outside its fundamental niche in the case of source-sink population, since individuals in sink populations are not in a suitable habitat that can sustain a positive growth rate (in this case the realised niche is wider than the fundamental one). Jackson & Overpeck (2000) introduced the concept of potential niche, which results from the intersection between the fundamental niche and the available environment in the geographical space. Since some environmental factor combinations may not be available at a particular time in the real world (there is a discrepancy between environmental and geographical spaces), the potential niche can be larger than the realised niche.

Finally, Pearson (2010), but also Peterson (2011), defined the occupied niche as the distribution of a species constrained by geographical or historical factors as well as biotic interactions, which can either be positive (*e.g.* symbiosis, positive density-dependence effect) or negative (*e.g.* competition, predation, parasitism, Allee effect). The modern version of Hutchinson's ecological concept

can be presented through the BAM diagram (Figure 7.1; Soberón 2007, Peterson 2011): the niche corresponds to the interaction between abiotic, biotic and dispersal factors.

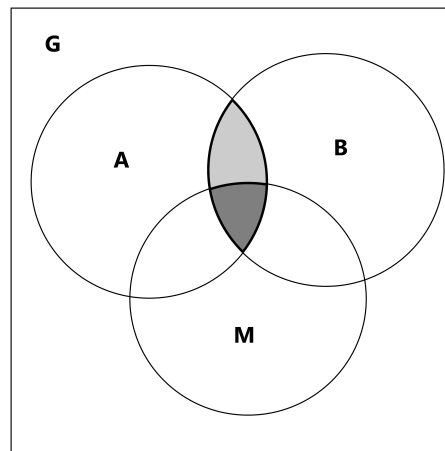


Figure 7.1 – The BAM diagram is representation of factors affecting the distribution of a species. **G** represents the total study area. **A** represents the abiotically suitable area, that is the geographical area where the intrinsic growth rate of the species would be positive. **B** represents the biotically suitable area, that is the geographical area where the species can exclude or coexist with competitors. **M** represents the total area that is accessible to the species (movement factor). The union between A and B (in light grey) represents the region in G where both abiotic and biotic factors are suitable, but inaccessible to the species. The species is viable only at the union between A, B and M (dark grey). Redrawn from Peterson (2011).

It can be noticed that all these definitions generally refer to species distributions, and attempt to explain the niches through these distributions. The BAM diagram, for example, is the formalisation of the niche concept into the geographical space. However, since the niche is thought to be a function of the species (Hutchinson 1957), the observed distribution of a species would only be an outcome of its niche (McInerny & Etienne 2012c), and could not be used to infer it completely. This misconception is at the origin of the confusion concerning what SDMs actually model. When we consider the distribution as an outcome of the ecological niche of a species, then we see that the processes that can be inferred from it can only represent a part of this niche. In this view, the problem is no more to know which niche do SDMs (and geographical distribution of species) refer to, but rather which part of it.

McInerny & Etienne (2012c) attempted to formalise a rejuvenated niche concept which would succeed in incorporating all the facets of its current use, would be independent of scale and would be relevant in all domains of ecology. They argued that the ecological niche, as suggested by Hutchinson (1957), is a facet (a function) of a species, not of the environment, and corresponded to its ecology: the niche of a species is the set of traits and adaptations that determines which biotic and abiotic factors a species interact with, how it responds to, and how it affects these variables. The niche of a species is therefore composed of conditions and resources, as defined in the introduction (Figure 7.2). This is the ecological niche definition that has been used all along this thesis dissertation.

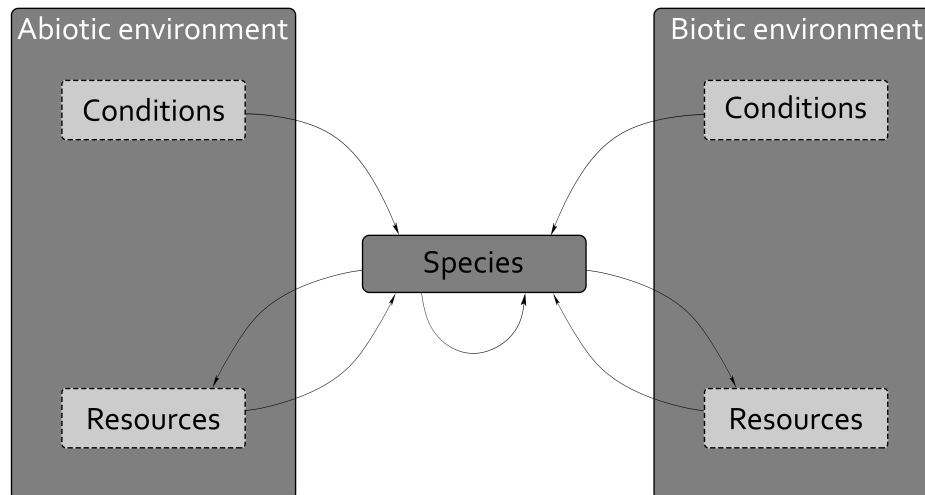


Figure 7.2 – *The ecological niche concept, which is also a conceptual representation of Ecology. Redrawn from McNerny & Etienne (2012c).*

While I agree with this definition of the ecological niche of a species, I believe the authors were then mistaken in their attempt to incorporate this definition within SDMs. By attempting to re-define the niche through the expectations and characteristics of SDMs, they recreated the shortcut implying that the niche would equate the distribution (McInerny & Etienne 2012c). In my view, any attempt to define the niche concept through species distribution is doomed to failure. According to the niche description above (Figure 7.2), the niche is a theoretical object of a species ecology which cannot be completely inferred, but is extremely useful to conceptualise and understand patterns exhibited by species. Indeed, all ecological studies based on observations could virtually never access the complete niche of a species, since these observations will always be outcomes of the niche. These observations only allow us to infer some part of it, and to which part of the niche refers any observation depends on the methodology used to explore it, and of the associated specific assumptions.

7.1.2 Ecological niche and geographic distributions

Given the definition above, I argue that what is called Ecological Niche Models (ENMs, often used as a synonym of SDM) would in fact refer to many studies, and not only to the ones based on species distributions. Therefore, ENMs are different from SDMs, contrary to what is often argued (e.g. McNerny & Etienne 2012a;c;b). Indeed, the niche can be inferred with other methods than those based on species distributions, which is for example the case of isotopic ratios analyses (e.g. Layman et al. 2007), explorations of predator-prey relationships, or mechanistic exploration of a species relationships to its environment.

In fact, I am not comfortable with the use of "Species Distributions Models" terminology. This neutral terminology has been set, with sense, to avoid any misleading due to the confusion in niche concept terminology (Elith & Leathwick 2009, McNerny & Etienne 2012c), but it gathers

many methodological techniques with very different scopes. In fact, SDMs do not only refer to Ecology, since SDMs can achieve prediction of species distribution without any environmental variables (as kriging, for example; Wagner & Fortin 2005): such spatial structuring of the distribution only relates to species biology, not to its ecology since it does not include any relationship to its environment. In accordance with Franklin (2010) and Soberón (2014), I would argue that the belonging of an SDM to ENMs completely depends on its assumptions. In order to be ENMs, SDMs have to be clearly related to a niche concept, especially in the choice of predictors, the expected forms of the relationship between the species and its environment, the type of model and the interpretation of results. Therefore, SDMs using environmental variables but aiming only to predict the species distribution, without aiming at explaining factors driving distribution (Shmueli 2010), would not be ENMs. Environmental factors could well predict the distribution without having a particular biological meaning. This could be the case, for example, of horizontal distances to coast for oceanic marine species without any biological link to it.

Therefore, SDMs and ENMs only have a small intersection area. Most SDMs that can be referred to as ENMs are based on environmental conditions, without including resources variables, so these models would be related to the part of the niche corresponding to the habitat, *i.e.* they are habitat models as referred to within this thesis. However, SDMs will probably evolve toward the inclusion of resources variables and biotic interactions, thus extending the overlap between SDMs and ENMs to a wider part of the niche than just the habitat. Some SDMs are already used with the inclusion of resource variables, such as prey field, but without incorporating the impact of the species on it; they consider prey field as a habitat dimension, that is as a condition rather than as a resource. It also should be kept in mind that habitats can be assessed through other means than habitat modelling, as would be the case with isotopic ratios for example (*e.g.* Layman et al. 2007, Ramos et al. 2009, Praca et al. 2011, Méndez-Fernandez et al. 2013, Louis et al. 2014a, Campioni et al. 2015). These methods however cannot lead to prediction of distribution, which is why they are not SDMs.

Since habitat models are based on species distribution (the outcome of their niche), the results presented here are subject to some limitations concerning what they help us to infer of the species niche. The potential habitats of a species (Figure 7.3, bold envelop) are composed of the habitats a species can have access to, and into which it can sustain a positive growth rate (see Figures 7.1 and 2.6). However, these potential habitats are not always realised in the geographical space, due to the impact of interactions of the species of interest with its resources, and the availability of habitats in time (this is particularly a matter in pelagic ecosystems, where habitats can be ephemeral, so that some of them are not available within the geographical space all the time). Therefore, the habitats inferred through habitat modelling based on the species distribution can only infer the realised habitats (grey envelop), but the implementation of habitat models at various time periods and scales could allow to approach the potential ones, and help unveiling some interacting effects of resources. The inferred habitat is also dependent on the sampling protocol used and the representativity of the sampled distribution (see Figure 2.6).

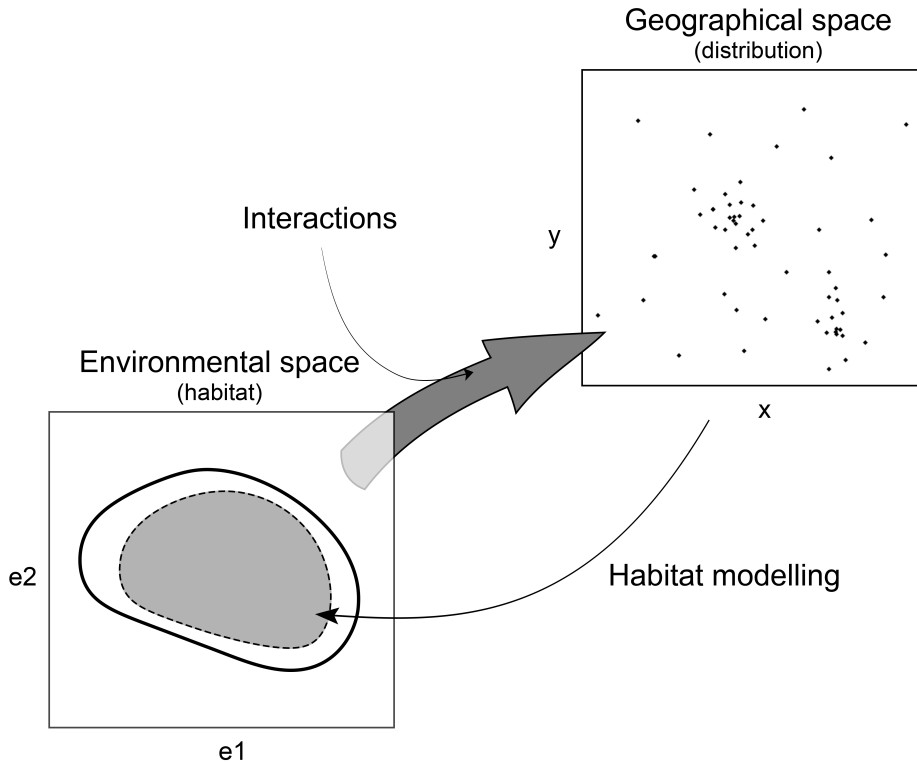


Figure 7.3 – Relationship between potential habitat, distribution, and inference from habitat models. The environmental conditions where a species can survive (the potential habitat, bold contour line, equivalent to A in the BAM diagram, Figure 7.1) are either reduced or extended by the interaction between the species and its resources, which drive the distribution pattern observed in the geographical space. From this distribution, habitat model can thus only infer the part of potential habitat the species actually realised through the influence of interactions (grey envelop).

7.2 TOP PREDATORS FACING OCEAN HETEROGENEITY: PUTTING THE PIECES TOGETHER

7.2.1 Conceptual framework and limitations

As seen in the Introduction, patchiness of the pelagic ecosystems has shaped life history traits of cetaceans and seabirds, leading to varying characteristics between species. This led us to expect cetaceans and seabirds to respond differently to ocean spatio-temporal variability. In particular, these responses were expected to drive specific habitat selection patterns according to the encountered environmental conditions and species characteristics. Since the pelagic ecosystem is a highly dynamic and varying environment, I expected species to exhibit a range of more or less overlapping sub-niches (in terms of habitat) depending on the considered temporal scales: a species could, for example, use different parts of its niche in winter compared to summer as both available environmental conditions and constraints of the species differ between seasons.

Although we cannot disentangle whether habitat selection drives life history traits evolution or whether life history traits condition habitat selection, here, I chose to discuss the results following the second perspective. Indeed, since I explored ecological patterns at rather small temporal scales with long-lived species, the results presented within this thesis could hardly be discussed within an evolutionary framework. Nevertheless, both processes surely influence each other at this scale. In the same way, exploring the potential impact of climate change would require much larger time scales than the ones considered here, as well as different methodologies, so I did not discuss the consequences of the present results within that framework.

As stated above, the niche of a species cannot be directly or fully inferred from distribution. Here, I mostly focused on the habitat component of this niche, with complementary exploration of the association of predators with their prey. By using habitat models, the results presented here are subject to the limitations detailed above regarding the inference of realised *versus* potential habitats (Figure 7.3). Besides, in the case of seabirds, the results presented here do not incorporate the ecological processes occurring at the colony as we only focused on at-sea habitats. Hence, the habitat component of seabird niches inferred here, as discussed below, was probably an under-estimation of the actual niche of these species. However, one could suppose this terrestrial component of the niche is not subject to temporal variability since, for many seabirds, the colony locations (and precise nest location in many case) are highly stable from one year to the next (Gaston 2004), albeit others like terns and some gulls can be more flexible. Therefore, the focus on at-sea foraging habitats probably provides a good representation of the effect of ocean temporal variability for these species.

Finally, environmental conditions used for habitat modelling were mainly distal, and so probably differed from the conditions which species actually responded to, although I was careful in the choice of environmental predictors. Therefore, habitats inferred from habitat models presented in this thesis are only proxies of habitats realised by the studied species. However, since I was careful in the choice of predictors, construction and choice of models, as well as in the construction of hypotheses and interpretations of results, these results were informative regarding both the so far poorly known habitat preferences of the species of interest and the overall effect of ocean temporal variability on the niche of top predators.

As expected, ocean heterogeneity did shape the habitat component of top predator niches, but species characteristics also conditioned their response to this variability at the different considered temporal scales considered here. In addition, these responses seemed to impact the predators association with their prey.

7.2.2 Accommodating seasonal variations

Concerning accommodation to ocean seasonality, various strategies were exhibited by the studied predators. If some of them adjusted their habitats to cope with the alternating of favourable and unfavourable seasons, other seemed to adjust other parameters (potentially foraging effort, although not measured in the present work). Two extreme cases of predator responses to ocean seasonality were identified from our results (Figure 7.4). In the first case, the species would respond to the seasonally alternating conditions by switching habitats between seasons, while in the second case the species mostly remains within the same habitat. The bold envelop represents the potential habitats a species is able to inhabit, while the grey envelops represent winter and summer habitats as inferred through habitat modelling.

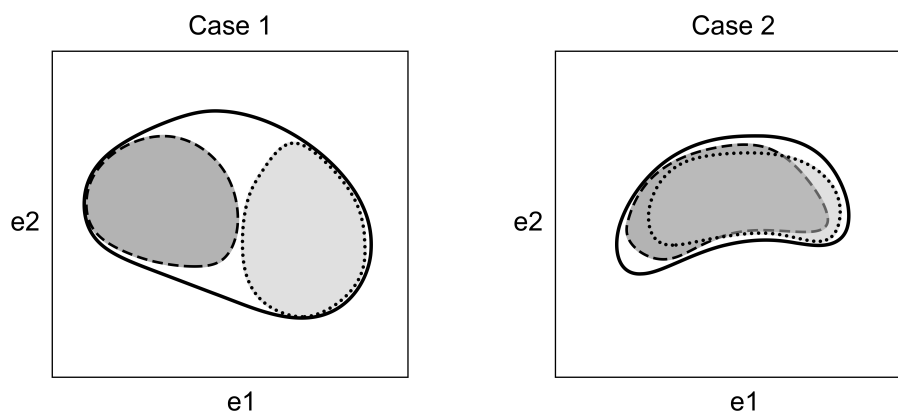


Figure 7.4 – Seasonal variations of habitat for two theoretical species. In bold is the species potential habitat, in dark grey the winter habitat and in light grey the summer habitat. In case 1, the species has two distinct habitats between the two seasons, while in the case 2 the two seasonal habitats overlap extensively. In both cases, the realised habitats are smaller than potential ones, due to biotic interactions.

Interestingly, the second case was mostly observed for species in the north-western Mediterranean Sea (NWMS): Globicephalinae in both basins, fin whales and small-sized delphinids as well as small and large-sized shearwaters in the NWMS. This could be linked to the low seasonality of the basin compared to the eastern North-Atlantic (ENA). Bottlenose dolphin was the only species in the NWMS to exhibit important variations in habitat preferences between seasons, which were supposed to be linked to reproductive constraints. In contrast, no species but the Globicephalinae did conserve the same habitat between winter and summer in the ENA, probably due to stronger variation in environmental conditions from winter to summer. For example, the summer habitat might either be no more available in the geographical space in winter, or could become too unfavourable for the species to survive.

The former strategy (second case, Figure 7.4) do not necessarily means that species occupy the same area in the geographical space between the two seasons. If it was the case for small-sized shearwaters, Cory's shearwaters (in the NWMS) are a good example of a species for which variations are reduced in the environmental space, but large in the geographical one. Indeed, we saw in

Chapter 3 that the species tracked the same habitat year-round, all along its large-scale migration pathway.

7.2.3 Accommodating interannual variations

In addition to these variations between seasons, habitats encountered at a particular season might vary according to years, because of the dynamic nature of pelagic ecosystems. Therefore, as for seasonal variations, top predators species can accommodate this variation in different ways. Based on the results presented here, I could identify two extreme cases (Figure 7.5). In the first case, the species habitat preferences are rather broad and the species is flexible, so that it can switch between several habitats according to conditions encountered each year. In the second case, the species habitat preferences are narrower and the species is less flexible, so that it uses the same habitat from year to year, irrespective of the encountered conditions.

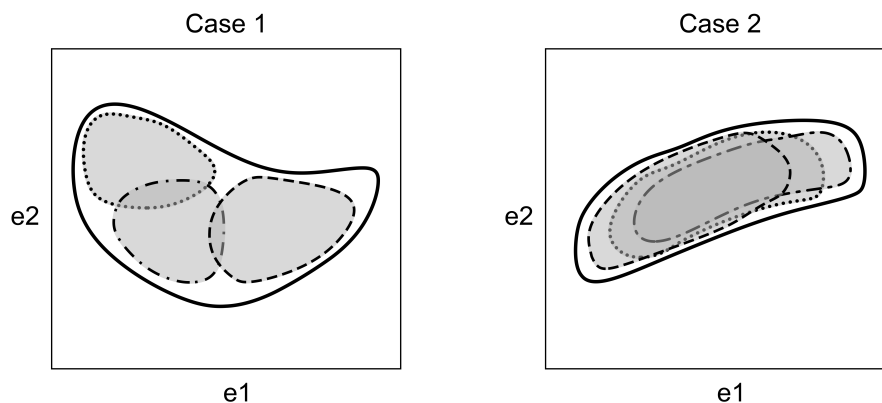


Figure 7.5 – Inter-annual variations of habitats during one season for two theoretical species. In bold is the complete potential habitat for the considered season, while the dashed envelopes are the habitats realised during different years (here, three). In case 1, the habitats used by the species vary extensively between years, while in case 2, a similar habitat is used from year to year.

The results presented here demonstrated that the studied species in fact represented a range between these two extremes. In particular, bottlenose dolphins and auks were shown to be affiliated to a particular habitat, illustrative of the second case. Their variations in distribution mostly mirrored that of the habitat. Such species would compensate poor years by varying other parameters than habitats, as their diet or foraging effort, or, potentially, their body condition. On the opposite, species like gannets are more flexible both in terms of habitats and diet, and thus were shown to adapt their habitat preferences according to the annual conditions (first case).

These different strategies should lead to similar outputs in terms of association with prey. However, we should expect some differences regarding the variability of this link. Indeed, in the first case (Figure 7.5), as the species always track the, supposedly, most favourable habitat, they should be strongly positively associated with their prey, and this association should not vary between years. However, in the second case, if the overall association with prey would also be positive,

we should expect this association to be variable between years, with potentially poor link during bad years. Such a pattern was found in the association with prey, since gannets were the only species for which the association was positive during the 11 years, while auks and dolphins had important variations between years.

7.2.4 An age-dependent response to temporal variability

In the previous sections, we considered species from a general point of view, but differences in age, maturity or breeding status between individuals might result in varying responses to ocean variability. For example, breeders are more constrained than non-breeders, and adult individuals are more experienced than younger ones. The impact of individual age on their ecology is a growing field in ecology, with several studies focusing on the differences between immature and adult birds in terms of habitat or foraging behaviour (Votier et al. 2011, Riotte-Lambert & Weimerskirch 2013, Campioni et al. 2015, Fayet et al. 2015, Missagia et al. 2015). However, most of these studies were biased towards individuals attending colonies, and limited information have been collected so far on young individuals not attending the colonies (but see the case of albatrosses; e.g. Riotte-Lambert & Weimerskirch 2013, Weimerskirch et al. 2014). Here, we focused on the northern gannet, the most abundant and easiest species to tell apart adult from young individuals. Thanks to the large scale of the surveys, we had access to a large part of the population, and particularly to the younger birds (1–3 years) not attending colonies.

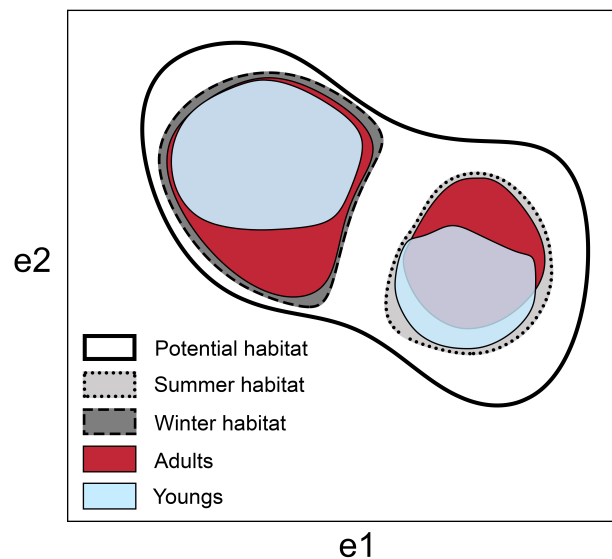


Figure 7.6 – Seasonal variations of habitat according to experience, as a schematic representation of results for northern gannets shown in Chapter 5. In bold is the potential habitat of the species, in dark grey the winter habitat and in light grey the summer one. However, these potential seasonal habitats are used differently according to experience: in winter, adults and youngs share the same habitat, but the adult preferences are broader; in summer, adults have broader preferences but exclude younger birds from part of their summer habitat due to high intra-specific competition. However, this exclusion mainly impact the distribution, not the habitat preferences.

As expected, individual experience had an important effect on habitat preferences. For example, in winter (Figure 7.6), the range of habitats where the species was present was narrower for younger birds compared to adults, but their preferences were similar. However, in summer, the aggregation of breeders around colonies resulted in a strong intra-specific competition for food, which young birds cannot sustain due to their limited experience. Therefore, during the breeding season, there was a competitive exclusion between experienced adults and less experienced younger birds. Yet, this competition mostly impacted the distribution in the geographical space, but not the realised habitat in the environmental one. Indeed, adult and young birds mostly shared the same preference for tidal fronts in the Celtic Sea and the Channel despite this competition in the environmental space (overlap of the envelopes, Figure 7.6), their segregation being only visible in the geographical space.

7.3 THE CONSERVATION OF MOBILE MARINE PREDATORS

Given the numerous pressures exerted on the marine environment (Worm et al. 2006, Halpern et al. 2008, Game et al. 2009), conservation strategies have developed along two main lines: threat-based and site-based conservation instruments, generally called Marine Protected Areas (MPAs). MPAs designation has increased sharply during the last decades, accompanied by studies about their effects over marine ecosystems (Guisan et al. 2013, Butchart et al. 2015). These MPAs have various target and status of protection, and are implemented under different legal frameworks (Claudet et al. 2008, Lester & Halpern 2008). MPAs can either protect the sea floor or the water column, be fully or partially protected areas, be seasonal or year-round.

However, the value of MPAs have been criticised for their limited capacities to cope with mobile species, especially top predators. Initially, an MPA was considered to be useful only if it would encompass the whole distribution range of a species or a population (Boersma & Parrish 1999, Reeves 2000), which would be problematic for wide-ranging species like marine mammals and seabirds. Instead, MPA design has been optimised to protect key areas encompassing sites of aggregations containing a significant fraction of a population or being home to some vital functions, the so-called critical habitats. Critical habitats are the ecological units required for successful breeding, foraging or other vital functions ensuring population growth (Hooker & Gerber 2004).

Due to the more extensive knowledge about species distributions and threats within inshore waters, most current MPAs have been implemented within coastal waters (Game et al. 2009, Butchart et al. 2015). Coastal MPAs often rely on discrete sites used by seabirds or marine mammals for breeding, resting or moulting, or to restricted areas used by resident cetacean communities. These areas are often comparatively small and highly stable in time, with large aggregation of individuals within small surface areas, and are therefore easier to protect. Yet, for seabirds and pinnipeds, time spent within breeding and resting sites is often small compared to the time spent outside, while resident groups of cetaceans often represents small populations. Offshore habitats and resources used by these species are subject to a combination of major threats (acoustic and

chemical pollutions, physical habitat destruction, marine debris, overfishing, incidental catches etc.) and would require adequate protection (Hooker & Gerber 2004).

Current efforts aim to expand MPA networks in offshore waters in order to mitigate threats predators have to face while at-sea (e.g. Skov et al. 2007, Notarbartolo Di Sciara et al. 2008, Garthe et al. 2012, Delavenne et al. 2014, Heinänen & Skov 2015). The major limit to their implementation is the rather poor knowledge regarding the ecology and distribution of species while at-sea. In addition, remote offshore MPAs would be difficult to implement given the dynamic nature of pelagic ecosystems and species distributions. As shown within this work, critical habitats for particular species might change with time, and be subject to spatio-temporal fluctuations. In order to encompass this spatial variability, suggested offshore MPAs are often large-sized (the higher the mobility of target species, the larger the area has to be for an efficient protection; Lewison et al. 2015), which might give rise to administrative and political issues in the implementation and surveillance of such large and distant MPAs interacting with many different human activities.

Therefore, the temporal variability of spatial patterns exhibited by target species have become one of the main consideration when defining and proposing new areas of interest for the protection of pelagic species (Nur et al. 2011, Delavenne et al. 2014, Heinänen & Skov 2015). Several offshore areas are currently submitted for consultation to be implemented as MPAs that would explicitly consider this temporal variability. For example, the United Kingdom has recently confirmed the implementation of several large offshore MPAs for the protection of the harbour porpoise in the south-western North Sea, the Irish Sea and the Inner Hebrides (Heinänen & Skov 2015), and several large areas are being considered in the French Exclusive Economic Zone, especially along the shelf edge of the Bay of Biscay (Delavenne et al. 2014).

7.4 PERSPECTIVES

7.4.1 Anthropogenic pressures

Despite increasing efforts toward the protection of the ocean, anthropogenic pressures still are major threats to marine wild megafauna (Halpern et al. 2008). These pressures can occur at coarse scale (shipping traffic, fishing), but their consequences also are global (marine pollution, climate change).

Top predators might respond fairly differently to these pressures depending on their capacities, as they accommodate differently ocean variability. Indeed, we saw that auks or bottlenose dolphins are relatively faithful to particular habitat from year to year. We could therefore wonder what would be the consequences if that habitat ever disappeared? However, we suspected these species to be flexible regarding other parameters than habitat preferences, so they would be able to modulate their foraging effort or their diet at least to some extent. On the other hand, some species turned out to be highly flexible in their habitat preferences, and so would potentially be less sensitive to ecosystem changes, especially since they also have been shown to be able to

modulate their foraging effort to maintain chick provisioning rate for example (Hamer et al. 2007).

Although marine predators might be able to modulate their foraging effort in case of resource reduction, they are armless against pressures like acoustic pollution. This is one of the main anthropogenic pressure for cetaceans in the ENA (Southall et al. 2007). Our results showed that some cetaceans had critical habitats largely matching some major shipping lanes, as porpoises in the eastern Channel or fin whales in the Ligurian Sea (Halpern et al. 2008, Micheli et al. 2013). In the case of porpoises, they also have to face increasing numbers of constructing wind farm which generate important acoustic pollution. These levels of noise might have impact on mortality rate of porpoises, either directly through permanent or temporary hearing losses (King et al. 2015) or indirectly through disturbance of foraging activities (Wisniewska et al. 2016). In the case of fin whales, a major shipping lane crosses the core area of whales distribution in the NWMS (David et al. 2011), and, in addition to noise pollution generated by this traffic, collisions occurring each year represent the first cause of fin whale man-induced mortality in the Mediterranean (Notarbartolo-Di-Sciara et al. 2003, Panigada et al. 2006).

Porpoises and small dolphins are particularly exposed to by-catch in the ENA. From on board observer programs, it has been estimated that more than 1,000 dolphins are by-caught each year (IWC 2010), but studies based on stranded individuals suggested larger numbers, with more than 3,500 individuals per year only for common dolphins in the Bay of Biscay and western Channel alone (Peltier et al. 2016). Hence, the by-catch issue represents a major threat to these populations in the area. The knowledge of their temporal variation in distributions and foraging prey would thus be crucial to successfully mitigate them.

As a consequence, it would be relevant to expand the present work with the explicit consideration of these impacts, in order to attempt identifying areas of higher conservation concern or predicting future evolution of predators distribution under several scenarios (with and without mitigation for example).

7.4.2 Interspecific relationships

In this work, we studied species separately, without considering potential interactions between them. In marine habitat modelling, the effect of other species over habitat preferences of the studied species is often not included. In fact, ocean resources are implicitly considered as non-limiting, so that no competition occurs between species.

Yet, we saw with gannets that some competition indeed occurs and can lead to spatial segregation between individuals. In the case of gannets, this segregation was only spatial, not relative to habitat preferences. However, we could expect interspecific interactions to shape the response of species to environmental variability, potentially reducing the realised habitat of predators (Figures 2.6 and 7.3; Chase & Leibold 2003, Pearson 2010). These interactions might either be positive or negative. For example, cetaceans might facilitate the exploitation of a particular habitat to some seabird species through local enhancement (Harrison et al. 1991, Silverman et al. 2004), leading

them to use a habitat they could otherwise not exploit, while seabird species might compete for food resources around colonies or cetaceans relying on similar prey might be subject to competition (Herzing & Johnson 1997, Clua & Grosvalet 2001, Spitz et al. 2006; 2011).

The consideration of these interactions within habitat models could be done by incorporating the distribution of other species within the models. However, these interactions make the inference of species ecological niche highly complicated. As seen above, habitat models can only infer realised habitats, due to the inherent limitations of using distributional data (Figure 2.6 and 7.3). The quantification of the effect of inter- or intra-specific interactions on the habitat component of the niche could be assessed if we had access to the whole species range, under the condition that the effect of interactions only occurred over part of this range. In such a case, scrutinising the divergence in observed distribution compared to predicted one could help identifying where such interactions occur, allowing further exploration of the locally driving process. However, in some particular cases the effect of interactions can be more easily identified from habitat models, if it only impacts the distribution of species in the geographical space, as in the case of adult and young gannets.

7.4.3 A matter of scale

Within pelagic ecosystems, ecological processes are a matter of scale (Figure 1.3; Hunt & Schneider 1987, Kotliar & Wiens 1990, Fauchald 1999). In this work, we focused on the meso- to coarse scales for the habitat preference studies, and on the fine scale for the exploration of predator-prey associations. Given the hierarchical structure of oceanographic processes within pelagic ecosystems, it could be interesting to reiterate similar studies as conducted here but with varying scales. For example, with SAMM data we conducted the analyses with a small spatial resolution (10 km long segments and a prediction at a 0.05° resolution), but it would be interesting to explore whether the observed habitat preferences would be conserved at a coarser scale. Similarly, with PELGAS data we used a 0.25° resolution as it was the resolution at which environmental variables were available; a finer resolution might give access to a better description of habitats available to predators.

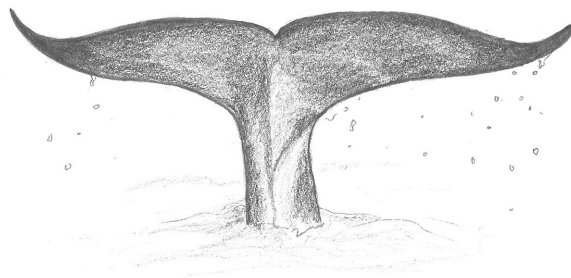
Besides, it would be interesting to conduct a similar study at the European scale. Indeed, as seen in Chapter 3, the individuals present in the study area in summer differ from those present in winter, especially for seabirds. Conducting a similar study at the European scale would allow to control for potential population-specific preferences. For example, this would allow to explore whether there is any differences in the way they answer seasonality or inter-annual variability between gannets breeding in northern Europe and gannets breeding in the Channel, or between porpoises of the northern North Sea and porpoises from the Channel.

Concerning the predator-prey association however, we guess the relationships highlighted here may not be found at a coarser scale, since the association is known to occur at fine scale due to the unpredictability of prey patch location. However, it could be interesting to further refine this work by using a higher resolution. A resolution less than one nautical mile would allow to explore

behavioural associations between the two compartments. It would potentially allow to explore the avoidance of predators that could occur for prey and bring some highlights on the reasons for the negative associations observed between cetaceans and their prey.

Finally, the exercise might also benefit from the exploration of whether predators respond better to instantaneous, contemporaneous or climatological environmental conditions. Here, I chose to use the most instantaneous conditions possible. Without *a priori* knowledge on the delay between ecological processes described by variables introduced within models (temperature, altimetry, primary production) and the availability of resources for predators, the use of two reduced temporal resolutions (7 and 28 days) for models based on SAMM data in Chapter 3 was a precautionary approach (Fernandez et al. 2015). However, in order to use data closest as possible from reality, the *in-situ* measured variables were used for models based on PELGAS data in Chapter 4.

Therefore, it would be interesting to explore how would the results vary when using environmental conditions at different temporal resolutions. For example, we could suppose a predator might respond better to climatological conditions rather than instantaneous ones if this predator relied on habitat only from memory, *i.e.* if this predator returns every year over the same habitat because he knows from experience this habitat is favourable in average. Such questioning are currently being investigated by habitat modellers due to the deep consequences the temporal resolution of variables might have on habitat models predictive capacities (*e.g.* Fernandez et al. 2015, Scales et al. 2016), and some preliminary results tend to show that a preferential response to contemporaneous *vs* climatological conditions might depend on the considered ecosystems and predator species.



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Appendices

Appendices

Appendix **A**

Chapter 2 - Supporting information

Supporting information to Chapter 2 (general methodology)

1 SAMM survey

1.1 Survey effort

Aerial surveys SAMM were conducted from November 17, 2011 to February 12, 2012 in winter and from May 16 to August 08, 2012 in summer. Hence, the monthly distribution of effort do not cover the entire studied area each month, especially in November, February, May and August (Figure 1).

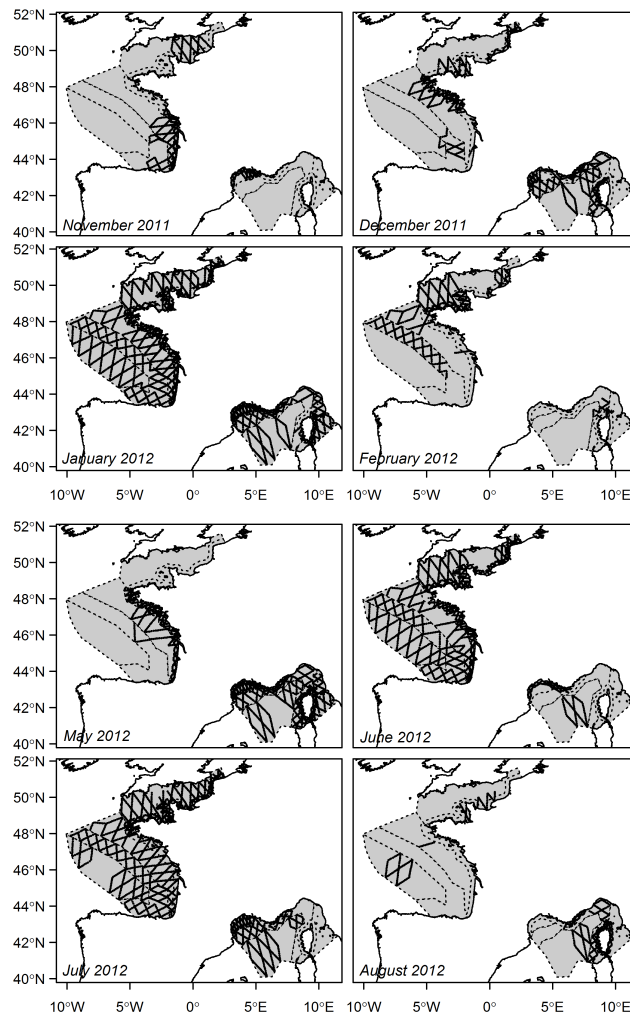


Figure 1. SAMM surveyed effort, for the four months of the winter (top) and summer (bottom) surveys.

1.2 Sightings

The observed distributions of the several groups presented in the Chapter 2 are detailed in the following sections (Figure 2–5), as well as the corresponding encounter rates, given in Table 1. These distributions and encounter rates were based on all sightings, in either good or poor observation conditions.

1.2.1 Cetaceans

Harbour porpoises were only present in the ENA, where they aggregated along the coast in winter (from Dover strait to Basque country), and dispersed more offshore in summer, especially in the Celtic Sea and western Channel (Figure 2). In the ENA, small-sized delphinids were distributed over the whole area except the EC, while in the NWMS they were present both over neritic and pelagic waters (Figure 2). Bottlenose dolphin was mostly distributed over the shelf in the ENA, with some sightings occurring in the EC and over pelagic waters, but in the NWMS sightings occurred both inshore (especially around Corsica) and offshore, especially during winter (Figure 2).

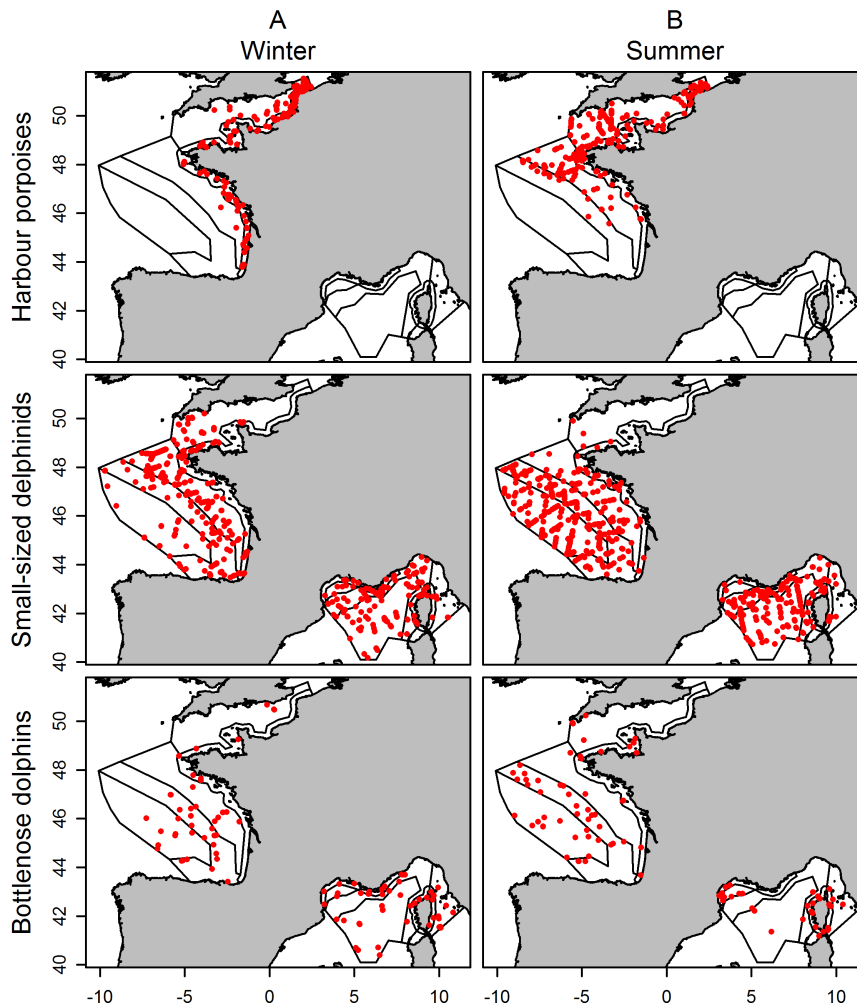


Figure 2. Distribution of sightings for harbour porpoises, small-sized delphinids and bottlenose dolphins in winter (A) and summer (B).

Long-finned pilot whales and Risso's dolphins were mostly sighted along the shelf edge, with some occurrence over pelagic waters and inshore in the western EC (Figure 3). Fin whale occurred mostly within the Ligurian Sea and along the shelf edge (Figure 3). All sightings unidentified with certainty within one of these groups were left apart.

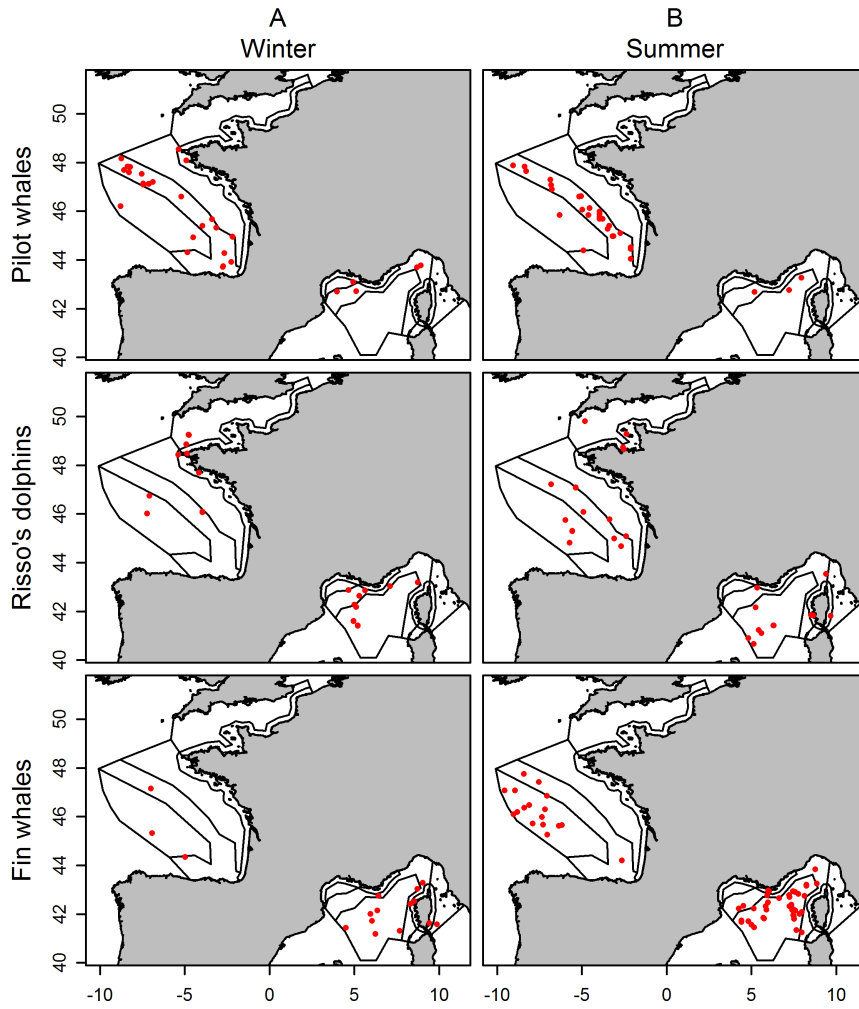


Figure 3. Distribution of sightings for long-finned pilot whales, Risso's dolphins and fin whales in winter (A) and summer (B).

1.2.2 Seabird

Northern fulmars had similar distribution between the two seasons, with most sightings occurring north of 45°N (Figure 4). Small-sized shearwaters had a low occurrence in winter in the ENA, and were mostly distributed around Brittany in summer, while in the NWMS the distribution was very similar between winter and summer, the group mostly occurring inshore (Figure 4). Large-sized shearwaters were absent from both basins in winter, but in summer the distribution were fairly contrasted (Figure 4): in the ENA, the group only occurred off the shelf edge, while in the NWMS it was mostly inshore. In the ENA, storm petrels exhibited a contrasted distribution between the seasons: mostly occurring in the southern BoB in winter, it was widespread over the ENA in summer, but avoiding the EC (Figure 4). In the NWMS, the species (the group being composed only of European storm petrels) was almost absent in winter but was widespread over the area in summer.

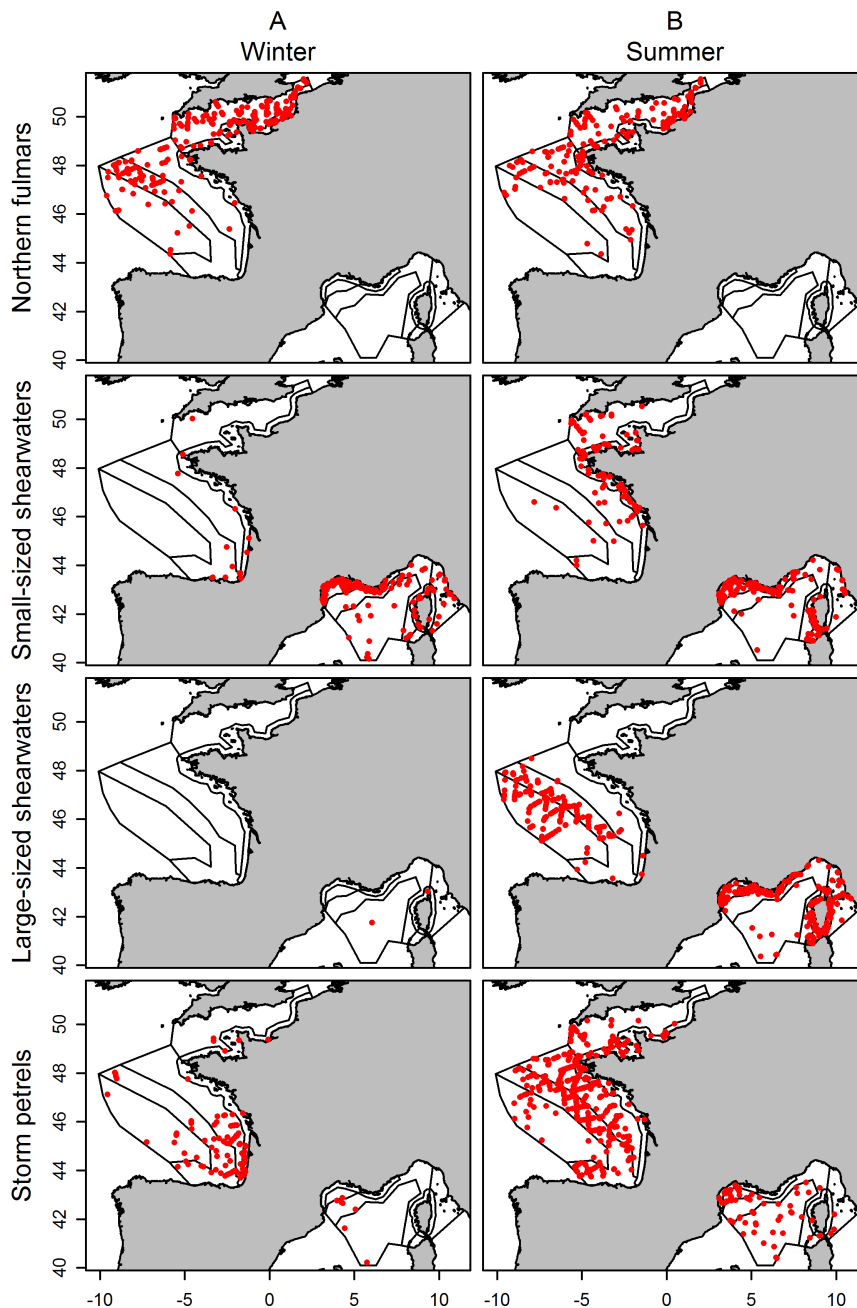


Figure 4. Distribution of sightings for northern fulmars, storm petrels, small- and large-sized shearwaters in winter (A) and summer (B).

Northern gannet was mostly occurring in the ENA (mainly over neritic waters, Figure 5), but sightings were also made in the NWMS, in coastal waters, but these sightings were not considered. Auks were widespread over the whole shelf in the ENA in winter, with some sightings occurring in the Gulf of Lion in the NWMS (Figure 5), but in summer, it only occurred along Brittany coast and in the EC. In winter, black-legged kittiwakes occurred over the whole ENA, but in summer the sightings were far less numerous, mostly occurring around colonies (mostly in EC and Brittany) and in pelagic waters of the BoB (Figure 5).

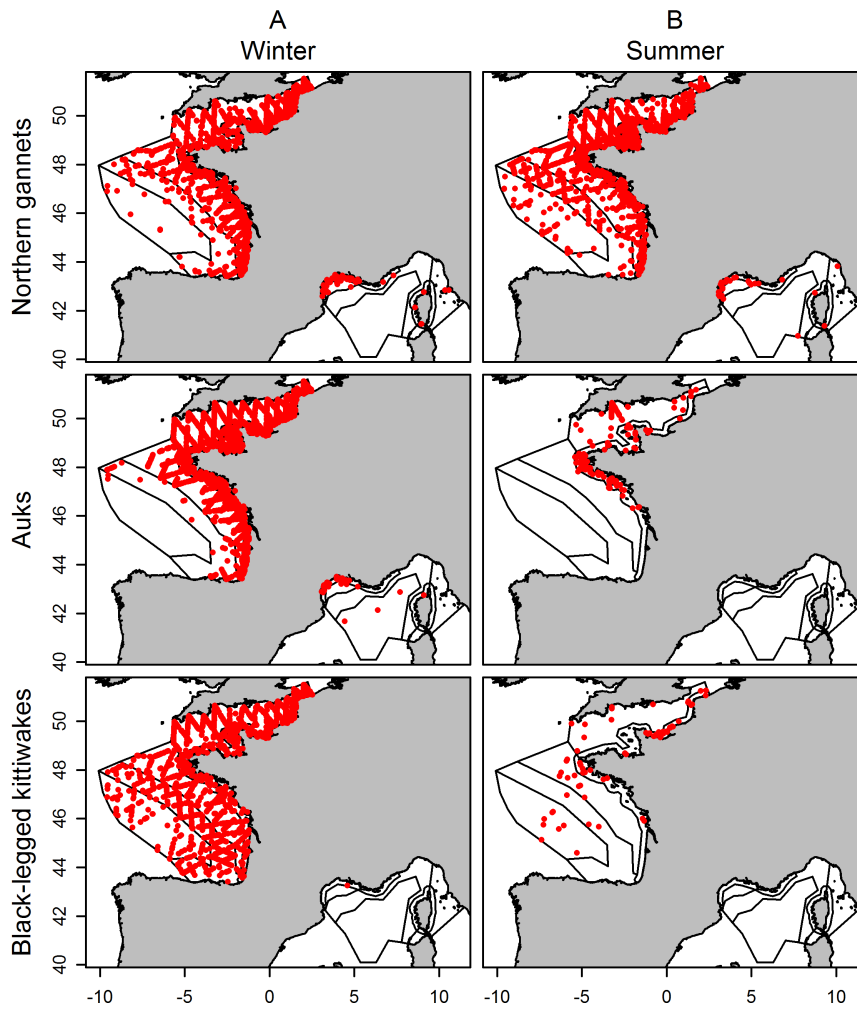


Figure 5. Distribution of sightings for northern gannets, auks and black-legged kittiwakes in winter (A) and summer (B).

Table 1. Number of sightings, number of individuals and encounter rates (individuals per km) for each studied groups in winter and summer from the SAMM survey in the NWMS and the ENA.

Basin	Species	Number of sightings	Winter Number of individuals	Encounter rate	Number of sightings	Summer Number of individuals	Encounter rate
NWMS	Small-sized delphinids	163	979	0.071	248	4288	0.230
	Bottlenose dolphin	56	209	0.015	51	355	0.019
	Globicephalinae	20	42	0.003	17	152	0.007
	Fin whale	13	13	0.001	48	63	0.003
	Small-sized shearwaters	411	1540	0.110	279	1381	0.075
	Large-sized shearwaters	2	2		318	988	0.054
	Storm petrels	7	13	0.001	74	101	0.005
	Northern gannet	87	190	0.014	43	60	0.003
	Auks	77	250	0.018	-	-	-
Black-legged kittiwake	1	2					
ENA	Harbour porpoise	279	481	0.015	272	423	0.012
	Small-sized delphinids	442	4737	0.146	680	16306	0.482
	Bottlenose dolphin	48	327	0.010	63	383	0.011
	Globicephalinae	40	130	0.004	57	241	0.007
	Fin whale	3	3		17	21	
	Northern fulmar	346	740	0.023	195	283	0.008
	Small-sized shearwaters	16	31	0.001	179	770	0.023
	Large-sized shearwaters	-	-	-	228	891	0.026
	Storm petrels	157	306	0.009	548	718	0.021
	Northern gannet	3697	11123	0.343	2540	1178	0.035
Auks	6221	16841	0.519	240	530	0.016	
Black-legged kittiwake	2255	3233	0.100	73	93	0.003	

2 PELGAS survey

2.1 Prey data

The following section will present the detailed annual distributions of the seven main small pelagic fishes detected during PELGAS surveys within both surface and deep layers.

Anchovies were mostly encountered over the shelf of the southern BoB, and along the coast from Brittany to Basque country (Figure 6). In 2011, anchovies were widespread over the whole shelf, from north to south. The distribution is rather similar between the two layers. Sardines were mostly encountered along the coast, but occurred more offshore than anchovies (Figure 7). In depth, they were only encountered along the coast in 2009–2010, but during the other years, more detections occurred over the shelf. In surface however, they occurred as much over the shelf, especially along the shelf edge, as along the coast. Concerning Atlantic mackerel, the distribution between the two layers were different (Figure 8). In depth, the species was detected over the whole shelf, except in 2010 and 2012 when the detections were more scarce, but in surface they were less detected, with most of occurrences along the coast (shallow waters) and over the outer shelf, although the species was fairly widespread in 2005–2007 and 2009. Pacific mackerel was less encountered, mostly over the southern shelf and avoiding coastal waters, except in 2006 when the species was found over the whole BoB (Figure 9). The species was mostly detected within deep layers, and occurrences within surface layer were scarce. The Atlantic horse mackerel was far more common in deeper layers, were the species was widespread over the shelf, but mostly avoided the areas of freshwater influence (Figure 10). It was absent from the surface layer, except for shallower waters when the two layers are gathered and in 2005 when the species occurred at the surface in the central part of the BoB shelf. Sprat had a distribution restricted to shallower waters, from Brittany to Arcachon, thus the distribution between the two layers were rather similar (Figure 11). Finally, the blue whiting only occurred in the deep layers, and was mostly detected over the northern BoB shelf, with some occurrence off Aquitaine (Figure 12). In 2008, 2009 and 2011 however, the species was more scarce, and mostly occurred along the shelf edge.

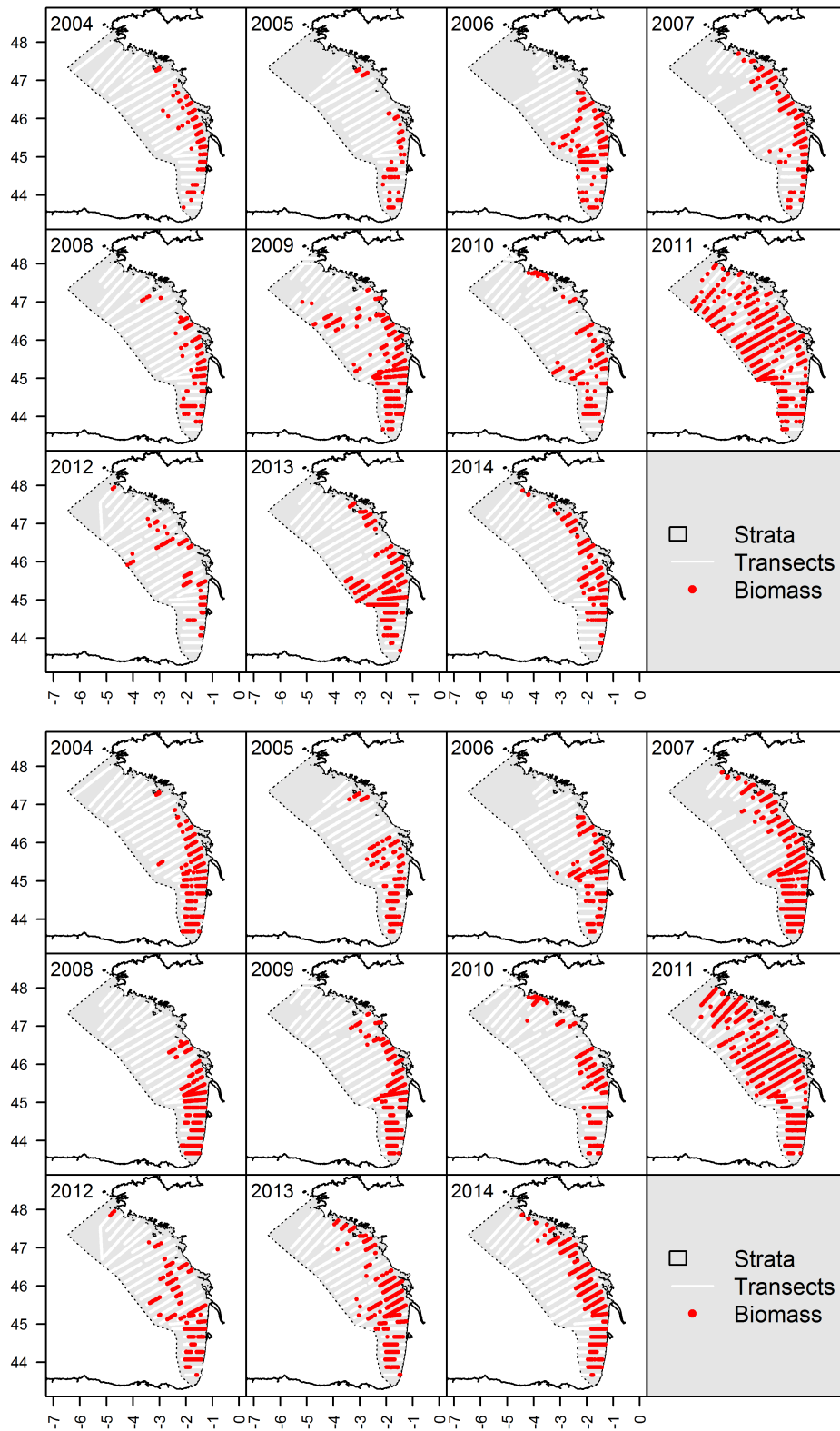


Figure 6. Distribution of anchovy acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

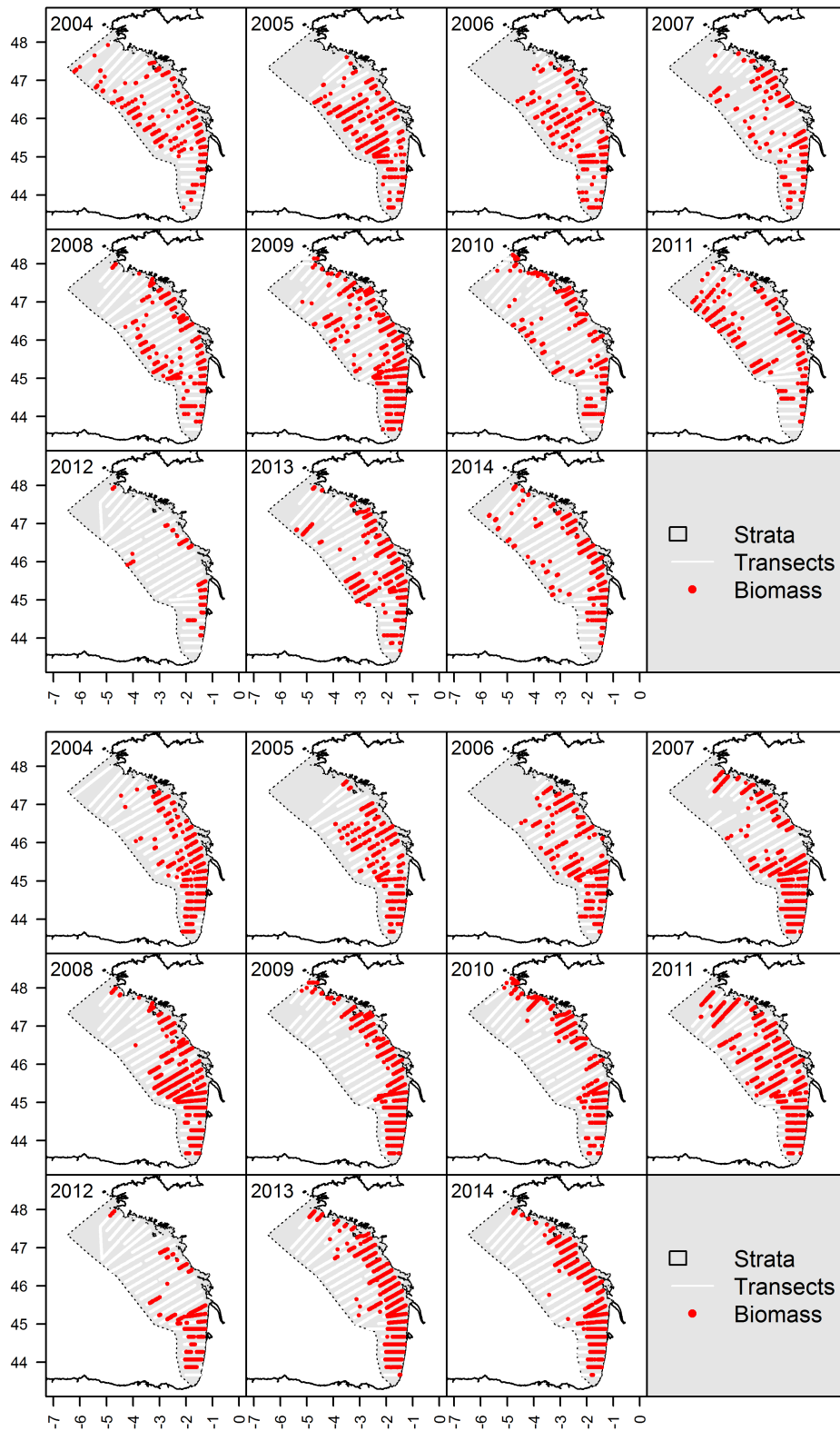


Figure 7. Distribution of sardine acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

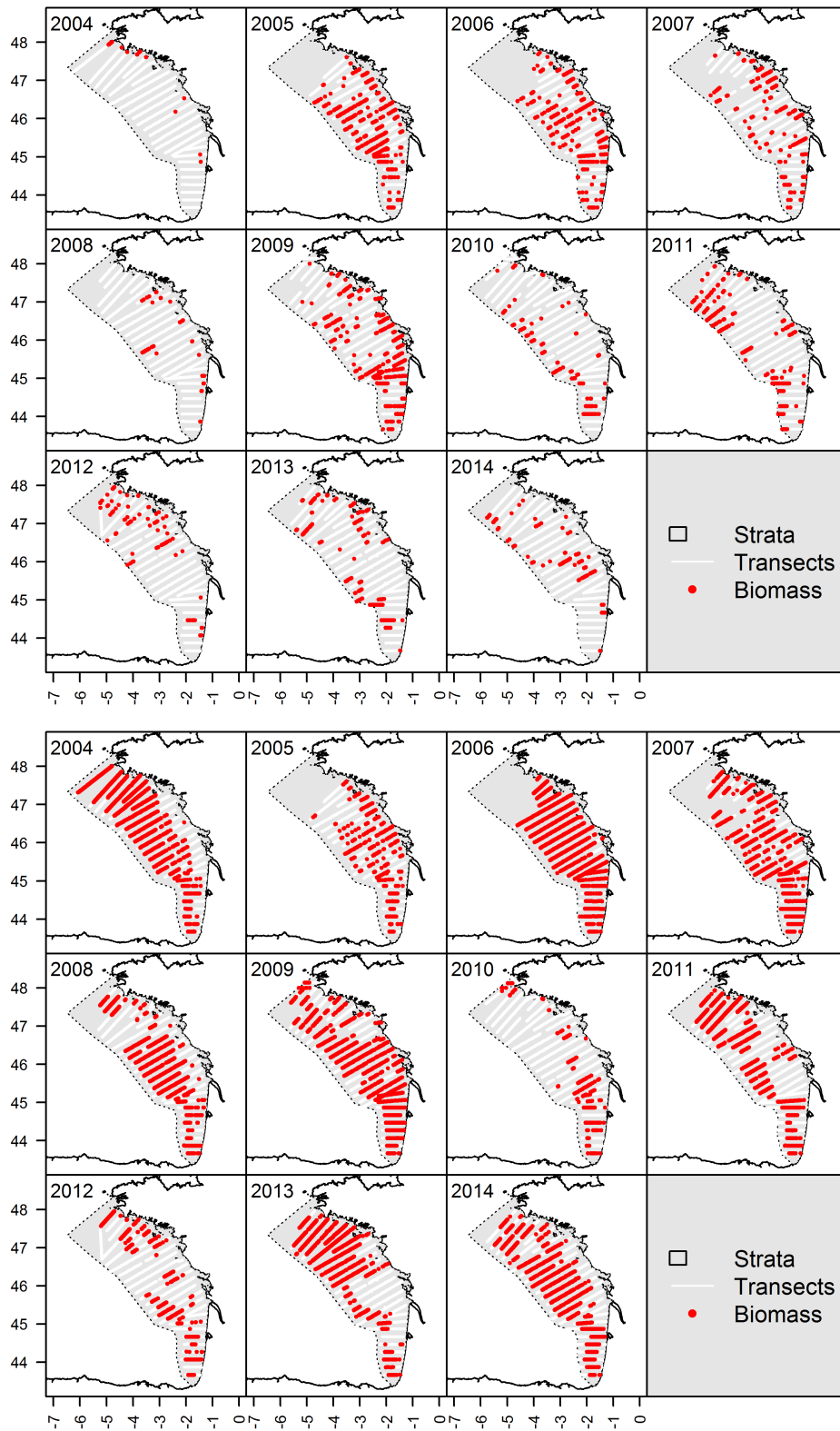


Figure 8. Distribution of Atlantic mackerel acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

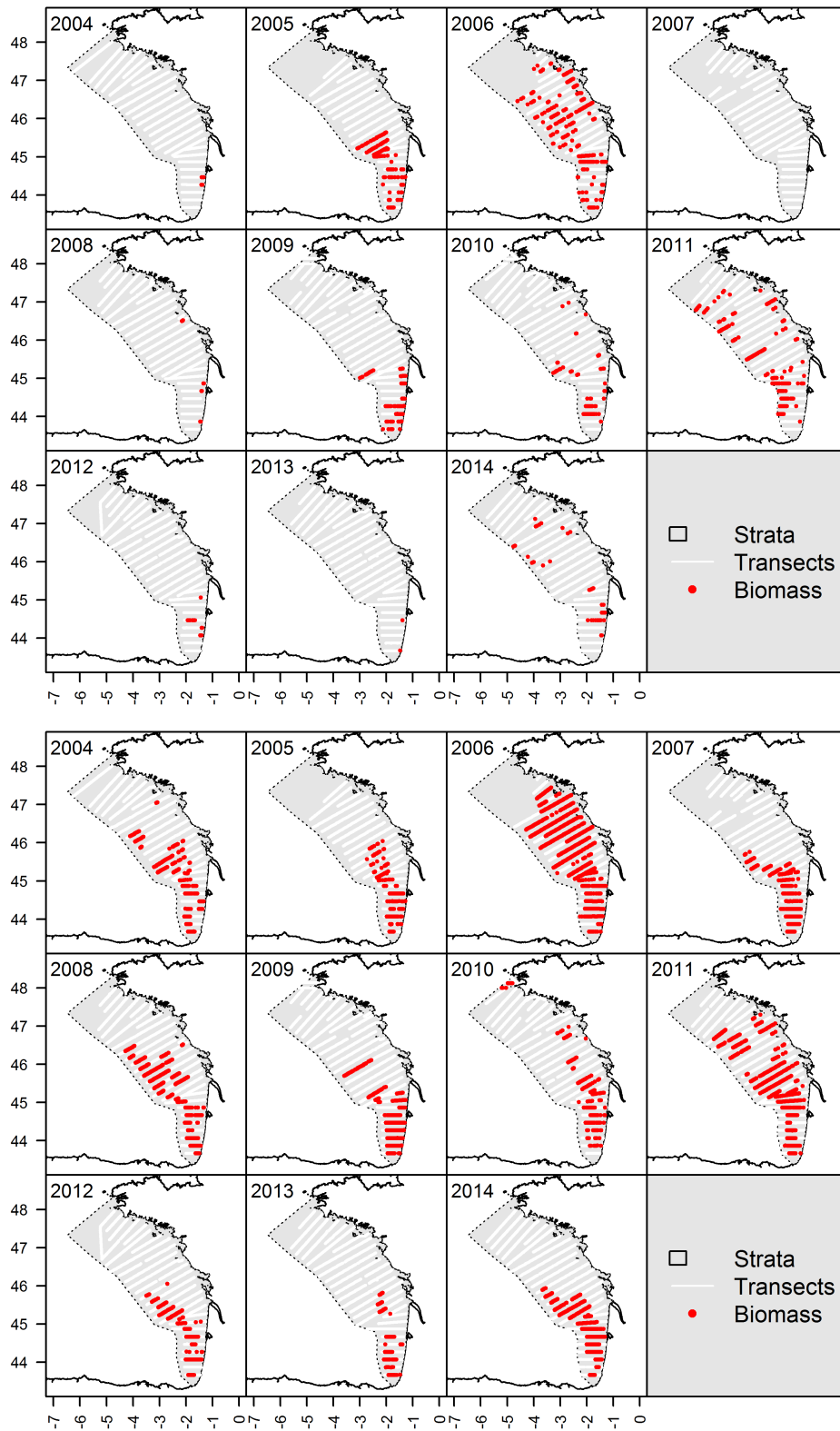


Figure 9. Distribution of Pacific mackerel acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

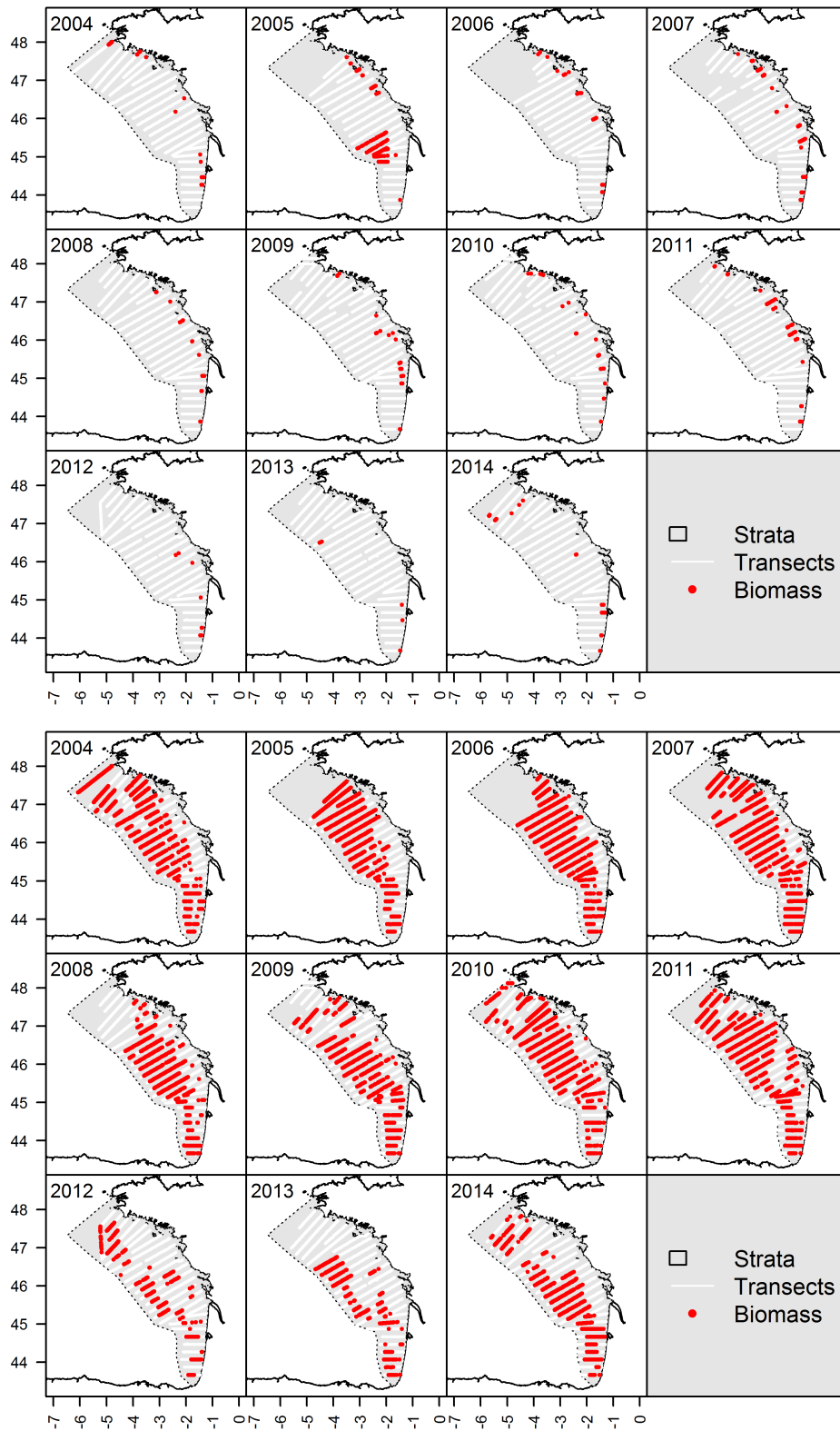


Figure 10. Distribution of Atlantic horse mackerel acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

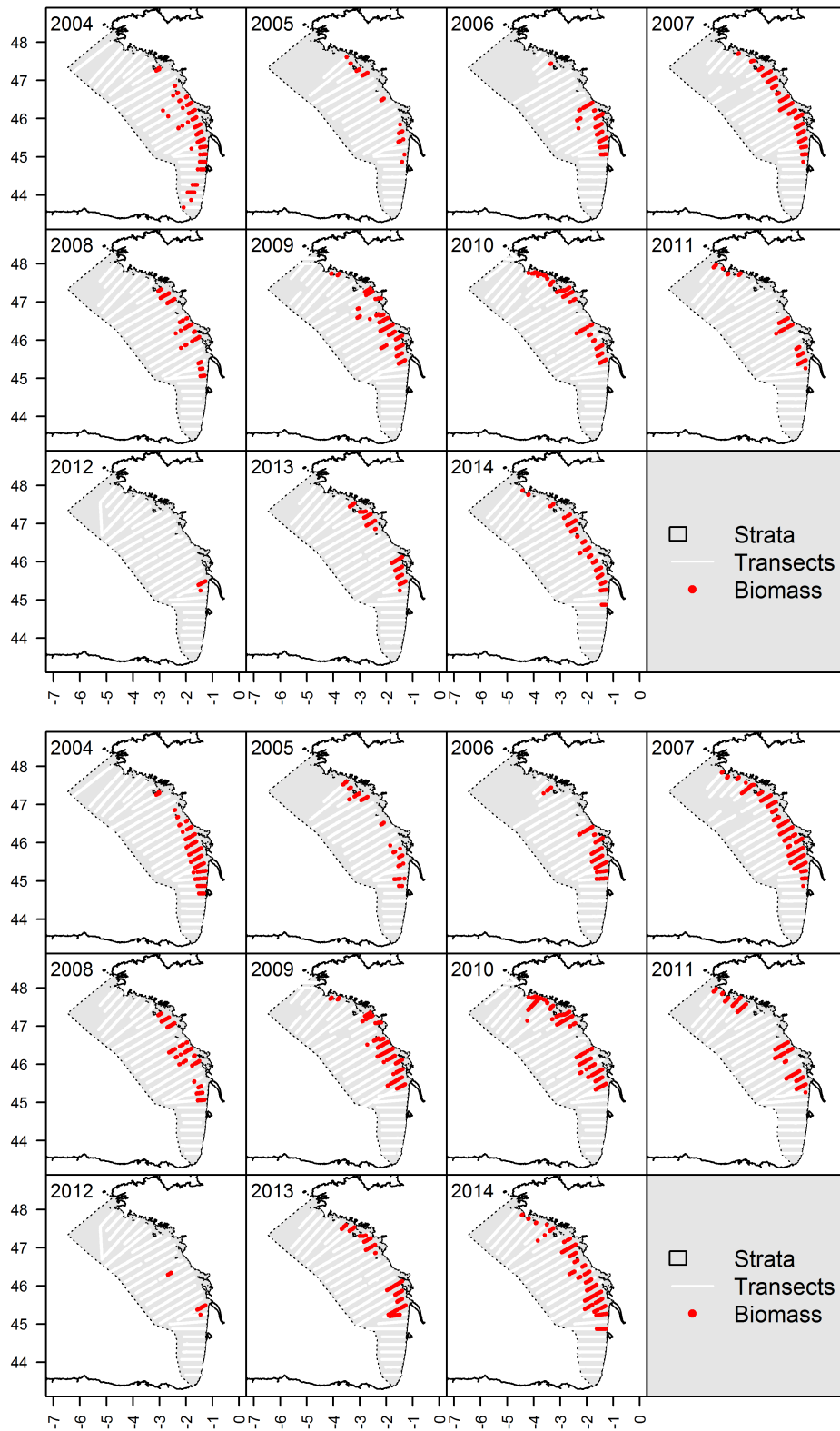


Figure 11. Distribution of sprat acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

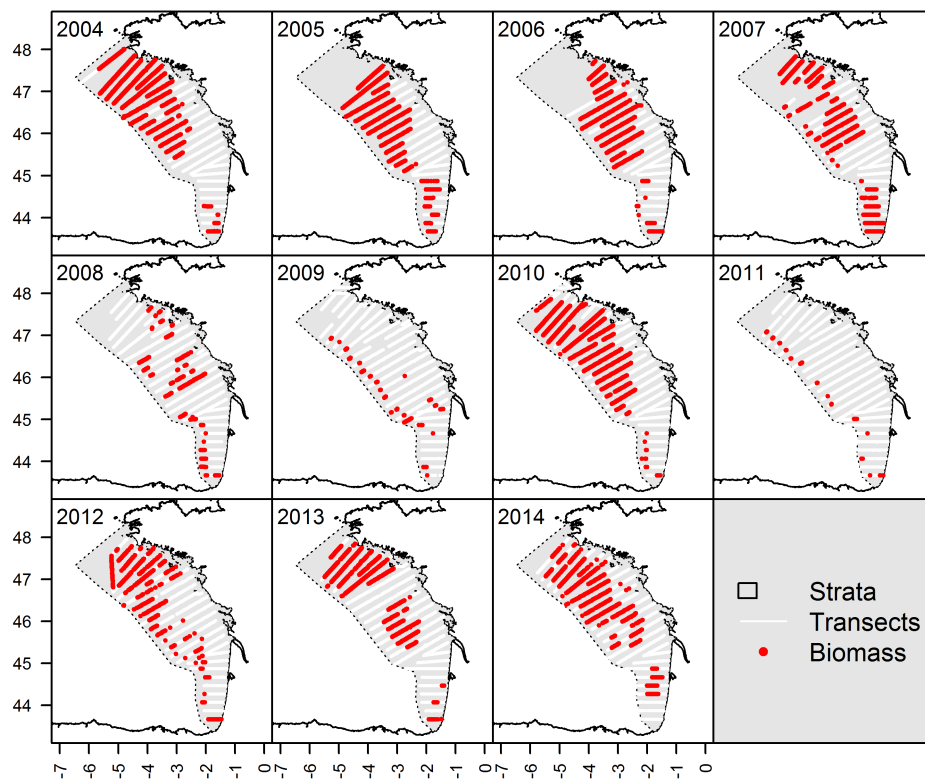


Figure 12. Distribution of blue whiting acoustic detections within surface (top) and deep (bottom) layers, in red. In white is indicated the acoustic sampling trace.

2.2 Predators sightings

The annual observed distribution and encounter rates of the nine studied groups of predators are presented in the following section. These distributions and encounter rates (Table 2), only include the effort made within the stratum (both good and poor observation conditions), but exclude all sightings of individuals attracted or repelled by the vessel, as well as sightings of individuals associated to fishing vessels.

Northern fulmar distribution did not exhibit many changes between years, although the encounter rates were higher in 2008–2009, the species being mostly distributed over the outer shelf, with some incursions inshore around Brittany (Figure 13). Northern gannet was the most abundant species, and was widespread over the whole BoB whatever the year (Figure 14). Auks were abundant, with a stable distribution through the years: they were distributed along the coast during the whole decade (Figure 15). Common dolphin occurrences were scarce, but their group sizes were important. Their distribution did not really vary between years, most of sightings occurring over the inner shelf despite some occurrence of the shelf edge (Figure 16). Finally, bottlenose dolphins also occurred in large groups despite low sighting numbers, and were distributed along the shelf edge throughout the decade (Figure 17).

Table 2. Predators annual encounter rates (individuals per km) for the ten studied years of the PELGAS survey, within the stratum.

Year	Northern fulmar	Northern gannet	Auks	Common dolphins	Bottlenose dolphins	Survey effort (km)
2004	0.0206	0.1507	0.0173	0.0220	0.0020	3590
2005	0.0305	0.2316	0.0101	0.0586	0.0635	3671
2006	0.0171	0.2146	0.0078	0.0360	0.0319	4861
2007	0.0348	0.0955	0.0163	0.0016	0.0445	4429
2008	0.0540	0.3345	0.0548	0.1494	0.0345	5109
2009	0.0444	0.1404	0.0232	0.1116	0.1059	5656
2010	0.0437	0.1268	0.0219	0.0514	0.0308	5838
2011	0.0274	0.0527	0.0705	0.0470	0.0109	5408
2012	0.0186	0.1583	0.0239	0.0512	0.0085	5059
2013	0.0272	0.5095	0.1806	0.0660	0.0320	4381
2014	0.0401	0.2517	0.0332	0.0342	0.0128	4060

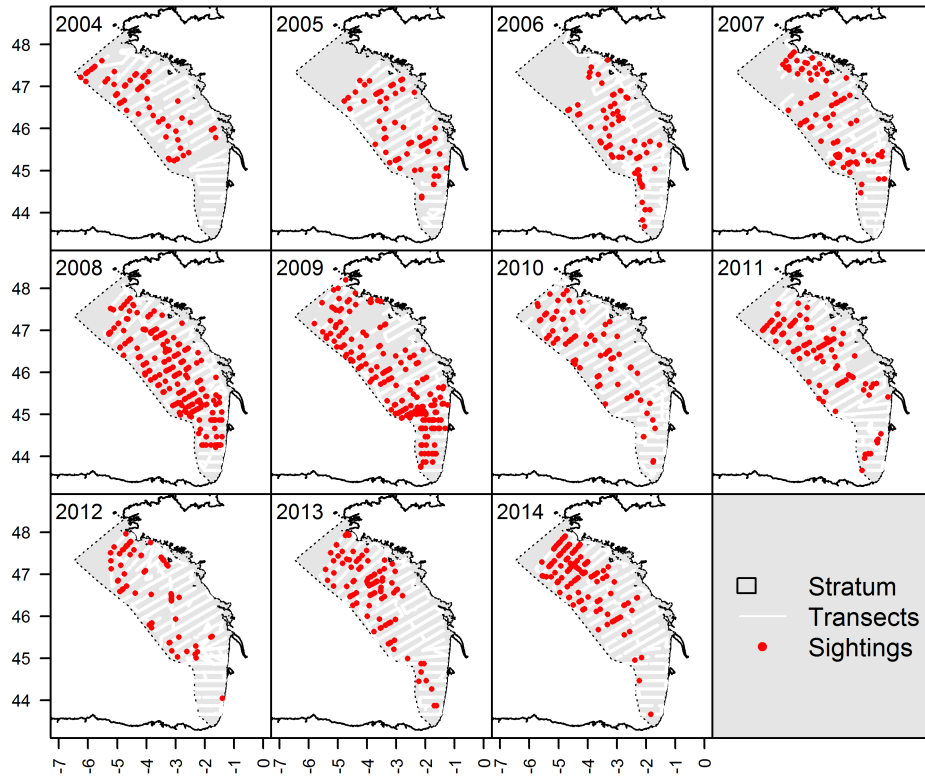


Figure 13. Northern fulmars sightings from 2004 to 2014. In white is the effort associated to the top predator survey.

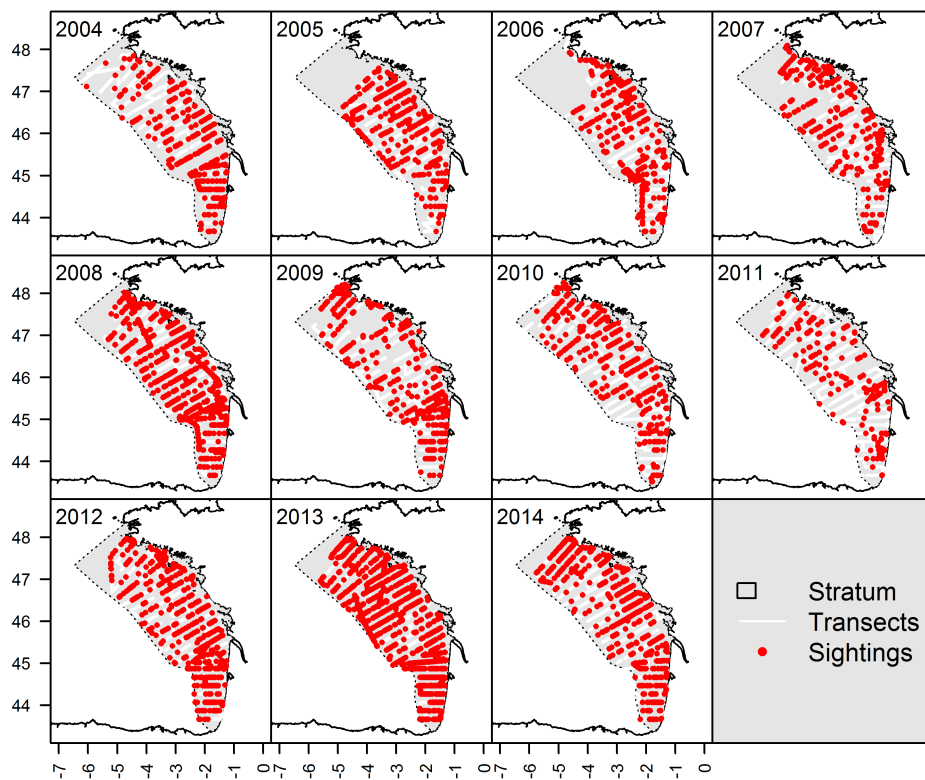


Figure 14. Northern gannets sightings from 2004 to 2014. In white is the effort associated to the top predator survey.

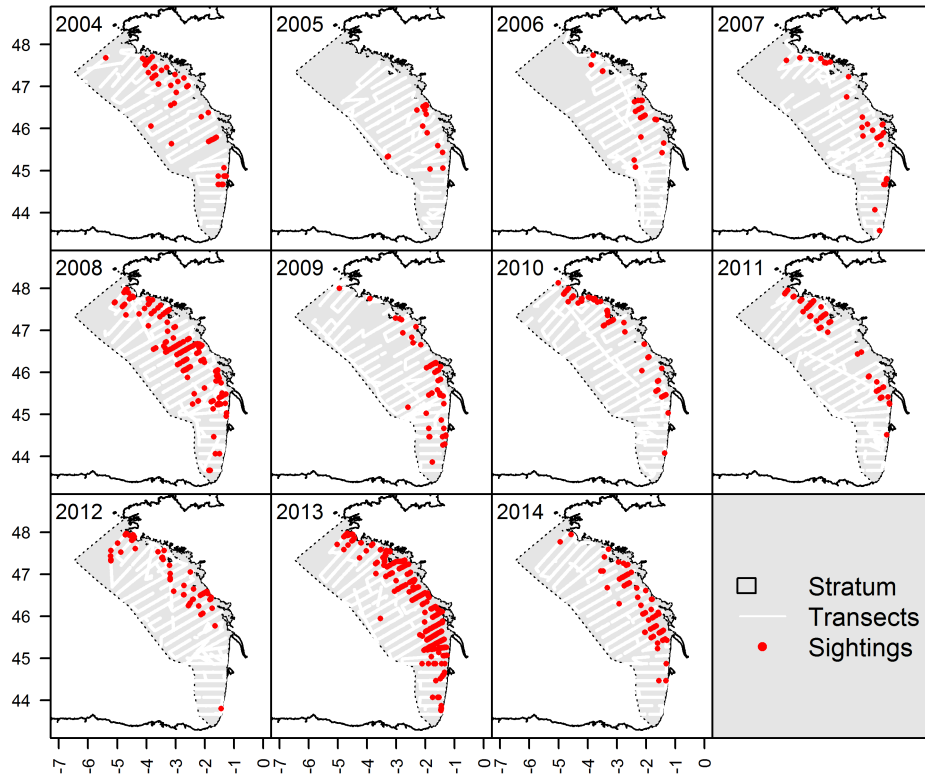


Figure 15. Auks sightings from 2004 to 2014. In white is the effort associated to the top predator survey.

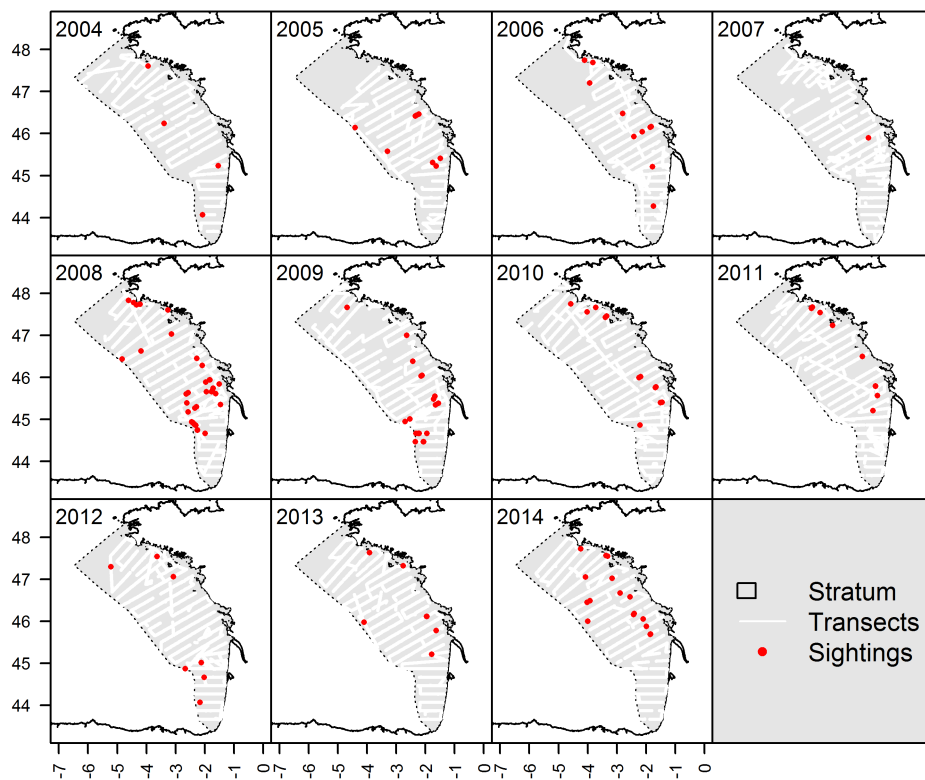


Figure 16. Common dolphins sightings from 2004 to 2014. In white is the effort associated to the top predator survey.

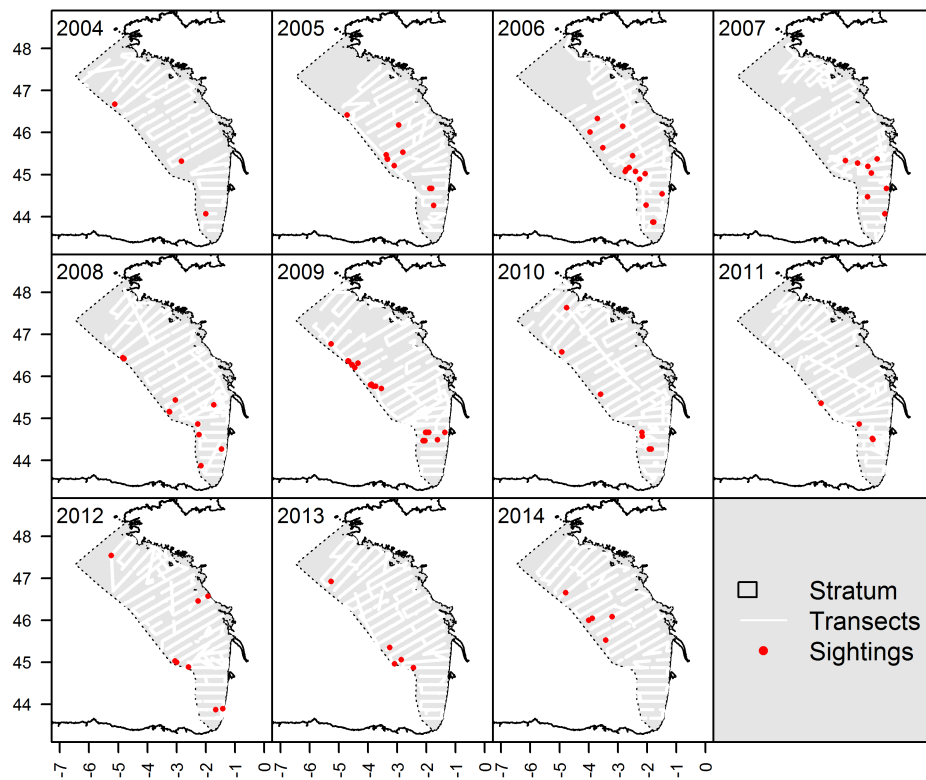


Figure 17. Bottlenose dolphins sightings from 2004 to 2014. In white is the effort associated to the top predator survey.

Appendix **B**

Chapter 3 - How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: the north-western Mediterranean Sea

Supporting information to Chapter 3: in press paper.

Contents lists available at [ScienceDirect](http://www.sciencedirect.com)

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Regular article

How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: The north-western Mediterranean Sea

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ABSTRACT

Contrasting to the overall oligotrophic Mediterranean Sea, the north-western basin is characterised by high productivity and marked by seasonality, which induces spatiotemporal heterogeneity of habitat. Cetaceans and seabirds are expected to perceive this repetition of the seasonal cycle and to anticipate the recurrent variability of their environment. Because phenology imposes strong constraints over marine predators, especially through reproduction, we expected them to exhibit variations in their habitat preferences over seasons. Indeed, during reproductive period, marine predators have to face their own needs and those of their young, while out of this period, they can focus on maximising their own survival only. We therefore hypothesised that some species would change their habitat preferences to exploit the most favourable habitat during each season, while other species might accommodate the same habitat all year-round, for example thanks to the use of an habitat favourable all the year. To explore these hypotheses, we used aerial surveys data conducted over north-western Mediterranean Sea during winter 2011–2012 and summer 2012. Generalised Additive Models were used to link the species density to a set of 12 physiographic and oceanographic predictors describing their environment. Habitat models resulted in deviances from 12 to 47%. Our results provided the first assessment of habitat preferences for the winter season for most of our studied species. Small-sized delphinids (mostly striped dolphins), fin whales, *Globicephalinae* (long-finned pilot whales and Risso's dolphins) and small-sized shearwaters (Yelkouan and Balearic shearwaters) exhibited no habitat variations between seasons, although for the first two, abundances were lower in winter. On the contrary, bottlenose dolphins switched from coastal habitat in summer to pelagic habitat in winter, while Cory's shearwaters and storm petrels exhibited the largest habitat variations between seasons with a complete absence during winter.

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1. Introduction

Physical and biological processes in marine ecosystems are generally strongly heterogeneous in space and time (Barry and Dayton, 1991). This high environmental variability in ecosystem conditions induces patchy and variable distributions of forage resources for top predators and, as a consequence, implies the necessity for predators to cope with such variability (Hunt and Schneider, 1987; Stewart et al., 2000). However, the degree of predictability and patchiness of resources for predators depends on scales: spatial and temporal scales are known to be linked and generally to increase together (Wiens, 1989). For example, spatially large-scale features tend to be recurrent or permanent and are

highly predictable; in contrast, coarse and fine-scale processes tend to be shorter and less predictable. Seasonality is a major contributor to temporal variability and operates at an intermediate temporal scale (infra-year) and from fine to large spatial scales; its effects are strongly predictable from year to year. Indeed, the winter mixing of the water column induces enrichment of the upper layer in nutrients, which allows the growth of phytoplankton when incident light and temperature increase in summer, the so-called phytoplankton bloom (Sverdrup, 1953). The development of phytoplankton then induces an impoverishment of the upper layer and, since the summer stratification of the water column inhibits the renewal of nutrients, a reduction of production occurs in summer.

Seasons result from the angle between the polar rotation axis of the earth and its revolution plan around the sun. This angle has been fairly stable with time, and hence the earth has experienced a seasonal regime for periods comparable to evolutionary times. The

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amplitude of seasonal variation is minimal at the equator and increases with latitude. The location and intensity of the main seasonal processes can vary between years according to decadal fluctuations (*i.e.* north Atlantic oscillation) or longer-term trends (*i.e.* climate change). Marine mammals and seabirds living at temperate latitudes have thus evolved in a seasonal environment that has shaped their life traits and migration patterns according to the main recurrent large-scale features in physical and biological characteristics of the ocean. We define the phenology of these species as their annual cycle in distribution and associated vital functions such as reproduction, migration, and foraging.

In addition to this, meso- and micro-scale processes add less predictable heterogeneity to the marine environment that top predators have to cope with by adaptive behavioural responses largely dependent on their individual sensory and communication skills, possibly enriched by the memory of previous experiences as well as by social (horizontal transmission between individuals of the same generation) and cultural (vertical transmission between individuals of consecutive generations) traits.

Hence, we could reasonably expect top predators to perceive the repetition of the seasonal cycle (Simmonds, 2006), and to anticipate this recurrence of their environment. Since phenology imposes strong constraints over species on an annual basis, especially through reproduction, we could expect predators to change their habitat preferences seasonally to find the best compromise between ocean conditions and their own constraints during each season. For example, during the reproductive period, marine mammals and seabirds face increased energetic demands to answer both their own needs and those of their young (Stearns, 1992). As an answer, adults adapt their behaviour during the reproductive season to equilibrate the compromise between investing in their own survival or in reproduction: diet and/or foraging strategy flexibility, variations of foraging areas, increase of foraging effort in the case of an unfavourable year. Out of the reproductive season, predators are released from this compromise and can modulate their habitat preferences to optimise their own survival.

This study will focus on the north-western Mediterranean basin (hereafter NWMS). This long considered oligotrophic sea (Margalef, 1985) is today known as strongly heterogeneous. The eastern basin is oligotrophic, but the north-western basin exhibits the highest productivity of the whole Mediterranean, showing

similarities with the eastern North Atlantic regarding its marked seasonality (D'Ortenzio and Ribera d'Alcalà, 2009). The NWMS is home to a diversified and abundant community of cetaceans and seabirds (see Laran et al., *this issue*; Pettex et al., *this issue*). Cetacean populations are mostly confined to the Mediterranean, whereas seabird populations include species with a permanent presence in the basin, as well as populations that predominantly use the area either during their breeding season, or conversely during non-breeding or inter-nuptial periods of their life cycles (del Hoyo et al., 2010). Few of them have been investigated for habitat use so far and, when so, mostly in the summer (*e.g.* Péron et al., 2013; Péron and Grémillet, 2013). Hence, basin-wide seasonal changes in distribution and habitat use by marine top predators are still poorly known.

By using observational data from aerial surveys conducted in the NWMS during both the summer and winter seasons, the present study was aimed at testing whether predators modulated their habitat preferences in response to seasonal changes of their environment, and explore which parameters were involved in these potential variations. To do so, we investigated seasonal changes in habitat preferences of species underlying their changes in distribution through habitat modelling using Generalised Additive Models (GAMs) to seasonally model the relationships between species density and a set of variables describing their environment. This approach allowed us both to provide robust insights into those relationships and to compute predictions of potential species distributions based on their observed habitat preferences.

2. Material & methods

2.1. Study region

The NWMS is characterised by a complex topography, with large continental shelves in the Gulf of Lion and the Tyrrhenian Sea and steep slopes indented by numerous canyons elsewhere (Fig. 1). The general circulation is dominated by deep Atlantic-originated waters entering the area from the eastern Mediterranean through the Tyrrhenian Sea, and flowing across the Ligurian Sea to the Balearic Sea, along the continental slope. This current is known as the Liguro-Provençal or Northern Current (Millot, 1999).

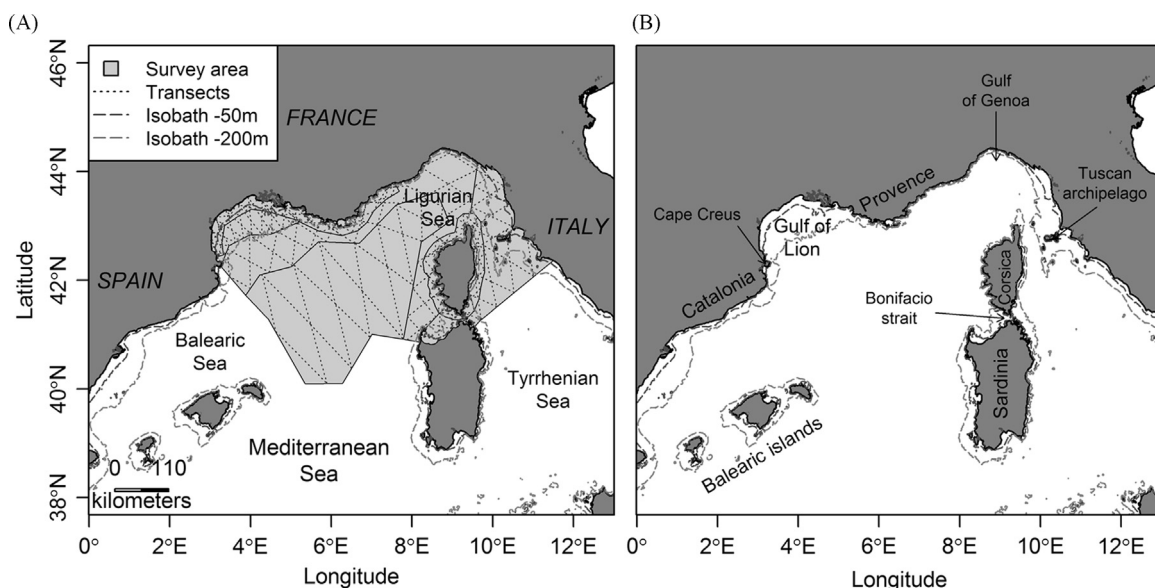


Fig. 1. Study area, with survey area and sampled transect (A), and geographical names (B).

Wind regime, topography and general circulation generate two permanent fronts: the Ligurian Front along the steep slopes of the Ligurian Sea and the North-Balearic Front (Sournia et al., 1990). The Gulf of Lion remains a particular area within the NWMS, where the combined effect of winds and fluvial discharge, mainly from the Rhône river, generates high productivity throughout the year (Morel and André, 1991). The Rhône river plume spreads out up to hundred kilometres from the river delta (Sournia et al., 1990; Morel et al., 1990).

The strong NWMS seasonality (D'Ortenzio and Ribera d'Alcalà, 2009) is characterised by a strong summer stratification limiting phytoplankton growth and overall biological production, whereas water mixing during winter due to the combination of low surface temperatures and strong winds results in the breakdown of water stratification and in deep water nutrients being upwelled to the surface layer. This enrichment of the euphotic layer allows phytoplankton bloom and mesotrophic conditions to develop in the NWMS from late winter to spring (Auger, 2011; Morel and André, 1991; Sournia, 1973; Bosc et al., 2004).

2.2. Aerial survey and data collection

SAMM (*Suivi Aérien de la Mégafaune Marine*, Aerial Census of Marine Megafauna) aerial surveys were conducted from late November to mid-February 2012 (13,762 km of sampled transect) and from mid-May to early August 2012 (18,451 km of sampled transects). Sampling transects followed a zig-zag layout, and were manually designed to both maximise the use of flight time and cover the variety of marine habitats found in the NWMS, while ensuring an equal coverage probability within each stratum. Effort covered most of the NWMS north of 41° N (Fig. 1).

Observations were conducted following a standardised protocol designed for aerial surveys. For cetaceans, the protocol was based on line-transect methodology (Buckland et al., 2001): all sightings of cetaceans were recorded with the declination angle, measured with a hand-held clinometer. Along with flight altitude, this angle allowed the determination of the half-effective strip width (ESW) sampled on each side of the plane. For seabirds, the strip-transect methodology was used (Certain and Bretagnolle, 2008): seabirds were recorded within a band of 200 m on each side of the transect, under the assumption of perfect detection. Transects were sampled at a ground speed of 167 km/h and an altitude of 182 m.

Survey platforms were high-wing aircraft, equipped with bubble windows, allowing observation right under the plane. Sightings and group size were recorded, alongside observation conditions (Beaufort sea-state, glare severity, turbidity, and cloud cover), by two trained observers who transmitted their information to a flight leader collecting the data on a laptop connected to a GPS. Sightings were recorded at the lowest taxonomic level possible, but groupings were done when species could not be unambiguously identified. The survey provided a census of all megafauna, including turtles, sharks, large fishes, cetaceans and seabirds but, in this study, we focused on four groups of cetaceans and three groups of seabirds.

Groups used for further analysis were compromises between using the lowest taxonomic level available, with as many observations as possible. Common and striped dolphins (*Delphinus delphis* and *Stenella coeruleoalba*) were grouped as small-sized delphinids since, for most observations, it was not possible to tell apart the two species with certainty; however, it is admitted that striped dolphin largely dominates in the NWMS (Forcada and Hammond, 1998). The bottlenose dolphins *Tursiops truncatus* were identified at the species level. All sightings of "unidentified dolphins" were removed from the dataset. Although they can easily be told apart, long-finned pilot whales *Globicephala melas* and

Risso's dolphins *Grampus griseus* were pooled together (the *Globicephalinae* group) due to low sighting numbers for each species taken separately. Fin whales *Balaenoptera physalus* could not be confused with any other cetacean in the area. Regarding seabirds, we focused on three groups of procellariiforms: storm petrels *Hydrobates pelagicus*, Cory's shearwaters *Calonectris diomedea* and small-sized shearwaters, including both the yelkouan *Puffinus yelkouan* and Balearic *P. mauretanicus* shearwaters (two species indiscernible from the air). As for delphinids, unidentified procellariids were left apart.

2.3. Habitat modelling

Transects flown in effort were first subdivided into legs of identical observation conditions and then into 10 km-long segments. For each segment, numbers of sighted individuals of each group were summed up. To perform habitat modelling on the best quality data, we retained only segments with a Beaufort sea-state from 0 to 3, and subjective conditions from medium to excellent, representing 95% and 93% of the total survey effort in winter and summer, respectively.

Generalised Additive Models (GAMs) were used to model the relationship between the number of individuals per segment (response variable) and several environmental predictors (Hastie and Tibshirani, 1990; Wood, 2006) with a quasi-Poisson distribution, due to the over-dispersion of our data (Hedley and Buckland, 2004). We used a log-link function to relate the response variable to predictors, and set the sampled area per segment as model offset. The sampled area associated with each segment was the segment length multiplied by twice the corresponding ESW for cetaceans (see Laran et al., this issue, and Appendix S2 for more details), or by twice 200 m for seabirds.

We used a set of twelve environmental predictors (Table 1). First, we included four physiographic variables: bathymetry (depth), its gradient (slope), distance to the closest coast and distance to the closest colony for seabirds. Colony locations were compiled from several sources and geolocated (Appendix S1). Second, we included eight oceanographic variables: sea surface

Table 1

Environmental predictors used for habitat modelling and their source. GEBCO-08 database was used to compute depth, slope and distance to closest coast (<http://www.gebco.net/>). Aqua MODIS sensor products were used to compute surface chlorophyll and euphotic depth (<http://oceancolor.gsfc.nasa.gov/cgi/13>), and Eppley-VGPM model based on MODIS products was used to compute surface Net Primary Production (<http://www.science.oregonstate.edu/ocean.productivity/>). The ODYSSEA product from Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu/>) was used to compute mean, variance and gradient of sea surface temperature. The Mediterranean Sea Physics Analysis and Forecast (MSPAF) products from My Ocean project were used to compute mean and standard deviation of sea surface height.

Type	Environmental predictors	Units	Source
Physiographic	Depth	meters	GEBCO-08
	Slope	degrees	
	Distance to the closest coast	meters	Manually referenced
	Distance to the closest colony	km	
Oceanographic	Mean surface Chlorophyll a	$g \cdot m^{-2}$	MODIS
	Mean surface Net Primary Production	$g \cdot m^{-2} \cdot day^{-1}$	
	Mean euphotic depth	meters	ODYSSEA
	Mean SST	°C	
	Variance of SST	°C	
	Mean gradient of SST	°C	
	Mean sea surface height	meters	MSPAF
	Standard deviation of SSH	meters	

temperature (SST) mean, variance (SST_{var}) and gradient (SST_{grad} , computed as the difference between minimum and maximum values among the eight neighbours of each cell), sea surface height (SSH) mean and standard deviation (SSH_{SD}), surface chlorophyll *a* concentration (Chl), surface net primary production (NPP) and mean euphotic depth (Zeu). These oceanographic predictors were dynamic and, hence, introduced with two temporal resolutions: dynamic predictors were summarised over the 7 and 28 days prior to each sampled day. An overview of environmental conditions in the study area was obtained by averaging predictors over the survey period for winter and summer seasons (Fig. 2). These predictors were all distal variables, given that no proximal

variables (*i.e.* prey) were available at this scale for the study periods. Although proximal variables are expected to better explain the distributions of species, the variables used here were environmental characteristics of known importance to approximate the distribution of prey.

We implemented a selection procedure which tested models with at least one and up to four covariates (including covariates at both temporal resolutions) and excluding all combinations of covariates with an absolute value of correlation higher than 0.7 (correlation matrices are presented in Appendix S3). The maximum degree of freedom for smoothers was constrained to 3 to avoid over-fitting of the data (4, considering the offset). The

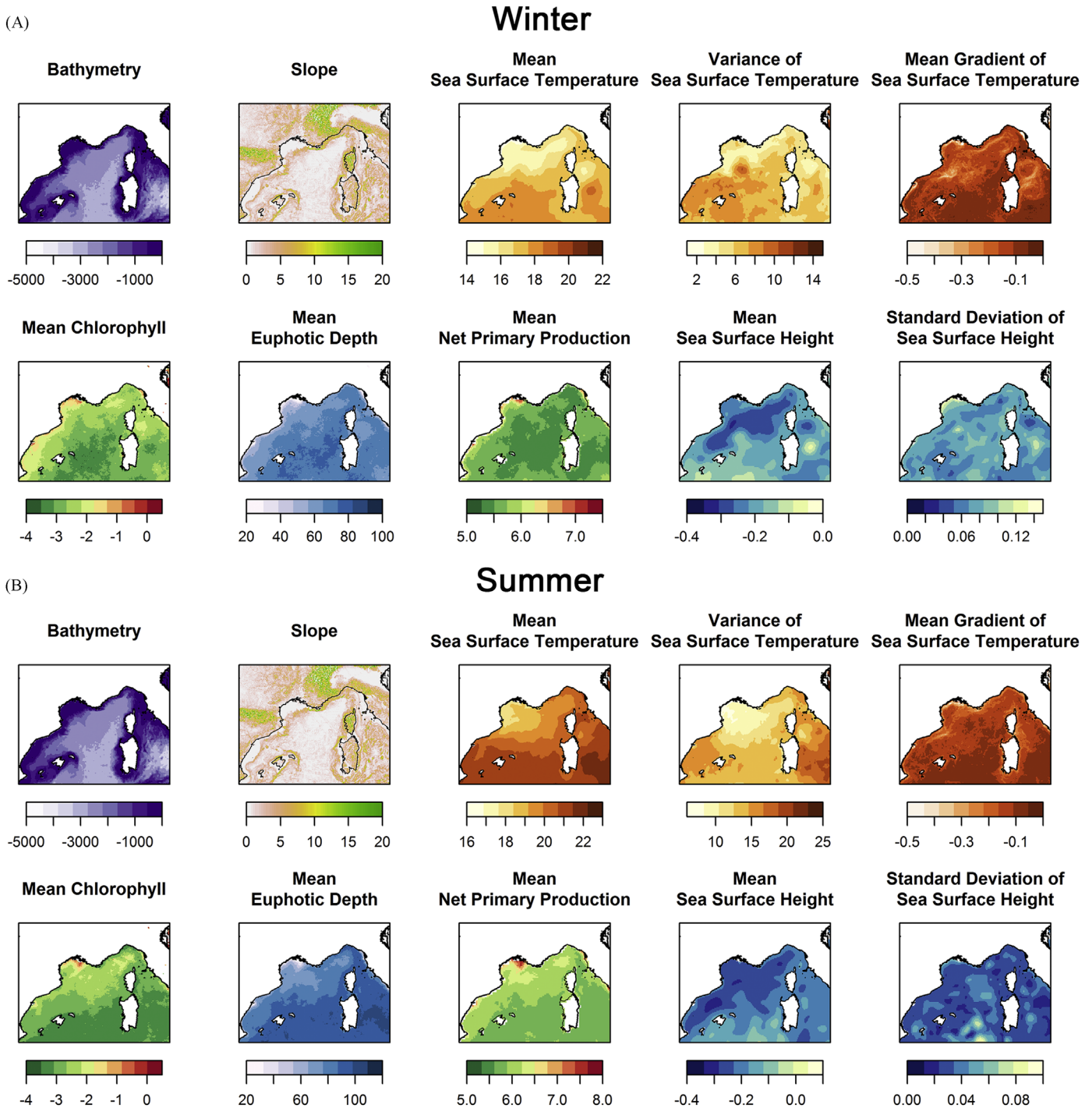


Fig. 2. Environmental conditions averaged over the two study periods. A – averaged conditions in winter (from late November 2011 to mid-February 2012); B – averaged conditions in summer (from mid-May 2012 to early August 2012).

selection procedure was based on the Generalised Cross-Validation criterion (GCV, the lower the better). Once a model was selected, we extracted the contribution of each covariate in the linear predictor by segments. These contributions were computed using the `predict.gam` function within the `gam` package, setting the `type` argument as “terms” (Wood, 2006): this provides a matrix with each component of the linear predictor separately (here, the smoothed covariates); see function description for more details. The contributions were then mapped to explore the local variations in the importance of each selected covariate.

Predictions were then produced for each day encompassed in the survey periods, then daily predictions were averaged to get winter and summer predictions. In order to limit extrapolation, we only performed predictions within the sampled environmental envelope. Variance around those overall predictions were computed as the sum of variance around mean prediction and mean of daily variances, and then the coefficient of variation was calculated as $CV = \sqrt{\text{seasonal variance}/\text{seasonal mean}}$. All analyses were done in R version 2.15.3 (R Core Team, 2014).

3. Results

3.1. Sightings

The four groups of cetaceans were present in both seasons, but the only seabirds to be abundant in both seasons were the small-sized shearwaters (Table 2, Appendix S4). For the two other seabird groups, numbers of sightings in winter were too low to allow habitat modelling.

3.2. Seasonal habitat models and predicted distributions

3.2.1. Small-sized delphinids

In winter, the selected habitat model for small-sized delphinids accounted for 11.8% of the total deviance (Table 3, Fig. 3A). The selected covariates were depth, slope, Zeu (7d) and SSH_{SD} (28d). The most contributing covariate was depth, with a relationship highlighting a preference for deep waters (3000–1500 m deep). The SSH_{SD} had overall important contributions, with a preference for medium values (the lower the value, the higher the water column stability). The relationships to Zeu and slope, respectively, indicated a preference for oligotrophic waters and high slope values. This model predicted an exclusively oceanic distribution, completely avoiding shelves (Fig. 4A).

In summer, explained deviance reached 20.5% (Table 4, Fig. 3B), with depth, mean SST (7d), SST_{var} (7d) and Chl (28d) as selected covariates. As in winter, depth was the most important covariate, with a similar relationship. Chl seemed to be an important covariate as well, with a relationship indicating a preference for oligotrophic waters, inducing negative contributions in the Gulf of

Lion (which was productive). Then, the relationships with the last two covariates showed a preference for cooler waters and a fairly high weekly variance of SST. The model predicted small-sized delphinids to be present in oceanic waters, with higher densities in the southern, deep oligotrophic waters (Fig. 4B). CVs were overall low for both seasons, with higher CVs in the Gulf of Lion and along northern Tuscan coast in winter, but higher CVs outside the studied area in summer (Appendix S5, Figure S5.1).

3.2.2. Bottlenose dolphins

The bottlenose dolphin winter model explained 20% of deviance (Fig. 5A). Selected covariates were mean SST (28d), SST_{var} (28d), SST_{grad} (28d) and Zeu (28d). According to the contribution maps, all covariates seemed to be more or less equivalent in their overall contributions. Relationships indicated a preference for deep Zeu, for high monthly variations of SST, warmer waters and an avoidance of medium monthly thermal fronts. According to the model, bottlenose dolphins were predicted to spread across oceanic waters (Fig. 4A), with higher densities in the strong frontal zone off Catalonia and in the frontal zone induced by the interaction between cyclonic and anticyclonic eddies in the Tyrrhenian Sea.

In summer, the model explained 27.1% of deviance (Fig. 5B). Selected covariates were depth, mean SST (28d), mean SSH (28d) and SSH_{SD} (28d). Once again, the four selected covariates resulted in similar importance in the linear predictor. Bottlenose dolphins showed a preference for waters deeper than 1000 m, waters around 22, low SSH and SSH_{SD} . This model predicted a more coastal distribution for bottlenose dolphins in summer (Fig. 4B), the species being predicted all along the slope from Catalonia to the Gulf of Lion, the Ligurian Sea shelf, around Corsica and Sardinia, the Tuscan Archipelago and the northern Tyrrhenian Sea. However, coupled with a preference for high SST, highest densities were predicted in the Balearic shelf and west of Sardinia, two areas located outside the surveyed area. CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.3. *Globicephalinae*

Given the small sample size and the absence of *Globicephalinae* from the Gulf of Lion, the effort conducted in the area has been excluded from the dataset prior to performing habitat model selection, since when the Gulf was included, no habitat models stood out. Explained deviances for the selected model were quite high, with 53.1% in winter and 39.6% in summer (Fig. 6A, B). In winter, selected covariates were depth, SST_{grad} (7d), mean SST (28d) and SSH_{SD} (28d). Mean SST was the most contributing covariate, especially along the slope and the oceanic area off the Gulf of Lion, with a relationship denoting a preference for cooler waters. Relationship to depth highlighted a preference for shallower waters, inducing positive contributions along the coasts, while the relationship to SST_{grad} indicated a preference for

Table 2
Number of sightings, number of individuals and encounter rates for each studied groups in winter and summer.

Species	Winter			Summer		
	Number of sightings	Number of individuals	Encounter rate (ind. km ⁻¹)	Number of sightings	Number of individuals	Encounter rate (ind. km ⁻¹)
Small-sized delphinids	163	979	0.071	248	4288	0.230
Bottlenose dolphins	56	209	0.015	51	355	0.019
<i>Globicephalinae</i>	20	42	0.003	17	125	0.007
Fin whales	13	13	0.001	48	63	0.003
Small-sized shearwaters	411	1540	0.110	279	1381	0.075
Cory's shearwaters	2	2	1.45 · 10 ⁻⁴	318	988	0.054
Storm petrels	7	13	0.001	74	101	0.005

Table 3
Summary of selected models for winter. Selected covariates for each group are indicated with the tick mark for physiographic variables, but with their temporal resolution (7 or 28 days) for oceanographic variables. All selected covariates were significant.

Winter	Small-sized delphinids	Bottlenose dolphins	<i>Globicephalinae</i>	Fin whales	Small-sized shearwaters
Distance closest coast					✓
Distance closest colony					
Depth	✓		✓	✓	
Slope	✓				
Mean SST		28d	28d		
SST _{var}		28d		28d	28d
SST _{grad}		28d	7d		
Chl					28d
NPP				7d	
Euphotic depth	7d	28d			
Mean SSH				28d	
SSH _{SD}	28d		28d		7d
Explained deviance (%)	11.8	20.0	53.1	24.8	46.6

medium weekly thermal gradients, hence positive contributions along the slope. The relationship with the last covariate indicated a preference for reduced SSH_{SD}. The model predicted *Globicephalinae* to be present mostly in the cooler waters of the Liguro-Provençal Current, and east of Corsica (Fig. 4A).

In summer, the selected covariates were NPP (7d), Zeu (7d), SST_{var} (28d) and SSH_{SD} (28d). Zeu and NPP were the most important covariates, with similar contributions. Their relationships indicated a preference for high productivity areas (hence positive contributions for NPP along the Liguro-Provençal Current), and for deep Zeu (positive contributions for Zeu within oceanic waters and the Tyrrhenian Sea). For the remaining two covariates, contributions were lower and positive all over the area. Their relationships indicated a preference for low monthly variance of SST and low SSH_{SD}. This model predicted highest densities along the slope and shelf of the Iberian coast and Balearic Islands, and around the Tuscan Archipelago (Fig. 4B). CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.4. Fin whales

The winter model-explained deviance was 24.8% (Fig. 7A), with depth, NPP (7d), SST_{var} (28d) and mean SSH (28d) as selected variables. Depth was the most important covariate, with high contributions over the whole area highlighting a clear preference for deep waters. NPP had high positive contributions in the Gulf of Lion and around the Tuscan Archipelago due to a relationship indicating a preference for productive areas. The other two covariates were less important, with a relationship denoting a preference for high variance of SST and lower mean SSH. The resulting prediction showed the species being distributed over all deep waters across the region (Fig. 4A).

In summer, the selected model resulted in 33.3% of explained deviance (Fig. 7B). Depth and NPP (28d) were the most important covariates, with high contributions all over the area. The relationships showed a preference for deep waters on one hand, and productive waters on the other. The relationship with the two other covariates (SST_{var} 28d and mean SST 7d) indicated a preference for low weekly variance of SST and warmer waters. This model predicted fin whales to be present in high densities in all oceanic zones from the Ligurian Sea to the Balearic Front (Fig. 4B), where high productivity was coincident with deepest waters. CVs were overall low for both seasons, with no pattern (Appendix S5, Figure S5.1).

3.2.5. Small-sized shearwaters

Small-sized shearwater models resulted in explained deviances of 46.6% in winter and 41% in summer (Fig. 8A). In winter, distance to the closest coast was the most important covariate, with a

relationship indicating a preference for 50 km from the coast, and inducing positive contributions along the coasts. The other selected covariates were SSH_{SD} (7d), SST_{var} (28d) and Chl (28d). Relationships showed a preference for reduced SSH_{SD} (negative contributions in the Gulf of Lion), high monthly variations of SST and high Chl (positive contributions in the Gulf of Lion). This model resulted in higher predicted densities where high Chl were close to shores, in the Gulf of Lion (especially in the Rhône river plume) and off the Catalanian and Tuscan coasts (Fig. 9A).

In summer (Fig. 8B), the most important covariates were depth and mean SSH (7d). The two other selected covariates, SST_{var} (7d) and SST_{grad} (7d) had lower contributions. The relationships indicated a preference for shallow waters, medium SSH, reduced weekly variance of SST and strong weekly thermal gradients. This model predicted a summer distribution pattern quite similar to the winter one, with highest densities mostly predicted in coastal frontal zones, especially in the Gulf of Lion, the northern Tuscan coast and over the Sardinian shelf (Fig. 9A). CVs were overall low for both seasons, with no pattern in summer but higher CVs both close and far away from coasts in winter (Appendix S5, Figure S5.2).

3.2.6. Cory's shearwaters

The summer model for Cory's shearwaters gave 37.5% of explained deviance (Fig. 10), with depth as the most important covariate, and mean SST (28d), NPP (28d) and distance to the closest colony as the three other selected covariates, with similar overall contributions. Relationships highlighted a preference for shallow waters (positive contributions along the coast), warmer waters (negative contributions in the Gulf of Lion and Tyrrhenian Sea) and productive waters (positive contributions over the Liguro-Provençal Current) within 50 km of colonies. The predicted distribution was quite contrasted (Fig. 9B), the species being predicted in highest densities in shallow, warm and productive waters close to shores, such as the Tuscan shelf, western Sardinia, around the Balearic Islands and in the Gulf of Lion (particularly in the Rhône river plume). In winter, Cory's shearwater sightings were too scarce for habitat modelling. CVs were low, with higher values within the Tyrrhenian Sea (Appendix S5, Figure S5.2).

3.2.7. Storm petrels

The summer model resulted in 23.4% of explained deviance (Fig. 11). Selected covariates were mean SST (7d), SST_{grad} (7d), SSH_{SD} (7d) and mean SSH (28d). According to the contribution maps, mean SST and mean SSH were the most important covariates. The relationships indicated a preference for 22°C, medium SSH, low weekly thermal gradients and strong SSH_{SD}. The model predicted quite homogeneous distribution (Fig. 9C), the species

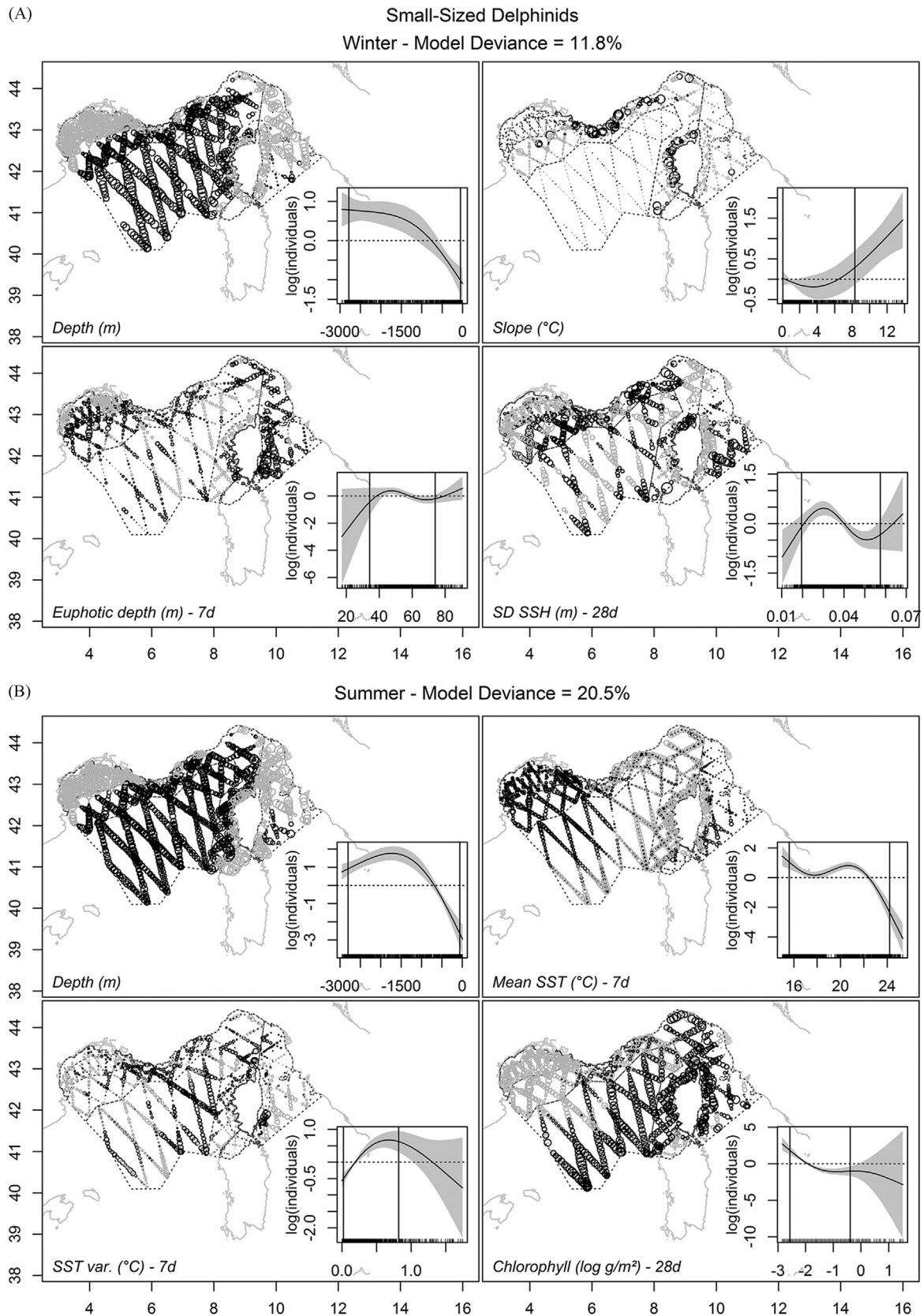


Fig. 3. Habitat model selected for small-sized delphinids A – in winter (explained deviance=11.8%), B – in summer (explained deviance=20.5%). Each panel spatially represents the contribution of the concerned covariate to the linear predictor for each sampled segment, with the dot size proportional to the covariate relative contribution regarding the three other covariates contributions in that point. Grey dots represent points with negative covariate contribution, black dots where it is positive. Corresponding GAMs curves are inserted in corresponding panels, representing the relationship between the covariate (abscissa) and the linear predictor (log(individuals) ordinate). The two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range must be avoided, since the smooth splines might not be reliable.

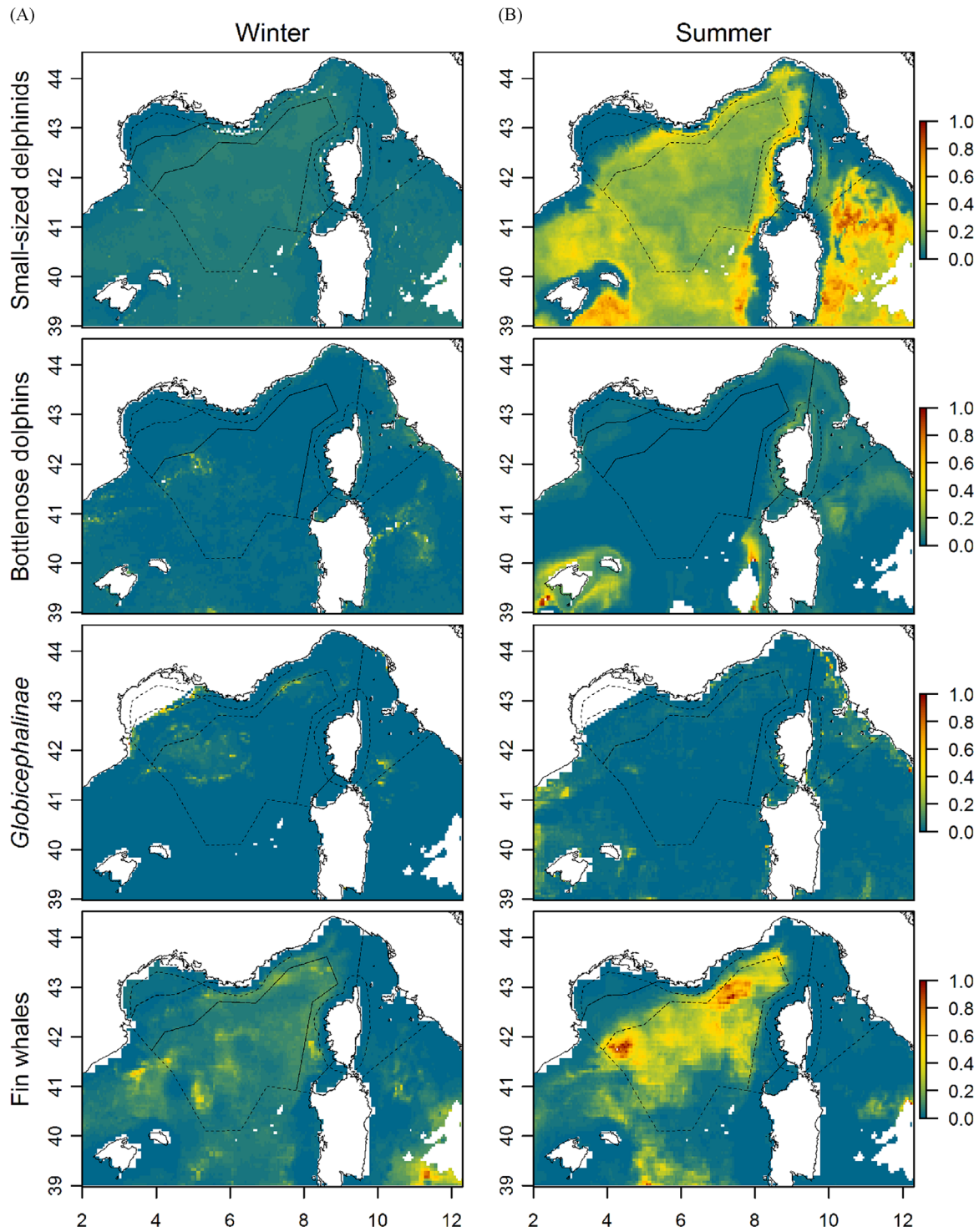


Fig. 4. Predicted distributions of cetaceans based on habitat models in winter (A) and summer (B). Distributions were scaled in relative densities: densities were divided by the maximum predicted density over the two seasons, for each group. As a consequence, scales are not comparable between groups. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1).

being predicted mostly over deep oceanic waters north of 40 °N up to the Gulf of Lion, and deep waters of the Ligurian Sea. High densities were also predicted in the southern Tyrrhenian Sea. As for Cory's shearwaters, in winter, storm petrels sightings were too scarce to permit habitat modelling, and no model was fitted. CVs were low and without clear pattern (Appendix S5, Figure S5.2).

4. Discussion

4.1. General

The present work analyses the summer and winter distribution and habitat used by marine mammals and seabirds in the NWMS, an area of major importance with regard to human activities at

Table 4

Summary of selected models for summer. Selected covariates for each group are indicated with the tick mark for physiographic variables, but with their temporal resolution (7 or 28 days) for oceanographic variables. All selected covariates were significant.

Summer	Small-sized delphinids	Bottlenose dolphins	<i>Globicephalinae</i>	Fin whales	Small-sized shearwaters	Cory's shearwaters	Storm petrels
Distance closest coast							
Distance closest colony						✓	
Depth	✓	✓		✓	✓	✓	
Slope							
Mean SST	7d	28d		7d		28d	7d
SST _{var}	7d		28d	28d	7d		
SST _{grad}					7d		7d
Chl	28d						
NPP			7d	28d		28d	
Euphotic depth			7d				
Mean SSH		28d			7d		28d
SSH _{SD}		28d	28d				7d
Explained deviance (%)	20.5	27.1	39.6	33.3	41.0	37.5	23.4

sea. Relative densities were modelled under GAMs by using a variety of physiographic and oceanographic variables of potential biological importance to the different taxa of interest. While fitting the models, variables that contributed the most to the heterogeneity of seabird and cetacean densities were identified in the selection process and provided some representation of the habitat preferences of each taxon. Major strengths of the two seasonal data sets include: (1) the synoptic view of two seasonal situations in a large marine area permitted by an airborne survey methodology; (2) the homogeneity of treatment, both during the sampling phase and the analytical phase, between seasons and taxa allowing ample comparisons; (3) the unprecedented amount of effort per unit surface area yielding large data sets; and (4) the simultaneous sampling of multiple target taxa of the marine megafauna that not only reduces relative costs of data sets but also allows more ecosystemic analyses and interpretations. The main weaknesses are mostly related to the downside of the survey strategy: (1) no specific protocol was implemented within this particular aerial survey to allow detection probability to be properly estimated; (2) identification at specific level from the air can be impaired for groups of species with similar colour, shape and size patterns such as small-sized delphinids, auks and several groups of larids; (3) the timing of the surveys relative to the dynamic of marine ecosystems makes it impossible to provide instant views of summer or winter cetacean and seabird distributions, instead the two seasonal data sets correspond to composite sampling over periods of 2–3 months of predominantly summer or winter conditions; and finally (4) the phenology of the different taxa cannot always match the timing of the surveys. The results have thus to be interpreted and discussed within these limitations.

So far, no similar synoptic and multitarget survey has been conducted in such a large area with a dual seasonal focus to the summer and winter seasons as well. However, many studies, although of taxonomically and spatially more limited scope, provided insights into the distribution and habitat preferences of cetacean and seabirds in the NWMS, but mostly during the summer season. These studies encompassed some dedicated shipborne surveys of cetaceans (Cañadas et al., 2002), observer programs from platforms of opportunity with yearly coverage as well as some telemetry studies on seabirds (mainly shearwaters; Péron and Grémillet, 2013). Only a few surveys included a seasonal component, but did not focus on such a large area (see for example Panigada et al., 2011). Therefore, in complement with these previous studies, our results provided the first assessment of habitat preferences driving the seasonal distributions of some poorly known species in the area, such as storm petrels, and provided

refined understanding of habitat preferences for some species such as bottlenose dolphins.

4.2. Ecological preferences

Small-sized delphinids: The small-sized delphinids oceanic distribution was driven by a clear preference for deep and oligotrophic waters in both seasons, and a preference for moderate to low monthly eddy dynamic and steep slope in winter. Those two last conditions were met along the Provençal coast and in the deep Ligurian Sea, where higher densities were predicted, and could match an optimum for prey habitat. In summer, their overall preferences for oligotrophic waters shifted towards areas with SST around 21°C, and moderate weekly variations in SST. Those optimum conditions were met in the Tyrrhenian Sea, along the lower slope of the western Sardinia/Corsica margin and the south Balearic Islands. These areas of high density were consistent with the habitats of the known forage species, such as blue whiting *Micromesistius poutassou* for example (Würtz and Marrale, 1993).

Small-sized delphinids were mostly composed of identified striped dolphins and unidentified small-sized delphinids (unidentified between striped or common dolphin: 23% of sightings in summer, 42% in winter), with only one identified common dolphin in summer. This composition of aerial survey data is consistent with previous knowledge in the NWMS (Bearzi et al., 2003). The clear oceanic pattern revealed in this study also concurs with the majority of unidentified sightings being of striped dolphins, since both the observed and predicted distribution patterns were well consistent with the known ecology of the species (Forcada and Hammond, 1998; Cañadas et al., 2002).

Bottlenose dolphins: Concerning bottlenose dolphins, the seasonality resulted in a complete inversion of habitat preferences from winter to summer. Seasonal changes in preferences might be linked to a compromise equilibrium set in favour of the optimisation of phenological constraints, with bottlenose dolphins moving inshore during summer for calving and growth of their young. Indeed, the bottlenose dolphin is a plastic species and can adapt to changing conditions, hence the species could easily sustain such a compromise.

Bottlenose dolphins showed the most contrasted predicted distribution between seasons among all studied cetaceans. Indeed, in winter, the species was overall oceanic, avoiding the northern NWMS, from the Gulf of Lion to the Ligurian Sea, and aggregated over the predictable and monthly frontal zones of the Balearic and Tyrrhenian Seas. Contrastingly, in summer, the species was more inshore, with a preference for warmer waters (22°C, as for small-sized delphinids) with calm hydrography. It was only around the Tuscan Archipelago, eastern Corsica and in the Ligurian Sea that

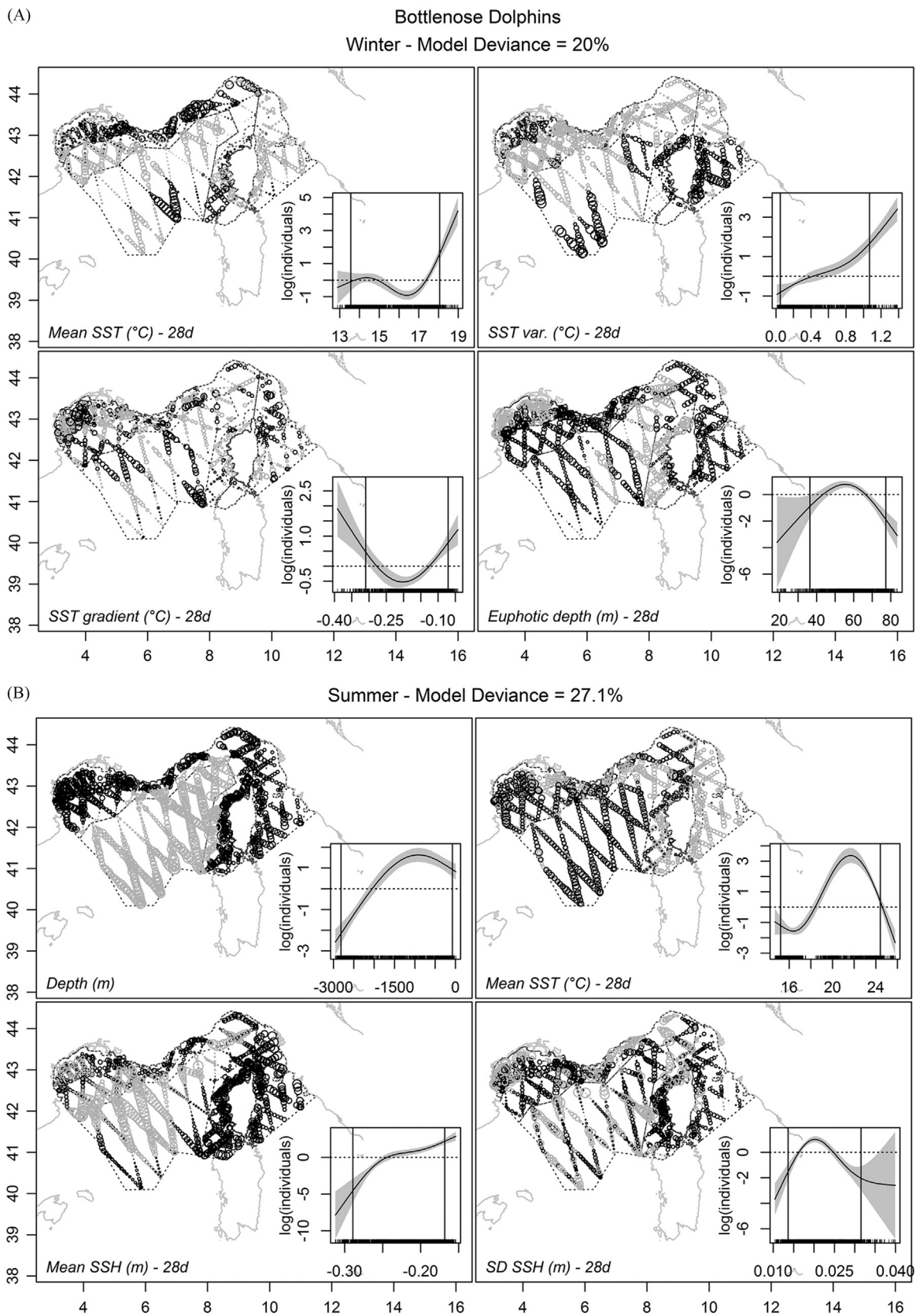


Fig. 5. Habitat model selected for bottlenose dolphins A - in winter (explained deviance=20%), B - in summer (explained deviance=27.1%). See Fig. 3 for figure explanation.

coastal waters were used throughout the year. This contrast in seasonal distribution has, to our knowledge, never been described in the NWMS, since the bottlenose dolphin is considered

inhabiting mainly continental shelves: previous studies reported bottlenose dolphins to be present only over the shelf, within the 200 m isobath (Cañadas et al., 2002; Gnone et al., 2011). In

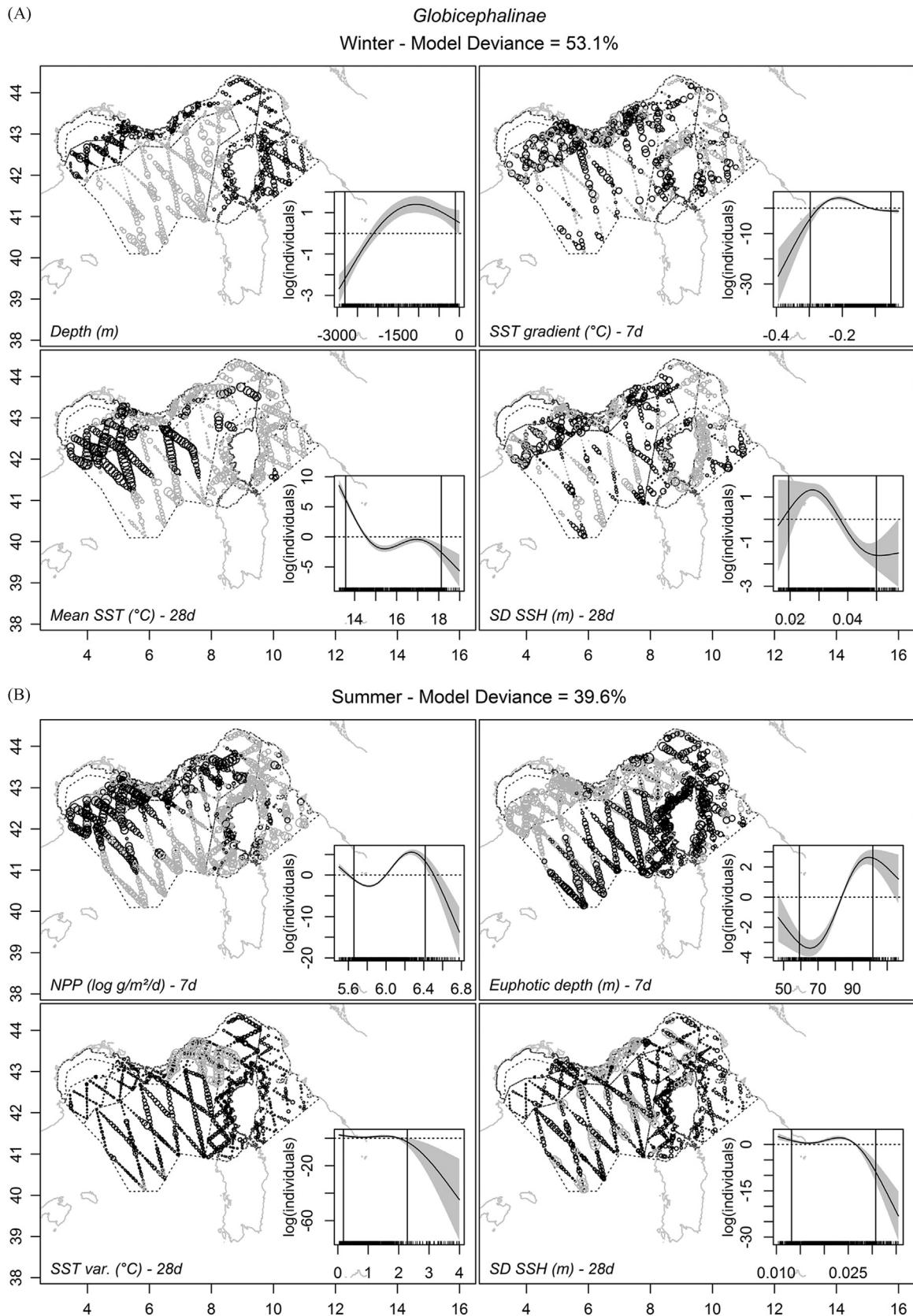


Fig. 6. Habitat model selected for *Globicephalinae* A - in winter (explained deviance=53.1%), B - in summer (explained deviance=39.6%). See Fig. 3 for figure explanation.

contrast, we showed here that, even in summer, bottlenose dolphins were also frequent in offshore waters up to 1000 m deep. To our knowledge, only one study suggested variations in abundance

between seasons within the shelf, around the Balearic Islands (Forcada et al., 2004). Considering our results, these variations of abundance might be due to movements between neritic and

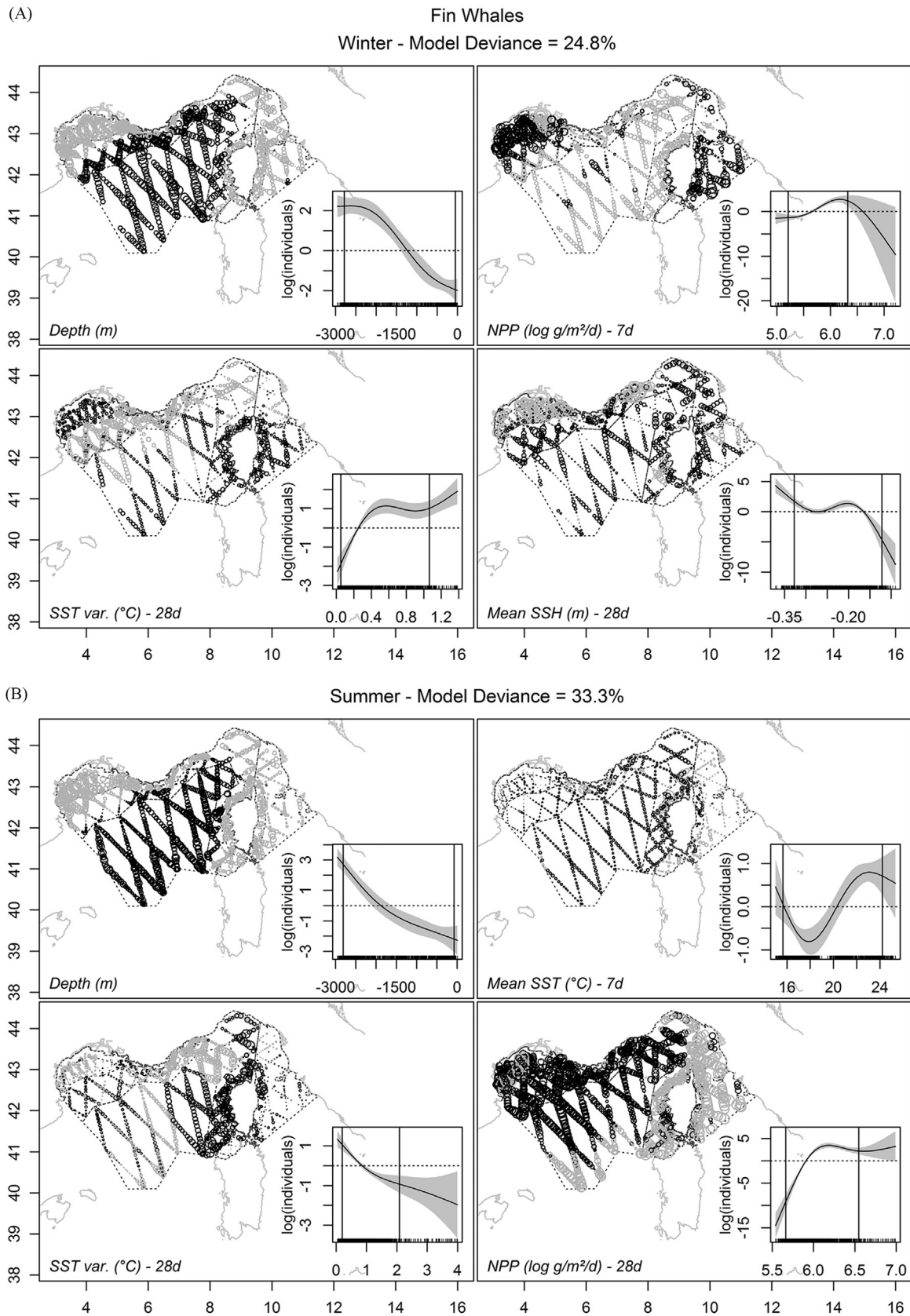


Fig. 7. Habitat model selected for fin whales A – in winter (explained deviance=24.8%), B – in summer (explained deviance=33.3%). See Fig. 3 for figure explanation.

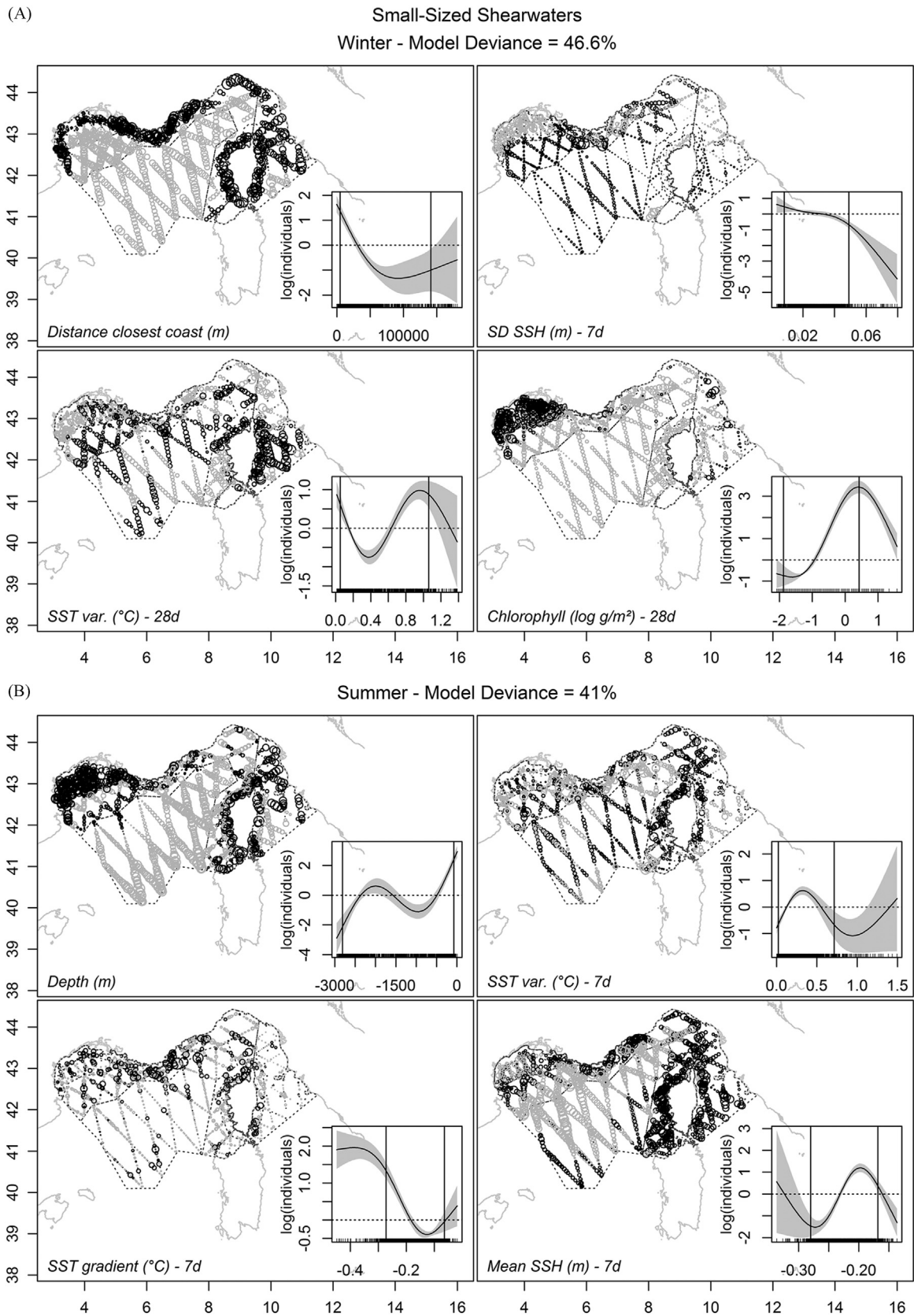


Fig. 8. Habitat model selected for small-sized shearwaters A – in winter (explained deviance = 46.6%), B – in summer (explained deviance = 41%). See Fig. 3 for figure explanation.

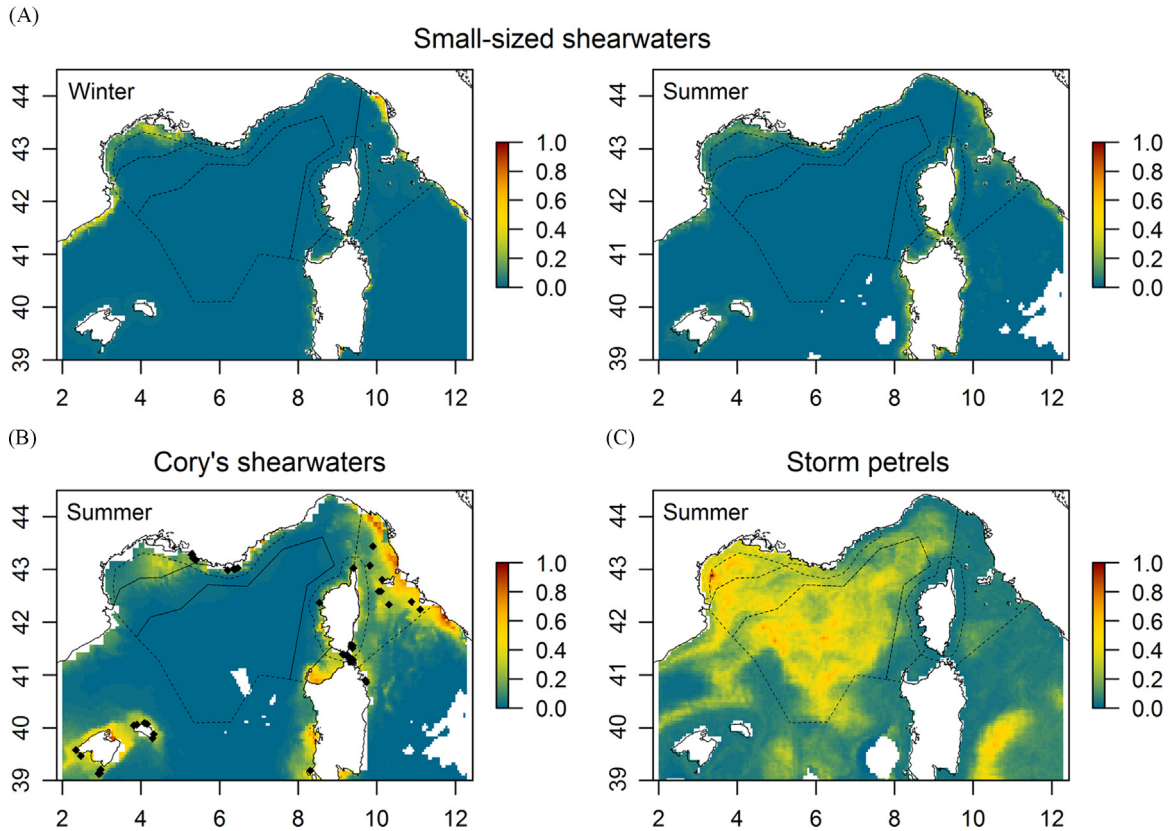


Fig. 9. Predicted distributions of seabirds based on habitat models, for small-sized shearwaters (A), Cory's shearwater (B) and storm petrels (C). Distributions were scaled in relative densities: densities were divided by the maximum predicted density over the two seasons, for each group. As a consequence, scales are not comparable between groups. Empty cells were due to the limitation of the prediction within the range of sampled covariates, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1). Black dots on Cory's Shearwaters prediction (B) are colonies locations.

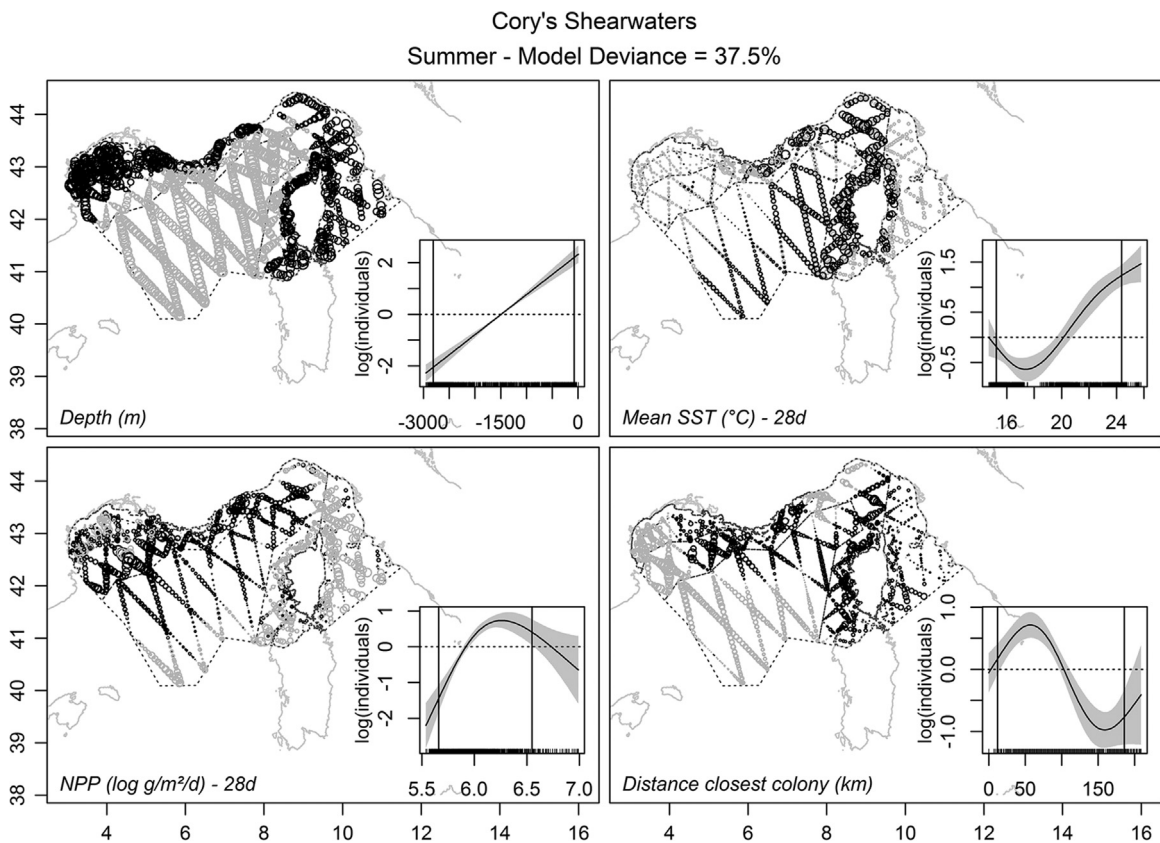


Fig. 10. Habitat model selected for Cory's shearwaters in summer (explained deviance=37.5%). See Fig. 3 for figure explanation.

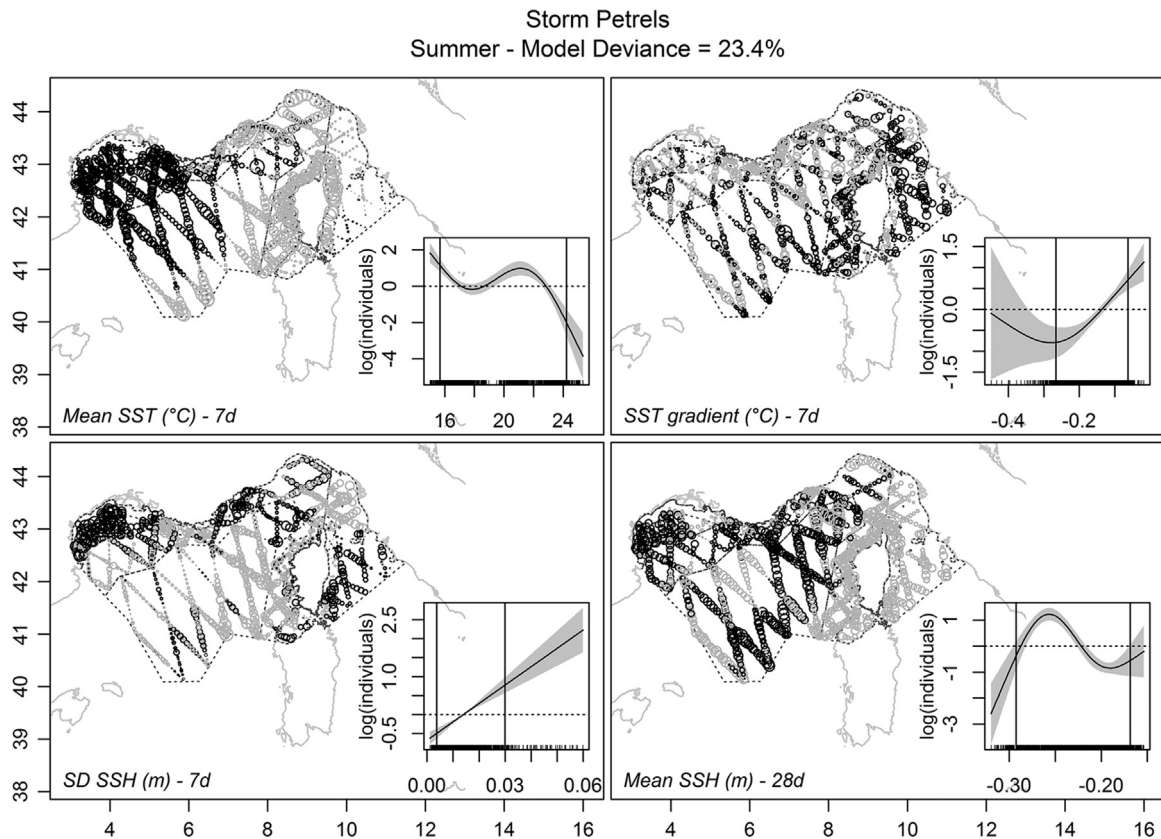


Fig. 11. Habitat model selected for storm petrels in summer (explained deviance=23.4%). See Fig. 3 for figure explanation.

oceanic waters. Interestingly, although habitat preferences were contrasted between winter and summer, bottlenose dolphins were always related to monthly covariates, indicating a preference for more persistent patterns.

The observed shift in habitat use may be due to different reasons, such as a shift in main prey, a seasonal migration of prey, or phenological constraints. The calving period for this species occurs during summer (between July and August), and it is thought that females favour shallower waters during this period, for shelter against open-ocean agitation or predation (Blanco et al., 2001). Moreover, they could find prey without having to perform long dives, thus calves could easily learn to forage (Blanco et al., 2001). According to stranding data (mostly spring and summer strandings; Blanco et al., 2001), bottlenose dolphins in the NWMS would mainly forage on demersal and benthic prey (mainly hake), with occurrence of epipelagic species (pilchard and anchovy, possibly due to indirect ingestion, given that these species are fed on by hake). The authors hypothesised that the highlighted differences in diet according to sex and age might be due to lactation or calf care. Given that the selected model for summer corresponded to warm, shallow and calm waters, during summer, a significant fraction of bottlenose dolphin populations would dwell in coastal waters for calving and thus forage on demersal and benthic prey, whereas in winter, when calves are older, they would switch towards deep oceanic waters where they would have to forage on different species.

Globicephalinae: Most studies exploring long-finned pilot whales and Risso's dolphins habitat preferences in the NWMS used physiographic covariates, including depth, slope and distance to the shore or to the 200 m isobath, as well as oceanographic variables such as SST, always in summer (Cañadas et al., 2002; Praca and Gannier, 2008). However, our results showed that the taxon was more related to dynamic processes enhancing

productivity in both seasons. In winter, they showed a preference for the frontal zone in the Ligurian Sea and the deep convection area off the Gulf of Lion (Auger, 2011), both variables being involved in the enrichment of the surface layer in nutrients. In summer, these species showed a preference for productive and dynamic waters occurring from the Balearic to the Ligurian Sea associated to the Liguro-Provençal Current, as well as for productive waters around the Tuscan Archipelago.

Fin whales: Fin whales, unlike bottlenose dolphins and *Globicephalinae*, proved to be similarly distributed between the two seasons, albeit at a lower density in winter. In the NWMS, in summer, fin whales are known to forage mostly on *Meganyctiphanes norvegica*, which has a patchy distribution with the main concentration found in the Liguro-Provençal Front (Astruc et al., 2005). Parameters selected for the summer model were precisely related to the anticlockwise gyre of the Liguro-Provençal Current, hence fin whales were predicted to be the most abundant in this area. Our model therefore seemed to relate fin whales directly to habitats where krill concentrations are the most predictable. Moreover, summer habitat preferences were consistent with previous studies in the same season, showing that fin whales preferred waters with a SST around 23°C (Laran and Gannier, 2008; Panigada et al., 2008) and depth around 2500 m. Beside this, during periods of low productivity, fin whales were shown to respond to weekly environmental processes (Littaye et al., 2004), while during periods of high productivity they responded to monthly processes (spring bloom). Our results were consistent with this, since the summer best model related fin whales to 28 days NPP, while the winter model related them to 7 days NPP.

In winter, information concerning habitat preferences of fin whales is scarce, but it is admitted that the population would migrate to other Mediterranean subregions, such as the central Mediterranean Sea. Fin whales may perform a migration from the

PELAGOS sanctuary to around Lampedusa Island, through the Messina Strait (Aïssi et al., 2008). Other studies have shown that some animals fitted with Argos tags moved to the Alboran Sea and the Gibraltar Strait (Cotté et al., 2009). These movements might explain the lower predicted densities in winter. Some studies demonstrated a shift in foraging strategies potentially linked to variations in resource availability between regions, as was the case for fin whales around Lampedusa Island foraging on *Nyctiphanes couchii* rather than *Meganyctiphanes norvegica* (Canese et al., 2006). However, in the NWMS, we could reasonably suggest that wintering fin whales remaining in the area still forage on krill during winter since they exhibit the same habitat preferences as in summer.

Small-sized shearwaters: Habitat models clearly indicated that small-sized shearwaters exhibited no seasonal variations of their preferences for coastal waters. In winter, they showed a clear preference for inshore rich waters (high Chl) averaged at a monthly scale. They were concentrated north of the study area, mostly in the Gulf of Lion, and Catalanian Tuscan coasts. In summer, their distribution was similar, but higher densities were predicted around Sardinia, the Balearic Islands and the Tuscan Archipelago. Interestingly, this pattern reproduced well the distribution of known colonies for Yelkouan and Balearic shearwaters, although distance to the closest colony was not selected in the best model; this suggests that colonies would be established close to recurrently favourable habitats. Indeed, our results indicated that during summer, individuals relied on predictable weekly frontal zones over the plateau. Yelkouan and Balearic shearwaters therefore seemed to select similar coastal habitats throughout the year, although the drivers were a bit different.

This summer distribution was consistent with known foraging habitats of these two species. Yelkouan shearwaters breeding on the Provençal coast islands are known to perform most of their foraging trips to the Gulf of Lion with some flights up to Cape Creus (Péron et al., 2013; Péron and Grémillet, 2014). The Catalanian coast, around Cape Creus, was identified as an important foraging ground for Balearic shearwaters breeding in Balearic colonies (Louzao et al., 2011), but the Gulf of Lion was recently shown to be regularly used by Balearic shearwaters in spring (Meier et al., 2015). When comparing results from telemetry (Péron et al., 2013; Péron and Grémillet, 2014) and predictions from habitat models presented in this study, it seems surprising that our model does not predict the high densities of individuals close to the Provençal colonies. However, individuals sighted around those colonies were very coastal, and predictors used for this study did not provide any information for very coastal cells, depending on their resolutions. Therefore, no prediction was available in those areas.

Cory's shearwaters: The summer Cory's shearwater predicted distribution was quite similar to that of small-sized shearwaters. However, the environmental parameters driving this distribution were different. The selected model indicated that Cory's shearwater preferred monthly averaged warm productive waters close to their colonies, where they could find reliable and easily accessible resources during the breeding period. A tracking study of Cory's shearwaters tagged during aerial survey periods provided consistent results (Péron and Grémillet, 2014): individuals breeding in the colonies of the Provençal coast performed foraging trips in the Gulf of Lion and on the Catalanian coast (Cape Creus), while individuals tagged in northern Corsica used the south Ligurian Sea, close to the Tuscan Archipelago, and individuals tagged in southern Corsica moved across the whole Bonifacio Strait. The absence of Cory's shearwaters from the area in winter has recently been confirmed by telemetry study (Péron and Grémillet, 2013), revealing migration from the Mediterranean Sea to western Africa in autumn for all adults, juveniles and immature individuals.

Storm petrels: Storm petrels showed a predicted distribution almost opposite to that of shearwaters. Indeed, the species was predicted across all oceanic waters from the Balearic to Ligurian Seas, as well as in the Gulf of Lion, as an answer to their preference for stable waters with negative SSH and reduced surface temperature. This oceanic distribution was fairly similar to that of the fin whale, which might be linked to a partially overlapping diet between both taxa, since storm petrels are known to forage over plankton, although with a wider spectrum than whales. They forage over microzooplankton and ichthyoplankton from oceanic to coastal waters, but also over small fishes, squids, whale carcasses and offals (del Hoyo et al., 2010).

4.3. Accommodating seasonal variations

Small-sized shearwaters, *Globicephalinae*, small-sized delphinids and fin whales were characterised by the consistency of their habitat preferences from winter to summer. The small-sized shearwaters answered the seasonality of their environment by targeting areas exhibiting reduced seasonality: the coastal year-round productive habitats. Doing so, they exploited a habitat ensuring the satisfaction of their needs throughout the year, during the non-reproductive period as well as during the high-cost breeding and chick-rearing periods. The overall seasonality of the NWMS seemed to have no impact on the *Globicephalinae* habitat preference, the species being able to switch between habitats with enhanced productivity from season to season. This might be explained by the reduced energetic needs of the species linked to their deep-diving capacities, allowing them to target layers little concerned by surface seasonality. For the last two groups, habitat preferences did not vary between seasons, but a part of the population seemed constrained to migrate out of the area during the unfavourable season; e.g. fin whales and small-sized delphinids had lower abundance in winter compared to summer (see Laran et al., this issue), but their habitat preferences remained similar in both seasons. Around the Channel Islands, California, whales were also found to have consistent preferences across seasons (Croll et al., 1998): the authors demonstrated that whales exploited highly predictable patches of euphausiids that aggregate above topographic breaks when upwelling is more active, these processes being sufficiently consistent across seasons and years to correctly predict the distribution of whales. Although at a finer scale, fin whales in the NWMS showed the same pattern of foraging consistency between seasons, if not years, at least for the part of the population remaining in the area throughout the year. For these two groups, then, the habitat remained favourable throughout the year but a part of the population seems to move out of the NWMS for some unknown reasons.

In contrast to the above groups, species characterised by high plasticity seemed to have the possibility to switch between the most favourable habitats between seasons rather than accommodating the same habitat all year round. For migrating seabirds, this variation was extreme: although the NWMS seemed a good reproductive ground for Cory's shearwaters and storm petrels, once the central-place foraging constraint was released, the two species migrated out of the Mediterranean Sea (Péron and Grémillet, 2013). This migration could indicate that the area might not, during winter, represent an optimal foraging ground, and once reproductive constraints are released, they leave the NWMS for better places. Finally, bottlenose dolphins exhibited the widest shift in habitat preferences among the cetaceans studied here, using coastal habitats during the calving period then moving to oceanic waters when calves could follow the adults. This is a good example of the well-known foraging plasticity of the species.

5. Conclusion

In the present work, our goal was to test whether the seasonality of the environment induces a modification in ecological processes underlying seasonal changes in the distribution of species, and we provided insights on which mechanisms drive the spatial distribution of species in each season.

The knowledge of habitat preferences for the studied species in the NWMS were scarce, and mostly relied on physiographic parameters such as depth or slope, plus some dynamic parameters such as SST, but always at low temporal resolution. Here, we incorporated all predictors potentially involved in the processes underlying distributions for these species. The use of two temporal resolutions (7 and 28 days) allowed consideration of the temporal lags between oceanographic processes and predator responses. Therefore, our study provided a first insight into habitat preferences of several taxa, and for all taxa the first description of their winter preferences in the NWMS.

Our goal was to test whether the seasonality of the environment induces a modification in ecological processes underlying seasonal changes in species distribution, and we showed that both ecological processes driving distributions and top predator relationships with these processes vary through seasons. The highlighting of this seasonal variation of habitat preferences implies some important advice for habitat modelling: our results clearly demonstrated that we must not try to extrapolate habitat preferences and distributions based on one season to another. That is, we should not use a summer model to predict a winter distribution or vice-versa. Indeed, the first assumption of extrapolation is that processes are stationary and are similar, in their distribution and importance for species, in the forecast region and forecast time (Elith and Leathwick, 2009), which in the present study was clearly demonstrated as wrong concerning season.

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Appendix A. Supplementary data

Supplementary data associated with this paper can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.06.012>.

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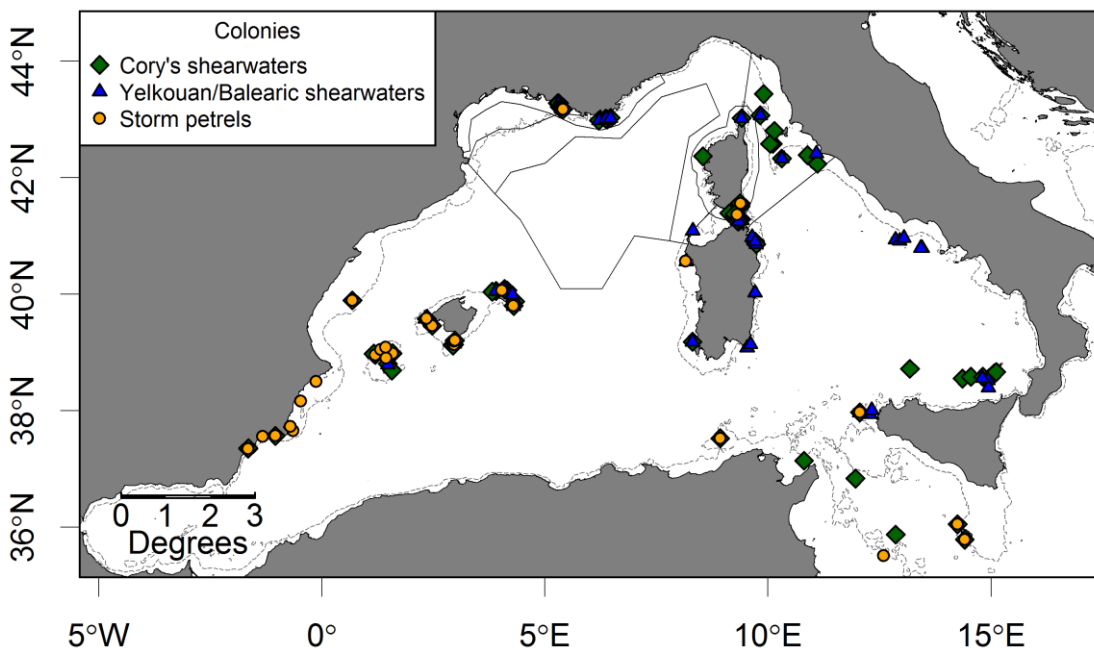
Appendix S1

Colonies Locations

Colonies locations for studied seabird species in north-western Mediterranean Sea have been compiled from several authors in France, Italy and Spain (Figure 2). In France, Yelkouan Shearwaters breed in Proquerolles Islands, Port-Cros, Frioul and Riou archipelagos and in Giraglia, Corsica (Bourgeois, 2012; Cadiou et al., 2005). The species may also present in Baleares, in sympatry with Balearic Shearwaters, in Cabrera and Menorca Islands (Martin et al., 2000). In Italy, the species breeds in Sardinia, Tuscany, Ponziane, Egadie and Aeolian archipelagos (Bourgeois, 2012). Balearic Shearwaters breed in all islands of Balearic archipelago, from Menorca to Cabrera and Pitiüses (Catchot, 1992; Genovart et al., 2007).

Cory's Shearwater colonies are present all around Mediterranean Sea. In France, the species is present Porquerolles Islands, Port-Cros, Frioul and Riou archipelagos and on several islands around Corsica (Cadiou et al., 2005). In Spain, Cory's Shearwaters breed in Baleares and on several islands along Iberian coast (Aguilar, 1992; Catchot, 1992; Martin et al., 2000). Colonies are also found in Sardinia, Sicily and in Egadi, Pelagie, Aeolian and Tuscany archipelagos for Italy, in La Galite and Zembra Islands in Tunisia, and in Filfla and Gozo Islands in Malta (Anselme and Durand, 2012; Martin et al., 2000; Sultana et al., 2012).

In France, European Storm Petrels only breed in Riou Islands and Bonifacio Strait (Cadiou et al., 2005). Several colonies are present in Baleares archipelago, in Cabrera, Mallorca, Menorca and Ibiza (Aguilar, 1992; Amengual et al., 1999; Catchot, 1992; Martin et al., 2000). Other colonies are found in Iberian coast, from Murcia to Andalusia (Debize and Mante, 2012; Sultana et al., 2012), on Filfla and Gozo in Malta, on Lampedusa and Marettimo Islands and Sardinia in Italy, on La Galite in Tunisia (LoValvo and Massa, 2000; Sultana et al., 2012).



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Appendix S2

Distance sampling analysis

1. Method

Distance sampling was conducted on cetacean sightings to investigate the effect of distance and sighting conditions on the detection probability, and estimate the half-effective strip width (ESW). This estimation of ESW was performed by fitting detection functions to the perpendicular distances (extracted from the declination angle measured during sightings).

The analysis was carried out using DISTANCE 6.0 (Thomas *et al.*, 2010) on transects flown with good sightings conditions: Beaufort sea state ≤ 3 for all species, except for fin whales for which Beaufort sea-state of 4 was also considered. The 5-10% sightings detected at the longest distances were removed from the datasets prior to analysis (Buckland *et al.*, 2001). Different stratification were tested has potentially affecting the detection function: school size, season, sea-state, turbidity, glare severity, subjective conditions on both side of the plane and cloud.

2. Results

Beaufort sea-state significantly affected the detection function of small-sized delphinids, with ESW varying from 234 m for best conditions to 165 m for worse sea-states (Table S2). Concerning bottlenose dolphin, the detection function was affected by cloud coverage, with an ESW of 192 m for coverage from 0 to 4, and 144 m for coverage above 5. However, for *Globicephalinae* and fin whales no detection covariates affected the detection function, and their ESW were 252 m and 400 m, respectively.

3. References

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- L. Thomas, S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques & K.P. Burnham (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47(1), 5-14.

Table S2. Results of Distance Sampling analysis.

Selection for analysis	Cetacean groups	Stratification	Detection covariate	ESW (m)	Histograms of perpendicular distances and fitted detection functions	
	Small-Sized Delphinids	Half-normal (in black)	Beaufort sea-state	0, 1	234	
		Half-normal (in grey)		2, 3	165	
Beaufort sea-state ≤ 3 , Subjective Conditions > 3	Bottlenose Dolphins	Half-normal (in black)	Cloud cover	0 to 4	192	
		Half-normal (in grey)		5 to 8	144	
	<i>Globicephalinae</i>	Half-normal	-		252	
Beaufort sea-state ≤ 4 , Subjective Conditions > 2	Fin Whales	Half-normal	-		400	

Table S3.1

Correlation matrix, based on the Spearman correlation test. Correlations for winter variables are presented above the diagonal (in blue), while correlations for summer are presented below the diagonal (in orange). Correlation higher than |0.7| are in bold.

		7d										28d								
		Distance closest coast	Depth	Slope	Mean SST	SST var.	SST gradient	Chl. a	NPP	Euphotic depth	Mean SSH	SD SSH	Mean SST	SST var.	SST gradient	Chl.	NPP	Euphotic depth	Mean SSH	SD SSH
7d	Distance closest coast	1	-0,72	-0,20	-0,10	-0,05	0,19	-0,27	-0,26	0,26	-0,32	-0,42	-0,12	-0,09	0,12	-0,33	-0,42	0,31	-0,38	-0,26
	Depth	-0,77	1	-0,18	-0,07	0,04	-0,21	0,60	0,65	-0,60	0,20	0,51	-0,07	0,07	-0,18	0,64	0,74	-0,63	0,32	0,50
	Slope	-0,34	0,02	1	0,20	-0,05	0,11	-0,40	-0,38	0,39	0,14	-0,14	0,20	-0,10	0,13	-0,33	-0,30	0,34	0,09	-0,31
	Mean SST	0,05	-0,22	0,11	1	0,20	-0,16	-0,48	-0,36	0,49	0,81	-0,39	0,98	0,04	-0,12	-0,55	-0,34	0,59	0,78	-0,47
	SST var.	0,04	-0,20	0,07	0,30	1	-0,43	0,01	-0,08	-0,01	0,27	-0,02	0,25	0,29	-0,35	-0,13	-0,12	0,16	0,19	-0,08
	SST gradient	0,18	-0,19	0,01	-0,24	-0,28	1	-0,12	-0,14	0,12	-0,24	-0,05	-0,18	-0,21	0,77	-0,11	-0,16	0,09	-0,22	-0,03
	Chlorophyll	0,09	0,30	-0,32	-0,58	-0,12	-0,14	1	0,85	-0,99	-0,20	0,51	-0,46	0,22	-0,12	0,82	0,76	-0,82	-0,05	0,64
	NPP	0,15	0,10	-0,21	0,05	0,11	-0,31	0,64	1	-0,84	-0,13	0,39	-0,37	0,08	-0,17	0,79	0,87	-0,79	0,02	0,54
	Euphotic depth	-0,09	-0,29	0,32	0,58	0,13	0,14	-1,00	-0,63	1	0,21	-0,51	0,47	-0,21	0,12	-0,81	-0,75	0,82	0,06	-0,64
	Mean SSH	-0,54	0,35	0,33	-0,06	-0,28	0,18	-0,43	-0,52	0,43	1	-0,11	0,84	0,25	-0,13	-0,32	-0,12	0,35	0,91	-0,38
	SD SSH	-0,14	0,33	-0,15	-0,55	-0,40	0,02	0,41	0,06	-0,41	0,13	1	-0,35	0,11	0,00	0,49	0,36	-0,50	-0,08	0,45
	Mean SST	0,07	-0,22	0,11	0,98	0,27	-0,20	-0,60	0,03	0,60	-0,04	-0,54	1	0,18	-0,10	-0,58	-0,37	0,62	0,79	-0,48
	SST var.	0,07	-0,02	-0,15	-0,04	0,11	-0,23	0,27	0,16	-0,27	-0,33	0,21	-0,16	1	-0,16	-0,05	-0,01	0,07	0,23	0,02
	SST gradient	0,48	-0,44	-0,09	-0,25	-0,17	0,71	-0,07	-0,26	0,07	-0,03	-0,02	-0,22	-0,09	1	-0,15	-0,19	0,13	-0,13	-0,07
28d	Chlorophyll	-0,08	0,37	-0,22	-0,66	-0,14	-0,10	0,88	0,50	-0,88	-0,26	0,43	-0,68	0,30	-0,06	1	0,90	-0,99	-0,14	0,65
	NPP	0,10	0,15	-0,21	-0,10	0,03	-0,29	0,71	0,88	-0,71	-0,48	0,15	-0,13	0,24	-0,25	0,69	1	-0,88	0,05	0,58
	Euphotic depth	0,06	-0,35	0,24	0,64	0,13	0,11	-0,89	-0,52	0,89	0,29	-0,42	0,67	-0,29	0,06	-0,99	-0,71	1	0,18	-0,65
	Mean SSH	-0,56	0,38	0,28	-0,25	-0,19	0,21	-0,33	-0,55	0,32	0,91	0,12	-0,23	-0,32	0,04	-0,13	-0,49	0,16	1	-0,13
	SD SSH	-0,16	0,13	-0,12	-0,23	-0,04	-0,09	0,20	0,07	-0,20	0,00	0,29	-0,26	0,12	-0,11	0,25	0,14	-0,25	0,03	1

Appendix S4

Cetacean and seabird sightings

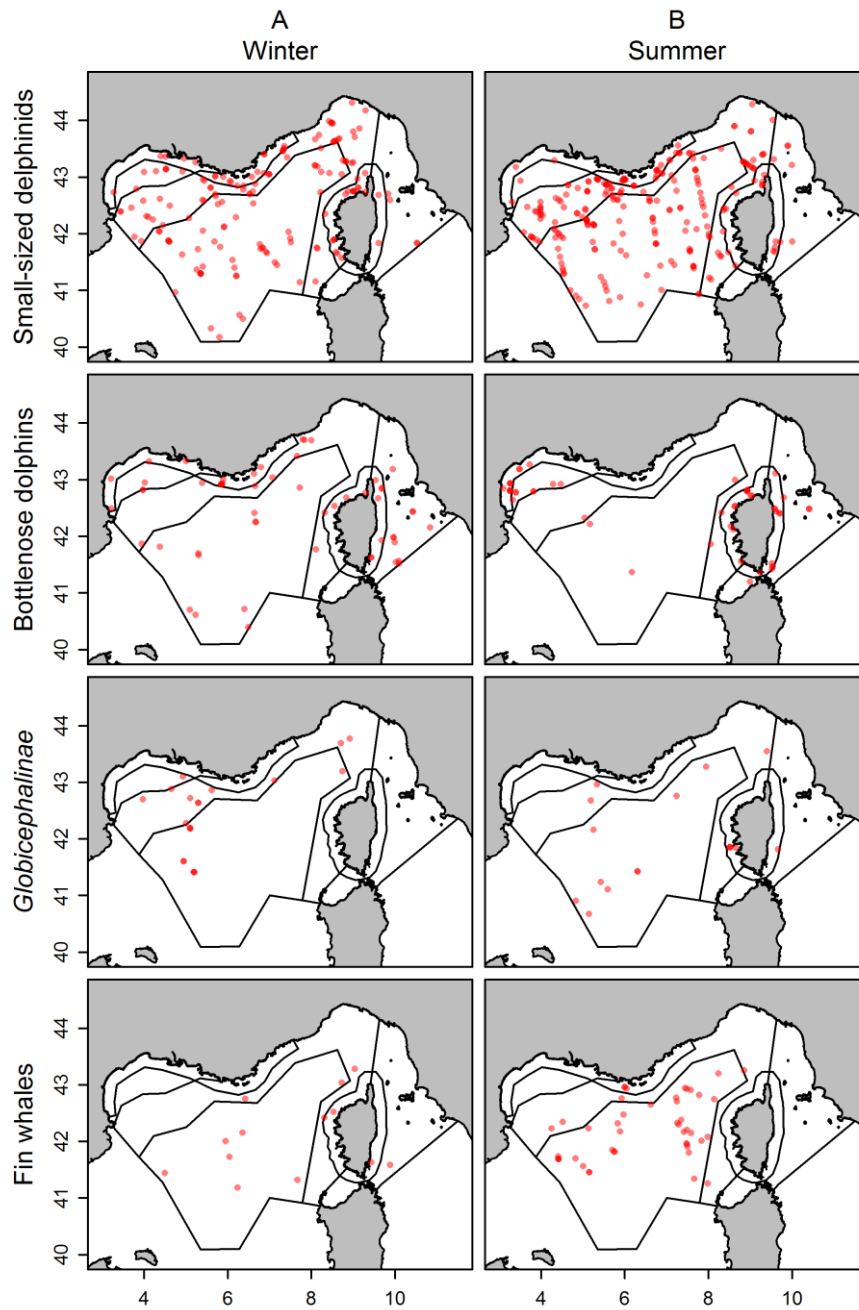


Figure S4.1 – The winter and summer cetacean sightings within northwestern Mediterranean Sea.

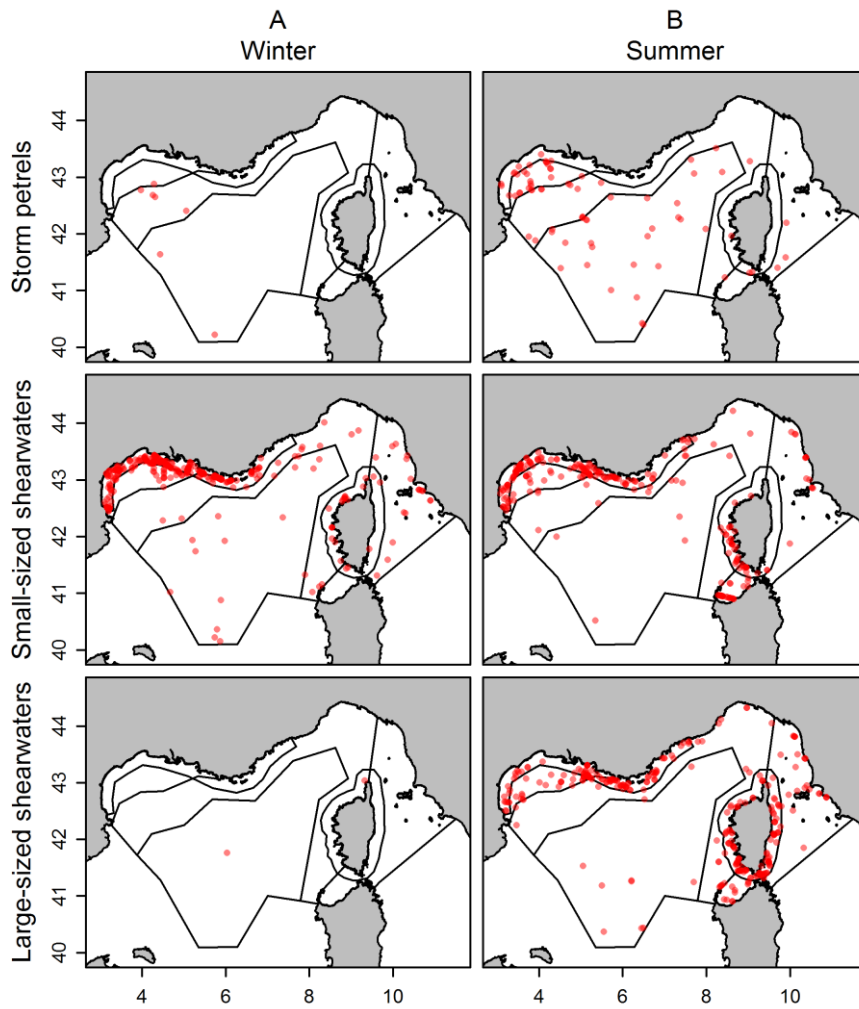


Figure S4.2 – The winter and summer seabird sightings within northwestern Mediterranean Sea.

Appendix S5

Coefficient of variations for cetacean and seabird predicted distributions

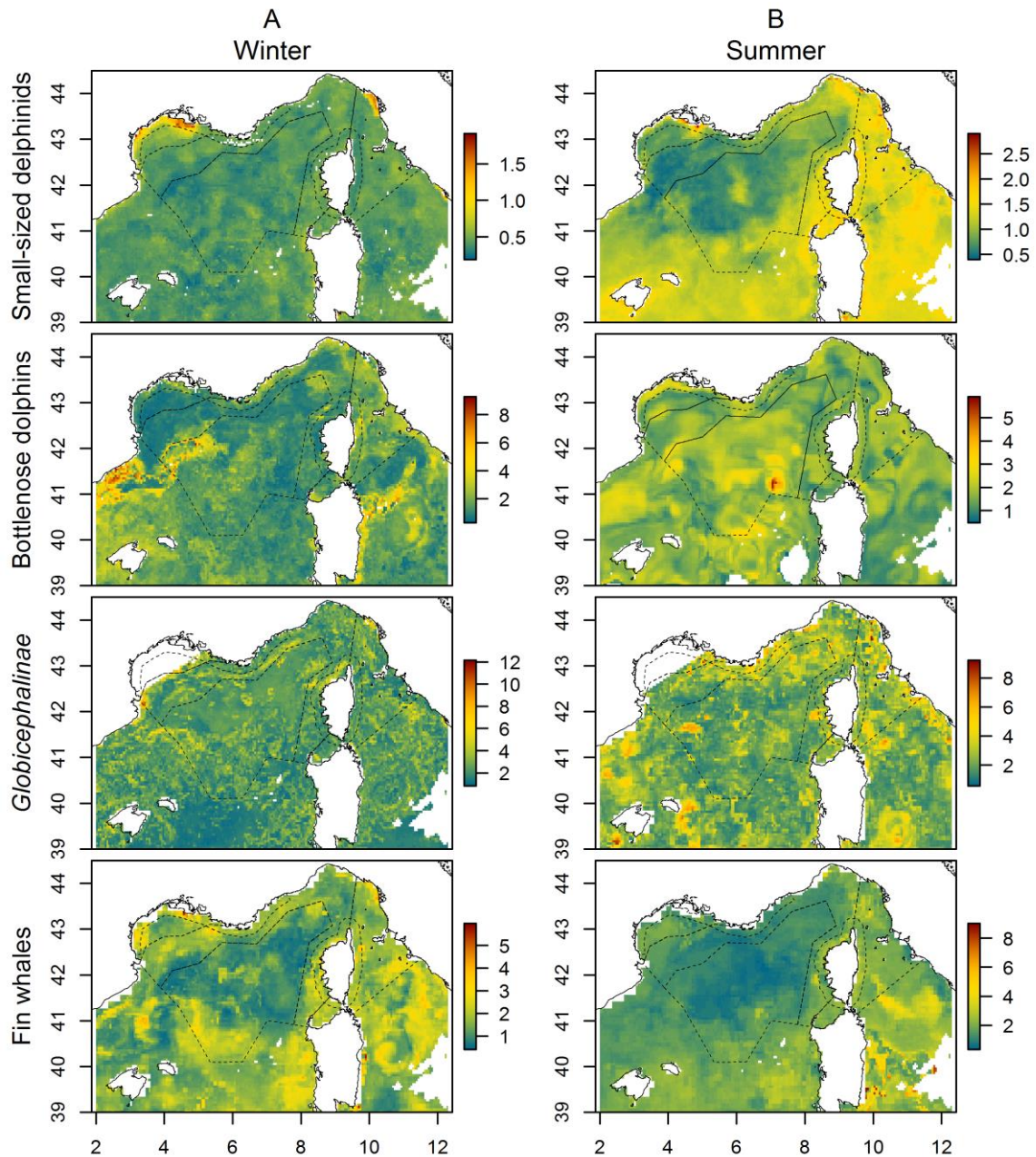


Figure S5.1 – Coefficient of variations around mean predictions of cetaceans based on habitat models in winter (A) and summer (B). Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

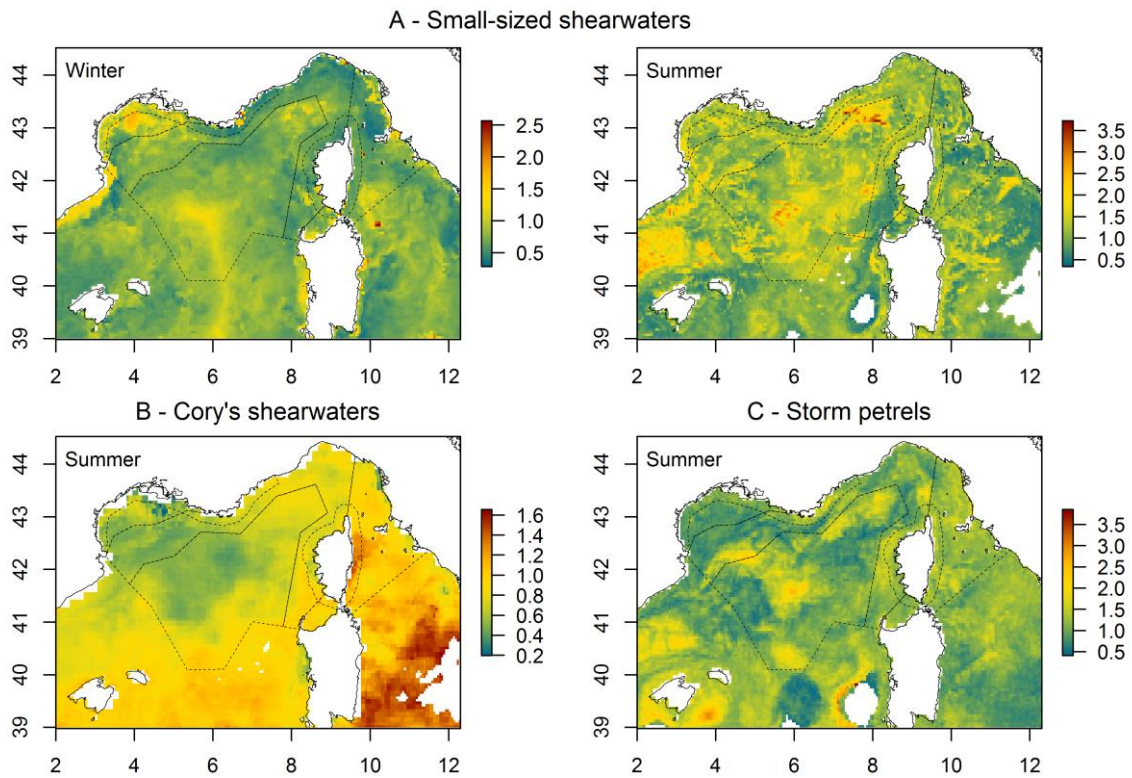


Figure S5.2 – Coefficient of variations around mean predictions of seabirds based on habitat models in winter (A) and summer (B). Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

Appendix **C**

Chapter 3 - How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: the eastern North-Atlantic

Supporting information to Chapter 3: in press paper.

Contents lists available at [ScienceDirect](http://www.sciencedirect.com)

Deep-Sea Research II

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Regular article

How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: The eastern North-Atlantic

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ABSTRACT

Marine ecosystems are characterised by strong heterogeneity and variability, both spatially and temporally. In particular, seasonal variations may lead to severe constraints for predators which have to cope with these variations, for example through migration to avoid unfavourable seasons, or adaptation to local modification of the ecosystem. In the Bay of Biscay and English Channel, ecosystem seasonality is well marked, especially over the shelf. Cetacean and seabird communities within the Bay of Biscay, Celtic Sea and English Channel were studied during aerial surveys conducted in winter 2011–2012 and summer 2012, following a strip-transect methodology deployed from the coast to oceanic waters. We explored seasonal variations of habitat preferences of four cetacean and six seabird groups through Generalised Additive Models, using physiographic variables and weekly- and monthly-averaged oceanographic predictors for both seasons. Our results provided the first overview at such a large scale of the variation of habitat preferences in response to the seasonality of the ocean by seabirds in that region, at such a large scale. Habitat models resulted in explained deviances from 13 to 55%. Predators answered the seasonality of their environment in different ways. Long-finned pilot whales and Risso's dolphins were the only studied group exhibiting no habitat variations between seasons, targeting the shelf break throughout the year. The other groups modulated their habitat preferences between seasons to optimise the compromise between the ocean seasonal variations and their own constraints: common and striped dolphins, bottlenose dolphins and harbour porpoises for cetaceans; northern gannets, auks, northern fulmars and kittiwakes for seabirds. For shearwaters, the seasonality had an extreme impact, inducing a complete absence from the region during the unfavourable season.

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1. Introduction

Marine ecosystems are characterised by strong spatio-temporal heterogeneity (Barry and Dayton, 1953), with a wide panel of ecological conditions subject to temporal fluctuations, at scales from hours to season, and years to decades. Seasonality is one of the major contributors to temporal variability, operating at an intermediate temporal scale (within year), from fine to large spatial scales, with effects strongly predictable from year to year. Temperate ecosystems typically show two blooms of phytoplankton production, the most important one in spring and a smaller one in autumn. Indeed, winter mixing of the water column induces nutrient enrichment in the euphotic layer, which allows

rapid growth of phytoplankton when incident light and water temperature increase in spring (Sverdrup, 1953).

Phytoplankton development in turn leads to nutrient depletion in the upper layer, and consequently a decrease in phytoplankton production as stratification of the water column impairs nutrient renewal in the summer. Later recycling of organic matter partly restores nutrient concentration and allows a second yet smaller peak of primary production in autumn. Despite this highly predictable cycle, the location and intensity of the main seasonal processes can vary between years according to decadal fluctuations or longer-term trends (*i.e.* climate change) as well as year-to-year variations in nutrient input of continental origin by river plumes (Pingree and Garcia-Soto, 2014).

Marine mammals and seabirds living at temperate latitudes have evolved in this highly seasonal environment that has shaped their life traits and migration patterns according to the main recurrent large-scale features in physical and biological characteristics of the ocean.

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Top predators have to cope with the seasonal heterogeneity by adaptive behavioural responses largely dependent on their sensory and communication skills, possibly enriched by the memory of previous experiences as well as by social and cultural traits (Simmonds, 2006). Hence, one could expect top predators to perceive the repetition of the seasonal cycle (Simmonds, 2006), and modulate their habitat preferences accordingly.

Within the eastern North-Atlantic (ENA), the Bay of Biscay (BoB), the Celtic Sea (CS) and the English Channel (EC) show particularly well-marked seasonality (Pingree and Garcia-Soto, 2014). The structure of the water column in summer is complex due to the strong interactions between tide currents, winds and thermal stratification, the two former locally preventing the latter, especially along the coasts. River inputs add to this complexity with several river plumes (Vilaine, Loire, Gironde and Adour estuaries within the BoB) associated with nutrient input and haline stratification.

The ENA is characterised by an important and diversified community of cetaceans and seabirds, most of them characterised by high mobility (Hammond et al., 2002, 2013; del Hoyo et al., 2010). Many studies, most often with a taxonomically limited scope, have provided insights into the distributions of several species in the area, mainly in summer. They included dedicated shipborne or airborne summer surveys for cetaceans (Hammond et al., 2002, 2013), cetacean and seabird observer programmes on recurrent oceanographic cruises at certain times of the year (Certain et al., 2008, 2011) or from platforms of opportunity with yearly coverage (Castéje and Hémerly, 2011; Kiszka et al., 2007), as well as telemetry studies on seabirds (Pettex et al., 2010; Péron and Grémillet, 2013, 2014). However, despite all the surveys, information on habitat preference is still acute in the winter season because of the lack of systematic survey during this season in the ENA at large.

The present paper is the second part of a larger work. Part I focused on the north-western Mediterranean Sea (NWMS, Lambert et al., *this issue*), where predators were shown to cope with the seasonal variability of their environment within the constraints of their own biological or physical characteristics. In a similar way, the present study was aimed at testing whether predators have the capacity to change their habitat preferences in response to seasonal changes of their environment, and explore which parameters are involved in these variations. We used observational data from synoptic multi-target aerial surveys conducted during both the summer and winter seasons in the BoB, CS and EC to investigate seasonal changes in habitat preferences. Seasonal variations in habitat preferences of cetaceans and seabirds were examined through habitat modelling by using Generalised Additive Models (GAMs).

2. Material & methods

2.1. Study region

The study encompassed two sectors, the EC, the southern CS and the BoB. The EC is an epicontinental sea of shallow depth (maximum 172 m in the Hurd Deep; Smith et al., 1975) characterised by a mega-tidal regime. The strongest tides in Europe, with larger tidal ranges and more efficient vertical mixing, are found along the French coast of the EC (Brylinski and Lagadeuc, 1990). The general circulation within the EC is mainly from the Atlantic to the North Sea. Seasonality is well marked, with vertically mixed waters in winter and stratified waters in summer. However, tidal currents and winds can locally prevent stratification, in particular along the coasts of the eastern EC.

On the other hand, the BoB is characterised by a broad continental shelf, from 20 km wide in the south to as much as 180 km in the north, and around 30–40 km wide along the Iberian coasts (Koutsikopoulos and Le Cann, 1996). The oceanic part of the BoB is from 2000 to 5000 m deep. The general circulation, originating

from the North-Atlantic Gyre, is weak and flows from north to south (Koutsikopoulos and Le Cann, 1996; Pingree and Garcia-Soto, 2014), while the slope current is strong and flows from the Iberian Peninsula to the northern BoB along the shelf break. The interaction between these two opposite circulations frequently results in mesoscale eddies that are relatively persistent in time (Pingree and Le Cann, 1992; Caballero et al., 2014). Over the shelf, currents are mainly driven by winds, tides or freshwater inputs, depending on the area. Tidal currents predominate in shallower areas that are more extended in the northern BoB, while wind-driven currents predominate elsewhere, generating an important spatio-temporal variability of local currents (Koutsikopoulos and Le Cann, 1996).

Seasonality is well marked, with the thermal stratification establishing during spring from south to north. In coastal waters, however, tidal forcing in the north and wind-driven coastal upwelling in the south preclude summer stratification (Koutsikopoulos and Le Cann, 1996). Interaction between tidal waves and the continental shelf edge also induces upwelling of colder and nutrient-rich deep waters associated with higher productivity, mostly around 47°N. In autumn, stratification breakdown starts by the northern BoB, and the whole shelf is vertically mixed in winter, although some thermohaline stratification is maintained in large river plumes (Loire and Gironde estuaries Jegou and Lazure, 2014). In terms of productivity, the main phytoplankton bloom occurs in spring, then productivity reduces in summer as a result of nutrient depletion, and a secondary bloom appears in autumn, mostly in coastal waters (Pingree and Garcia-Soto, 2014).

2.2. Aerial survey and data collection

SAMM (*Suivi Aérien de la Mégafaune Marine*, Aerial Census of Marine Megafauna) aerial surveys over the BoB and EC were conducted during winter 2011–2012 (late November to mid-February; 32443 km of sampled transects) and summer 2012 (mid-May to early-August; 33864 km of sampled transects, Fig. 1). Sampling transects followed a zig-zag layout, and were manually designed to both maximise the use of flight time and cover the variety of marine habitats found in the ENA, while ensuring an equal coverage probability within each stratum.

Observations were conducted following a standardised protocol designed for aerial surveys. For cetaceans, the protocol was based on line-transect methodology (Buckland et al., 2001): all sightings of cetaceans were recorded with the declination angle, measured with a hand-held clinometer. Along with flight altitude, this angle allowed determination of the half-effective strip width (ESW) sampled on each side of the plane. For seabirds, the strip-transect methodology was used (Certain and Bretagnolle, 2008): seabirds were recorded within a band of 200 m on each side of the transect, under the assumption of perfect detection. Transects were sampled at a ground speed of 167 km/h and an altitude of 182 m. See Lambert et al. (*this issue*) for further details.

Species groupings used for further analyses resulted from the difficulty to tell apart morphologically similar species and from a compromise between using the lowest taxonomic level available yet keeping datasets large enough to allow habitat modelling. Common *Delphinus delphis* and striped *Stenella coeruleoalba* dolphins were grouped together, since they could hardly be told apart with certainty. Bottlenose dolphins *Tursiops truncatus* were identified at the species level. All sightings of “unidentified dolphins” were removed from the dataset. Although they can easily be separated, long-finned pilot whales *Globicephala melas* and Risso’s dolphins *Grampus griseus* were pooled together (the *Globicephalinae* group) due to low sighting numbers for each species taken separately. Harbour porpoises *Phocoena phocoena* were always well identified.

Regarding seabirds, we focused on six groups, corresponding as much as possible to families. Thus, northern gannets *Morus*

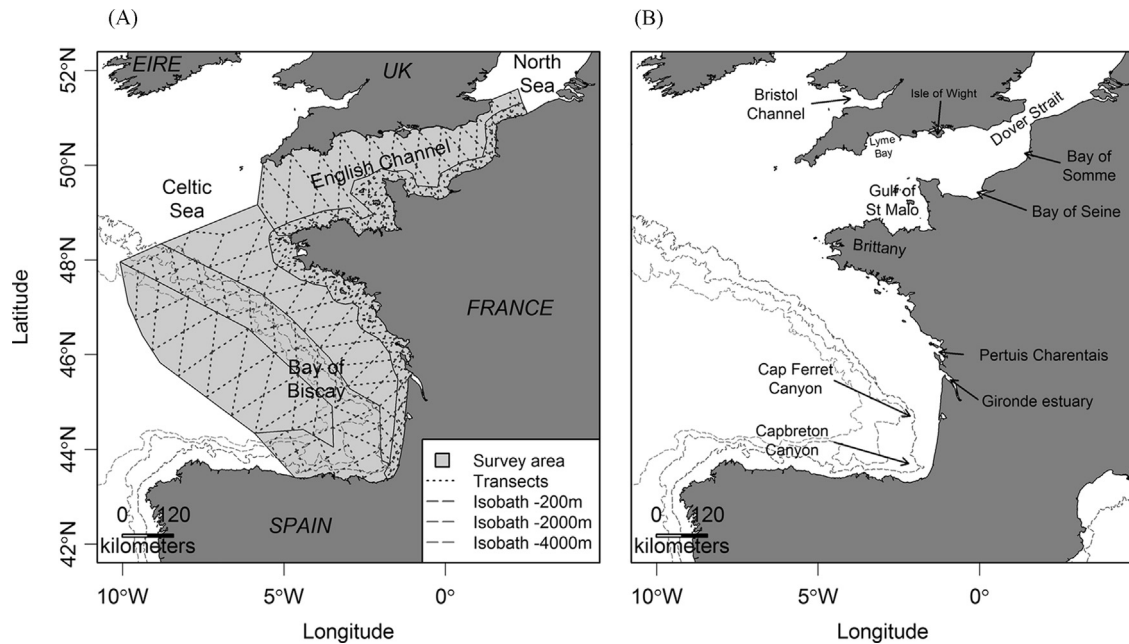


Fig. 1. Study area, with survey area and sampled transect (A), and geographical names (B).

bassanus were considered as one group, while auks were constituted of common guillemots *Uria aalge* and razorbills *Alca torda*, two species hardly discernible from the air. Procellariids were divided into two independent groups, the northern fulmars *Fulmarus glacialis* and the small-sized shearwaters, encompassing Manx Puffin *Puffinus puffinus* and Balearic *P. mauretanicus* shearwaters that are indiscernible from a plane. As for delphinids, unidentified procellariids were left apart. One species of larids was studied: the black-legged kittiwake *Rissa tridactyla*.

2.3. Habitat modelling

Transects were subdivided into 10 km-long segments of homogeneous conditions. Habitat modelling was then performed on best-quality data (Beaufort sea-state from 0 to 3 and subjective conditions from medium to excellent). The effort flown in good conditions represented 87% of the total survey effort in winter, 93% in summer. Habitat models were computed using GAMs to relate the response variable (number of individuals per segment) to predictors, with a quasi-Poisson error distribution, a log-link function and sampled area as model offset. The sampled area associated to each segment was the segment length multiplied by twice the corresponding ESW for cetaceans (see Laran et al., this issue, and Appendix S2 for more details), or by twice 200 m for seabirds.

We used four physiographic predictors: depth, slope, distance to the closest coast and distance to the closest colony (Appendix S1), the latter two for seabirds only; and six oceanographic predictors (Table 1): sea surface temperature (SST) mean, variance (SST_{var}) and gradient (SST_{grad}), sea surface height (SSH) mean and standard deviation (SSH_{SD}) as well as maximum tidal velocity (max. velocity). The latter was included in our set of predictors since tides in our study regions are among the most intense over the world, especially in the EC. All oceanographic predictors were summarised over 7 and 28 days prior to each sample day, to include both weekly and monthly temporal resolution. An overview of the environmental conditions in the study area for the two seasons was obtained by averaging predictors over the survey period for each season (Fig. 2).

Model selection was conducted following a procedure allowing a maximum of four covariates to be selected, excluding all

Table 1

Environmental predictors used for habitat modelling and their source. GEBCO-08 30 arc-second database was used to compute depth, slope and distance to closest coast (<http://www.gebco.net/>). The ODYSSEA product from Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu/>) was used to compute mean, variance and gradient of sea surface temperature. MARS-3D model from PREVIMER (<http://www.previmer.org/>) was used to compute mean and standard deviation of sea surface height (SSH), MARS-2D to compute maximum tidal velocity.

Type	Environmental predictors	Units	Source
Physiographic	Depth	meters	GEBCO-08 30 arc second
	Slope	degrees	
	Distance to the closest coast	meters	
	Distance to the closest colony	km	Manually referenced
Oceanographic	Mean SST	°C	ODYSSEA
	Variance of SST	°C	
	Mean gradient of SST	°C	MARS 3D
	Mean SSH	meters	
	Standard deviation of SSH	meters	
Maximum tidal velocity	$m.s^{-1}$	MARS 2D	

combinations of covariates with an absolute value of correlation higher than 0.7 (correlation matrices are presented in Appendix S3, and selecting best models on the basis of the Generalised Cross-Validation criterion (GCV, the lower the better). The maximum degree of freedom for smoothers was constrained to 3 to avoid over-fitting of the data (4, considering the offset). Once a model was selected, we extracted the contribution of each covariate in the linear predictor by segment. These contributions were computed using the `predict.gam` function within the `gam` package, setting the `type` argument as “terms” (Wood, 2006); this provides a matrix with each component of the linear predictor separately (here, the smoothed covariates); see function description for more details. The contributions were then mapped to explore the local variations in the importance of each selected covariates. Predictions were then produced for each day

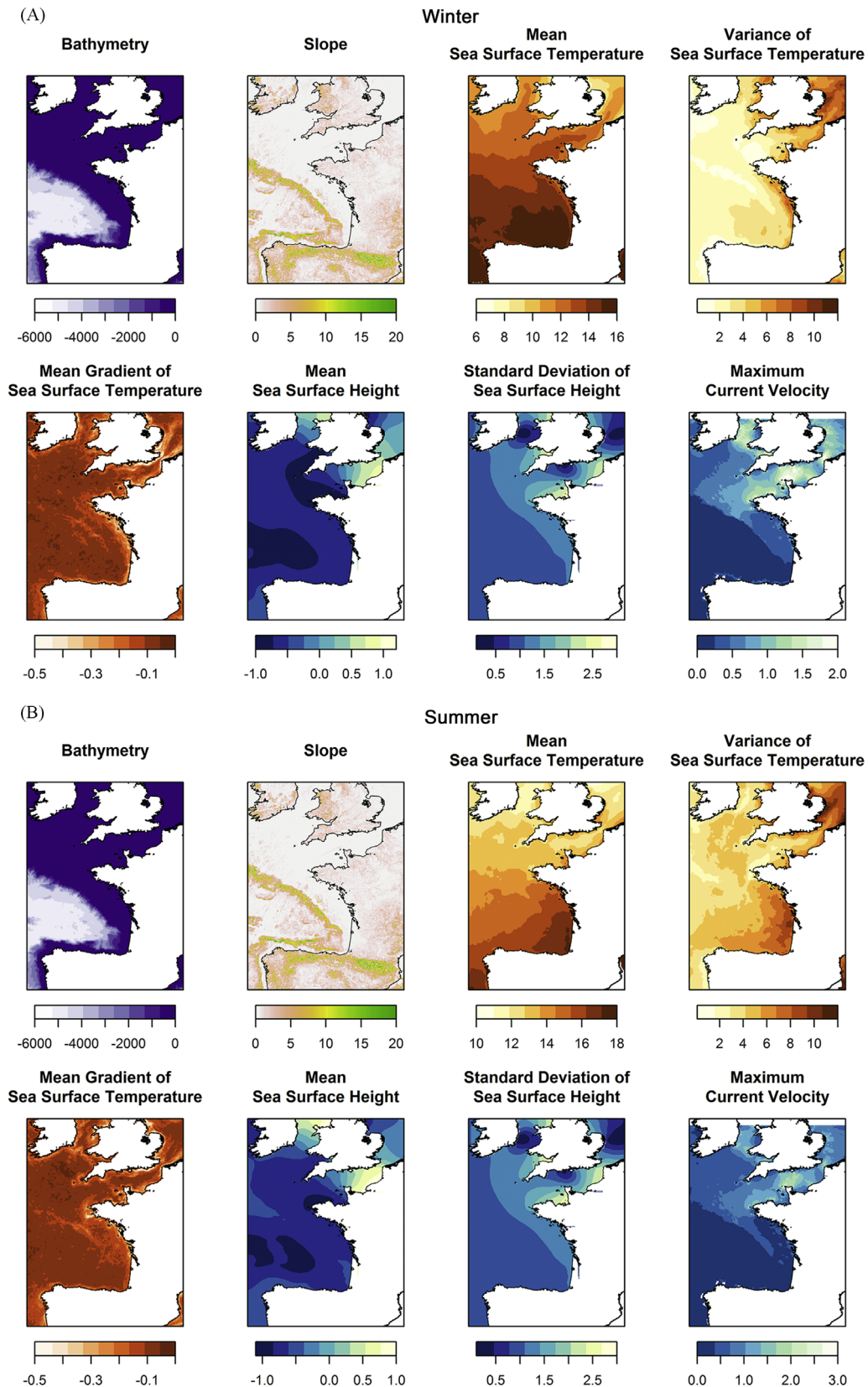


Fig. 2. Environmental conditions averaged over the two study periods. A – averaged conditions in winter (from late November 2011 to mid-February 2012); B – averaged conditions in summer (from mid-May 2012 to early August 2012). (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

encompassed in the survey periods, and daily predictions were averaged to get winter and summer predictions. Coefficients of variation (CVs) were produced from the variance around daily

prediction and the variance around the mean prediction ($CV = \sqrt{\text{seasonal variance}/\text{seasonal mean}}$). In order to limit extrapolation, we only performed predictions within the sampled

environmental envelope. All analyses were done in R version 2.15.3 (R Core Team, 2014).

3. Results

3.1. Sightings

All species groups were encountered in both seasons, although seabirds generally showed more contrasting abundances between the winter and summer seasons than cetaceans. The most abundant seabird species encountered were auks in winter and northern gannets in summer, while small-sized delphinids were the most abundant cetacean species in both seasons (Table 2, Appendix S4).

3.2. Seasonal habitat models and predicted distribution

3.2.1. Harbour porpoises

In winter, the harbour porpoises model resulted in an explained deviances of 39.6% (Table 3, Fig. 3A). The selected covariates were depth, SST_{var} (28d), mean SSH (28d) and maximum velocity (28d). Depth was clearly the most contributing covariate, with positive contributions over the continental shelf. The relationship indicated a preference for shallow waters. The three other covariates contributed less, with high contributions only over the shelf edge. Relationships showed a preference for strong variance of SST inducing positive contributions mostly along the coasts, a preference for positive SSH inducing positive contributions mostly in eastern the EC and southern BoB, and a preference for null (positive contributions within oceanic waters) or strongest monthly maximum tidal currents (EC). These relationships led us to predict a distribution mostly concentrated in the eastern EC and southern North Sea (Fig. 4A).

In summer, explained deviance reached 33.6% (Table 4, Fig. 3B), with mean SSH (7d), mean SST (28d), SSH_{SD} (28d) and maximum velocity (28d) as the selected covariates. The most important covariate was maximum velocity, with positive contributions over the continental shelf, north of 45°N, indicating a preference for high maximum tidal currents at the monthly scale. Mean SST was also a major contributing variable, with a preference for waters around 14°C. Mean SSH contributed mostly over the shelf, and the positive contributions (central EC and BoB) expressed a preference for null SSH. Finally, SSH_{SD} was the least contributing covariate, with a preference for fairly high values inducing positive contributions in the EC. These preferences resulted in harbour porpoises being distributed over the shelf in the western EC and CS, yet avoiding the coasts of Brittany, and with high densities north

of the Dover Strait (Fig. 4B). CVs were overall low for both seasons, with higher values in winter over oceanic waters (Appendix S5, Figure S5.1).

3.2.2. Small-sized delphinids

In winter, the small-sized delphinids model resulted in 17.3% of explained deviance (Fig. 5A), with mean SST (7d), SST_{grad} (7d), mean SSH (7d) and maximum velocity (28d) as selected covariates. The four covariates showed similar overall contributions (Fig. 5A). The relationship between the number of individuals and the mean SST indicated a preference for warmer waters, inducing positive contributions over the whole BoB and western EC. The relationship to SST_{grad} showed an avoidance of weekly thermal fronts, hence negative contributions along the BoB coasts and eastern EC. Similarly, the species preferred negative SSH, associated with negative contributions in the eastern EC. Finally, the relationship to maximum velocity highlighted a preference for reduced monthly maximum tidal current, and positive contributions were induced over the BoB shelf and EC (except its central part). This model predicted the species to be mostly present over the continental shelf, from the CS to the southern BoB, in lower densities in oceanic waters, and absent in the eastern EC (Fig. 4A). Highest densities were predicted along the external part of the shelf.

In summer, explained deviance reached 32.1% (Fig. 5B). Selected covariates were mean SST (7d), mean SSH (7d), SST_{grad} (28d) and SSH_{SD} (28d). As in winter, all covariates showed high contributions over the whole area, but mean SSH and SSH_{SD} were the two most contributing variables. Their relationships indicated a preference for negative SSH and lower SSH_{SD} , inducing negative contributions over the EC. The last two covariates showed similar contributions, with relationships highlighting a preference for warmer waters and reduced monthly thermal fronts. This latter relationship induced negative contributions along the coasts. Given these preferences, the summer distribution shifted toward a more oceanic pattern, with the species being present in higher densities along the shelf edge (Fig. 4B). The model predicted high densities over the external part of the shelf and in oceanic waters, but densities close to nil across the whole EC and eastern CS. In winter, CVs were small around the seasonal mean, but in summer they reached high values within the eastern EC (Appendix S5, Figure S5.1). These values were due to the large confidence interval around the relationship with mean SSH for high values, and confined to areas with predicted densities close to zero.

3.2.3. Bottlenose dolphins

The bottlenose dolphins winter model explained 24.9% of deviance (Fig. 6A). The selected covariates were slope, SST_{var} (7d), mean SST (28d) and SST_{var} (28d). The overall most contributing

Table 2

Number of sightings, number of individuals and encounter rates for each studied groups in winter and summer.

Species	Winter			Summer		
	Number of sightings	Number of individuals	Encounter rate (ind./km)	Number of sightings	Number of individuals	Encounter rate (ind./km)
Harbour Porpoise	279	481	0.015	272	423	0.012
Small-sized delphinids	442	4737	0.146	680	16,306	0.482
Bottlenose dolphins	48	327	0.010	63	383	0.011
<i>Globicephalinae</i>	40	130	0.004	57	241	0.007
Northern gannets	3697	11,123	0.343	2540	1178	0.035
Auks	6221	16,841	0.519	240	530	0.016
Northern fulmar	346	740	0.023	195	283	0.008
Small-sized shearwaters	16	31	0.001	179	770	0.023
Black-legged kittiwake	2255	3233	0.1	73	93	0.003

Table 3
Summary of selected models for winter. Selected covariates for each group are indicated with the tick mark for physiographic variables, with their temporal resolution (7 or 28 days) for oceanographic variables. All selected covariates were significant.

Winter	Harbour porpoises	Small-sized delphinids	Bottlenose dolphins	<i>Globicephalinae</i>	Northern gannets	Auks	Northern fulmars	Black-legged kittiwakes
Distance closest coast								
Distance closest colony								
Depth	✓				✓	✓		
Slope			✓	✓				
Mean SST		7d	28d		7d	7d	7d	7d
SST _{var}	28d		7–28d	28d				28d
SST _{grad}		7d		7d			7d	
Mean SSH	28d	7d			7d	7d		28d
SSH _{SD}				7d				28d
Max. velocity	28d	28d			28d	28d	7d	
Explained deviance (%)	39.6	17.3	24.9	23.4	24.9	44.8	22.4	13.2

covariate was SST_{var} (7d), followed by mean SST and SST_{var} (28d), and slope. The relationships highlighted a preference for reduced weekly variance of SST but for warmer waters, inducing positive contributions mostly within the BoB. The model also indicated a preference for reduced monthly variance of SST, inducing negative contributions along the coasts and in the southern BoB. Finally, the relationship to the slope indicated a preference for high values inducing positive contributions over the shelf edge. This model resulted in bottlenose dolphins being mainly predicted in the southern BoB, especially over the shelf edge, and in adjacent oceanic waters (Fig. 4A). The species was predicted to mostly avoid coastal and shelf waters during winter.

In summer, the explained deviance dropped to 15.4% (Fig. 6B). The overall most contributing covariate was mean SSH (7d). As for small-sized delphinids, the relationship indicated a preference for negative SSH, inducing negative contributions in the eastern EC. The other selected covariates were slope, SST_{var} (7d) and SSH_{SD} (28d). Their relationships indicated a preference for high slope values (hence the positive contributions over the shelf edge) and null or strongest weekly variance of SST and high SSH_{SD} values (hence positive contributions in the western EC). The model then predicted a distribution spread across the whole area, but with higher densities predicted over the shelf edge and in the Gulf of St Malo, and densities close to zero in the eastern EC (Fig. 4B). CVs were low in winter, while in summer, higher CVs were found in the eastern EC, linked to the uncertainty around high values of mean SSH (Appendix S5, Figure S5.1).

3.2.4. *Globicephalinae*

In winter, the selected model for *Globicephalinae* resulted in a deviance of 23.4% (Fig. 7A), with SST_{grad} (7d) and SSH_{SD} (7d) as the two most contributory covariates, selected with slope and SST_{var} (28d). The relationships with SST_{grad} highlighted a preference for reduced weekly thermal fronts (hence negative contributions along the coasts) and for reduced SSH_{SD} (negative contributions within the southern EC). However, the relationship with slope showed a preference for high values, inducing strong positive contributions along the shelf edge, while the relationship to SST_{var} indicated a preference for either null or strongest monthly variance of SST. This model predicted *Globicephalinae* mainly over the shelf edge of the BoB and Iberian shelves (Fig. 4A).

In summer, the explained deviance was higher at 34.3% (Fig. 7B). The selected covariates were slope, mean SSH (7d), mean SST (28d) and SST_{grad} (28d). Mean SSH was clearly the most contributing covariate, with the relationship indicating a preference for negative SSH, associated to negative contributions within the eastern EC. The other three covariates had low contributions. The relationships indicated a preference for high slope values, warmer waters and reduced monthly thermal fronts. As in winter, highest densities were predicted

along the shelf edge from the BoB to north-western Iberian waters (Fig. 4B). In winter, higher CVs were predicted within the Gulf of St Malo and Bristol Channel, but in summer higher values were reached in the eastern EC, as for small-sized delphinids and bottlenose dolphins (Appendix S5, Figure S5.1).

3.2.5. *Northern gannets*

In winter, the selected model for northern gannets resulted in an explained deviance of 24.9% (Fig. 8A), with, as selected covariates, depth, mean SST (7d), mean SSH (7d) and maximum velocity (28d). The most contributory covariate was depth, with positive contributions over the whole shelf induced by the preference for shallow waters. The preference for warmer waters induced strong and positive contributions in the southern BoB. Mean SSH contributed mainly in the EC and off Brittany, but the preference for high SSH values induced positive contributions only in the eastern EC. Finally, velocity had overall lower contributions, and the relationship indicated preference for low monthly maximum tidal currents, which induced negative contributions over the whole EC and off Brittany. This model corresponded to a distinctive pattern. Northern gannet distribution constituted of two main areas, driven by different habitat preferences: in the eastern EC, high densities were driven by a preference for shallow waters and strong SSH, while in the southern BoB and Iberian shelves they were driven by a preference for shallow warmer waters and low tidal currents (Fig. 9A). Lower yet substantial densities were also predicted in the western CS.

In summer, the model explained 21.9% of the deviance (Fig. 8B), with SST_{var} (7 and 28d), SST_{grad} (28d) and distance to the closest colony as selected covariates. Distance to the closest colony was the overall most contributing covariate, with a clear preference for areas close to colonies, inducing positive contributions up to 300 km from colonies. The relationships to the other three covariates indicated a preference for reduced weekly and monthly variance of SST, but for marked monthly thermal fronts (hence positive contributions along the coasts). These preferences reflected the distributions centred on colonies, with highest densities in western EC, south of Brittany, south-west of Ireland and off Wales (Fig. 9B). CVs were overall low in both seasons (Appendix S5, Figure S5.2).

3.2.6. *Auks*

The selected models for auks resulted in the best explained deviance in both seasons. In winter, it reached 44.8% (Fig. 10A). The most contributing covariate was depth, with a preference for shallow waters inducing positive contributions over the shelf. The three other selected covariates were mean SST (7d), mean SSH (7d) and maximum velocity (28d), with similar overall contributions. The relationships indicated a preference for cooler waters (hence positive contributions in the

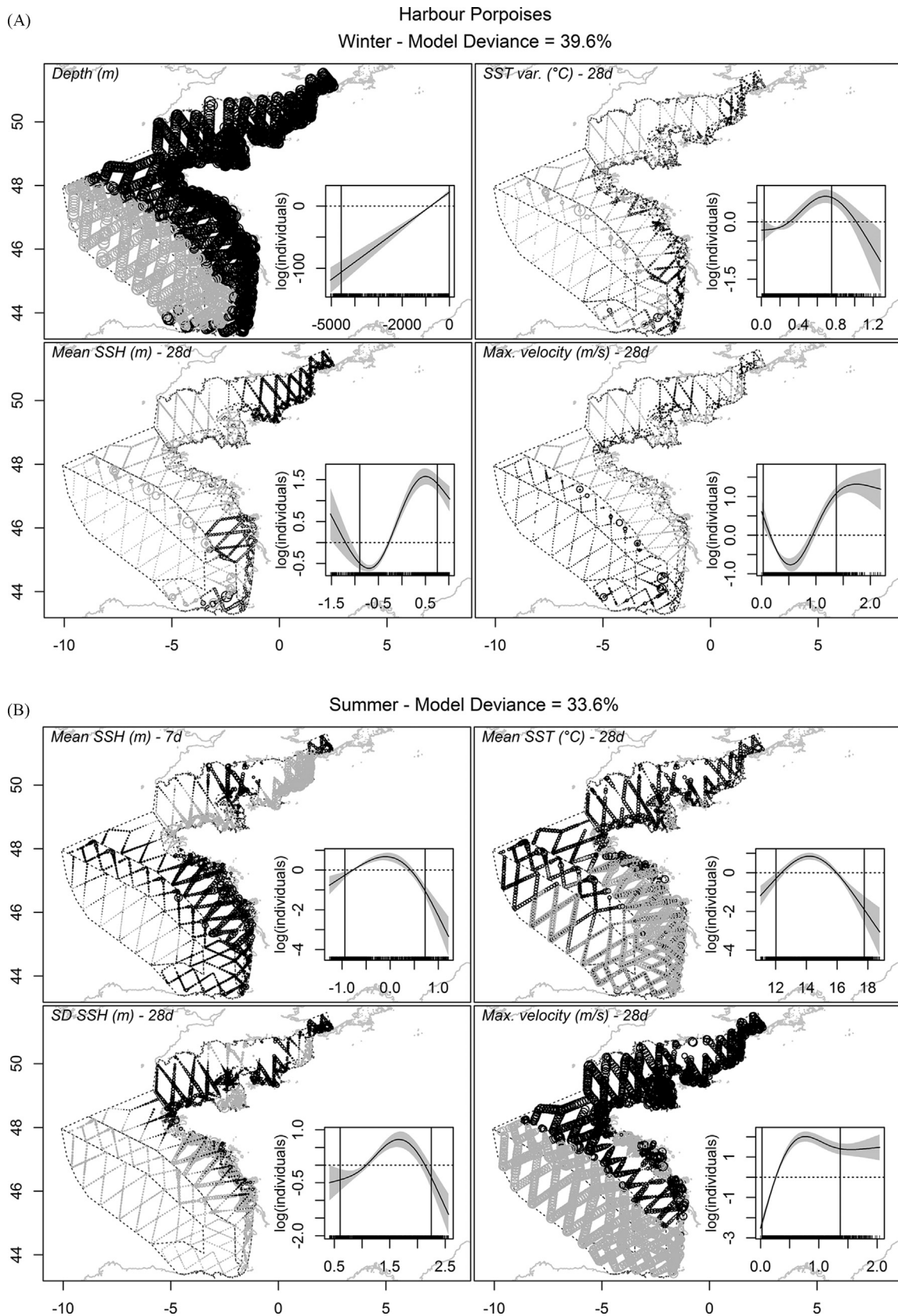


Fig. 3. Habitat model selected for harbour porpoises A – in winter (explained deviance=39.6%), B – in summer (explained deviance=33.6%). Each panel spatially represents the contribution of the concerned covariate to the linear predictor for each sampled segment, with the dot size proportional to the covariate relative contribution regarding the three other covariate contributions in that point. Grey dots represent points where the contribution of the covariate is negative, black dots where it is positive. Corresponding GAMs curves are inserted in corresponding panels, representing the relationship between the covariate (abscissa) and the linear predictor (log(individuals), ordinate). The two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range must be avoided, since the smooth splines might not be reliable.

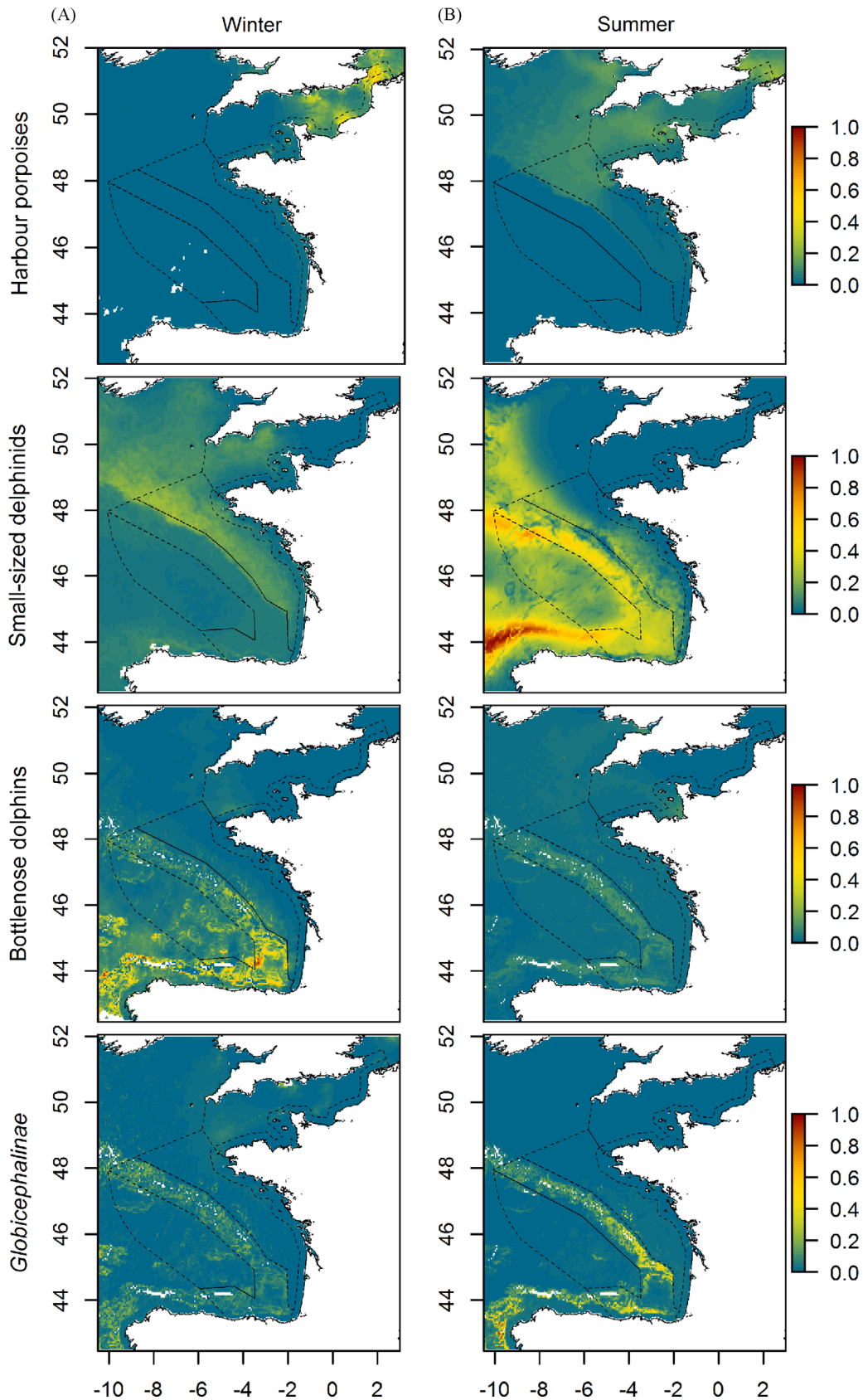


Fig. 4. Predicted distributions of cetaceans based on habitat models in winter (A) and summer (B). Distributions were scaled in relative densities: densities were divided by the maximum predicted density over the two seasons, for each group. As a consequence, scales are not comparable between groups. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1). (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

Table 4

Summary of selected models for summer. Selected covariates for each group are indicated with the tick mark for physiographic variables, with their temporal resolution (7 or 28 days) for oceanographic variables. All selected covariates were significant.

Summer	Harbour porpoises	Small-sized delphinids	Bottlenose dolphins	<i>Globicephalinae</i>	Northern gannets	Auks	Northern fulmars	Black-legged kittiwakes	Small-sized shearwaters
Distance closest coast							✓		✓
Distance closest colony					✓	✓	✓		✓
Depth							✓		
Slope			✓	✓					
Mean SST	28d	7d		28d			28d	7d	28d
SST _{var}			7d		7-28d	28d			
SST _{grad}		28d		28d	28d		28d	7d	
Mean SSH	7d	7d	7d	7d				28d	28d
SSH _{SD}	28d	28d	28d			28d			
Max. velocity	28d							28d	
Explained deviance (%)	33.6	32.1	15.4	34.3	21.9	55.2	17.5	17.4	38.1

northern BoB and in the EC), high positive SSH (positive contributions within the eastern EC) and low monthly maximum tidal currents (negative contributions in the EC). These preferences reflected a distribution mainly centred on the eastern EC (Fig. 9A), with lower densities in shelf waters in the CS and BoB, and an absence from oceanic waters.

In summer, the model explained deviance was 55.2% and, as in winter, depth as the most contributing covariate (Fig. 10B), with a similar preference and contribution pattern than in winter. SST_{var} (28d) was also selected, as well as SSH_{SD} (28d) and distance to the closest colony. The model indicated a preference for low monthly variance of SST, low monthly SSH_{SD} (associated with negative contributions in the EC) and a preference for areas within 350 km from colonies. The model then predicted highest densities around major colonies, mostly along the Irish and northern EC coasts, as well as at the tip of Brittany (Fig. 9B). CVs were overall low, with higher values over greater depths (Appendix S5, Figure S5.2).

3.2.7. Northern fulmars

The selected model for winter resulted in an explained deviance of 22.4% (Fig. 11A), with four selected covariates: mean SST (7d), SST_{grad} (7d), mean SSH (7d) and maximum velocity (7d). Mean SST was overall the most contributory covariate, with the preference for waters cooler than 13°C associated with positive contributions over the whole area except the southern BoB. The three other covariates had similar overall contributions. The relationships indicated a preference for reduced weekly thermal front (hence negative contributions along the coasts), positive SSH (hence positive contributions in the eastern EC and southern BoB) and medium weekly maximum tidal currents (positive contributions over northern BoB shelf and EC). The species was then predicted to be present over the shelf north of 47°N, and densities were fairly homogeneous throughout study area, yet with lower densities close to coasts (Fig. 9A).

In summer, the selected model explained 17.5% of the deviance (Fig. 11B). Selected covariates were the distance to the closest coast, mean SST (28d), SST_{grad} (28d) and distance to the closest colony. Distances to closest coast and colony were the two most contributory covariates, with opposite relationships: increasing with closest coast (positive contributions for distances > 50 km) and decreasing with closest colony (positive contributions for distances < 100 km). SST_{grad} and mean SST had lower contributions. Their relationships showed a preference for fairly marked weekly thermal fronts and cooler waters. This model resulted in a similar distribution to winter, yet at lower densities (Fig. 9B). CVs were overall low in both seasons, with higher values in the south (Appendix S5, Figure S5.2).

3.2.8. Black-legged kittiwakes

The winter model for black-legged kittiwakes explained 13.2% of the deviance (Fig. 12A), with mean SST (7d), SST_{var} (28d), mean SSH (28d) and SSH_{SD} (28d). All these covariates had generally similar contributions. The relationships highlighted a preference for cooler waters (hence negative contributions in the southern BoB), reduced monthly variance of SST (negative contributions along coasts), positive SSH (negative contributions in the western EC and oceanic waters) and medium SSH_{SD}. This model predicted black-legged kittiwakes to be widely dispersed over the whole region, especially over the shelf. However, the species was predicted to avoid northern Brittany coasts and west of the Isle of Wight, while slightly lower densities were also predicted over oceanic waters (Fig. 9A).

In summer, 17.4% of the deviance was explained by the selected model, containing mean SST (7d), SST_{grad} (7d), mean SSH (28d) and maximum velocity (28d) (Fig. 12B). Mean SSH and mean SST were the most contributory covariates, with a preference for waters around 14°C and positive SSH. The relationships with the last two covariates indicated a preference for low weekly thermal fronts and medium monthly tidal currents (mostly contributing over the EC). The model then predicted highest densities in the southern EC (Fig. 9B). CVs were low in both seasons (Appendix S5, Figure S5.2).

3.2.9. Small-sized shearwaters

The distribution of small-sized shearwaters was only modelled in the summer, because insufficient data was obtained in winter. The model explained 38.1% of the deviance (Fig. 13), with distance to the closest coast, mean SST (28d), mean SSH (28d) and distance to the closest colony as selected covariates. The most contributory was distance to the closest colony, with the relationship showing a preference for areas closer to colonies, inducing negative contributions for distances greater than 300 km. Similarly, distance to the closest coast also had a high contribution and the relationship highlighted a preference for areas very close to the shore, within 50 km from the coast (positive contributions only within this range). The relationship with the other two covariates indicated a preference for warmer waters and negative SSH values (hence negative contributions in the eastern EC). The model predicted small-sized shearwaters to be present around colonies throughout the BoB (Fig. 14), western EC and CS within the range of 50 km from the coast, and almost absent in the eastern EC and Atlantic oceanic waters. CVs were overall low (Appendix S5, Figure S5.3).

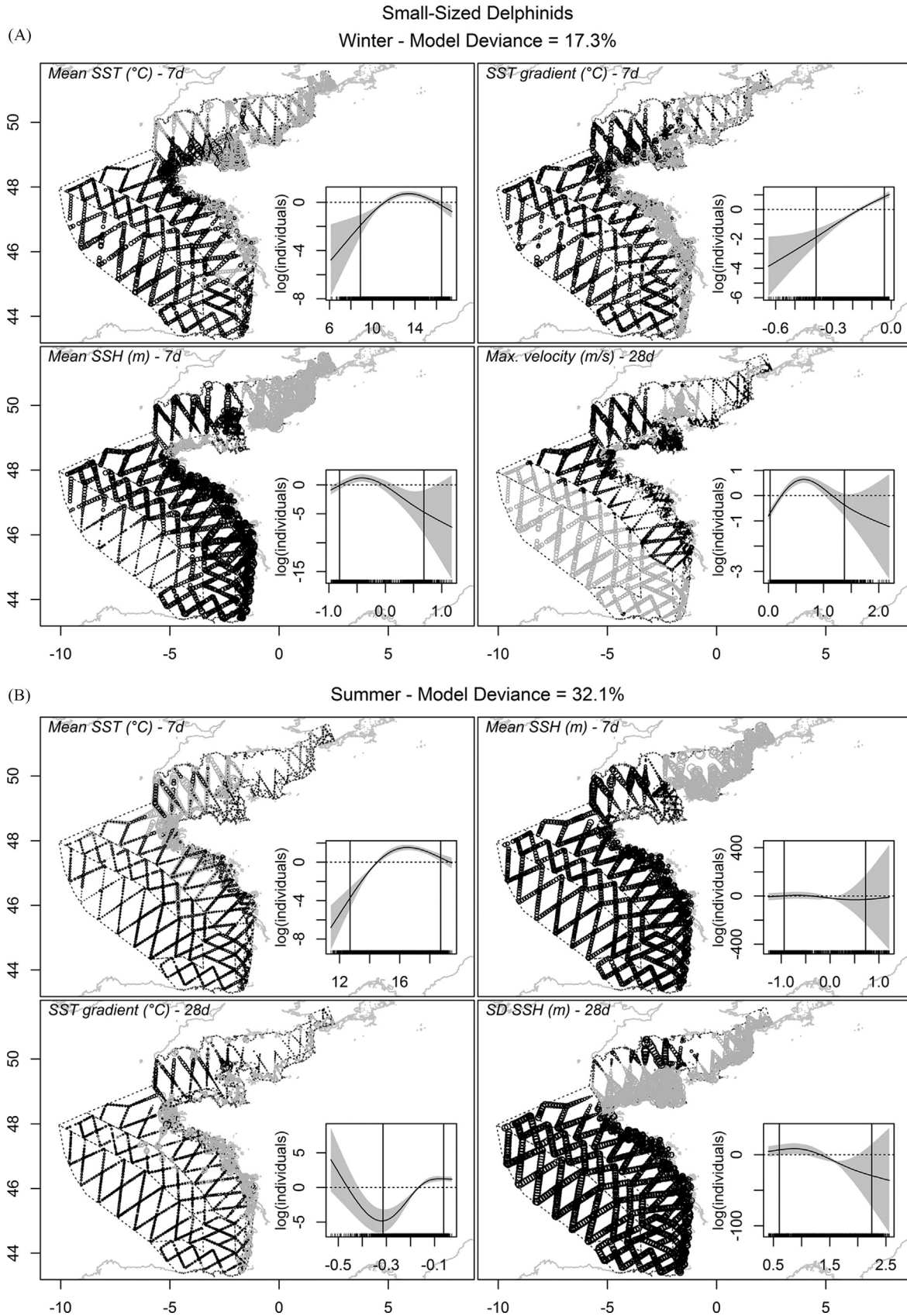


Fig. 5. Habitat model selected for small-sized delphinids A - in winter (explained deviance=17.3%), B - in summer (explained deviance=32.1%). See Fig. 3 for figure explanation.

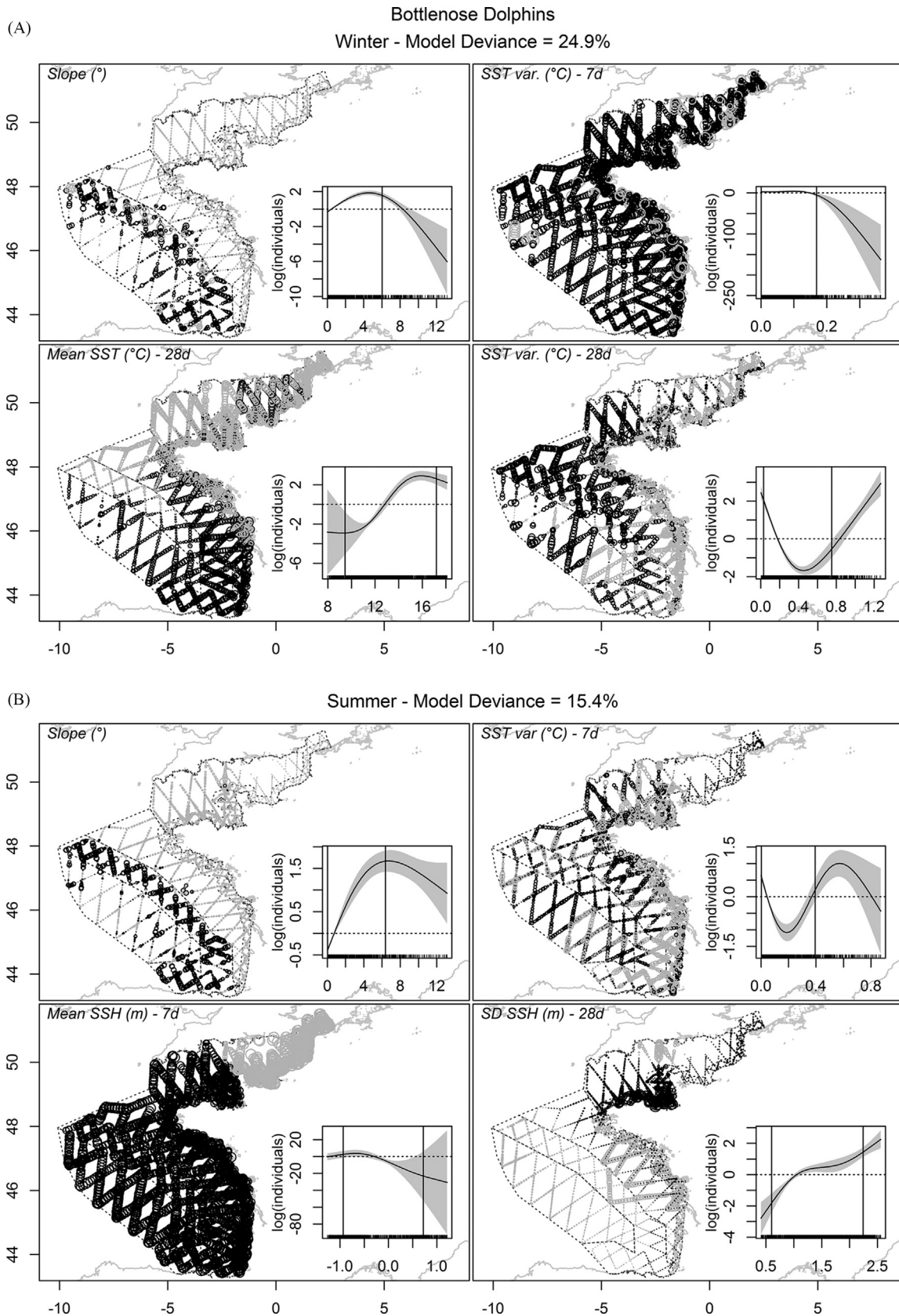


Fig. 6. Habitat model selected for bottlenose dolphins A - in winter (explained deviance=24.9%), B - in summer (explained deviance=15.4%). See Fig. 3 for figure explanation.

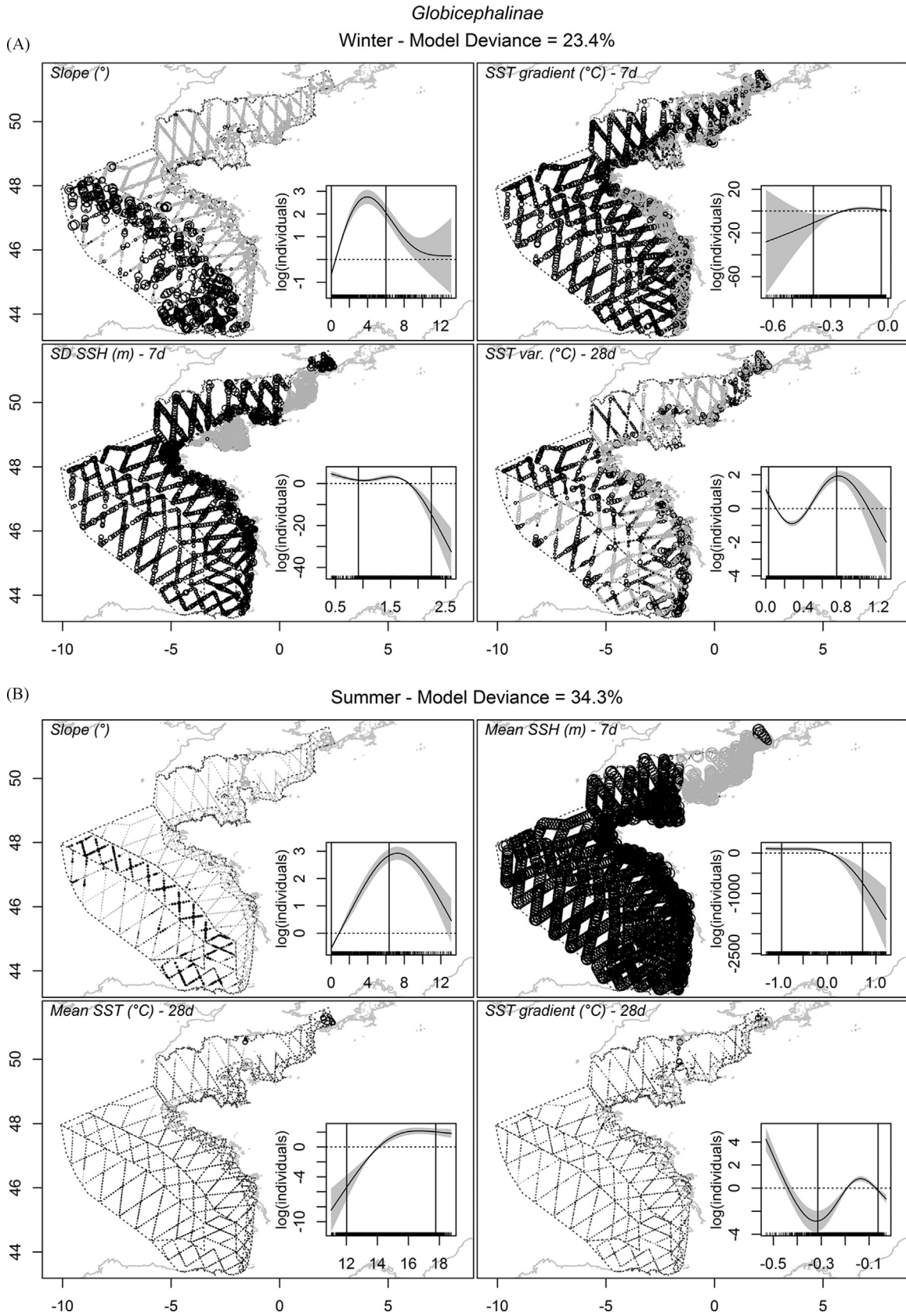


Fig. 7. Habitat model selected for *Globicephalinae* A – in winter (explained deviance=23.4%), B – in summer (explained deviance=34.3%). See Fig. 3 for figure explanation.

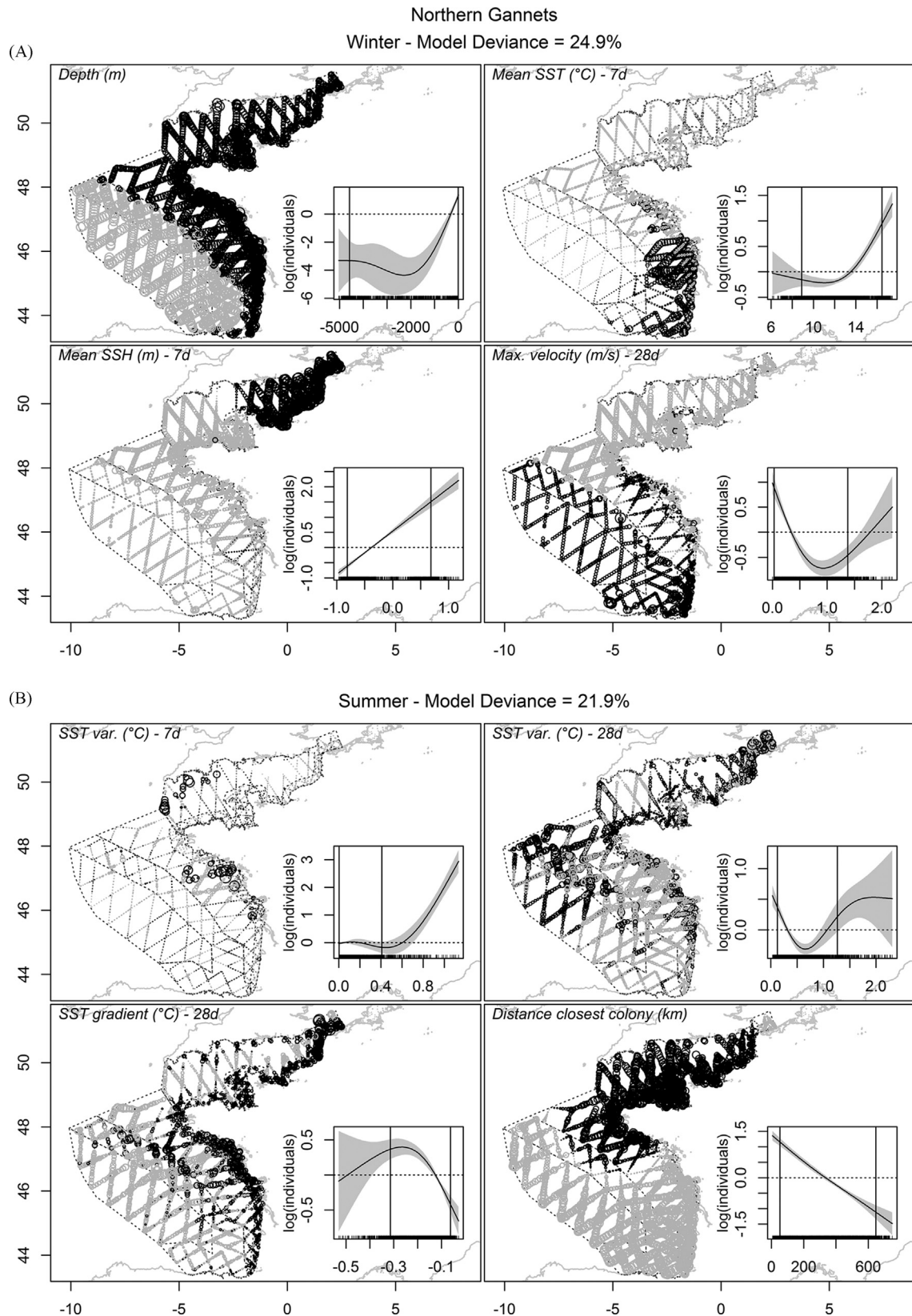


Fig. 8. Habitat model selected for northern gannets A – in winter (explained deviance=24.9%), B – in summer (explained deviance=21.9%). See Fig. 3 for figure explanation.

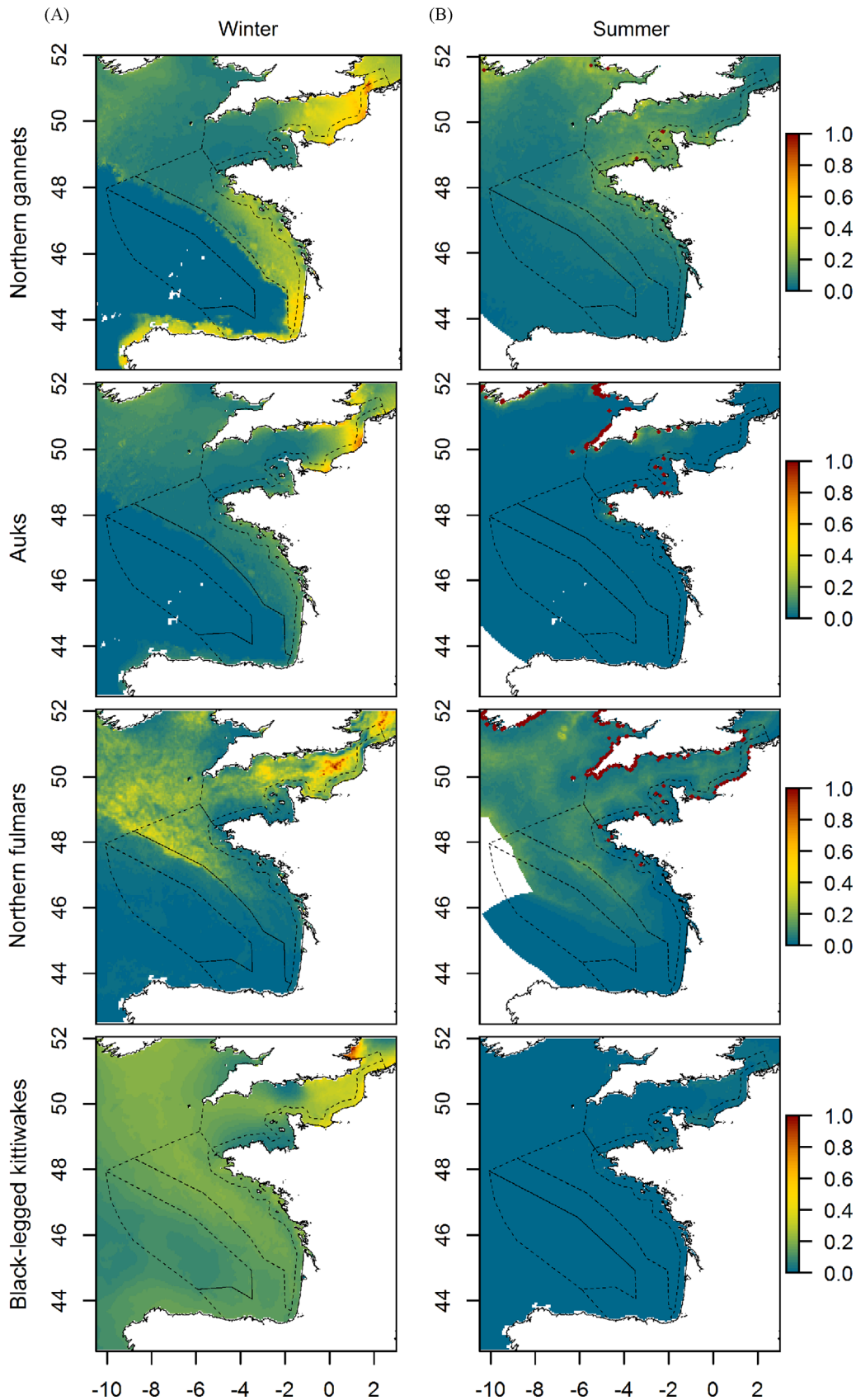


Fig. 9. Predicted distributions of seabirds based on habitat models, in winter (A) and summer (B). Distributions were scaled in relative densities: densities were divided by the maximum predicted density over the two seasons, for each group. As a consequence, scales are not comparable between groups. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1). Dark red dots on prediction are colonies locations (shown when the distance to closest colony was selected as covariate). (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

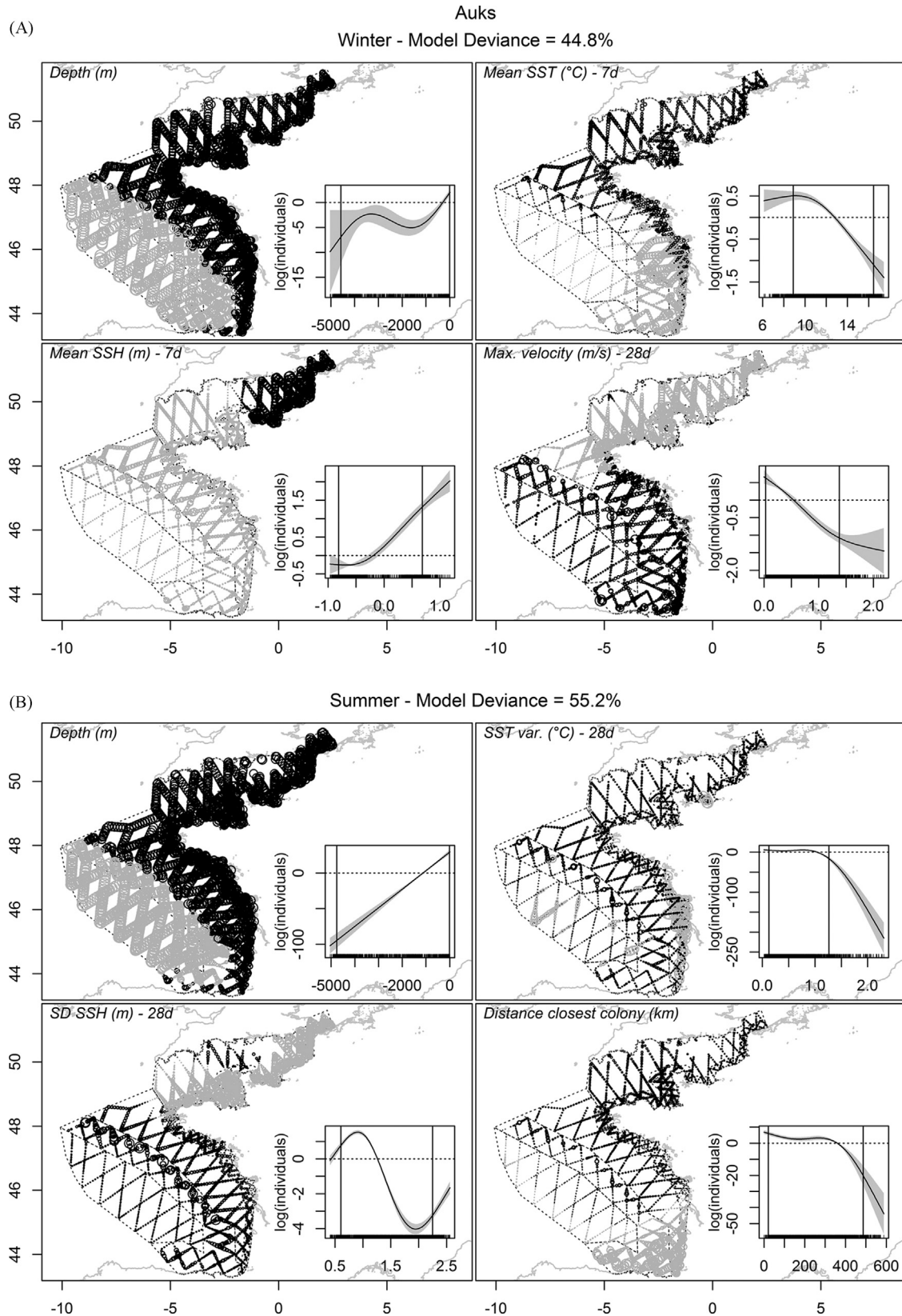


Fig. 10. Habitat model selected for auks A - in winter (explained deviance=44.8%), B - in summer (explained deviance=55.2%). See Fig. 3 for figure explanation.

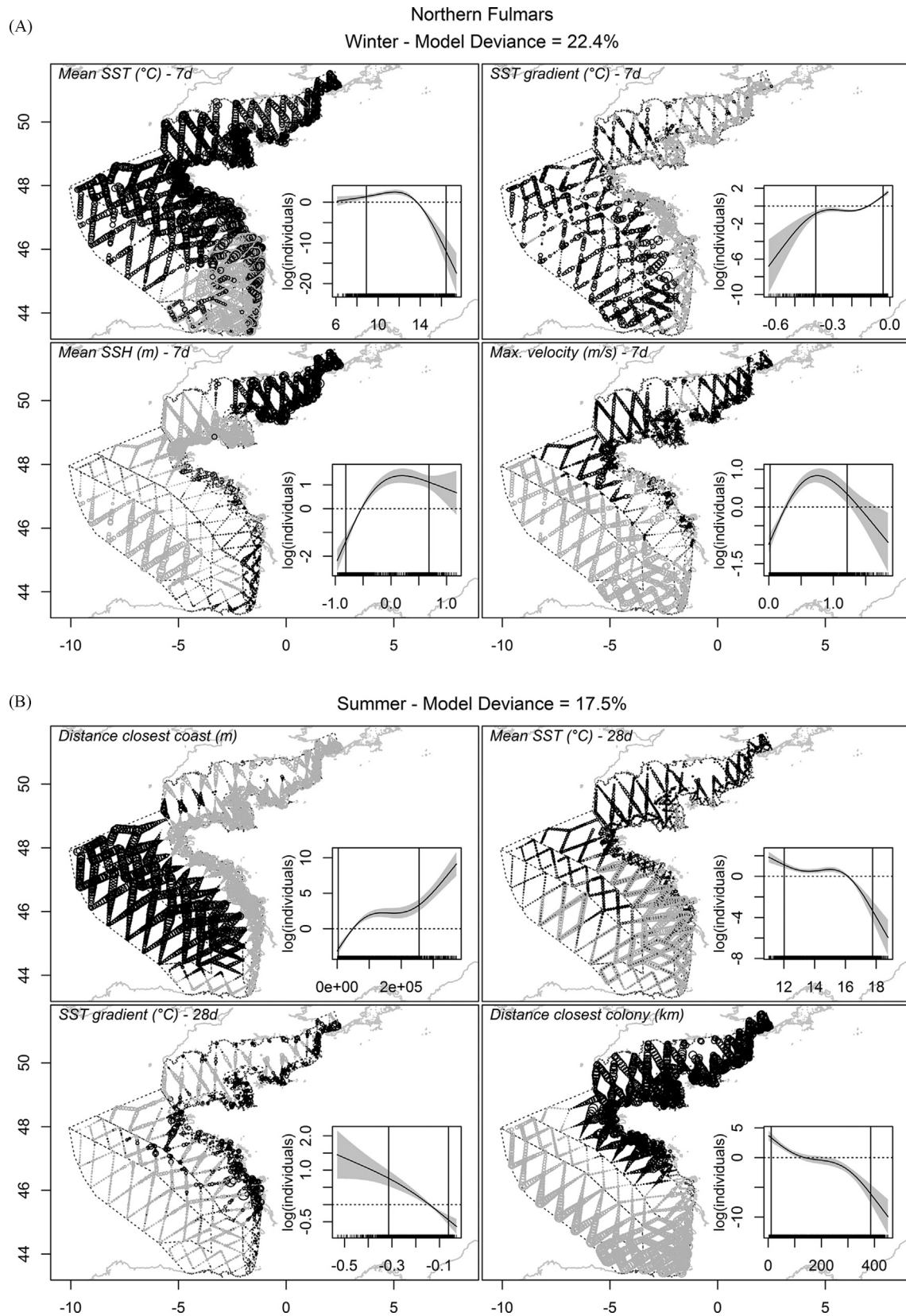


Fig. 11. Habitat model selected for northern fulmars A - in winter (explained deviance=22.4%), B - in summer (explained deviance=17.5%). See Fig. 3 for figure explanation.

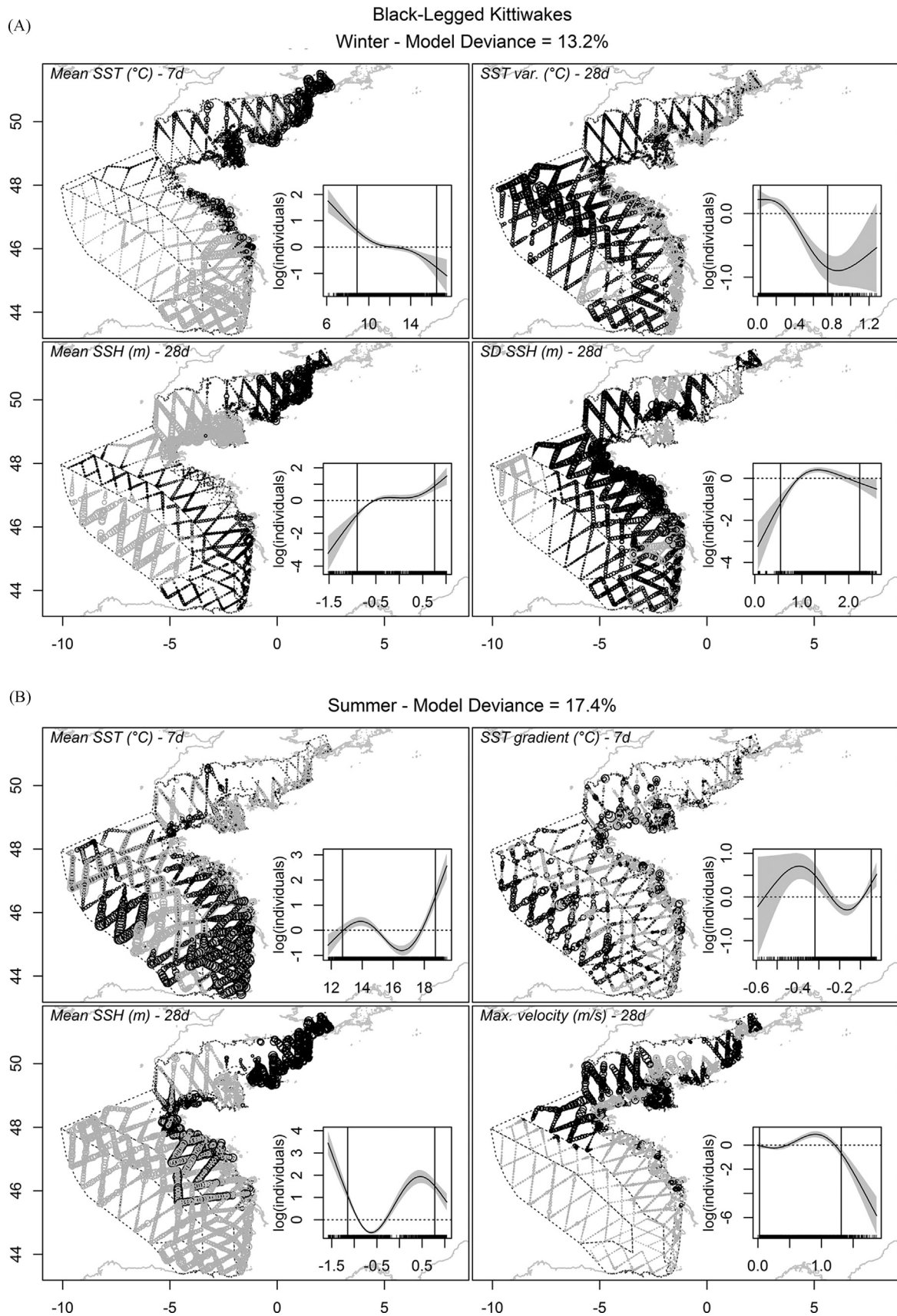


Fig. 12. Habitat model selected for black-legged kittiwakes A - in winter (explained deviance=13.2%), B - in summer (explained deviance=17.4%). See Fig. 3 for figure explanation.

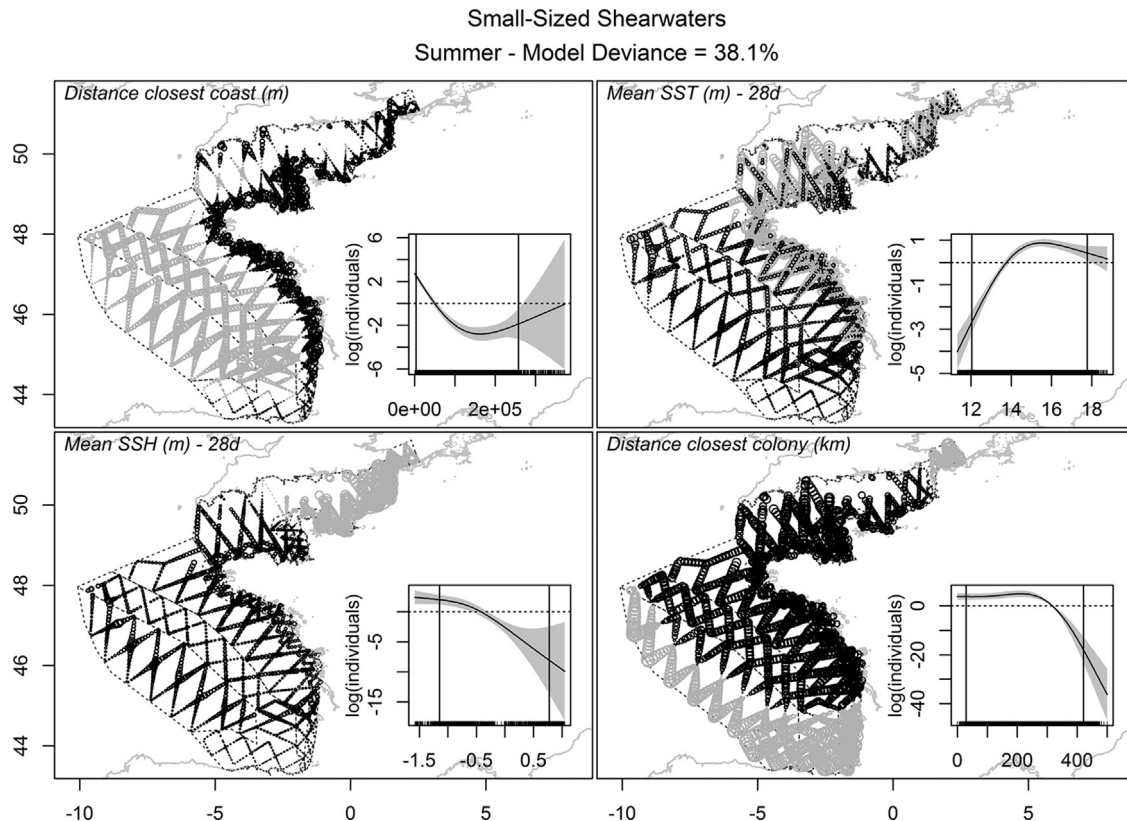


Fig. 13. Habitat model selected for small-sized shearwaters in summer (explained deviance=38.1%). See Fig. 3 for figure explanation.

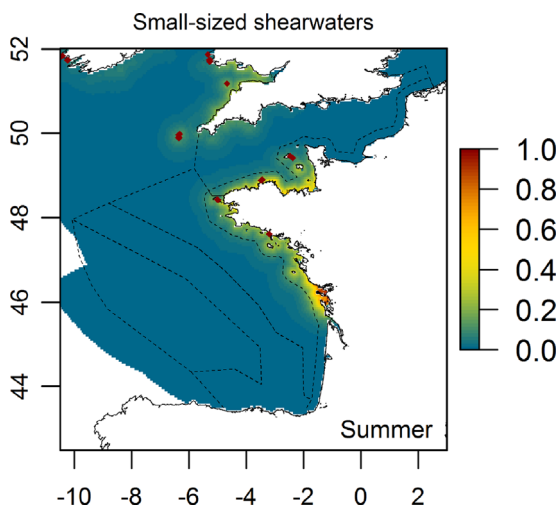


Fig. 14. Predicted distributions of small-sized shearwaters based on habitat models. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariate, in order to avoid extrapolation. Thick dotted lines materialised the survey area (see Fig. 1). Dark red dots on small-sized shearwaters prediction are colonies locations. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

4. Discussion

4.1. General

The present work explored the winter and summer habitat preferences exhibited by cetaceans and seabirds in the ENA by modelling the relative densities with GAMs by using a variety of physiographic and oceanographic variables of potential biological importance to the different taxa of interest. The use of aerial

survey observational data as input to habitat modelling necessarily comes with both strengths and limitations. The major strengths are the synoptic view of the two main season situations over a large marine area, leading to an unprecedented amount of effort per unit surface in the ENA; the simultaneous sampling of both cetaceans and seabirds, along with other marine megafauna not treated here, allowing the homogeneity of treatments between seasons and taxa required for ample comparisons, and more ecosystemic analyses and interpretations. Limitations are shared with all aerial surveys, and mainly concern species identification. Indeed, species-level identification is complicated by the high flying speed and by the morphological resemblance of several species when observed from above, with similar colour, shape, size patterns, etc. This was, for example, the case of small-sized delphinids, auks and some larids.

Despite these several limitations, all fixed as well as possible (e.g. by grouping some taxa), the present study provided a first assessment of habitat preferences driving the seasonal changes in at-sea distributions of several species in the western European waters. Concerning some poorly known species, this assessment furnished one of the first information sets on habitat preferences and distribution over such large areas at the population level in the ENA (e.g. shearwaters, fulmars). This was achieved through the model selection, which identified the variables that contributed the most to the heterogeneity of seabird and cetacean densities, approximating the habitat preferences of each taxon in both seasons.

In the NWMS, characterised by reduced seasonality compared to the ENA, three cetacean groups among four exhibited a clear consistency in their habitat preferences between seasons, as well as one seabird group among three (see Lambert et al., *this issue*). Here, in the ENA, the pattern was different: only one among ten cetacean or seabird groups exhibited similar habitat preferences between seasons. This group were the *Globicephalinae*, associated with the shelf break

throughout the year. This habitat might remain favourable even during winter since, as in the NWMS, they probably exploit deep layers little affected by surface layer seasonality. The seasonal variations of other cetaceans habitat preferences seemed to be linked to different parameters. The variations observed for harbour porpoises and small-sized delphinids could be related to the variation of their prey distributions, while for bottlenose dolphins, the seasonal variations might be related to calving and nursing. Indeed, bottlenose dolphins in the ENA exhibited a similar pattern as in the NWMS (see Lambert et al., [this issue](#)), although less marked, with part of the population moving inshore during the calving period.

The seasonality of the environment is known to induce migrating strategies in many species (Shaw and Couzin, 2013). Indeed, here, most studied seabirds engaged in more or less important migration as they moved from breeding to wintering grounds. For small-sized shearwaters, the migration was extreme with only a few individuals remaining within the study area in winter. For some other groups, the species were still present in winter, but individuals in the study region did not necessarily belong to the same populations as those present in summer. It was notably the case for gannets and kittiwakes, for example, for which most of the individuals present in winter actually breed in northern Europe in summer. This pattern explains the higher densities encountered in winter compared to summer for these groups (see Pettex et al., [this issue](#)). This pattern allows birds to optimise their survival as they can forage on optimal grounds when released from reproductive duty and central-place foraging constraints to replenish their reserves before the next reproductive period.

4.2. Ecological preferences

Harbour porpoises: In winter, the presence of harbour porpoises was mainly driven by a clear preference for shallow waters, and strong hydrological activity at the monthly scale (SSH). The presence of harbour porpoises in these waters was then modulated by a preference for highest spring tide currents (the monthly-scale current velocity reflecting the velocity during the preceding spring tide), and strong monthly variance of temperature. The association of these two parameters might indicate a preference for features where spring tides result in strong tidal currents, and induced the formation of locally enhanced productivity and local prey aggregation, through a complete mixing of the water column resulting in important variance of SST. This pattern explains the highest densities found in the Dover Strait, but the overall preference for dynamic shallow waters also explains why harbour porpoises can be found up to the Basque country along the coast in winter (Fig. 3, Marcos et al., 2010). This preference for structures induced by interactions between seabed topography and tidal currents during ebb tides has been demonstrated by several studies (Goodwin, 2008; Pierpoint, 2008). We could hypothesise that the preference for shallow dynamic waters reflects a preference for prey aggregation structures highly predictable in time and location, as shown at finer scale in the North Sea (Skov and Thomsen, 2008).

In summer, the species exhibited a more offshore distribution, avoiding the eastern EC, the Isle of Wight and the coast of Brittany, where hydrological activities remain strong all year round. Indeed, the species still showed a preference for strong spring tide currents, coupled with a preference for waters with medium standard deviation during the preceding month, which was an indicator of the dynamism of the water column during the past month. Hence, harbour porpoises seemed to target habitats where the mixing of the water column has been important during the past month, potentially inducing a break down of the stratification and an enrichment of the surface layer through the injection of nutrients. Following this enrichment, all trophic levels would rise in turn, up

to predators, thus the harbour porpoises would exploit these areas with a monthly lag. Such a migration has been described in other areas of the harbour porpoise range: from the Baltic to the North Sea through Kattegat and Skagerrak (Sveegaard et al., 2012; Benke et al., 2014), as well as in the Bay of Fundy (Neave and Wright, 1968; Read and Westgate, 1997; Johnston et al., 2005). In these areas, the mechanisms inducing these broad-scale movements are quite unknown, but potentially linked to sea-ice, availability of prey, or movement to calving grounds. Here, we could hypothesise a link to prey availability. Nevertheless, the importance of tides in porpoise habitats seems to be consistent through seasons and across regions.

Small-sized delphinids: Our results for small-sized delphinids were consistent with the observed large-scale seasonal changes in distribution of the species, especially the overall inshore movement during winter, up to the western EC (Murphy et al., 2013). Previous studies performed in summer found similar preferences for waters warmer than 15°C and from 400 to 1000 m deep along the shelf edge (Cañadas et al., 2009). These studies also found similar distribution during the calving and mating period (from April to September Murphy et al., 2013) with highest densities along the shelf edge in the whole study region, coupled to an avoidance of the EC and coastal waters of the BoB (Kiszka et al., 2007; MacLeod et al., 2009; Cañadas et al., 2009). This changing distribution between the seasons could be linked to the migration of pelagic prey (small schooling fishes; Pusineri et al., 2007; Meynier et al., 2008), moving from the shelf edge in summer to more inner shelf in winter. Hence, this seasonal movements would be a case of foraging optimisation.

Bottlenose dolphins: Our results indicated that, during winter, the majority of the bottlenose dolphin population exploited highly predictable aggregation structures within shelf break and oceanic waters while, in summer, part of the population shifted towards neritic habitats while the remaining population still exploited the shelf break. Such a pattern might be consistent with the hypothesis of a shift towards the exploitation of neritic strata linked to reproductive constraints. This was also quite similar to, although less pronounced than, results obtained for bottlenose dolphins in the NWMS (see Lambert et al., [this issue](#)).

The known strong preference for the BoB shelf break was confirmed (Certain et al., 2008, 2011). In winter, our model suggested that the species favoured mesoscale and monthly oceanographic features associated to the southern BoB shelf edge, especially eddies and upwellings induced by canyons (Cap-Ferret, Capbreton): the species showed a preference for warmer waters of the southern BoB, coupled with fairly high SST variations during the preceding month, an indicator of monthly structures allowing for the enrichment of the trophic web up to top predators. In summer, the distribution was still concentrated along the shelf break but extended more widely over the shelf compared to winter. Unlike in winter, predicted densities in the Gulf of St Malo were similar to that over the shelf break. This was consistent with the well-studied resident population present all year-round (Louis et al., 2014), and the increase of coastal and neritic populations might be linked to an influx of pelagic individuals. The species therefore showed a slight dispersion movement from offshore to more inshore waters in summer, at least for part of the population. For coastal populations exhibiting the same patterns (Mexico, Florida), this was often interpreted as a shift towards more protected habitats during the calving period (Shane et al., 1986). Hence, we hypothesised that the seasonal modifications of preferences could be linked to a compromise equilibrium related to phenological constraints, with the necessity for some bottlenose dolphins to move inshore during summer to ensure optimal conditions for calving and nursing.

Globicephalinae: The *Globicephalinae* were less abundant in winter than in summer, and were distributed over several habitats, from coastal to oceanic waters with a strong preference for the shelf edge. This was previously described in the area, especially for *Globicephala melas* (Kiszka et al., 2007; Certain et al., 2011). Our model predicted lower densities over shelf habitats of the BoB, western EC and CS, consistent with the disparate yet regular incursions of the species within these shallower waters (Kiszka et al., 2004). The presence of *Globicephalinae* within both oceanic and shelf waters was consistent with the known diet of the two species in the area: oceanic squids, benthic octopods and neritic fishes in the BoB (Spitz et al., 2011), cuttlefish in the EC (De Pierrepoint et al., 2005) for long-finned pilot whales; benthic cuttlefish for Risso's dolphins in the BoB (Spitz et al., 2011).

Northern gannets: Northern gannets exhibited strong seasonal variation in their habitat preferences, inducing contrasted distributions between seasons. Tracking studies following gannets from European colonies during their post-breeding movements have shown that the species exhibited several large wintering areas: individuals from northern colonies overwintered within the southern North Sea and eastern EC; individuals from eastern UK colonies (Bass Rock and Grassholm) overwintered within our study area, while individuals from the French colony of Rouzic overwintered in western Africa (Fort et al., 2012). Therefore, the gannets sighted during winter were of a different population than those sighted in summer. Although the BoB, CS and EC were identified as wintering grounds for gannets, this study only identified broad areas, due to the uncertainty around geolocations and the very large scale of the study (Kubetzki et al., 2009; Fort et al., 2012).

Habitat modelling over this specific area therefore allowed identification of precise finer-scale overwintering grounds of the species. The results highlighted two main areas, characterised by different oceanographic processes, thus habitat preferences exhibited by gannets varied accordingly. The first wintering ground was the eastern EC, where they used shallow depth combined with important positive SSH; the second was the southern BoB, where they preferred shallow and warmer waters combined with low tidal currents. Substantial densities were also predicted in the western CS, where ecological characteristics were similar to that of the southern BoB shelf. This dichotomy in wintering grounds choice illustrates the known flexibility of gannets: they selected wintering areas of different characteristics among favourable areas available within the maximum range around colony of origin (up to 5000 km, Fort et al., 2012).

During reproductive seasons, the species was strongly linked to colonies, with predicted densities linearly decreasing with increasing distance from colonies, to a maximum distance of 250 km. This range matched the known mean foraging range for European colonies in the UK and France, which was between 100 and 223 km (Grecian et al., 2012). Within this range, the species targeted habitats with strong monthly variations of SST and thermal fronts persistent at the monthly scale, mainly corresponding to coastal and central EC tidal fronts. This attraction to these particular persistent structures has already been shown for northern gannets (Grémillet et al., 2006; Pettex et al., 2010; Scales et al., 2014).

Auks: Wright and Begg (Wright and Begg, 1997) in Scotland, found the link of common guillemots to shore relaxed during post-breeding season, when guillemots were linked to shallow depth and low tidal strength. Here, we showed that this preference might depend on areas. Indeed, in the southern BoB, auks targeted shallow depth and low tidal velocity but, in contrast, auks wintering in the eastern EC clearly targeted shallow cool waters associated with strong SSH. In the eastern EC they were mostly predicted within embayments (Bay of Somme, Bay of Seine and

along the English coast). Globally, a similar overall pattern was shown for auks as compared to gannets, but with reduced bimodality between the eastern EC and southern BoB. During breeding seasons, auks were, as expected, concentrated around colonies, within a range of 50 km. The highest densities were predicted around colonies between Lyme Bay and the Isle of Wight, and around Irish colonies. Auks seemed to avoid French coasts of the EC, where SSH was too high. Therefore, our result confirmed the expectation of a very strong tie of auks to their colony during breeding season, with a reduced foraging range compared to some other seabirds (del Hoyo et al., 2010; Wright and Begg, 1997).

Northern fulmars: The study area represents the southern range of the species (Cadiou et al., 1997; del Hoyo et al., 2010). Our results for the winter season seemed to locate this limit around 46°N, and the sharp drop in the relationship to SST might indicate that the species do not wander over waters with a temperature warmer than 12°C. In summer, the southern limit of its range was still visible, with a strong drop of densities for waters warmer than 16°C. The species ranged within 100 km from colonies, preferably beyond 50 km from the coast. Within these limits, the species seemed to target weekly frontal zones. Overall, the abundance of the species remained lower than in winter, when migrants overwinter in the area. These results were consistent with tracking studies that have shown the species to forage far from colonies, up to hundred kilometres away, and over thermal fronts (Weimerskirch et al., 2001; Mallory, 2006; Edwards et al., 2013).

Black-legged kittiwakes: Black-legged kittiwakes breeding in western Europe have extended populations from the BoB to the Barents Sea, with the bulk of the breeding population in the British Isles and further north. Colonies in France and Spain are at the southern limit of the species range and are small compared to those located further to the north (Cadiou et al., 1997). Breeding populations tend to concentrate around colonies in summer and disperse widely across ENA waters in winter (Frederiksen et al., 2012). This pattern is in line with the strong difference in densities predicted in the present study region between the two seasons, with far fewer birds in summer.

This might also explain the overall preference for cooler waters in both seasons. In winter, the species targeted cool water areas with moderate hydrological activity and low thermal variations at the monthly scale while in summer it showed different preferences in the EC compared to the pelagic waters of the BoB. In the EC, the species, probably locally breeding individuals, targeted cooler waters with strong thermal gradient, important SSH and spring tide currents, corresponding to waters close to local colonies along the French and English EC coasts. However, non-nil densities were also predicted across waters with other characteristics: high values of mean SST and lower values of mean SSH (Fig. 12), related to some birds sighted over oceanic waters during the summer season, hence exhibiting sharply different habitat preferences. These individuals might be either non-breeders or failed breeders foraging farther from their colonies compared to most individuals.

Small-sized shearwaters: Small-sized shearwaters were mostly present during the reproductive season, in summer. The group exhibited a clear preference for coastal waters (less than 50 km from the coast), within a range of 250 km from their colony. This pattern, coupled with a preference for warm waters, explained the latitudinal gradient in densities, increasing up to the Gironde estuary. The group avoided the eastern EC. However, the high density predicted within Pertuis-Charentais might be an extrapolation, since no/few shearwaters are seen in the area during summer.

5. Conclusion

We provided the first assessment of habitat preferences over such a large spatial scale for many species in the area. For example, for many seabird species, knowledge came only from colony-based and tracking studies, and was therefore only based on a limited number of individuals and mostly during breeding season. Here, we provided a complementary population-wide view of the ecology of these species with, in addition, an insight of preferences over both summer and winter seasons. This latter being little if at all documented for most species, we furthermore provided the first assessment of habitat preferences and distribution during winter, especially during the poorly known non-breeding period of seabirds. This was especially the case for fulmars, auks, gannets and kittiwakes. Although their winter distributions were approximated, the ecological processes driving these distributions were up to now mostly ignored.

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Appendix A. Supplementary data

Supplementary data associated with this paper can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.06.011>.

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Appendix S1

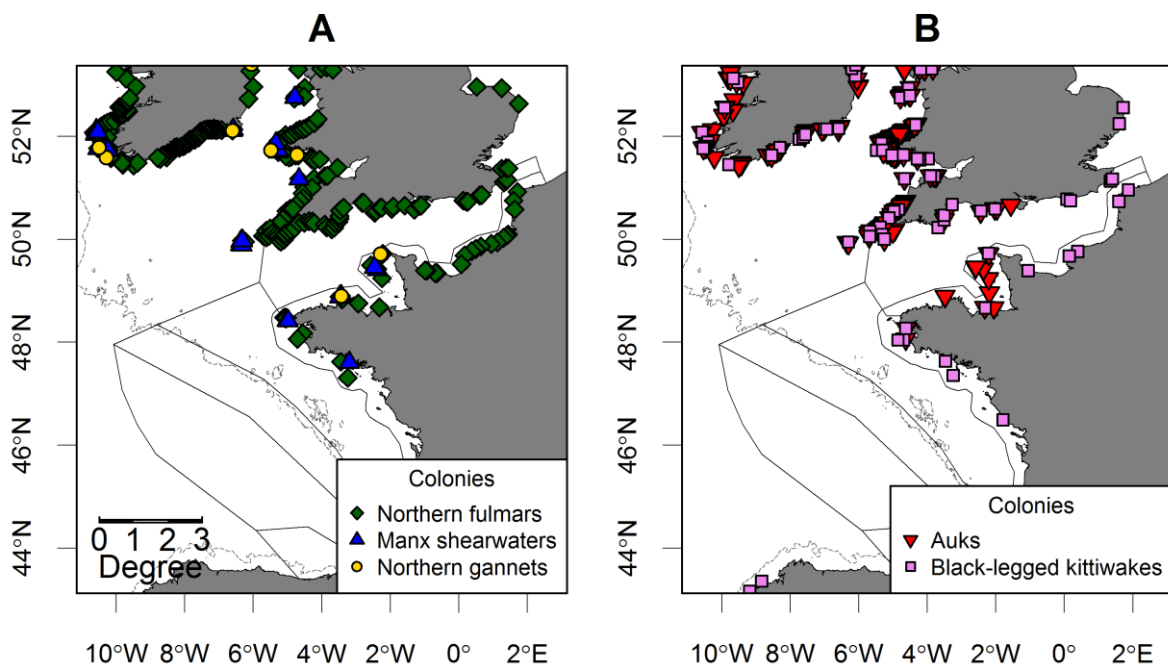
Colonies Locations

Colony locations for studied seabird species in the eastern North-Atlantic have been compiled from several authors in France, Ireland, Great Britain and Spain (Figure 2). Northern gannets breed on discrete locations (Nelson, 2002), well documented and surveyed, with one large colony in France (Rouzic), two colonies in Channel Islands (Les Etacs and Ortacs), two colonies in Wales (Grassholm and St Margaret's Island), five in Ireland (Bull Rock, Little Skellig, Great Saltee, Ireland's Eye and Lambay Island - not seen in the map) and one in England (Flamborough Head, not seen in the map).

On the contrary, northern fulmar colonies spread along the Irish and western UK coasts (Fisher and Waterston, 1941). In France, the northern fulmars is at its southern range limit, hence colonies installed along eastern Channel French coast and up to southern Brittany are very recent (Kerbiriou et al., 2012). However, colonies in Brittany are scarce, and for some of them not stable over years (Cadiou et al., 2005).

Manx shearwaters breed on several islands, with some colonies common with gannets (Mavor and others, 2005). In Ireland, sixteen colonies spread over Dublin, Wexford, Galway and Kerry provinces; five colonies in Wales; five in Scilly Islands; two on Channel Islands and one in Calf of Man. Finally, five colonies are found in Brittany (Cadiou et al., 2005).

Auks breed along Irish, Welsh, western and southern English coasts, as well as on Channel Islands and some Brittany islands (Birkhead, 1977; Cadiou et al., 2005; Mavor and others, 2005; Reed et al.,



2006; Southern et al., 1965). Finally, black-legged kittiwakes breed all along Irish, western UK coasts, French and English coasts of the Channel, and some colonies in Brittany (Cadiou et al., 2005; Mavor and others, 2005).

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Appendix S2

Distance sampling analysis

1. Method

Distance sampling was conducted on cetacean sightings to investigate the effect of distance and sighting conditions on the detection probability, and estimate the half-effective strip width (ESW). This estimation of ESW was performed by fitting detection functions to the perpendicular distances (extracted from the declination angle measured during sightings).

The analysis was carried out using DISTANCE 6.0 (Thomas et al., 2010) on transects flown with good sightings conditions: Beaufort sea-state ≤ 3 for all species, except for fin whales for which Beaufort sea-state of 4 was also considered. The 5-10% sightings detected at the longest distances were removed from the datasets prior to analysis (Buckland et al., 2001). Different stratification were tested has potentially affecting the detection function: school size, season, sea-state, turbidity, glare severity, subjective conditions on both side of the plane and cloud.

2. Results

ESW was different between English Channel and Bay of Biscay for harbour porpoise, with lower ESW in the first sector (104 m) compared to the second (145 m, Table S2). Beaufort sea-state significantly affected the detection function of small-sized delphinids, with ESW varying from 234 m for best conditions to 165 m for worse sea-states. Concerning bottlenose dolphin, the detection function was affected by cloud coverage, with an ESW of 192 m for coverage from 0 to 4, and 144 m for coverage above 5. However, for *Globicephalinae* no detection covariates affected the detection function: the ESW was 252 m.

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Table S2. Results of Distance Sampling analysis.

Selection for analysis	Cetacean groups	Stratification	Detection covariate	ESW (m)	Histograms of perpendicular distances and fitted detection functions	
	Harbour porpoises	English Channel	Negative exponential (in grey)	104		
		Bay of Biscay	Hazard (in black)	145		
Beaufort sea-state ≤ 3, Subjective Conditions > 3	Small-Sized Delphinids	Half-normal (in black)	Beaufort sea-state	0, 1	234	
		Half-normal (in grey)		2, 3	165	
	Bottlenose Dolphins	Half-normal (in black)	Cloud cover	0 to 4	192	
		Half-normal (in grey)		5 to 8	144	
	<i>Globicephalinae</i>	Half-normal	-	252		

Table S3.1 Correlation matrix, based on the Spearman correlation test. Correlations for winter variables are presented above the diagonal (in blue), while correlations for summer are presented below the diagonal (in orange). Correlations higher than $|0.7|$ are in bold.

		7d									28d					
		Distance closest coast	Depth	Slope	Mean SST	SST var.	SST gradient	Mean SSH	SD SSH	Max. velocity	Mean SST	SST var.	SST gradient	Mean SSH	SD SSH	Max. velocity
7d	Distance closest coast	1	-0,88	0,38	0,36	-0,41	0,67	-0,31	-0,68	-0,49	0,31	-0,49	0,73	-0,16	-0,58	-0,52
	Depth	-0,89	1	-0,51	-0,45	0,44	-0,68	0,42	0,74	0,62	-0,40	0,45	-0,72	0,26	0,64	0,63
	Slope	0,42	-0,53	1	0,34	-0,24	0,37	-0,17	-0,55	-0,62	0,32	-0,15	0,38	-0,01	-0,49	-0,61
	Mean SST	0,26	-0,30	0,27	1	-0,07	0,32	-0,07	-0,46	-0,54	0,99	0,01	0,35	0,09	-0,55	-0,52
	SST var.	-0,21	0,18	-0,11	0,22	1	-0,46	0,32	0,32	0,18	-0,01	0,55	-0,44	0,31	0,24	0,18
	SST gradient	0,58	-0,58	0,25	0,07	-0,29	1	-0,36	-0,51	-0,37	0,27	-0,46	0,87	-0,22	-0,45	-0,37
	Mean SSH	-0,18	0,30	-0,08	0,06	-0,08	-0,09	1	0,11	0,25	-0,04	0,42	-0,39	0,82	0,09	0,21
	SD SSH	-0,72	0,77	-0,57	-0,32	0,04	-0,44	0,09	1	0,68	-0,43	0,30	-0,53	-0,01	0,90	0,70
	Max. velocity	-0,58	0,70	-0,63	-0,45	0,09	-0,39	0,18	0,75	1	-0,53	0,10	-0,40	0,07	0,66	0,96
	Mean SST	0,26	-0,29	0,27	0,98	0,14	0,07	0,10	-0,29	-0,44	1	0,11	0,30	0,11	-0,52	-0,50
28d	SST var.	0,02	-0,05	0,05	0,38	0,26	-0,05	-0,10	-0,13	-0,27	0,25	1	-0,49	0,38	0,21	0,11
	SST gradient	0,64	-0,65	0,27	0,03	-0,23	0,80	-0,21	-0,46	-0,38	0,01	-0,03	1	-0,25	-0,45	-0,41
	Mean SSH	-0,20	0,34	-0,14	0,17	0,06	-0,22	0,67	0,19	0,28	0,18	0,07	-0,27	1	-0,14	0,06
	SD SSH	-0,50	0,53	-0,41	-0,03	0,06	-0,35	0,17	0,80	0,63	0,04	-0,20	-0,40	0,31	1	0,65
	Max. velocity	-0,58	0,68	-0,63	-0,51	0,04	-0,38	0,17	0,74	0,98	-0,48	-0,31	-0,37	0,26	0,60	1

Appendix S4

Cetacean and seabird sightings

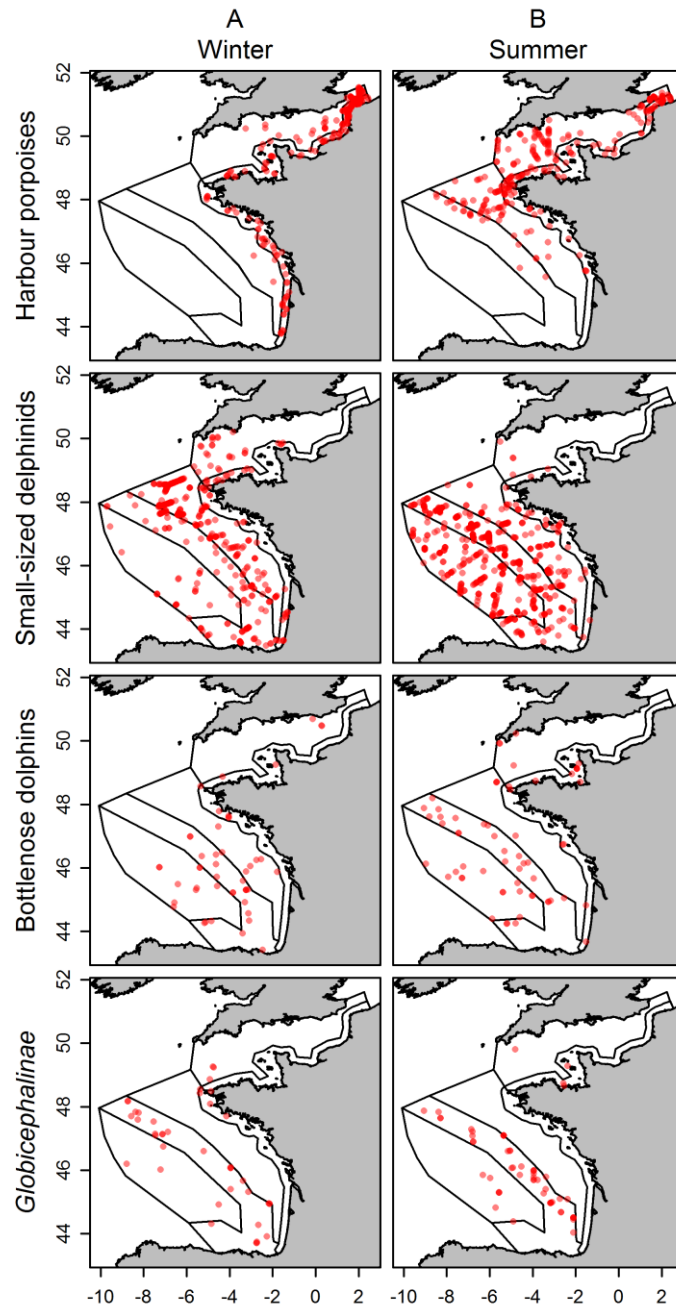


Figure S4.1 – The winter and summer cetacean sightings within eastern North-Atlantic.

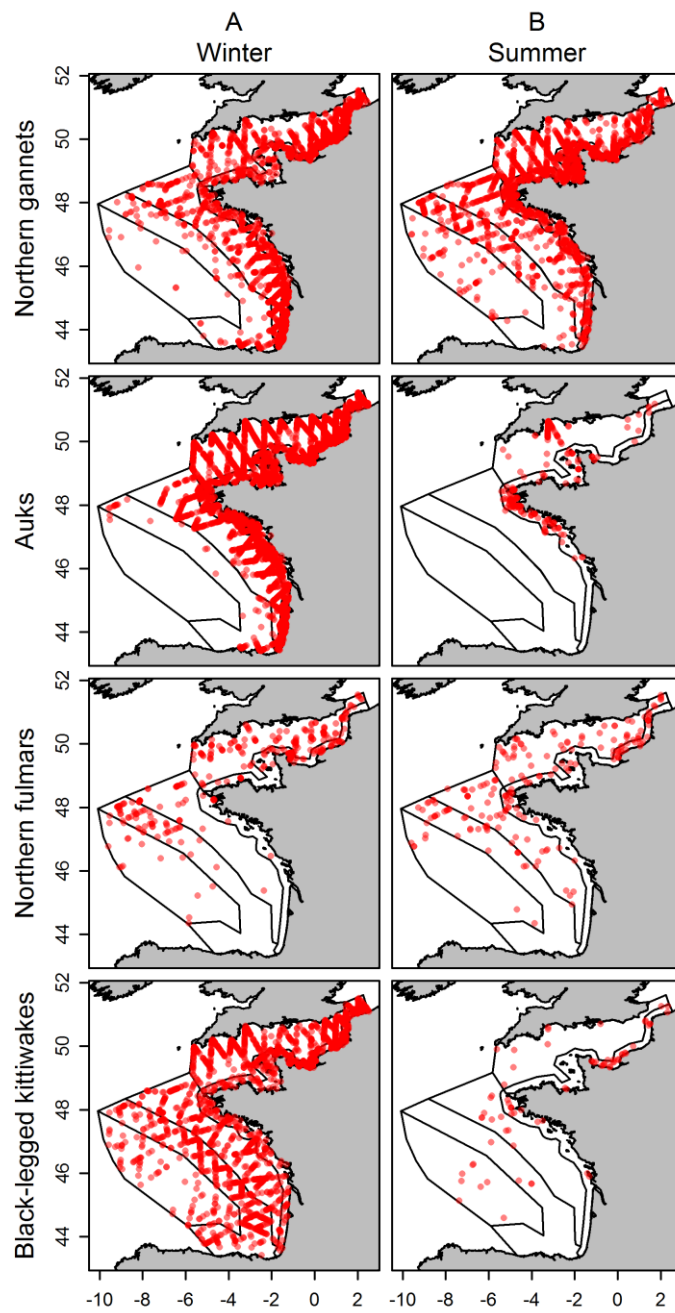


Figure S4.2 – The winter and summer seabird sightings within eastern North-Atlantic.

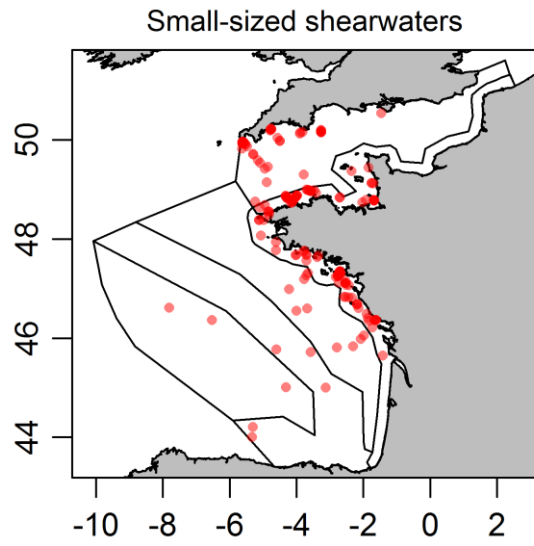


Figure S4.2 – The summer sightings of small-sized shearwaters within eastern North-Atlantic.

Appendix S5

Coefficient of variations for cetacean and seabird predicted distributions

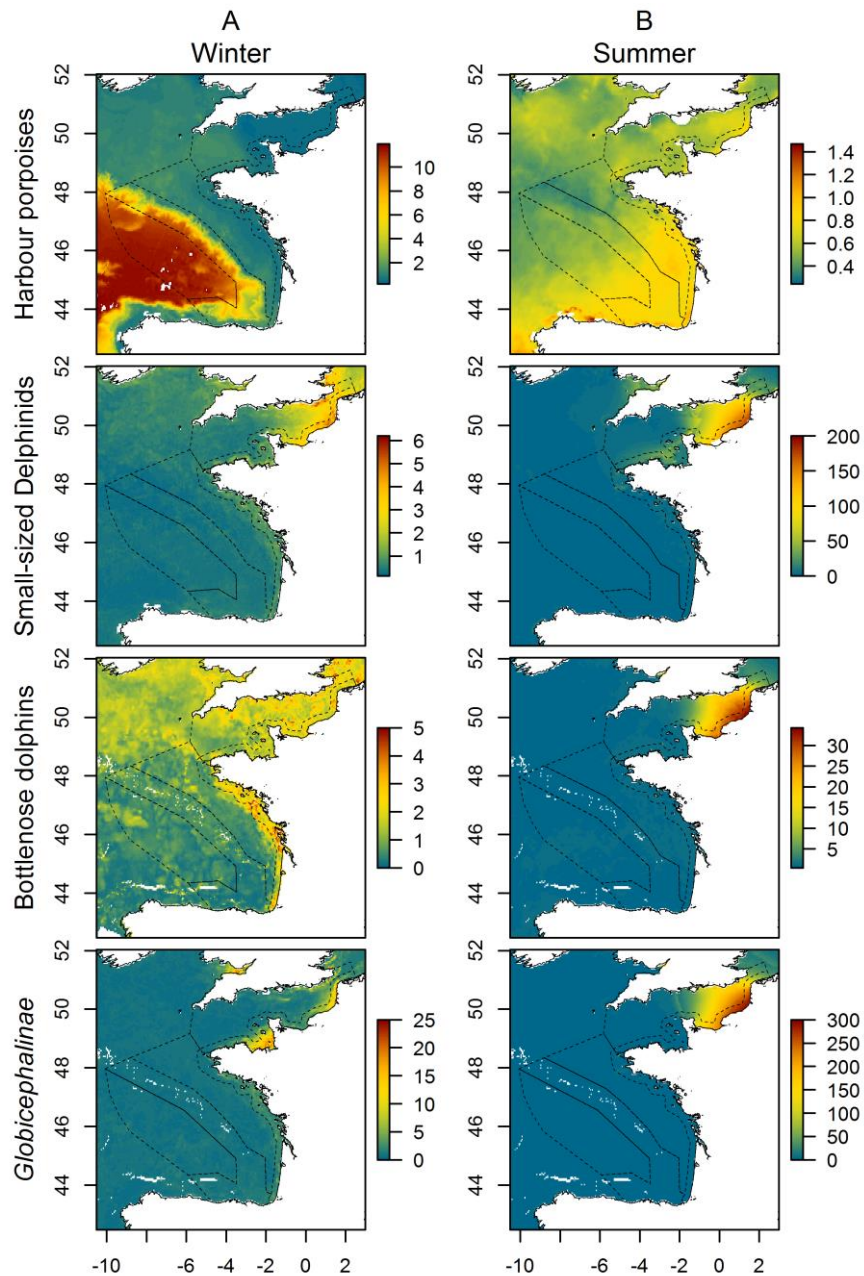


Figure S5.1 – Coefficient of variations around mean predictions of cetaceans based on habitat models in winter (A) and summer (B). Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

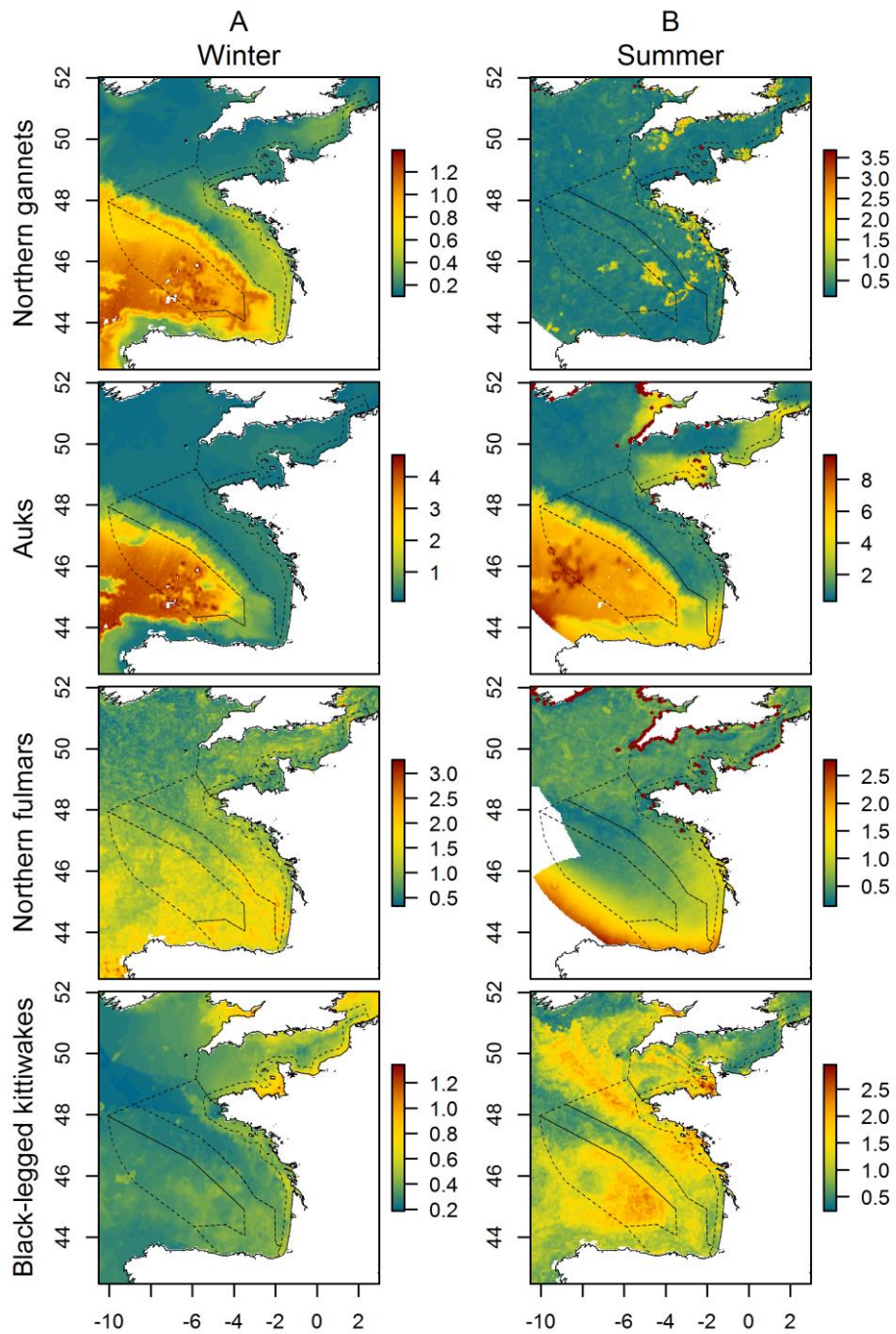


Figure S5.2 – Coefficient of variations around mean predictions of seabirds based on habitat models in winter (A) and summer (B). Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

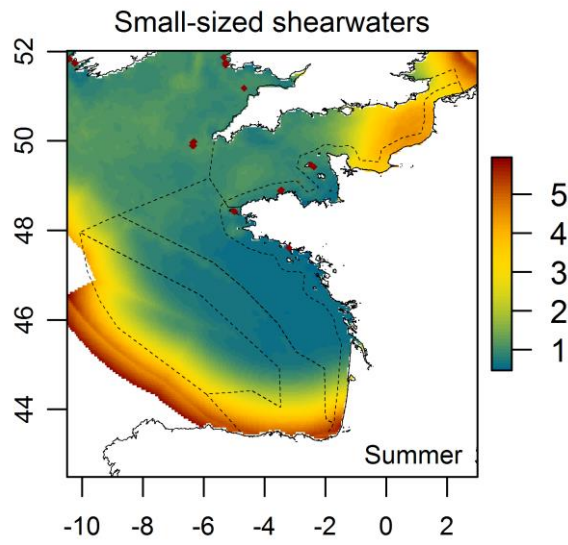


Figure S5.3 – Coefficient of variations around the mean predictions of small-sized shearwaters based on the summer model. Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

Appendix **D**

Chapter 4 - Ocean inter-annual
variability impacts the stability of
highly mobile top predators habitat
preferences

Supporting information to Chapter 4: in preparation paper.

Ocean temporal heterogeneity impacts the stability of top predators habitat preferences

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Abstract

Most oceanographic systems are characterised by interannual variability in the timing, extent and intensity of their seasonal patterns, especially shelf ecosystems. These interannual variations in habitat availability have important consequences for top predator's ecology. The purpose of this study was to explore the potential variations of habitat preferences exhibited by five mobile top predators species within the Bay of Biscay (BoB), throughout an entire decade thanks to oceanographic cruises performed every spring since 2004. This was achieved through the summary of environmental conditions within the BoB with a Principal Component Analysis (PCA), which identified three habitats spatially varying among years. The PCA dimensions were used to explore the habitat preferences of predators through Generalised Additive Models. We fitted a model without and with year as an interaction term in order to quantify the annual variations in habitat preferences. Our results showed that predators exhibited a gradual response to the ecosystem interannual heterogeneity, from bottlenose dolphins and auks with a narrow habitat preference particularly stable over the decade, to northern gannets with wider habitat preferences pretty varying among years.

Keywords: habitat preference, flexibility, temporal variability, cetaceans, seabirds, Bay of Biscay

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1 Introduction

The marine environment is often characterized by a large spatial and temporal variability (Barry & Dayton, 1991), from small to large scales, in particular in the case of the pelagic ecosystem. In the last years, the knowledge regarding the adaptation and response of mobile predator species to these several scales of variability has been improved. For example, several top predators has been shown to target predictive structures such as shelf edges, frontal zones associated to upwellings or eddies (*e.g.* Begg & Reid (1997); Weimerskirch (2007); Scales *et al.* (2014); Cotté *et al.* (2015)). To overcome the alternate of favourable and unfavourable seasons, some species perform long-range migrations to ensure they frequent favourable habitat throughout the year (Shaffer *et al.*, 2006; Egevang *et al.*, 2010), or switch between habitats through their life-time as an answer to the encountered constraints (Weimerskirch *et al.*, 2014; Lambert *et al.*, 2016a,b).

However, the pelagic ecosystem is also characterised by interannual variability in the timing, extent and intensity of their seasonal patterns, as for example over the shelves where the pelagic ecosystem is highly dependent on the nutrient inputs from river discharges for example (Longhurst, 2007). This variability leads to a dynamic mosaic of habitats, which are variable in both space and time, and thus can be difficult to locate and track. Although we know top predators are able to track some spatial variations in the localisation of particular features, especially if these variations are predictable (*e.g.* southward movement of eddies in the Mozambic Channel by frigatebirds, Kai *et al.* (2009)), some predators might also cope with this variability by switching between available habitats depending on years.

Top predators do not forage randomly over the ocean but target favourable and predictable areas to sustain their energetic needs at lower cost (Fauchald, 1999). However, all predators do not exhibit the same constraints and some are more flexible regarding their foraging habitat than other, since they are able to forage on a wider range of prey for example (*e.g.* northern gannet, dolphins, Nelson (2002)), while some species rely exclusively on one or two high quality prey species, and thus are dependent on particular habitat, sometimes leading to collapse in population when perturbations are introduced in the system (*e.g.* auks in the North Sea, Wanless *et al.* (2005)).

This study aimed at exploring the temporal variability of top predators habitat preferences among years. The goal was to address whether the strategies of predators regarding this interannual variability depends on their intrinsic characteristic or whether we could define a global pattern of top predators response to the temporal heterogeneity of the ocean. Depending on species characteristics, we expected two main strategies: (i) some species would use the same pelagic habitat year after years, hence spatial variations of distribution would express spatial variations in habitat, leading to the absence of species in case of habitat absence; (ii) other species would exhibit greater variability in habitat preferences among years, either because they would use all available habitats or remain within the same area irrespective of whether the corresponding habitat changed.

To explore habitat preferences among years however, we first had to characterize these habitats. As previously stated, the pelagic habitats are highly dynamic and are often difficult to segregate (Barry & Dayton, 1991; Longhurst, 2007). Here, we chose to identify the several habitats available within the study area, and their interannual variations, thanks to an ordination technique (Principal Component Analysis, PCA). Such technique allows to summarize the environmental conditions to identify particular environmental features. Then, Generalized Additive Models (GAMs) were used based on these habitats to highlight the habitat preferences of several predators, and whether these preferences varied among years. This study was based on a decadal oceanographic survey (2004-2013) conducted within the Bay of Biscay (BoB), north-eastern Atlantic shelf, which provided in-situ environmental variables concurrently with observational data of cetacean and seabird species.

2 Material & Methods

2.1 Survey data

The study was based on the pelagic oceanographic PELGAS (PELagique GAScogne) surveys, conducted by IFREMER onboard the R/V Thalassa, to study the abundance and distribution of small pelagic fish and monitor the BoB pelagic ecosystem. These surveys are conducted every spring since 2000, sampling parallels transects from the coast to the shelf break, orthogonal to the main isobaths (Figure 1, Doray et al. (2014)). Actual sampling design and total survey effort varied each year depending on the annual extent of the survey, sometimes extending farther than the shelf edge. However, in the present work, we only conducted the analyses on the area commonly sampled during all the studied years to ensure comparability.

Top predator observations were carried out from 2003 onwards following a line transect protocol (Buckland et al., 2001), but the study focused on a period from 2004 to 2013. Effort spanned from sunrise to sunset whenever the vessel was moving at ≥ 8 kn, while prospecting a transect or *en route* between two transects. Effort stopped during trawlings. The main observation platform was the upper deck of the R/V Thalassa (16 m above sea level), but when weather deteriorated (strong winds or rain), observation platform switched to the ship bridge (14 m above sea level). Two trained observers scanned with naked eyes the 180° ahead of the bow, each observer scanning 90° on each side of the bow. Observation bout duration was no longer than one hour. Observation conditions (Beaufort sea-state, swell, glare, cloud cover, platform) were recorded every hour, or whenever observation conditions changed. For each sighting, species composition, number of individuals, behaviour, distance and angle to the observer were recorded. Attention was paid not to record individuals attending the vessel. In-situ environmental variables were routinely collected along transects, such as surface and bottom temperature, salinity, mixed layer depth and surface chlorophyll a concentration (Doray et al., 2014).

2.2 Habitats availability over years

In order to explore the several habitats available and their extent variations over the decade, we performed a PCA over environmental data. The in-situ variables available for all years were summarised over a 0.25° grid (Appendix A): sea surface temperature (SST), sea bottom temperature (SBT), mixed layer depth (MLD), sea surface salinity (SSS). SST gradient (SSTg) was computed over the same grid as the largest difference between each cell and its neighbours. Bathymetry and slope aspect were summarised in the same way from the GEBCO database. Unfortunately, surface chlorophyll concentration measured in-situ was not available over the whole area for the whole decade, hence we instead used MODIS monthly composite surface chlorophyll a (CHL) concentration (in May, <http://oceancolor.gsfc.nasa.gov>), and Eppley-VGPM net primary productivity (NPP) at the same temporal resolution (<http://www.science.oregonstate.edu/ocean.productivity>). These two variables were then summarised over the PELGAS grid.

We then performed a hierarchical cluster analysis on the PCA result in order to identify habitats available in the BoB. The resulting clusters were plotted each year to visually assess their spatial variations. PCA was carried out in R version 3.2.3 (R Core Team, 2015) with the package FactoMineR (Husson et al., 2016), the hierarchical cluster analysis with the function `hclust` using the "ward.D" method.

2.3 Species habitat preference per year

The exploration of habitat preferences over the decade was performed through habitat modelling for five group of species: northern fulmar (*Fulmarus glacialis*), northern gannet (*Morus bassanus*), auks (common guillemot *Uria aalge* and razorbill *Alca torda*), common dolphin (*Delphinus delphis*) and bottlenose dolphin (*Tursiops truncatus*).

We first transformed sighting data into the same format as the covariates, the 0.25° grid. Firstly, we summed the numbers of observed individuals per cell as well as the effort deployed in each cell by multiplying the lengths of all segments falling within a cell by twice the Effective Strip Width (ESW) of each species. Hence, the effort

associated to observations was species-specific. The distance sampling analyses performed to obtain these ESW are detailed in Appendix B. These analyses were performed only over effort realized with Beaufort sea-state lower than 4 and subjective conditions excellent to medium. All sightings related to individuals recorded as attracted or repelled from the boat were removed, as well as individuals coming to the bow, scavenging behind fishing vessels or coming from the back of the observation platform.

To explore habitat preferences of species, habitat modelling was performed using GAMs (Wood, 2006) relating the number of individuals (response variables) to predictors through a logarithmic link function with the Tweedie error distribution, and with the sampled area as an offset. The Tweedie is an exponential family distribution with variance proportional to the power θ of the mean. A Tweedie random variable with $1 < \theta < 2$ is a sum of N gamma random variables where N has a Poisson distribution: when $\theta = 1$, the Tweedie is a generalization of a Poisson distribution, when $\theta = 2$ the Tweedie distribution is a gamma distribution. The choice of the best θ value is automatically made when fitting the model ("tw" function from the `mgcv` package, Wood (2011)).

Two kinds of models were computed. First, the null model (*i.e.* model supposing no variation across years, a basal model providing "mean" preferences) included the three main axes of the PCA as well as the distance to the closest colony for seabirds as simple terms (See Appendix A). Second, the interaction model included the same four variables, but with year as an interaction term. The inclusion of year as an interaction term allowed the relationships between response variable and covariates to be different for each year. The maximum degree of freedom for smoothers was constrained to 3 to avoid over-fitting the data (4, considering the offset). Explained deviances as well as p-values of each terms were examined.

From the two models, predictions were made for each year. In order to compare the variations of distribution between the two models, we computed their difference for each year. First, we standardised the yearly predictions from each model by their maximum predicted density so that the computed difference do not reflect the variation in abundance between the two models, but only the spatial pattern of their distribution. Then the difference was computed as the prediction from the interaction model minus the prediction from the null model.

To explore preferences for any habitats identified in the BoB among years, we extracted the abundances within each habitat clusters and related it to their respective surfaces, by years. To allow the comparison between the two models, the predicted densities were standardised by the maximum predicted density that can be encountered within the BoB for that particular year. These analyses allowed to compare the annual variation of preferences compared from a basal model, *i.e.* to test whether the preferences for a year diverged from the basal ones (the "mean" preferences as identified from the ten years as a row).

The model fitting and the predictions were done by using R 3.2.3 "Wooden Christmas-Tree" (R Core Team, 2015) using the `mgcv` package, while the prediction differences and the extraction of density within available habitats were done in R version 2.15.3 "Security Blanket" using the `raster` package (Hijmans et al., 2014).

3 Results

3.1 Habitats availability over years

The three first PCA dimensions accounted for 68.7% of the variance of the data. The first dimension explained 36.0% of the variance, the second one 17.1% and the third 15.7% (Figure 2a). The first dimension (Dim 1, Figure 2b, c) was mainly related to SSS, bathymetry and slope (highly correlated) with higher values to the right end of the axis, as well as by CHL and NPP with higher values to the left end of the axis. Hence, shallow waters with reduced salinity were more productive than deep waters with high salinity. The second dimension (Dim 2, Figure 2b, d) was mainly explained by temperature, with high values of SST, SSTg and SBT for negative values of the dimension. The MLD was similarly important over the two PC, with negative correlation to CHL/NPP for the first dimension, and negative correlation to temperature for the second dimension. The third dimension (Dim 3, Figure 2c, d) summarised all variables, with MLD and SSS opposite to the other seven variables.

The hierarchical cluster analysis over the PCA resulted in three main habitats (Figure 3a). Habitats 1

and 2 were related, while habitat 3 was well separated. The three clusters were mainly separated over the first PCA dimension (Figure 3b–d): (1) shallowest waters with lowest salinities, and highest NPP and CHL; (2) waters with shallower depth, lower slope/CHL/NPP and higher SST compared to the averaged situation; (3) deepest waters associated with steep slope and high salinities, as well as lower CHL/NPP. The first two clusters corresponded to the shelf habitat, the first being the coastal productive habitat mainly associated to river plumes, the second gathering shelf waters associated to shallow waters and low CHL/NPP. The third cluster corresponded to the shelf break (Figure 3). The spatial extent of these habitat varied among years, with for example the habitat 1 almost absent in 2011, or the habitat 3 spreading farther over the shelf in 2004, 2005 and 2010 (Figure 4). Interestingly, on the second axis, driven by the SST, clusters 1 and 3 were both colder than the cluster 2.

3.2 Sightings data

Over the whole PELGAS surveys, yearly encounter rates were low for most species (Table 1) except northern gannet, which was the most sighted species, with up to 92.6 individuals per sampled 100 km². However, these encounter rates showed strong spatial patterns (Figure 5), with some variations among years (see Appendix C for sightings and encounter rate maps per year). Overall, fulmars were mostly found over the outer shelf in the northern BoB; gannets were widely dispersed over the whole BoB; auks were concentrated along the coast; common dolphins were found over the whole shelf, especially in the central part and bottlenose dolphins were mostly encountered along the southern BoB shelf edge (Figure 5).

3.3 Species habitat preference per year

3.3.1 Northern fulmars

The null model resulted in a explained deviance of 21.8%, with axes 1 and 3 as well as the distance to the closest colonies as significant variables (Table 2). The northern fulmars exhibited a preference for the positive values of the dimension 1, for low positive values of the third dimension and for distance to the colonies lower than 200 km (Figure 6a). The prediction from the null model was overall even among years, with highest densities along the outer shelf and the species absent from the southern BoB, although high densities also occurred over the central shelf in 2007 and 2011 (Figure 7a).

In the interaction model, the four interaction terms were significant and the explained deviance was higher, with 34.5% of the deviance explained by the model (Table 2). The significance of the interaction terms and the higher explained deviance indicated that the relationship described above varied among years. Hence, some differences among years were predicted (Figure 7b). The overall pattern was still predicted, but some variations of densities among years occurred, with a peak in 2011 and lower densities in 2004 and 2013. In addition, the distribution pattern was more variable among years.

The difference between the standardized predictions from the interaction and null models, indeed revealed some spatial variations in the predicted distributions (Figure 7c). For example, in 2005–2008 the northern fulmar was predicted farther south by the interaction model than by the null model, while in 2010–2013 it was the opposite, which differences were probably linked to the relationship variations to distance to the colony. In 2004–2007 the species was less predicted along the shelf edge than by the null model, but more over the shelf. In 2010–2013, this species was overall less predicted over the shelf than by the null model.

This was confirmed by the predicted densities by habitat clusters (Figure 7d). In 2004–2006, as noticed by the difference maps, the interaction model predicted the species in higher densities in the habitat 2 than the null model, while in 2010–2013 it was predicted less. Despite these differences, both models predicted a gradient of preference from the habitat 3 to 1 in all ten years. This indicated that the global preference remained consistent over years, but still exhibited some spatial variations.

3.3.2 Northern gannets

The null model for northern gannets explained 18.2% of the deviance, with all terms significant (Table 2). The species avoided the lowest positive values of the first dimension, preferred the highest negative values of the second dimension, preferred the negative values of the third dimension and seemed to prefer either areas closer than 200 km or larger than 400 km from closest colony (Figure 6). The species was mainly predicted along the coast of Brittany, with high densities in the southern BoB during all years except 2007, 2008 and 2011. High densities were also predicted along the southern shelf edge in 2004 (Figure 8a).

The inclusion of the year as interaction term clearly improved the model, with 34.9% of explained deviance and all terms significant (Table 2). This interaction seemed to mainly capture the variation of overall density observed among years (Figure 8b), but some variations in distribution compared to the null model also appeared. In 2004 for example (Figure 8c), the species was less present over the shelf than predicted by the null model, but more predicted off the Gironde estuary; in 2008 it was less predicted along the coast than by the null model; in 2006–2007 the northern gannets were more predicted over the central northern shelf than by the null model. However, in 2010–2011 the spatial distribution was predicted the same with both models.

The null model highlighted a gradient from habitat 1 to 3, except in 2004, 2007 and 2012 when some differences occurred (Figure 8d): in 2004, the density in habitat 1 and 3 were equivalent, while in 2007 and 2012 the predicted density were equal in all three habitats. Despite the spatial differences, this overall pattern was also predicted by the interaction model, except in 2007 when it predicted a gradient from habitat 3 to 1.

3.3.3 Auks

The auks null model explained 35% of the deviance, with dimensions 1 and 3 significant (Table 2). Auks preferred highest negative values over the two dimensions (Figure 6). The model clearly predicted the species associated to the river plumes (Figure 9a). The explained deviances of the interaction model reached 54.1%, and all the variables were significant (Table 2). The overall predicted distribution was similar to the null model, but the interaction model clearly accounted for the increasing of auks density over the decade (Figure 9b). Nevertheless, some little spatial variations occurred.

In 2004, 2005, 2009, 2012 the auks were less present in the Gironde estuary than predicted by the null model, while in 2005–2007 it was more predicted off the Adour estuary and in 2008 it was more predicted over the Loire estuary (Figure 9c). Despite these spatial variations, both the null model and the interaction model clearly predicted a preference for the habitat 1 (Figure 9d). In 2008, the species was predicted in higher densities in the habitat 1 by the interaction model than by the null model, while in 2004 and 2012 it was predicted less. Some differences also occurred for the other two habitats, such as in 2004 and 2006 when the interaction model predicted higher densities in the habitat 3 than predicted by the null model, or in 2006–2008 when it predicted higher densities in the habitat 2 compared to the null model.

3.3.4 Common dolphins

The null model explained 11% of the deviance despite the non-significance of the three variables included in the model (Table 2). Indeed, the relationships between the number of individuals and the three PCA dimensions were flat (Figure 6). As a result, the prediction was homogeneous (Figure 10a), and predicted densities were equivalent for the three clusters (Figure 10d). The interaction model did not improved the model fit, with only 13% of explained deviance and none variables statistically significant (Table 2, Figure 6).

3.3.5 Bottlenose dolphins

The null model for bottlenose dolphins reached 32.9% of explained deviance, with dimensions 1 and 3 as significant variables (Table 2). The species preferred high positive values over both first and third dimensions (Figure 6). This preference resulted in the species being predicted mostly over the shelf edge (Figure 11a). The interaction model exhibited the same significant variables, for an explained deviance of 37.9% (Table 2). The

predicted distribution was overall the same as with the null model (Figure 11b,c). The bottlenose dolphins hence clearly preferred the habitat 3, with no variations among years (Figure 11d). However, in 2005–2008, some individuals were also predicted over the shelf, and the predicted densities within habitat 2 were higher than predicted by the null model, although these densities remained low compared to habitat 3.

4 Discussion

4.1 Methodological consideration

The purpose of this study was to explore potential variations of habitat preferences exhibited by five mobile top predator species in the BoB, over a decade (2004–2013). To do so, we first described the habitats available over the BoB thanks to a PCA, which is a conventional method to describe and highlight relationships between a set of variables (Jongman et al., 1995), here the environmental conditions at a 0.25° grid cells.

An interest of a PCA is the reduction of dimensions describing the dataset, through the summary of a set of variables into a reduced number of dimensions (here, from nine to three). In addition to this reduction, the PCA dimensions also consider the combinations of variables occurring within the dataset. Hence, using PCA dimensions rather than raw variables in the habitat modelling had several advantages. The interpretation of results is facilitated by the lower number of covariates included in the model, and the model consider both the effect of variables taken independently and the potential effect of combinations of these variables, rather than their simple additive effects. These combinations are incorporated directly in the model through the PCA dimensions, without having to fit interaction terms between raw environmental variables as in a traditional GAM.

To infer the habitat preferences of species, we could have explored the position of sightings over the multi-variate space of the PCA, however this method cannot help assessing any spatial variations in these preferences. This spatial dimension is included within the habitat models, which allows spatialize these preferences through the mapping of predicted densities.

Finally, the PELGAS survey aimed at studying small pelagic fishes and therefore is constrained to the BoB shelf. Yet we know from larger scale survey (*e.g.* Lambert et al. (2016b) in the area), that both common and bottlenose dolphins preferentially target the slope. Given the slope was only marginally sampled with the PELGAS survey (only the upper slope), habitat preferences highlighted here should be considered as a subset of the habitat preferences of these two pelagic species, only based on their neritic populations.

4.2 Pelagic habitats availability

Thanks to the PCA, we were able to identify three main pelagic habitats in the BoB, and to describe their variability in spatial distribution and extent among years, that is their availability (Figures 3 and 4). The PCA highlighted two independent environmental gradients in the BoB (the two first PCA dimensions) driving the segregation between pelagic habitats. The first gradient segregated the river plumes (habitat cluster 1) characterized by high values of CHL/NPP and low SSS from the shelf edge (habitat cluster 3) characterized by high depth, steep slopes and high SSS.

The second gradient was independent from the previous one. It was mainly driven by temperature variables, which were opposed to other variables. This gradient did not segregate between the first two habitats, both characterised by cold waters, but segregated a third habitat from the other two, corresponding to the shelf (habitat cluster 2), characterized by warmer temperature but reduced CHL/NPP and depth/slope. The habitat clusters 1 and 3 were both characterized by low SST, but for different reasons since river plumes had low SST due to freshwater inputs (Jegou & Lazure, 1995), while slope was associated to upwelling of colder deep oceanic water (Green et al., 2008).

As it was associated to a topographic feature, the habitat cluster 3 was the less varying habitat among years, although it spread farther over the shelf during some years (2004–2005, 2010). On the opposite, the habitat

cluster 1 was associated to the more dynamic feature, by nature, and its extent varied extensively among years. Indeed, the extent of river plumes depends on the freshwater run-offs, that is on the rainfall within drainage basins during the previous months, as well as on wind patterns. For example, the habitat cluster 1 was almost absent in 2011, when the river plumes were reduced due to severe rainfall shortage in April, while in 2009 strong winds extended the river plumes offshore.

4.3 Top predators response to the decadal spatio-temporal variability of available habitats

The comparison between models with and without the year as interaction term allowed us to assess whether the habitat preferences of species varied among years. Given we had both specialized and plastic species, we expected to find two strategies: (i) species with similar habitat preferences among years versus (ii) species exhibiting important variability in their habitat preferences.

In contrast with that expectation, our results showed a gradual response to the ocean interannual variability across species, associated to their flexibility. The species showing narrower habitat preferences exhibited the stronger stability in these preferences among years while the species with loose preferences exhibited higher variability among years.

The most extreme case was bottlenose dolphins, for which no difference occurred between the null and the interaction models, neither in terms of explained deviance, predictions nor predicted densities per habitat. Bottlenose dolphins were confined to the shelf edge during the whole decade, with densities an order of magnitude higher within habitat cluster 3 compared to the other two habitats. This preference was in line with the known ecology of the species in the area, either from large-scale surveys (Lambert et al., 2016b) or from diet analyses (Spitz et al., 2012), despite the fact the PELGAS survey is constrained to the shelf and only touches on the upper shelf break. Nevertheless, the model predicted some bottlenose dolphin intrusion within the shelf, especially in 2005–2008, even up to the coast in 2007. This preference for the shelf edge was also consistent with the known ecotype of bottlenose dolphin individuals within the BoB, which have been genetically identified as pelagic (Louis et al., 2014).

The auks also exhibited a sharp preference for a particular habitat, but for the habitat cluster 1, corresponding to the river plumes. However, unlike bottlenose dolphins, some differences occurred among years, as indicated by the improvement of the explained deviance with the inclusion of the year. Although the inclusion of the year mostly allowed the model to predict the increasing in overall abundance of the auks over the decade, auks also exhibited some spatial differences in the use of river plumes among years. Some plumes were preferentially used compared to others depending on the year, such as, for example, in 2004, 2005, 2012 when the auks were less present in the Gironde estuary than predicted by the null model. Despite these small variations, the distribution of auks was mostly linked to spatial variations of the habitat 1, but when this habitat was reduced or particularly contracted, as in 2010–2012, the species occurred over the surrounding habitat 2 as well, hence the not-so-small predicted densities for the habitat cluster 2.

91.6% of auks sightings were of common guillemots, while only 2.0% were of razorbills and 6.4% of sightings were unidentified between the two species. The number of breeding pairs of common guillemots in the western Brittany colony is known to be very low, with only 14 individuals in average between 2000 and 2011 (Cadiou, 2014). Given these numbers, we can reasonably postulate that most of auks sighted within the BoB during the survey period were non breeding individuals. We nevertheless included the distance to closest colony within the models, but this variable revealed to be poorly relevant. Given auks are known to be tightly linked to their colony during the breeding season (del Hoyo et al., 2010; Wright & Begg, 1997), this loose link to colony seemed consistent with the hypothesis of sightings being mainly composed of non-breeders.

Northern fulmars had a clear preference, but the gradient was smoother than for the the two former species which preferred a unique habitat. Fulmars thus exhibited increasing densities from habitat cluster 1 to 3. However, as indicated by the improvement of explained deviances and the predicted densities by habitat, this preference spatially varied among years. This was particularly visible regarding the extension of the species'

range toward southern BoB. If the overall gradient of preference remained stable through the decade, variations occurred in the amplitude of differences in predicted density between habitats: for example, in 2010 and 2011 the preference was clearly for the habitat 3, while in 2004–2006 the preference was equal for the habitats 3 and 2. These variations reflected the more or less widespread presence of the species over the shelf, related to the southward extension of the species' distribution, compared to the shelf edge. However, the species avoided the coastal habitats during the ten years. This preference was in line with known ecology of the species during the breeding period in the area (Weimerskirch et al., 2001; Mallory, 2006; Edwards et al., 2013; Lambert et al., 2016b).

Finally, gannets were the more flexible of the five studied groups of species. The results indicated a strong influence of the year over their habitat preferences. In addition to the improvement of the explained deviance with the inclusion of the year as interaction term, the predictions from this model better corresponded to the observations. This result was pretty consistent with the known plasticity of northern gannets and their flexibility across time (Nelson, 2002). Overall, a gradient of preference from the habitat 1 to 3 seemed to emerge from the data, but the amplitude between the predicted densities varied substantially among years, with no differences between the three habitats during some years. Despite these variations, a distribution with higher densities in the southern Brittany and along the coast up to Gironde, with some occurrence along the shelf edge during some years, was a recurring pattern.

Gannets breeding in the Channel and the Irish Sea, where are found the closest colonies from the BoB, are known to target discrete predictable favourable features, especially the Channel and Irish Sea tidal fronts, and Celtic Sea slope upwelling (Pettex et al., 2010; Scales et al., 2014; Lambert et al., 2016b). The consistency of such a result between studies from different colonies, different years and different methodology (telemetry and aerial survey) suggests a low interannual variability in this habitat preference for breeding gannets in the Channel and the Irish Sea. This would be in line with the overall preference for the productive habitat cluster 1 highlighted here, but not with the overall looser preferences and the important variability among years highlighted by our results.

The higher variability exhibited by gannets in BoB during the PELGAS survey compared to literature might originate from their reproductive status. Indeed, we hypothesized that the sighted gannets were actually non-breeders for several reasons. In our data, most of sighted gannets were identified as immature or juvenile birds (not shown), but there also was significant proportions of adults. To our knowledge, no breeding gannets from French, Irish or Welsh colonies have ever been shown to cross the Brittany tip to forage into the BoB, although breeding gannets from Grassholm (Wales) can perform trips up to southern Celtic Sea (Patrick et al., 2014), and the predicted foraging range around the Rouzic colony was restricted to the northern Brittany (Wakefield et al., 2013). However, since no incubating birds (the activity gannets are involved in during our survey period; Nelson (2002)) have been tagged with GPS, to our knowledge, we cannot completely exclude the possibility that some incubating individuals forage farther south than shown with chick-rearing individuals.

Since non-breeders are less energy-demanding and not central-place constrained, individuals might be more flexible in their foraging habitat compared to breeding gannets, thus explaining the higher variability shown here compared to habitat preferences of breeding adult gannets within the Channel and Irish Sea. This higher interannual variability in habitat preferences for non-breeders compared to breeders would be consistent with the known ecology of the species, which is known to be particularly plastic and flexible once released from reproductive duty (Nelson, 2002).

The common dolphin was excluded from this classification since both models failed to capture the observed variations in their distribution. The small variations predicted by the interaction model did not correspond to the observed distribution, which was consistent with the non-significance of the three variables used for the models. This result suggests that environmental variables used within the PCA were uninformative regarding the ecology of common dolphin, which might probably be driven by other parameters than those used during this study.

5 Conclusion

The purpose of this study was to explore the potential variations of habitat preferences exhibited by five mobile top predator species within the BoB, throughout an entire decade (2004–2013). This was achieved through the summary of environmental conditions within the BoB thanks to a PCA, further used to explore the habitat preferences of predator species through habitat modelling. The use of a PCA allowed us to successfully segregate three pelagic habitats, and to assess their spatial variations among years.

Our results showed that predators exhibited a gradual response to the interannual variability of their ecosystem, from bottlenose dolphins and auks with a narrow habitat preference particularly stable over the decade, to northern gannets with wider habitat preferences pretty varying among years. There was no relationship between the type of habitat and the stability of predator preferences, since the two species with the most stable preferences targeted opposite habitats. Indeed, bottlenose dolphins targeted the habitat associated to the shelf edge, which is highly stable across time since it is associated to topographic features; while auks were associated to river plumes, which were the more spatially variable habitat identified here (Figure 4).

Thus, top predator answered differently to the temporal variations in habitat (and probably prey) availability. Species like gannets or fulmars would modulate their habitat preferences, while species like bottlenose dolphins and auks would remain within their most favourable habitats, where they would probably modulate foraging efforts or prey (Fort et al., 2013).

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Tables

Table 1. Encounter rates from 2004 to 2013, in individuals per 100 km². FULGLA: northern fulmar; SULBAS: northern gannet; ALCURI: auks; DELDEL: common dolphin; TURTRU: bottlenose dolphin.

Year	FULGLA	SULBAS	ALCURI	DELDEL	TURTRU
2004	4.93	25.65	4.89	1.67	0.10
2005	5.66	32.96	3.48	4.76	5.50
2006	3.49	29.22	2.30	2.53	2.45
2007	7.09	13.07	5.46	0.13	4.04
2008	10.91	53.40	15.10	10.26	2.61
2009	7.86	17.21	8.57	9.78	9.39
2010	8.56	23.15	7.58	3.83	2.52
2011	4.95	10.00	31.66	4.24	1.22
2012	3.52	25.52	9.11	4.67	0.61
2013	3.72	92.61	70.66	4.97	2.91

Table 2. Generalised Additive Models results for the five studied species. The explained deviances (in %) are given, as well as the significance levels for the four covariates, for the null model and the interaction model. FULGLA: northern fulmars; SULBAS: northern gannets; ALCURI: auks; DELDEL: common dolphins; TURTRU: bottlenose dolphins.

		FULGLA	SULBAS	ALCURI	DELDEL	TURTRU
Global model	Explained deviance (%)	21.8	18.2	35	11	32.9
	Dimension 1	***	***	***		***
	Dimension 2		*			
	Dimension 3	**	***	***		***
	Distance to closest colony	***	***		-	-
Interaction model	Explained deviance (%)	34.5	34.9	54.1	13	37.9
	Dimension 1, Year	***	***	***		***
	Dimension 2, Year	***	***	***		
	Dimension 3, Year	***	***	***		***
	Distance to closest colony	***	***	***	-	-

Figures

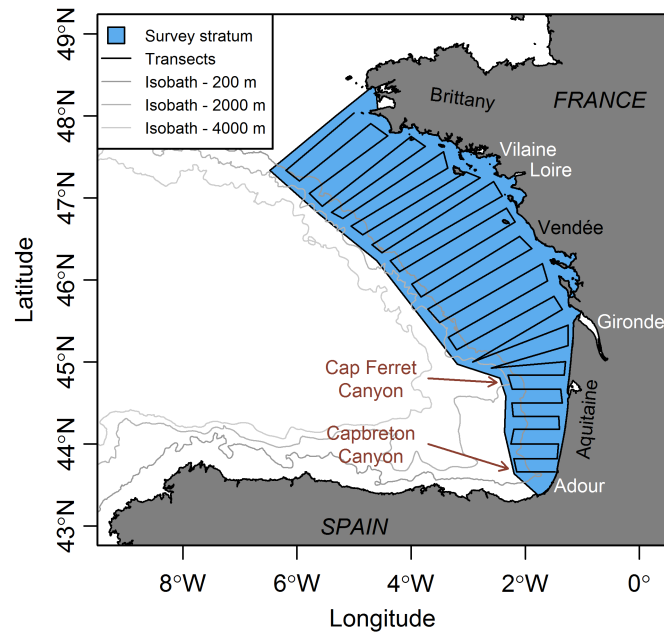


Figure 1. Survey area and theoretical sampling design of PELGAS survey. The isobaths are indicated in grey, the four main estuaries in white, the geographical localities in black and main canyons in brown.

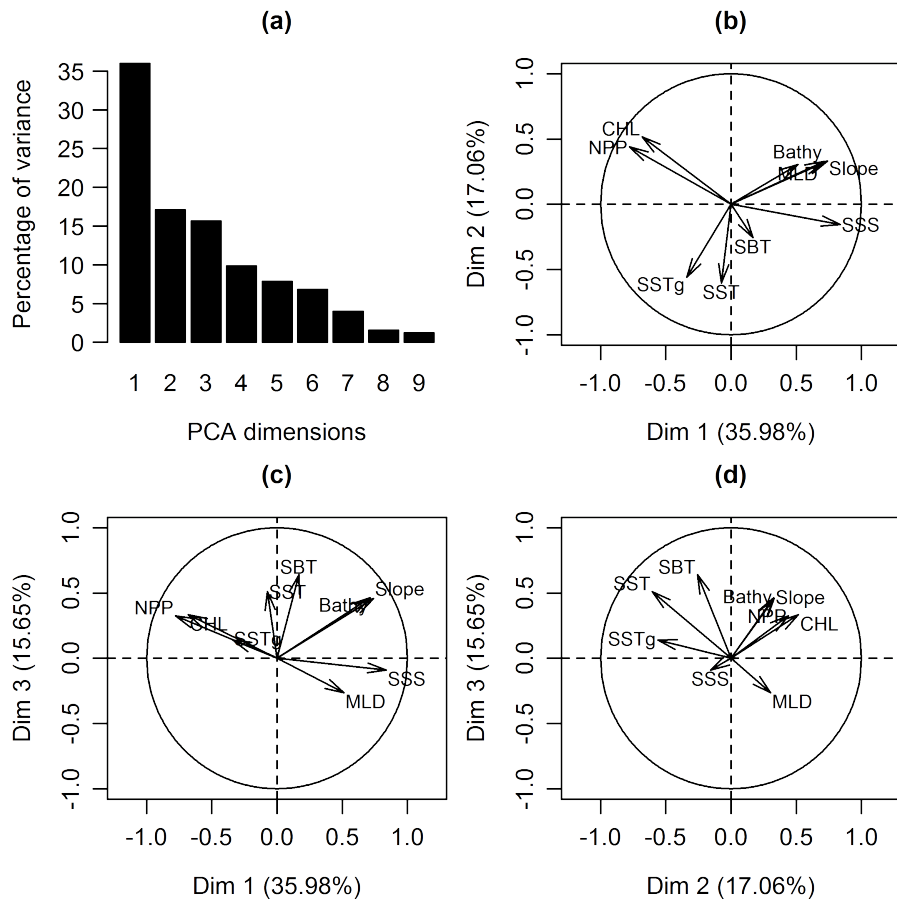


Figure 2. (a) Percentage of variance explained by each of the nine Principal Component Analysis (PCA) dimensions; (b) PCA correlation circle for the first and second dimensions; (c) PCA correlation circle for the first and third dimensions; (d) PCA correlation circle for the second and third dimensions. SST: Sea Surface Temperature; SSTg: SST gradients; SBT: Sea Bottom Temperature; SSS: Sea Surface Salinity; MLD: Mixed Layer Depth; CHL: surface Chlorophyll a concentration; NPP: Net Primary Production.

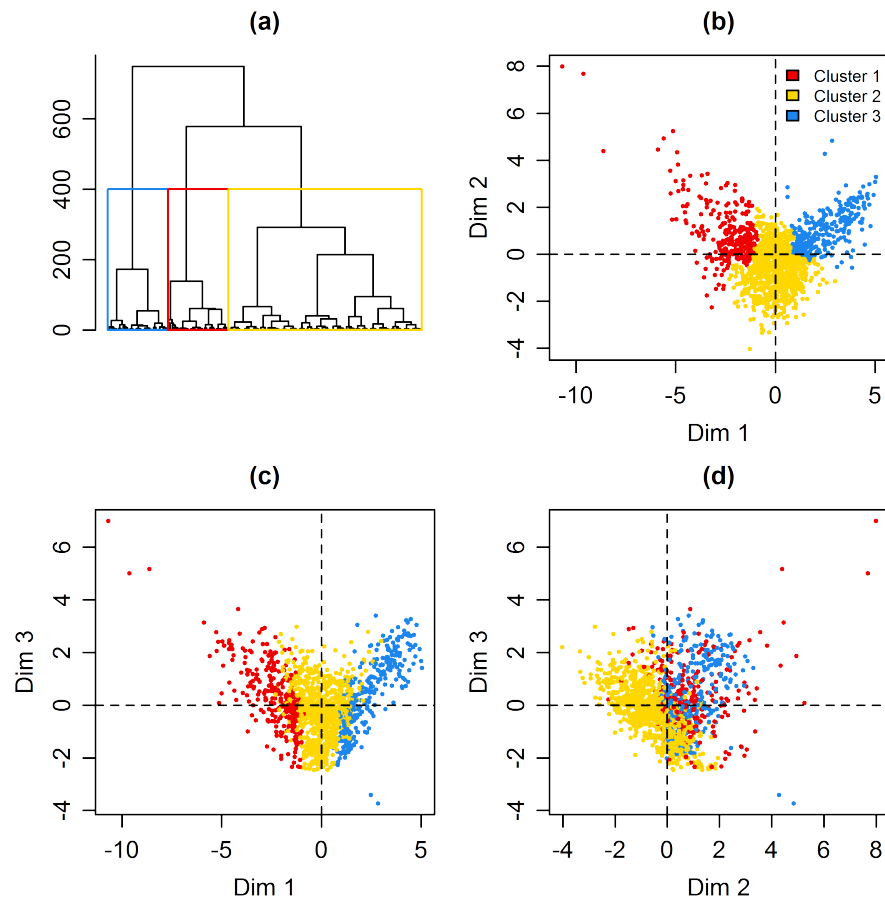


Figure 3. (a) The hierarchical cluster analysis performed over the Principal Component Analysis (PCA) result, segregating three different habitats; (b) The three clusters over the first and second PCA dimensions; (c) The three clusters over the first and third PCA dimensions; (d) The three clusters over the second and third PCA dimensions.

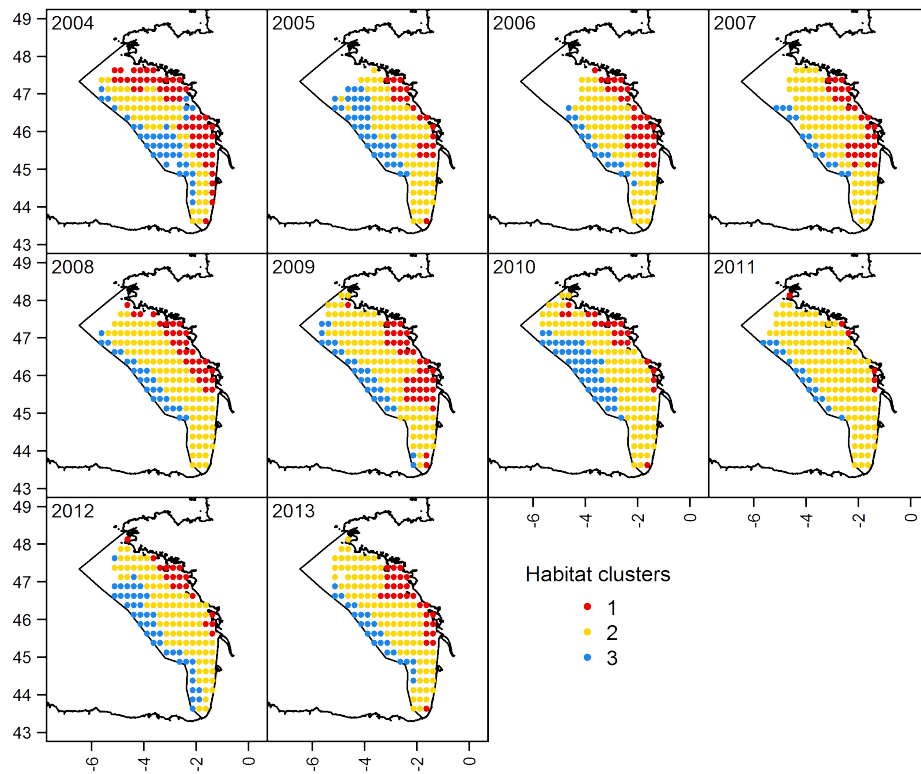


Figure 4. Yearly variations of the spatial extent of the three habitats available over the Bay of Biscay from 2004 to 2013.

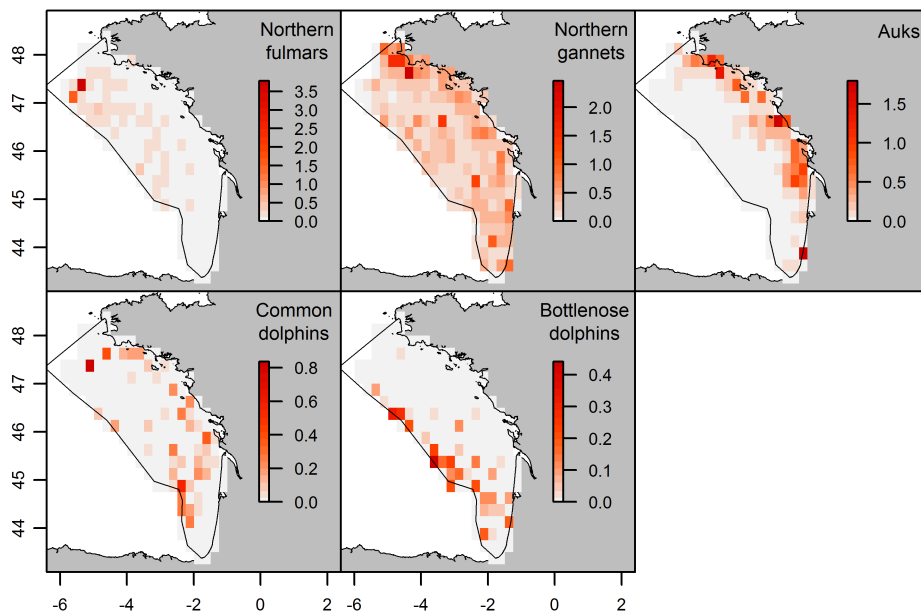


Figure 5. Mean encounter rates (individuals per sampled km²) for the studied species from 2004 to 2013.

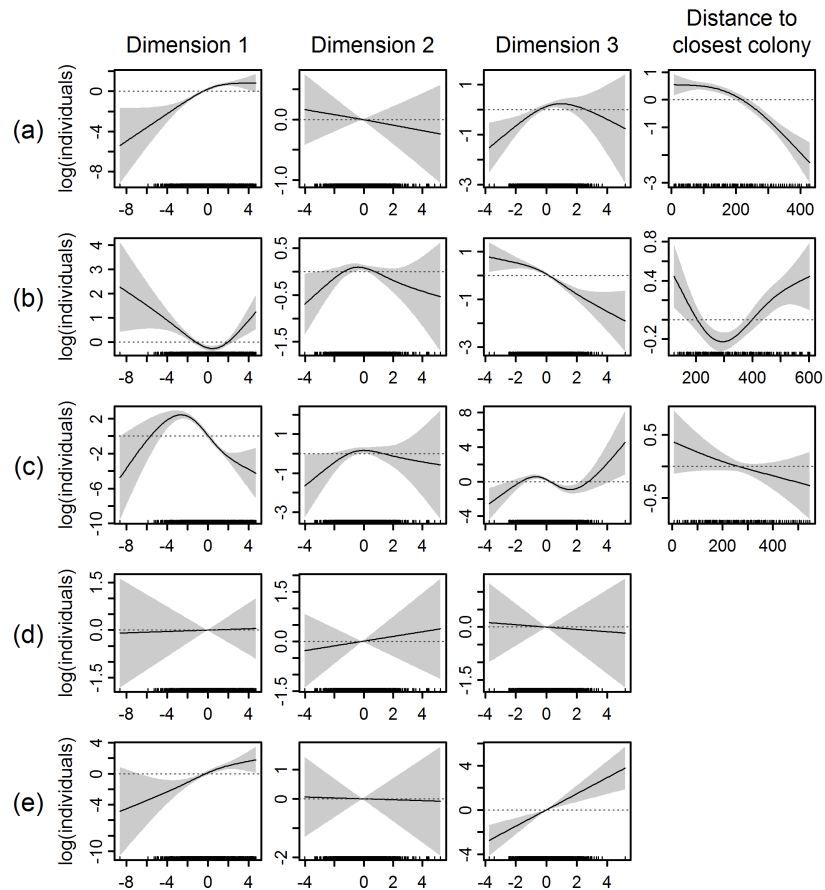


Figure 6. Generalized Additive Models for (a) northern fulmars, (b) northern gannets, (c) auks, (d) common dolphins and (e) bottlenose dolphins. The curves represent the relationship between the covariate (abscissa) and the linear predictor ($\log(\text{individuals})$, ordinate). The covariates are the three first dimension of the Principal Component Analysis, and the distance to closest colony for seabirds.

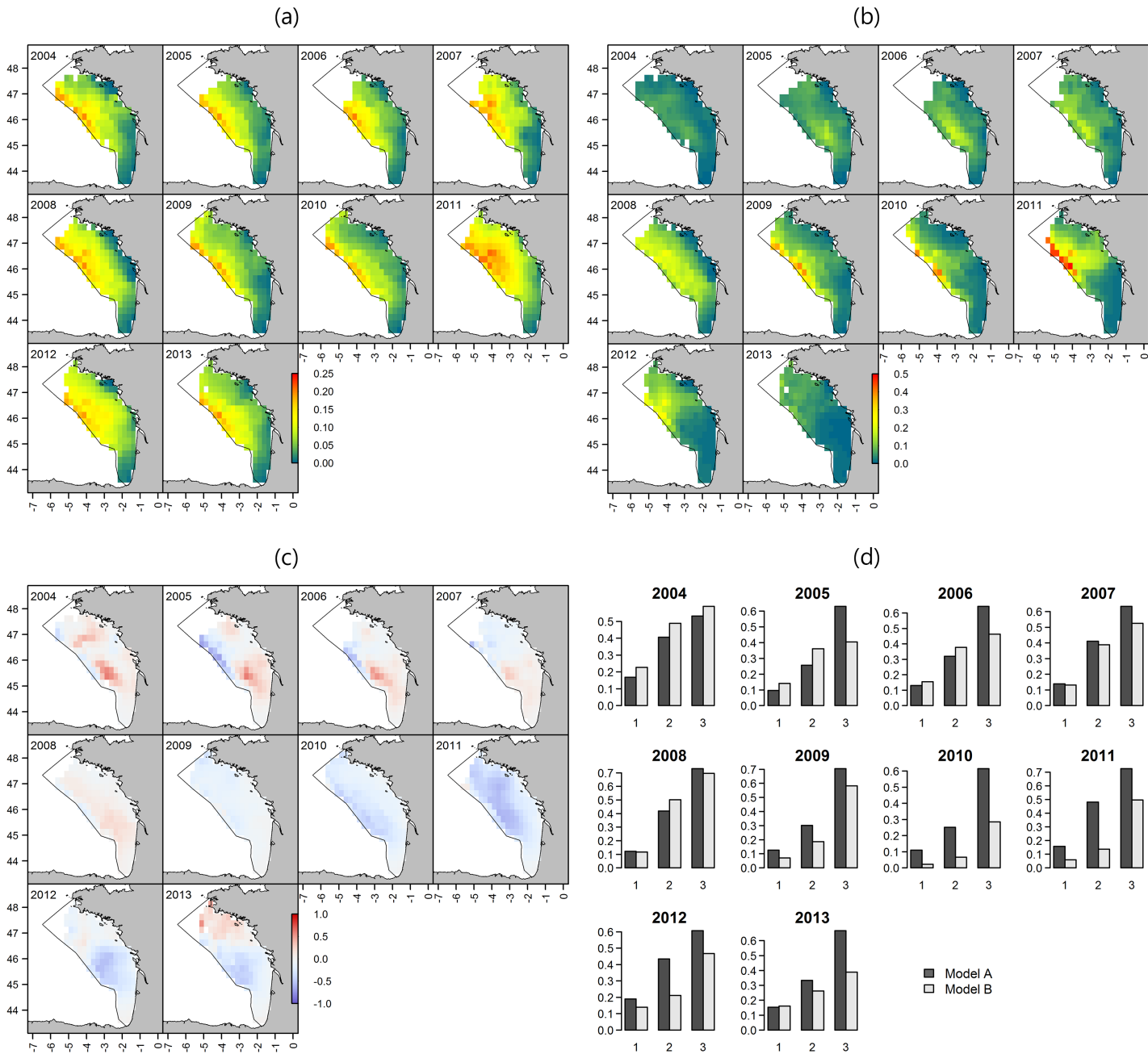


Figure 7. Results for northern fulmars: (a) the predicted distributions from the null model, in individuals per km²; (b) the predicted distributions from the model with interaction, in individuals per km²; (c) the difference between (b) and (a), red values indicating (b) was larger than (a), blue values the opposite (the predictions were standardised by years before the difference computation); (d) the predicted density by habitats, from null model in dark grey (Model A), from interaction model in light grey (Model B).

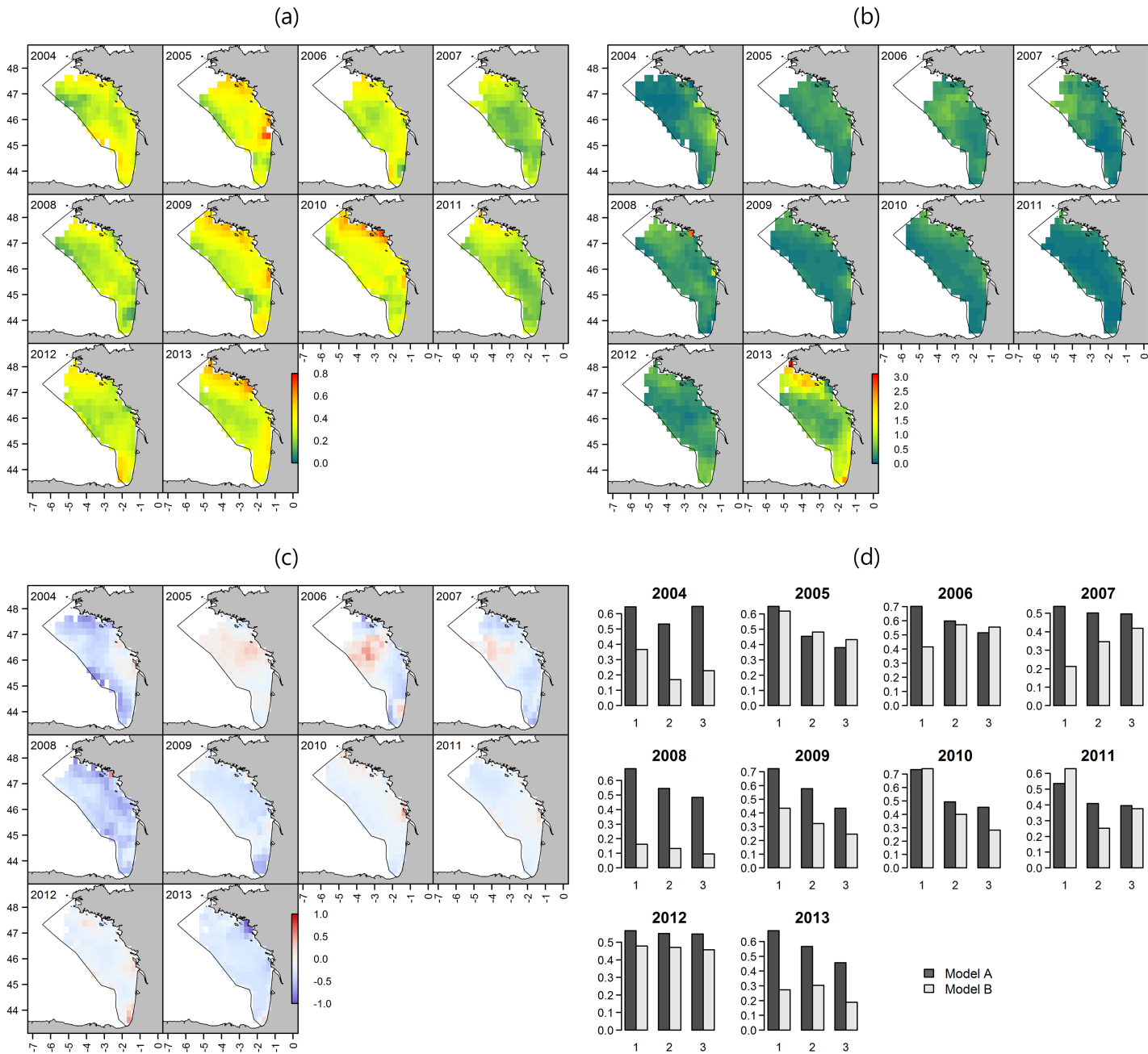


Figure 8. Results for northern gannets: (a) the predicted distributions from the null model, in individuals per km²; (b) the predicted distributions from the model with interaction, in individuals per km²; (c) the difference between (b) and (a), red values indicating (b) was larger than (a), blue values the opposite (the predictions were standardised by years before the difference computation); (d) the predicted density by habitats, from null model in dark grey (Model A), from interaction model in light grey (Model B).

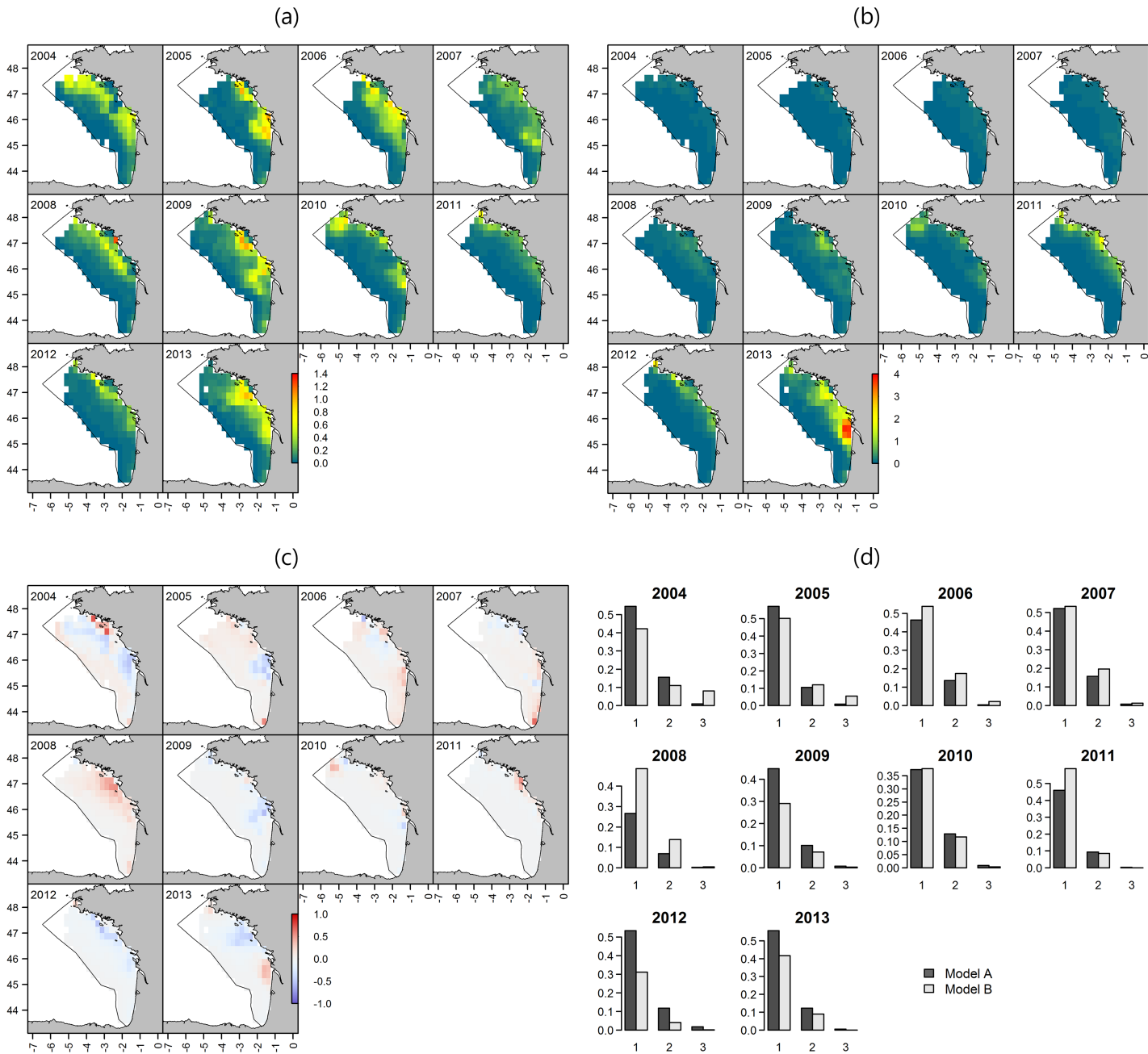


Figure 9. Results for auks: (a) the predicted distributions from the null model, in individuals per km²; (b) the predicted distributions from the model with interaction, in individuals per km²; (c) the difference between (b) and (a), red values indicating (b) was larger than (a), blue values the opposite (the predictions were standardised by years before the difference computation); (d) the predicted density by habitats, from null model in dark grey (Model A), from interaction model in light grey (Model B).

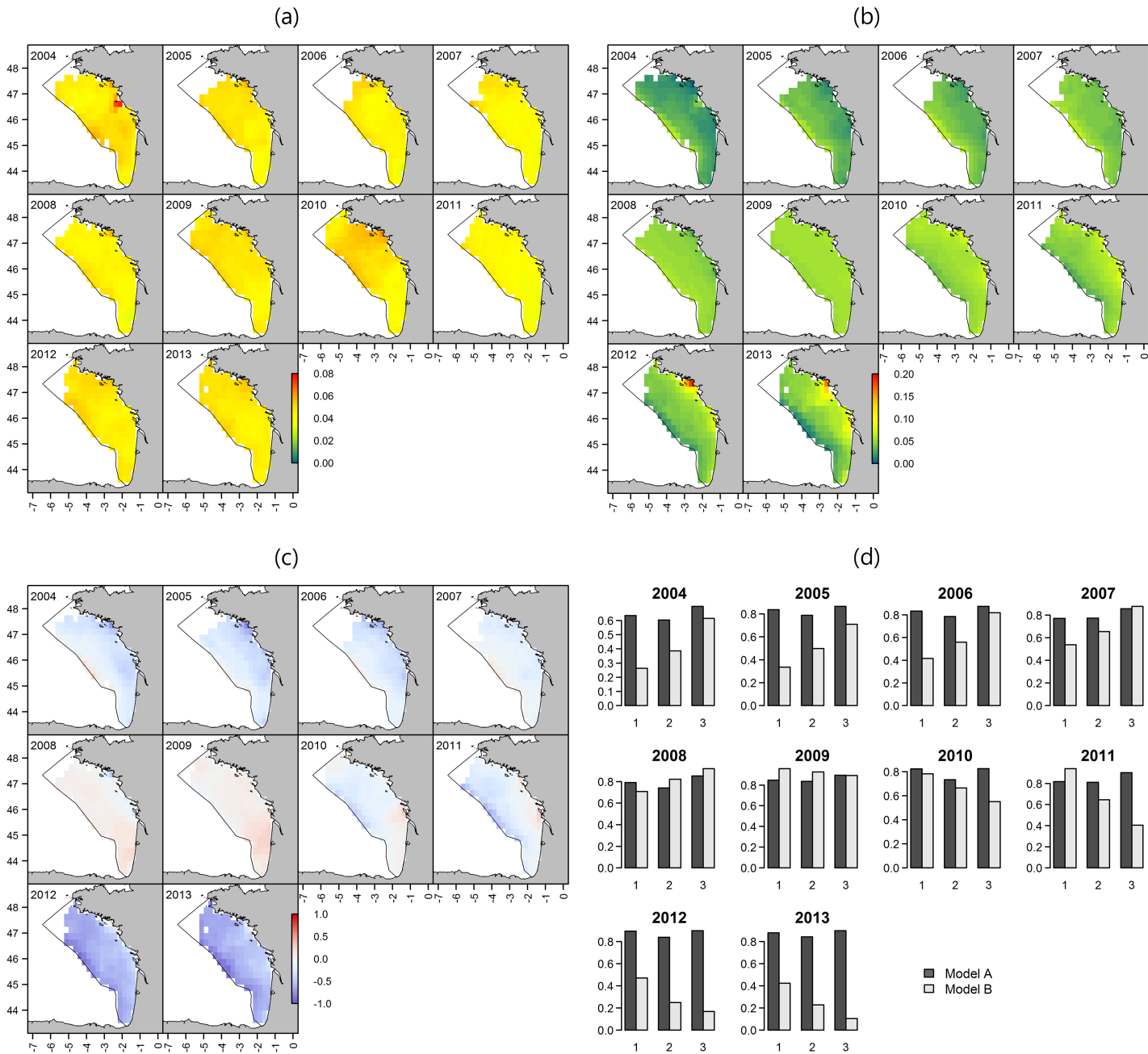


Figure 10. Results for common dolphins: (a) the predicted distributions from the null model, in individuals per km²; (b) the predicted distributions from the model with interaction, in individuals per km²; (c) the difference between (b) and (a), red values indicating (b) was larger than (a), blue values the opposite (the predictions were standardised by years before the difference computation); (d) the predicted density by habitats, from null model in dark grey (Model A), from interaction model in light grey (Model B).

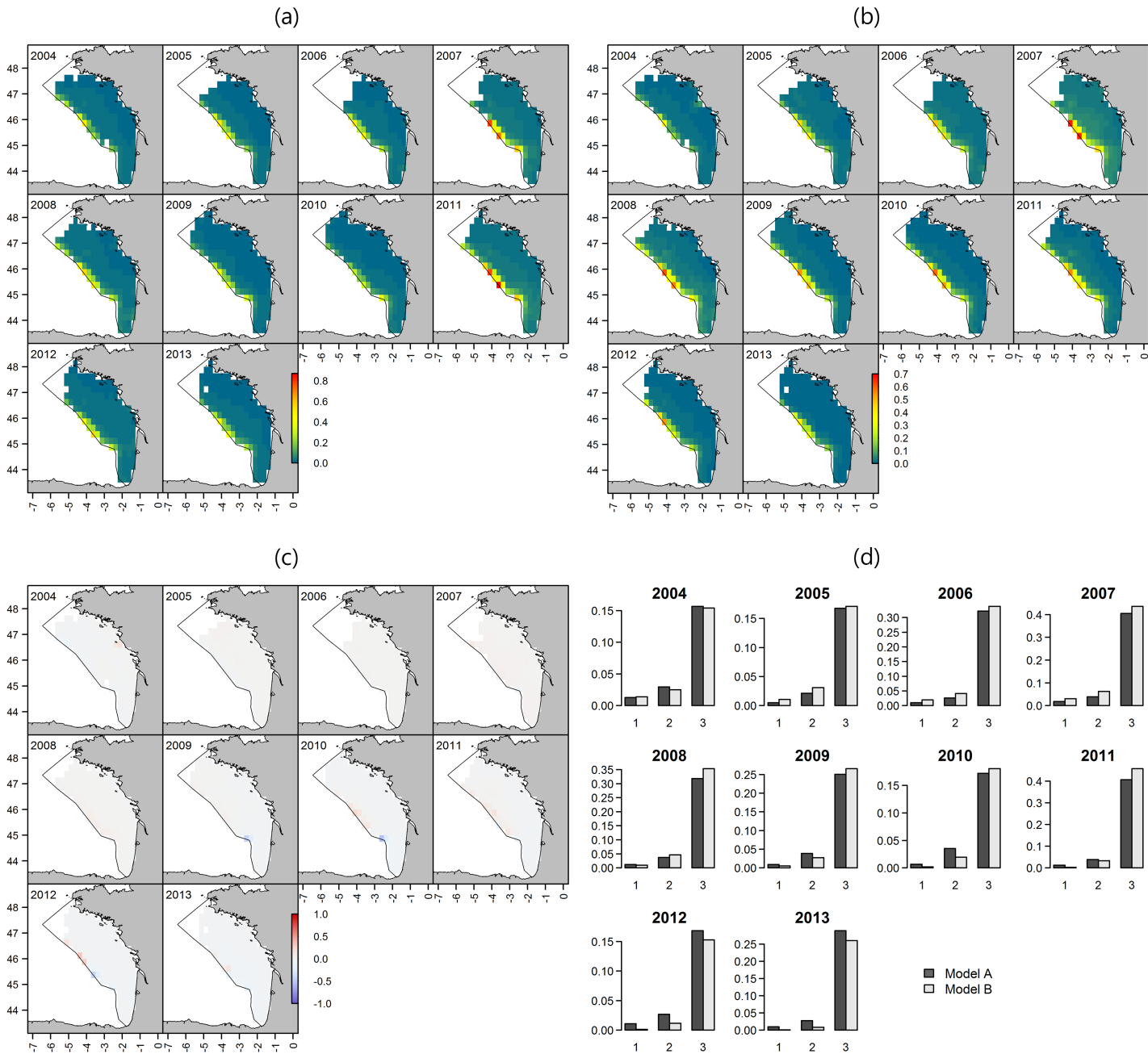


Figure 11. Results for bottlenose dolphins: (a) the predicted distributions from the null model, in individuals per km²; (b) the predicted distributions from the model with interaction, in individuals per km²; (c) the difference between (b) and (a), red values indicating (b) was larger than (a), blue values the opposite (the predictions were standardised by years before the difference computation); (d) the predicted density by habitats, from null model in dark grey (Model A), from interaction model in light grey (Model B).

Appendix A

Environmental variables

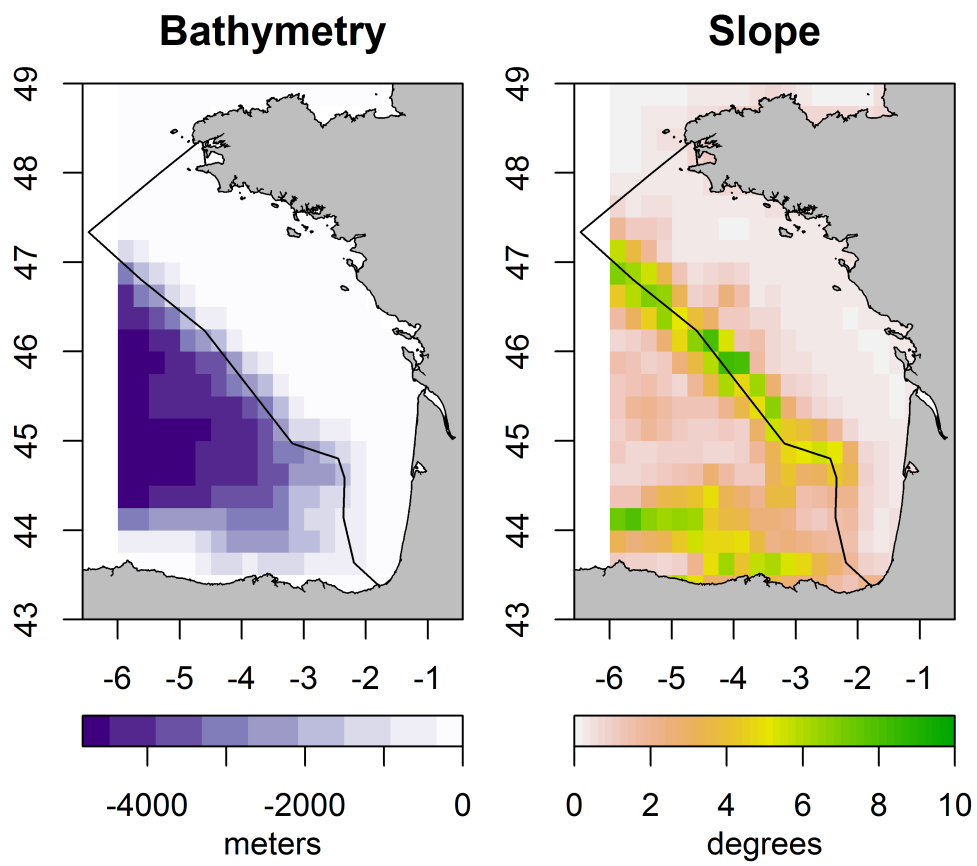


Figure 1. Physiographic variables used for the PCA.

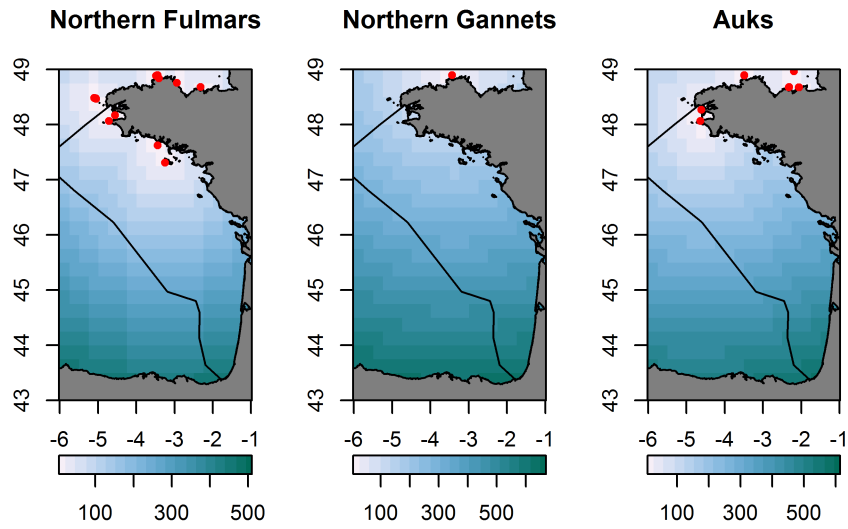


Figure 2. Colonies locations (red dots) and distance to closest colony across the study area for the six studied seabirds reproducing within the area used within habitat modelling.

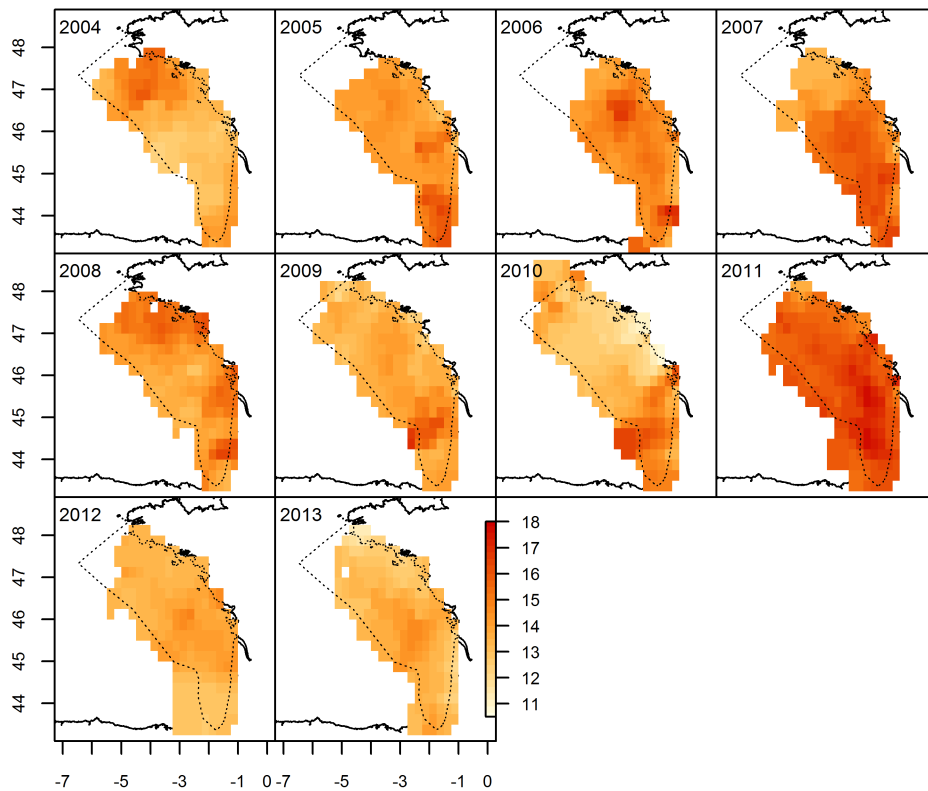


Figure 3. Sea surface temperature patterns from 2004 to 2013. In °C.

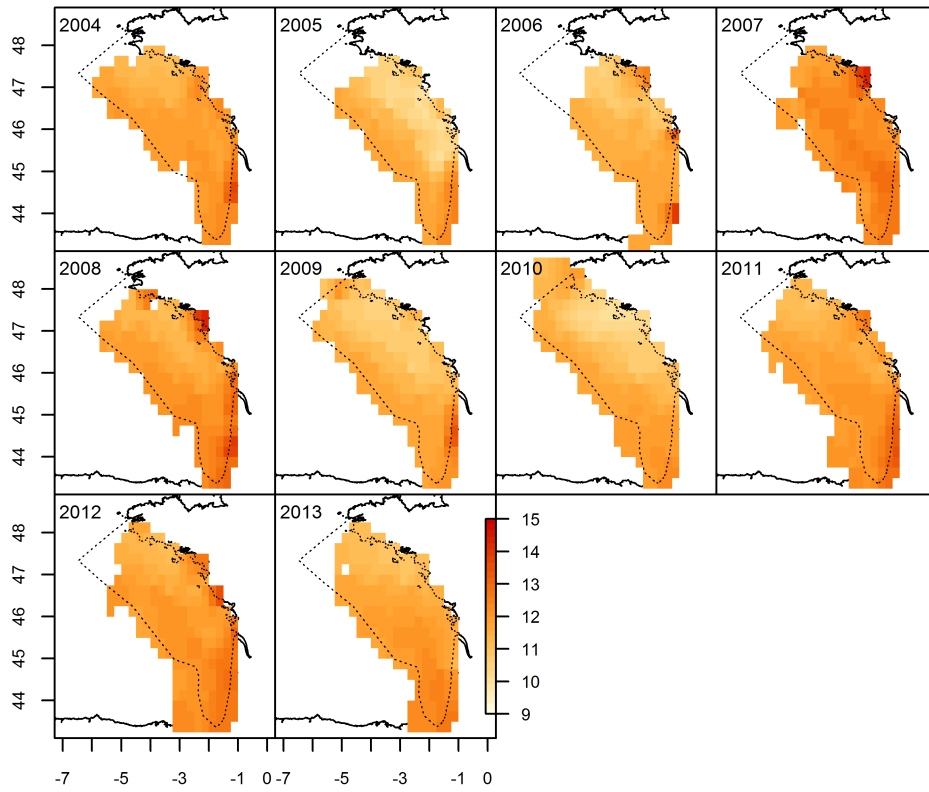


Figure 4. Sea bottom temperature patterns from 2004 to 2013. In °C.

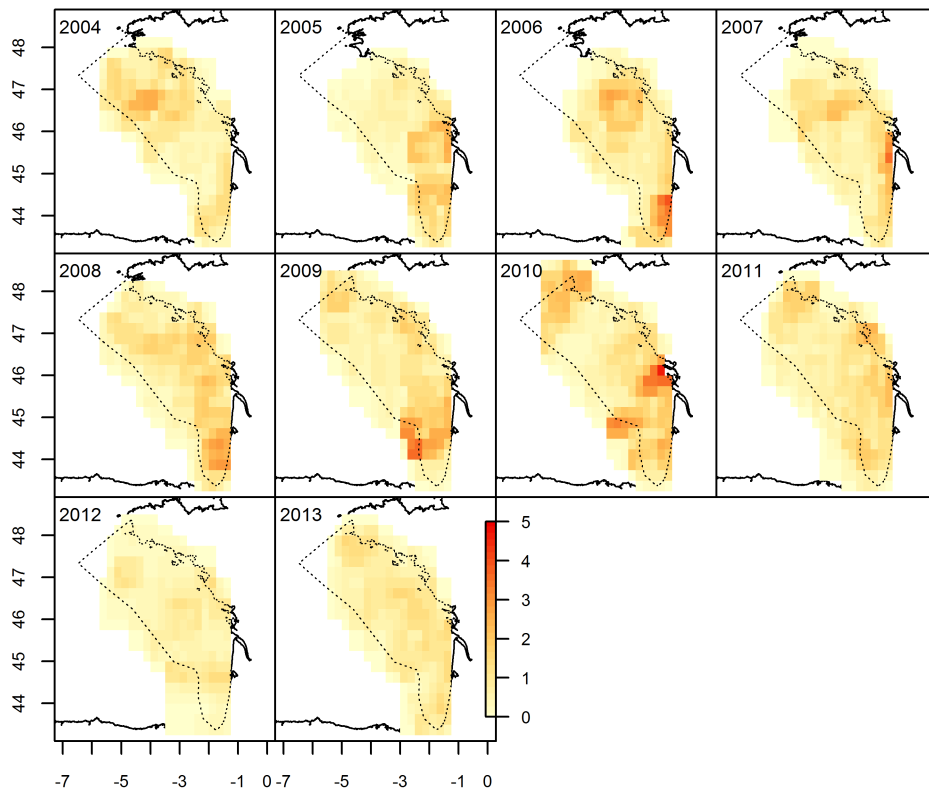


Figure 5. Patterns of sea surface temperature gradients from 2004 to 2013. In °C.

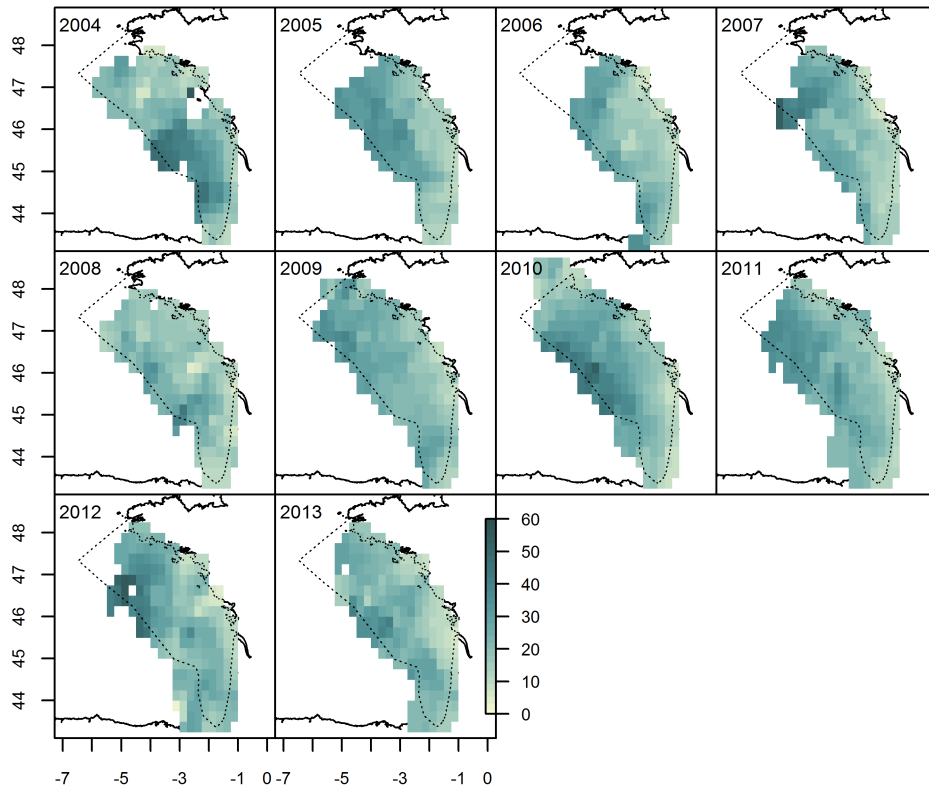


Figure 6. Patterns of mixed layer depth from 2004 to 2013. In meters.

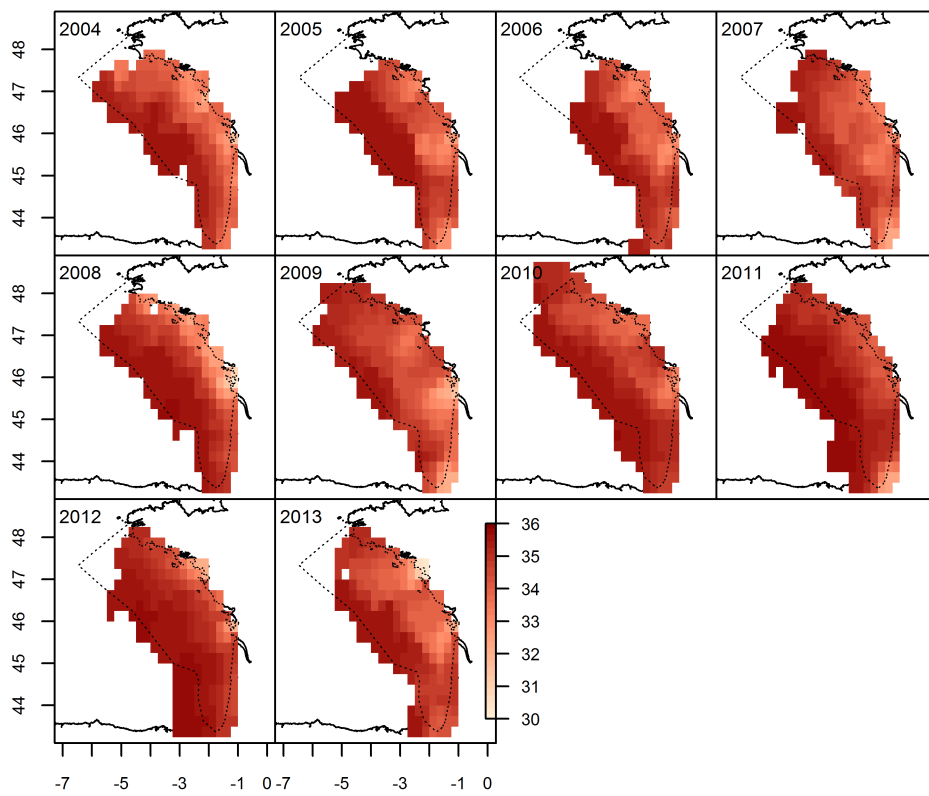


Figure 7. Sea surface salinity patterns from 2004 to 2013, without units.

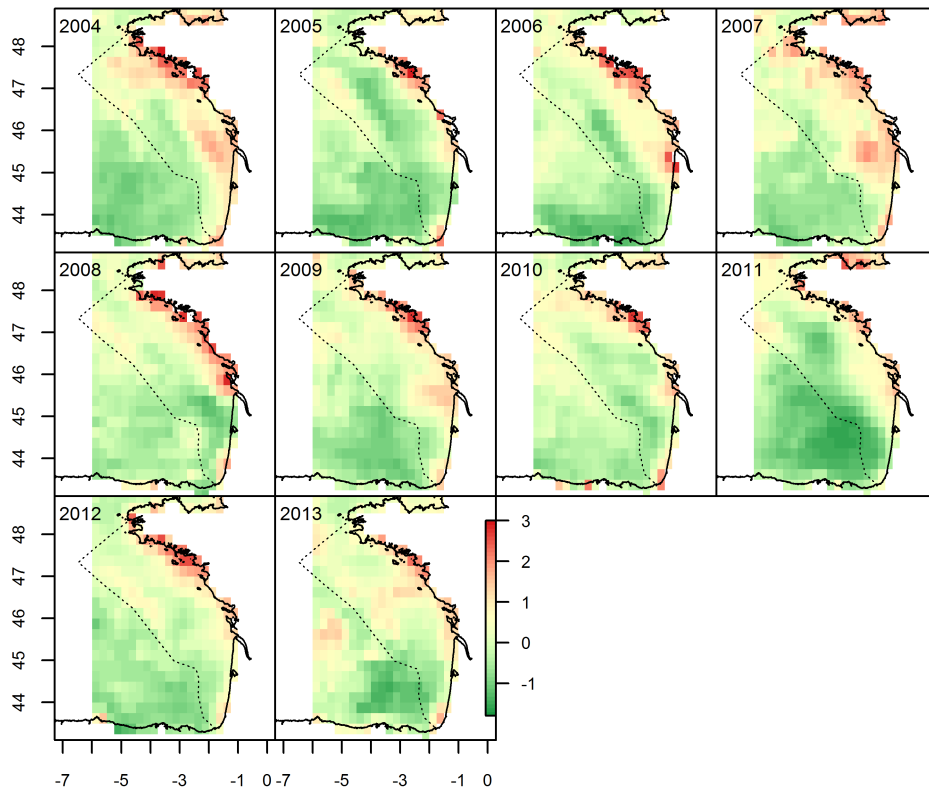


Figure 8. Surface chlorophyll a concentration patterns from 2004 to 2013. In $\log(\text{g}/\text{m}^2)$.

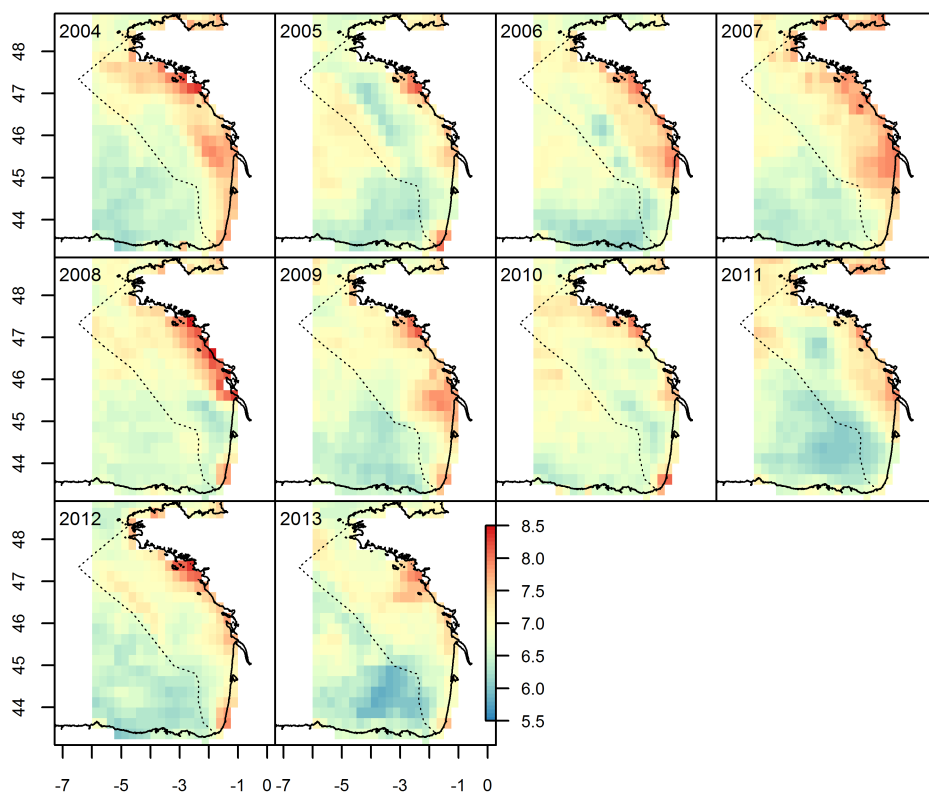


Figure 9. Surface net primary production patterns from 2004 to 2013. In $\log(\text{g}/\text{m}^2/\text{day})$.

Appendix B

Distance Sampling analysis

1 Methods

The distance sampling analysis was done over raw sightings, that is over point data, not yet summarized over the grid as for the habitat modelling analysis. Only the sightings recorded within the PELGAS stratum and during best detection conditions were used to performed the analysis, which was conducted using the `dsm` (Miller et al., 2013) and `Distance` (Miller, 2014) packages within R 2.15.3 "Security Blanket" (R Core Team, 2013). All sightings related to individuals recorded as attracted or repelled from the boat were removed, as well as individuals coming to the bow, scavenging behind fishing vessels or coming from the back of the observation platform. The distance of each sightings from the track-line was then calculated for each sighting as $distance_{(track-line)} = \sin(\frac{angle}{180} \times \pi) \times distance_{(observer)}$.

We tested the impact of seven factors (the "stratification" factors) on the detection function, in addition to the null model: years, Beaufort sea-state (3 classes: 0–1; 2–3; 4), subjective conditions and observation platform (either upper deck or the bridge). All these factors were tested with either half-normal or hazard function, in models with one to three variables. The best model was chosen based on the Akaike Information Criterion (AIC, the lower the better). Truncation was done prior the detection function modelling, as recommended by Buckland et al. (2001), *i.e.* the farthest sightings were removed (see Table 1 for corresponding distances). Once models chosen, the Effective Strip Widths (ESW) were computed. The ESW is extracted from the detection function as the distance for which the surface below the curve at its left equals the surface above the curve at its right.

2 Results

The detection of common dolphin (Figure 2A) and bottlenose dolphin (Figure 2B) were influenced by none of the tested stratification factors, with the null model selected for the two groups, using the half-normal function. The resulting ESWs were 804 m for common dolphin and 734 m for bottlenose dolphin, 299 m (Table 1).

The northern fulmar detection was influenced by the platform of observation (upper deck or bridge). The detection function used was the half-normal function (Figure 2C). For observations from the upper deck, the ESW for the northern fulmar was of 257 m, while from the ship bridge it was reduced to 203 m (Table 1).

The detection of auks varied with the Beaufort sea-state, with the half-normal function as detection function (Figure 2D). The ESWs were of 204 m for sea-states of 0–1, 194 m for sea-states of 2–3 and 160 m for sea-state of 4 (Table 1).

Northern gannet was the only species for which the detection functions varied between years, thus leading to detection models fitted for each year separately (Figures 2 and 2). In 2004, 2005, 2008, 2012 and 2013 the null models with half-normal function were selected, resulting in ESWs of, respectively, 321, 324, 328, 354 and 319 m (Table 1). In 2006, 2007 and 2011, null models were selected as well but

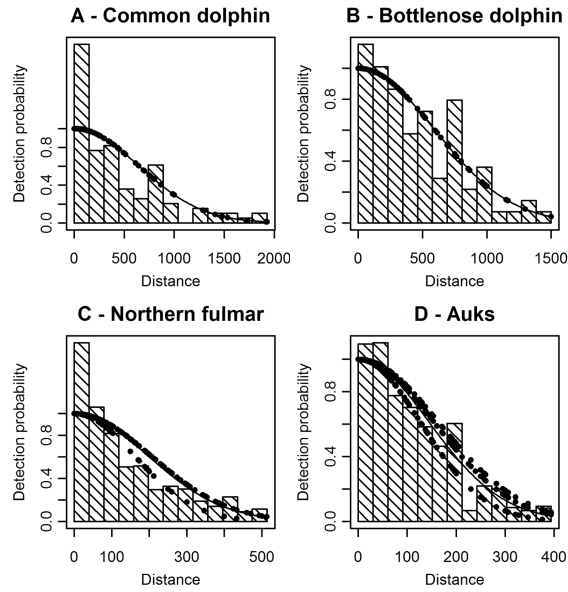


Figure 1. Detection models selected for (A) common dolphin, (B) bottlenose dolphin, (C) northern fulmar, and (D) auks. The histograms are the frequency of sightings per distance classes, the thin black lines are the mean detection functions and black dots are sightings fitting the detection functions per stratification levels, if any.

with hazard function, with ESWs of 387, 327 and 297 m respectively. In 2009, the detection model was fitted with the half-normal function, and varied with subjective conditions: for excellent conditions, the ESW was 334 m, 468 m for good conditions and 386 m for medium conditions. Finally, in 2010, the half-normal function was selected as well, but with Beaufort sea-state as stratification factor: 342 m for sea-state 0–1, 279 m for sea-state 2–3 and 255 m for sea-state 4.

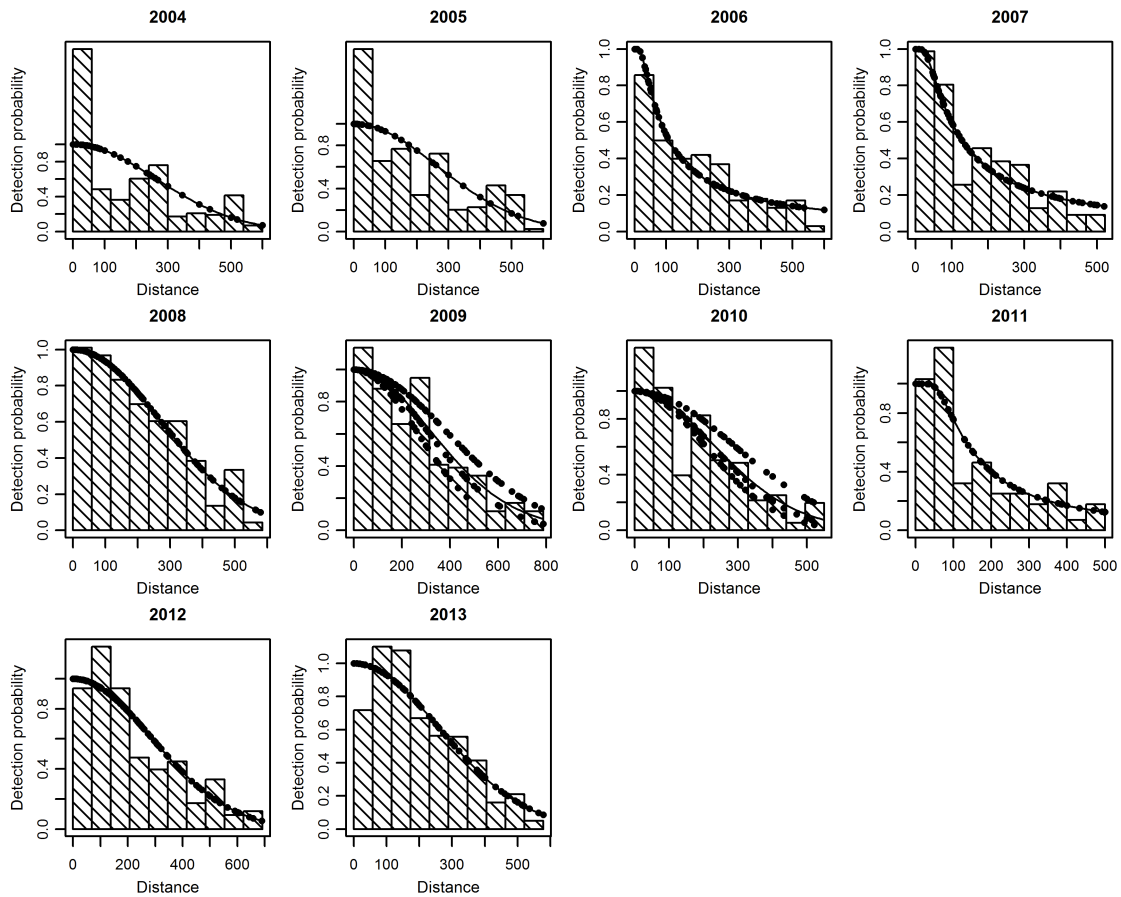


Figure 2. Detection models selected for the northern gannets for each year of the survey. The histograms are the frequency of sightings per distance classes, the thin black lines are the mean detection functions and black dots are sightings fitting the detection functions per stratification levels, if any.

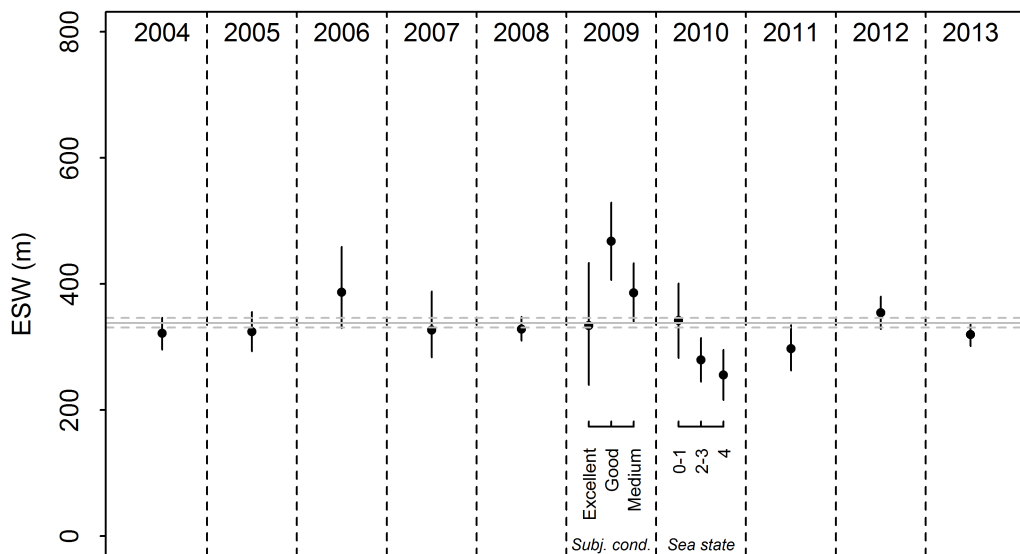


Figure 3. ESW resulting from the yearly detection models for the northern gannet. In grey, the ESW (thin line) and its confidence interval (dotted lines) for all years pooled ($338 \text{ m} \pm 7.5 \text{ m}$), for comparison.

Table 1. Truncation distances (beyond this limit, sightings were not considered), detection functions and stratification factors (if any) for each species, as well as resulting ESWs and their confidence intervals (lower and upper limits).

Species	Year	Truncation (m)	Detection function	Stratification		lower	ESW (m)	upper
Common dolphin	all	1828	Half-normal	-		720	804	886
Bottlenose dolphin	all	1500	Half-normal	-		622	734	848
Northern fulmar	all	514	Half-normal	Platform	Bridge	174	203	231
					Upper deck	243	257	270
Northern gannet	2004	600	Half-normal	-		296	321	347
	2005	600	Half-normal	-		293	324	356
	2006	600	Hazard	-		330	387	456
	2007	522	Hazard	-		283	327	388
	2008	585	Half-normal	-		310	328	348
	2009	787,8	Half-normal	Subjective conditions	Excellent	239	334	434
					Good	406	468	529
					Medium	340	386	433
	2010	550	Half-normal	Beaufort sea state	0&1	282	342	401
					2&3	245	279	314
					4	216	255	296
						263	297	335
	2011	500	Hazard	-		328	354	380
2012	691	Half-normal	-		301	319	336	
2013	578,5	Half-normal	-		184	204	224	
Auks	all	394	Half-normal	Beaufort sea state	0&1	184	204	224
					2&3	181	194	207
					4	148	160	173

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Appendix C

Sightings and encounter rates maps

Here are presented the sightings data for seabirds and cetaceans studied within this work, and the resulting encounter rates. These rasters were obtained from summarizing the number of individuals seen by squared kilometres of effort (see text for details), and corresponded to the response variables used within the habitat models.

On sightings maps are presented the sightings, with the size of points relative to the number of individuals seen per sightings, the sampled effort transects (in white) and the PELGAS stratum, in grey. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals.

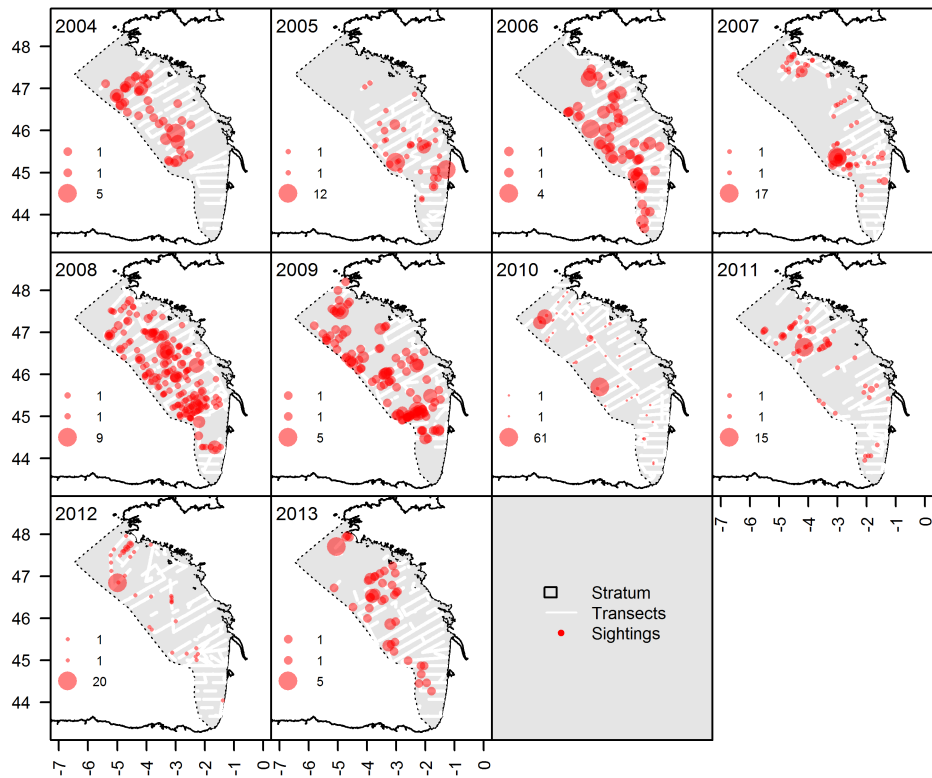


Figure 1. Sightings of northern fulmars for the ten studied years, in number of individuals. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals per sightings. The sampled transects are in white.

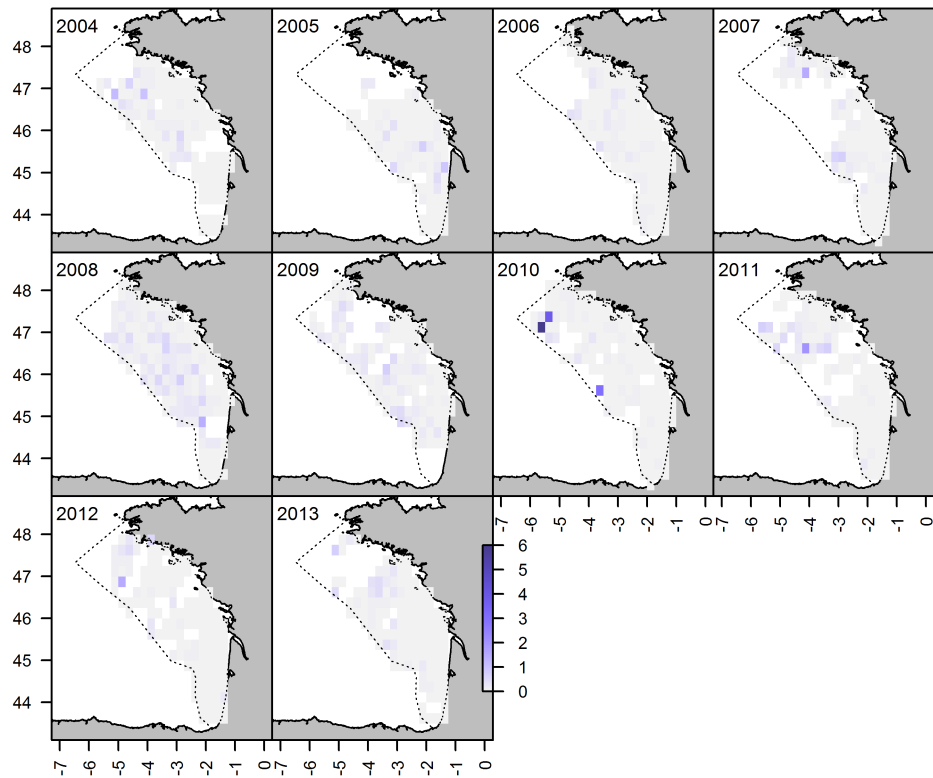


Figure 2. Encounter rates of northern fulmars for the ten studied years, in number of individuals per squared kilometres of effort.

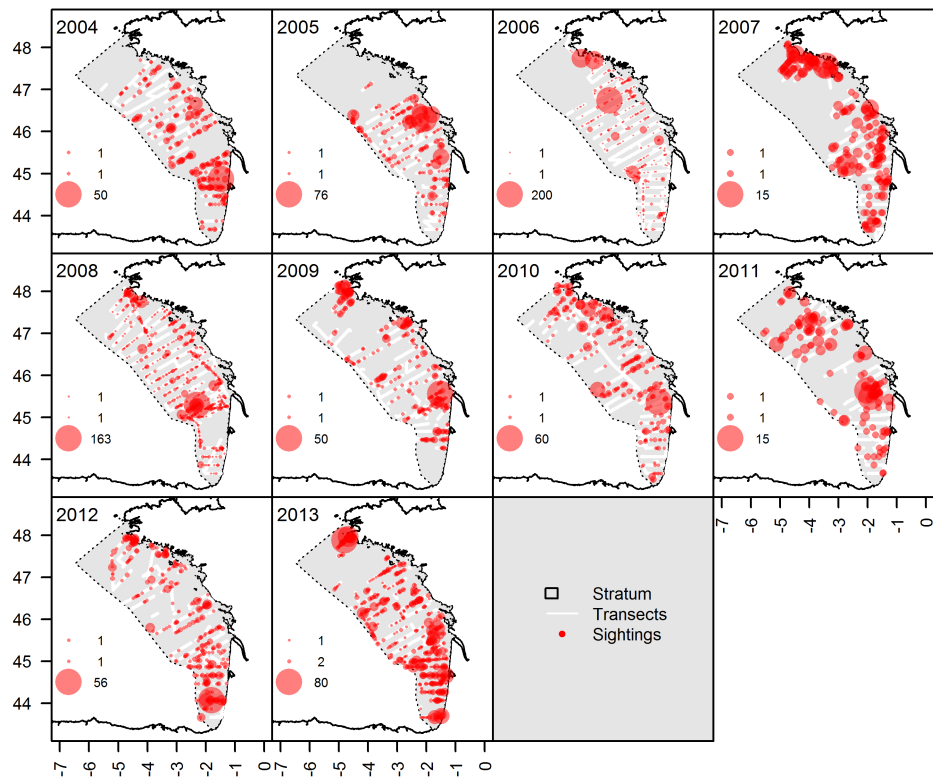


Figure 3. Sightings of northern gannets for the ten studied years, in number of individuals. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals per sightings. The sampled transects are in white.

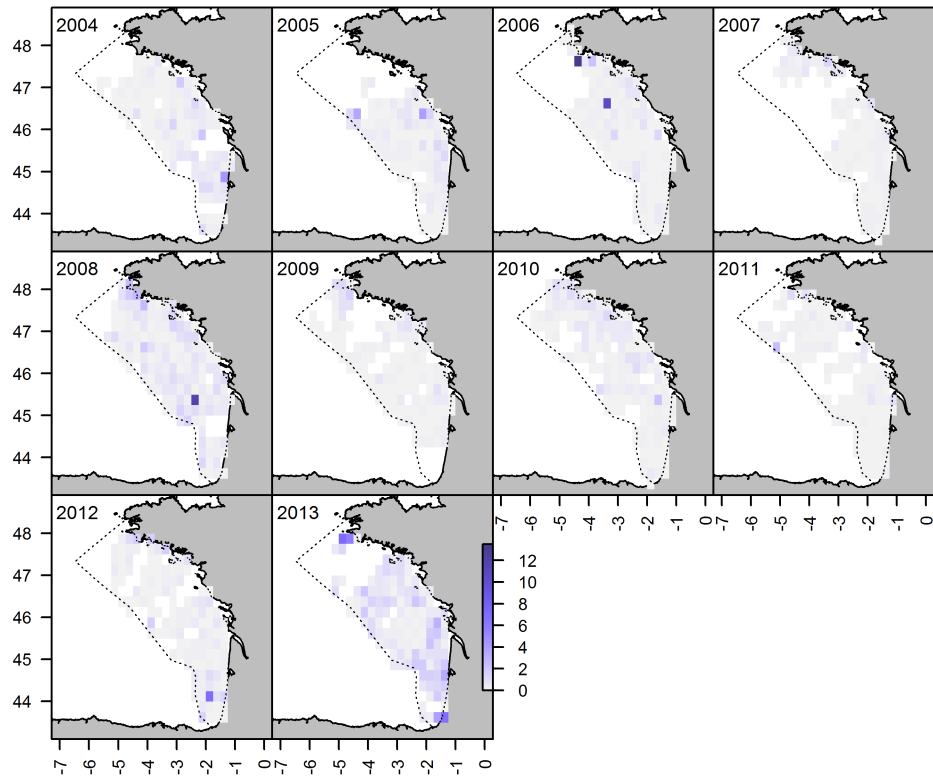


Figure 4. Encounter rates of northern gannets for the ten studied years, in number of individuals per squared kilometres of effort.

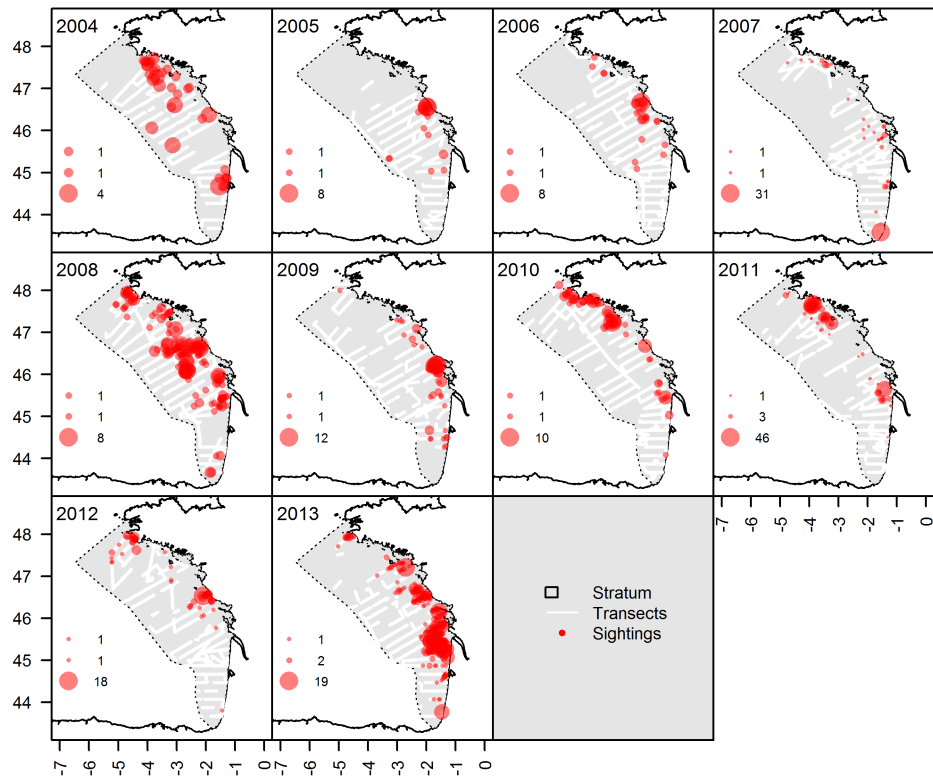


Figure 5. Sightings of auks for the ten studied years, in number of individuals. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals per sightings. The sampled transects are in white.

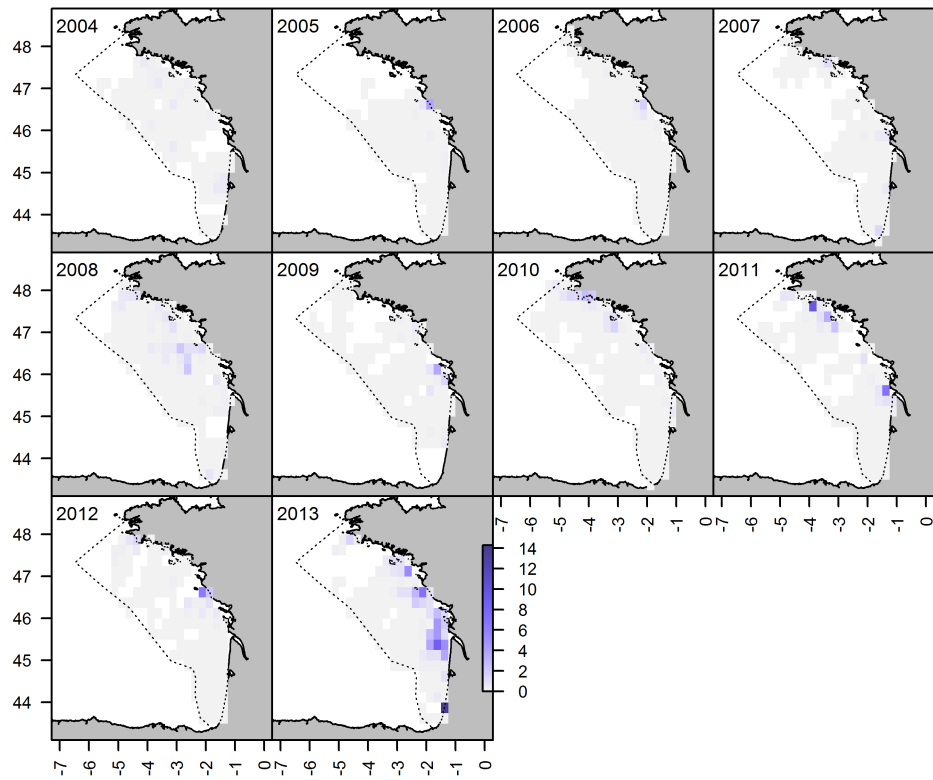


Figure 6. Encounter rates of auks for the ten studied years, in number of individuals per squared kilometres of effort.

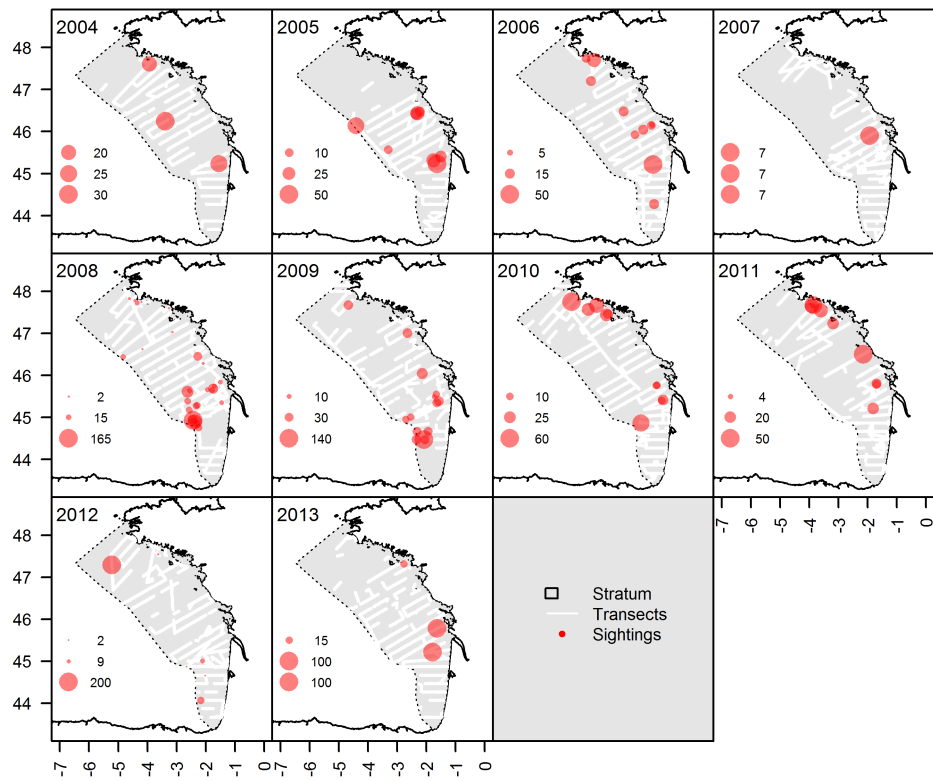


Figure 7. Sightings of common dolphin for the ten studied years, in number of individuals. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals per sightings. The sampled transects are in white.

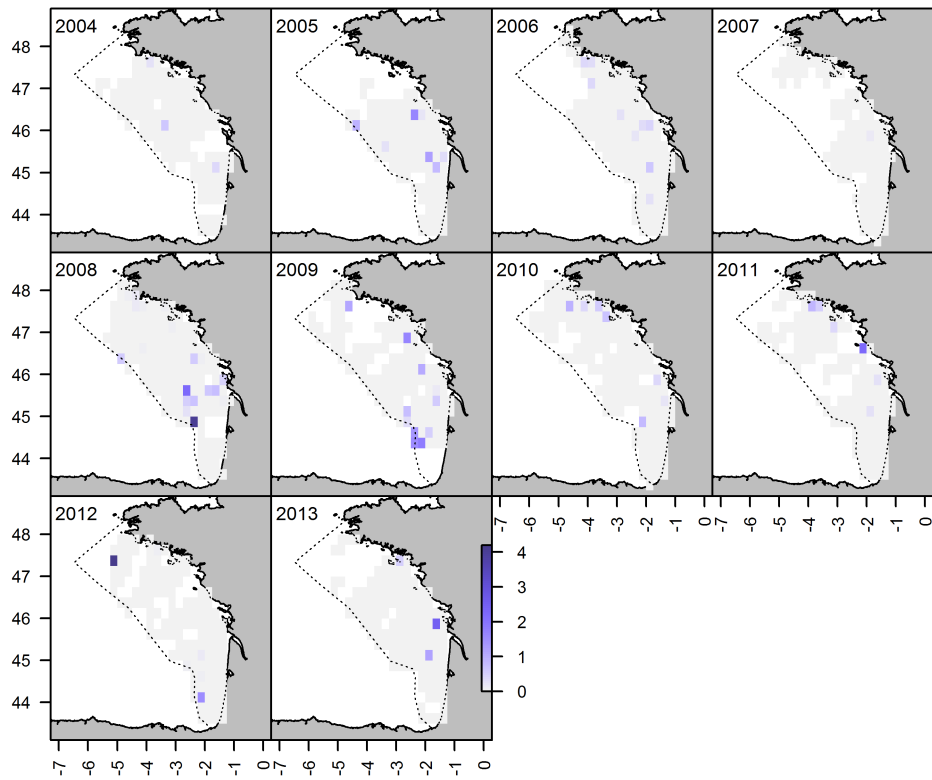


Figure 8. Encounter rates of common dolphin for the ten studied years, in number of individuals per squared kilometres of effort.

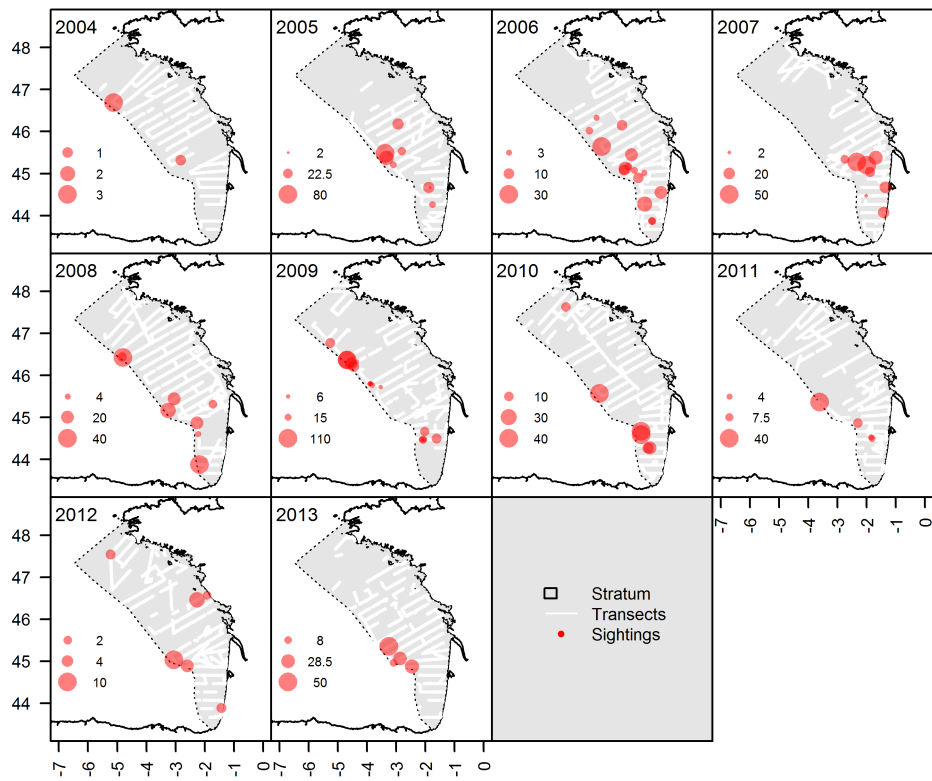


Figure 9. Sightings of bottlenose dolphins for the ten studied years, in number of individuals. The legend indicates the point size for the minimum, the quantile 50% and the maximum number of individuals per sightings. The sampled transects are in white.

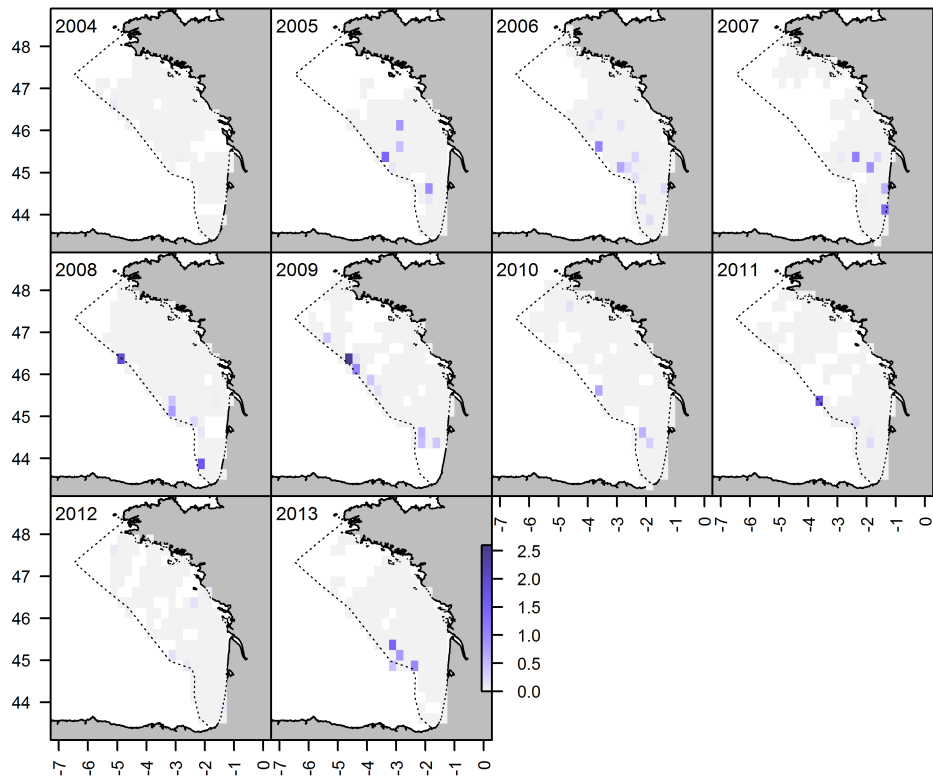


Figure 10. Encounter rates of bottlenose dolphins for the ten studied years, in number of individuals per squared kilometres of effort.

Appendix **E**

Chapter 5 - Seasonal distribution of
juvenile and immature Northern
Gannets reveals avoidance of
intra-specific competition with
breeding adults

Supporting information to Chapter 5: in preparation paper.

Seasonal distribution of juvenile and immature Northern Gannets reveals avoidance of intra-specific competition with breeding adults

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Keywords: intraspecific competition, Seabirds, Northern Gannets, Habitat modelling, north-east Atlantic, Seasons, Bay of Biscay, English Channel

1 Introduction

During their life, organisms have to face limited resource availability to meet their different vital needs. These constraints lead individuals to compete with conspecifics to access to the resource, but the competitiveness of each individual depends of its status, size, age or sex. Less competitive individuals may access the resource by developing adaptive strategies. Among possible foraging responses to competition, spatial segregation is observed in a wide range of species, either terrestrial (Ruckstuhl & Neuhaus, 2000; Bowyer, 2004) or marine species (Voight, 1995; Breed et al., 2006). When animals have to forage patchy resources, which location might be unpredictable, or exploit prey difficult to catch, the intra-specific competition may advantage most experienced foragers, whose foraging efficiency could be enhanced by a previous knowledge on food distribution using memory (Janson, 1998; Regular et al., 2013), more developed skills in predation (Sundström & Johnsson, 2001) or higher movement capacity (Riotte-Lambert & Weimerskirch, 2013).

Less experienced or skilled individuals, such as juvenile and immature individuals, could be competitively displaced towards more distant or less productive foraging grounds or select different prey of lower quality to avoid competition with adults. Spatial segregation between immature and adult individuals was described in several species, for which a lower foraging efficiency of immature individuals was involved (Daunt et al., 2007; Fayet et al., 2015). Despite an increasing interest for the subject (Campioni et al., 2015; Fayet et al., 2015; Haug et al., 2015; Missagia et al., 2015), the ecology and the distribution of immature individuals, as well as the role of the intra-specific competition with adults, remain poorly known, especially in marine species.

In this study, we compared the habitat preferences and the distribution of immature and adult northern gannets *Morus bassanus* (hereafter "gannet") over two contrasted seasons. The gannet is a long-lived pelagic seabird and a plunge-diver feeding on a wide range of prey (Montevecchi & Barrett, 1987; Hamer et al., 2007). The species is flexible and is able to cope with variability in food availability either by shifting between prey or by increasing their foraging effort (Garthe et al., 2011; Pettex et al., 2012). Gannets, which breed in large colonies, are mostly philopatric though immature individuals are known to prospect other colonies during their first years (Votier et al., 2011). During their two first years, immature gannets disperse at sea and return at the colony when two years old for regular visit, before the first breeding at 4-5 years old (Nelson, 2002). Adult gannets are central-place foragers during breeding period, which are constrained to return to the colony to incubate or to feed a single chick at short intervals.

Adult gannets are central placed foragers during the breeding period from May to August, as are constrained to return to the colony to incubate or to feed a single chick at short intervals. After the fledging of juveniles, adults migrate southwards to reach wintering ground (Fort et al., 2012; Fifield et al., 2014). During the breeding season, a strong intra-specific competition occurs between breeders within large colonies as density-dependent prey depletion forces them to forage further and longer (Lewis et al., 2001). Besides, Wakefield et al. (2013) showed that gannets breeding in neighbouring colonies forage in largely mutually exclusive areas, resulting in a marked spatial segregation induced by competition between individuals from different colonies. We can therefore wonder how this strong intra-specific competition between adults could affect less experienced seabirds, not constrained by central-place foraging, but displaying a potentially lower foraging efficiency.

In addition of the foraging experience, adults and immatures gannets also differ by their energetic requirements (Orians & Pearson, 1979). Therefore, since the energetic needs of the two stages differed, the first aim of this work was to explore whether the habitat preferences were similar between stages according to the season. Second, we tested for the hypothesis that if both stages exhibit similar habitat preferences, immature gannets would avoid the competition with breeding gannets and mostly forage outside of their range. This would result in a spatial segregation between immature and adult gannets during the breeding season. On the contrary, in winter, we hypothesised the density-dependent competition between gannets to be lower or absent, since outside the reproductive period, when breeding adults are released from central-place foraging and disperse throughout the north-Atlantic Ocean (Fort et al., 2012; Gremillet et al., 2015), the proximity of experienced adults could benefit to immature gannets.

To explore these hypotheses and to investigate habitat preferences of both stages during two contrasting seasons, we used Generalized Additive Models based on aerial surveys conducted over the Bay of Biscay (BoB), Celtic Sea (CS) and English Channel (EC) in winter 2011-2012 and summer 2012. The method allows to explore the relationship between the number of individuals and several environmental predictors, here physiographic and oceanographic variables. We therefore provided insights into the seasonal variations of habitat preferences of adult and immature Northern Gannets within the north-eastern Atlantic.

2 Material & Methods

This study was based on aerial surveys SAMM (Aerial Census of Marine Megafauna), conducted during the winter 2011-2012 (late November to mid-February: 32,443 km of effort) and the summer 2012 (mid-May to early-August 08: 33,864 km of effort) over the EC, BoB and CS (Figure 1). The strip-transect methodology was used to record seabird observations, using a band of 200 m on each side of the transect line, with perfect detection assumption. Along with seabird sightings and group size were recorded observation conditions (Beaufort sea-state, glare severity, turbidity, and cloud cover). Moreover, the age of sighted northern gannets were recorded when possible (immature, juvenile, adult or mix).

Individuals showing an adult-like plumage were gathered in the "adults" stage, though the breeding status remains unknown. Given the short time of observation and the distance from the plane, residual black feathers on the wing and tail of 4th year individuals were obviously not visible, therefore such individuals were often included within the adult stage. Concerning the 3rd year, individuals displaying few "piano key" secondary feathers might have been classified within adults as well. Individuals showing all stages of juvenile and immature plumage are hereafter called "immature".

Prior to analyses, transects flown in effort were subdivided in legs of homogeneous detection conditions and then in 10 km long segments. For each segment, numbers of sighted individuals were summed up, for adults at one hand, for immatures at the other hand. To perform habitat modelling on best quality data, we retained only segments with Beaufort sea-state from 0 to 3, and subjective conditions from medium to excellent. The effort flown in good conditions represented 87% of the total survey effort in winter, 93% in summer.

Habitats were then modelled using Generalized Additive Models (GAMs; Hastie & Tibshirani (1990); Wood (2006)) with a quasi-Poisson distribution to account for the over-dispersion of our data (Hedley & Buckland,

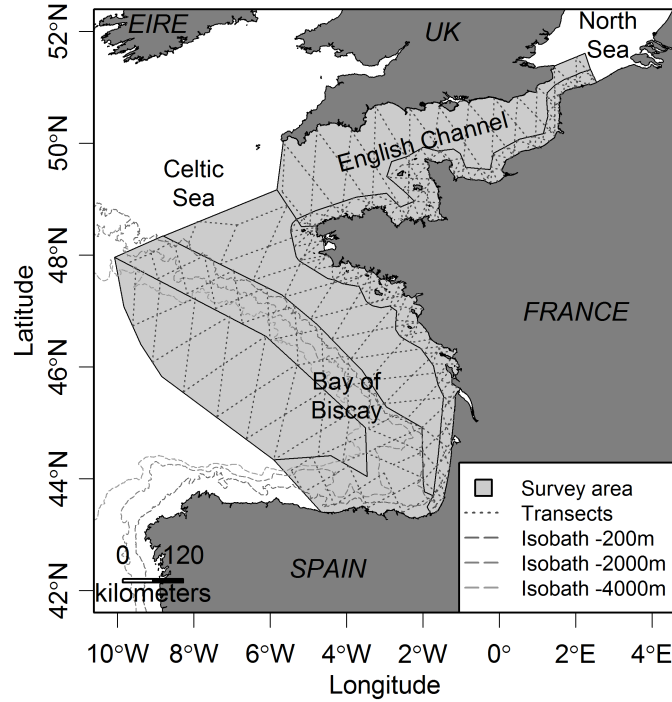


Figure 1. Study area, with survey area and sampled transects.

2004). The response variable (number of individuals per segment) was related to several environmental predictors with a log-link function and the sampled area per segment as model offset (segment length by twice 200 m). Two kind of environmental predictors were used (Supplementary Material, Figure A1). First, four physiographic variables were included (Table 1): bathymetry, its gradient (slope), distance to closest coast and distance to closest colony (only included for summer models). Colony locations were compiled from several sources and geolocated (Supplementary Material, Text A1). Second, we used six oceanographic predictors: sea surface temperature (SST) mean, variance and gradient, sea surface height (SSH) mean and standard deviation, and maximum tidal velocity. These dynamic variables were introduced into model selection with two temporal resolutions, environmental conditions being summarized over the 7 and 28 days prior to each sample day.

We implemented a model selection procedure based on GCV (the lower the better), allowing a maximum of four covariates by models and excluding all combinations of covariates with an absolute value of correlation higher than 0.7. The maximum degree of freedom for smoothers was constrained to 3 to avoid over-fitting of the data (4, considering the offset). Once a model was selected, we extracted the contribution of each covariate in the linear predictor by segments. These contributions were computed using the `predict.gam` function within the `mgcv` package, setting the `type` argument as "terms" (Wood, 2006): this provides a matrix with each component of the linear predictor separately (here, the smoothed covariates); see function description for more details. The contributions were then mapped to explore the local variations in the importance of each selected covariate. Predictions were then produced for every single day encompassed in the survey period, then these daily predictions were averaged over each season. In order to limit extrapolation, we only performed predictions within the sampled environmental envelope. Coefficients of variation associated to these predictions were computed as $CV = \sqrt{\text{seasonal variance} / \text{seasonal mean}}$.

Environmental predictors processing and analyses were performed using R version 2.15.3 (R Core Team, 2013), while survey data processing was performed in FME Desktop (ESRI Edition, 2014).

Table 1. Environmental predictors used for habitat modelling and their source. GEBCO-08 30 arc-second database was used to compute depth, slope and distance to closest coast (<http://www.gebco.net/>). The ODYSSEA product from Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu/>) was used to compute mean, variance and gradient of sea surface temperature. MARS-3D model from PREVIMER (<http://www.previmer.org/>) was used to compute mean and standard deviation of sea surface height (SSH), MARS-2D to compute maximum tidal velocity.

Type	Environmental predictors	Units	Source
Physiographic	Depth	meters	GEBCO-08 30 arc second
	Slope	degrees	
	Distance to the closest coast	meters	
	Distance to the closest colony	km	Manually referenced
Oceanographic	Mean SST	°C	ODYSSEA
	Variance of SST	°C	
	Mean gradient of SST	°C	MARS 3D
	Mean SSH	meters	
	Standard deviation of SSH	meters	
	Maximum tidal velocity	m.s ⁻¹	

3 Results

3.1 Sightings

Adults sightings were more numerous than immature sightings, especially in winter (Table 2). In winter, adults were more concentrated within southern BoB and eastern EC, while in summer they were concentrated around colonies of Rouzic and Les Etacs (Figure 2A). Immatures were more scarce in winter, but had overall distribution quite similar to adults, although only restricted to southern BoB and eastern EC (Figure 2B). In summer, they were mostly encountered within the BoB, especially along the coast and the slope. Sightings of mixed groups (adults mixed with immatures) were scarce in winter, with only 15 sightings in the southern BoB (Figure 2C). In summer, they were more numerous, spread over the EC and northern BoB. Given we had no estimation of the proportions of adult and immature gannets within mixed flocks, these sightings were left apart for the habitat modelling.

Table 2. Number of sightings and corresponding number of individuals for adults, immatures and mixed groups of gannets in winter and summer.

	Winter		Summer	
	Number of sightings	Number of individuals	Number of sightings	Number of individuals
Adults	1146	9332	833	2478
Immatures	68	144	478	973
Mixed groups	15	1644	59	735

3.2 Habitat modelling

The winter models reached fairly good explained deviances for both groups, with 26.5% for adults and 30.2% for immatures (Figure 3A). Their preferences were quite similar, with bathymetry selected for both groups as the most contributory covariate, according to the maps of covariate contributions to the linear predictor (Supplementary Material, Figure B1). Their relationship to the depth was negative, highlighting a preference for shallow waters. The maximum velocity (7d) was also selected for both groups, with an overall negative relation-

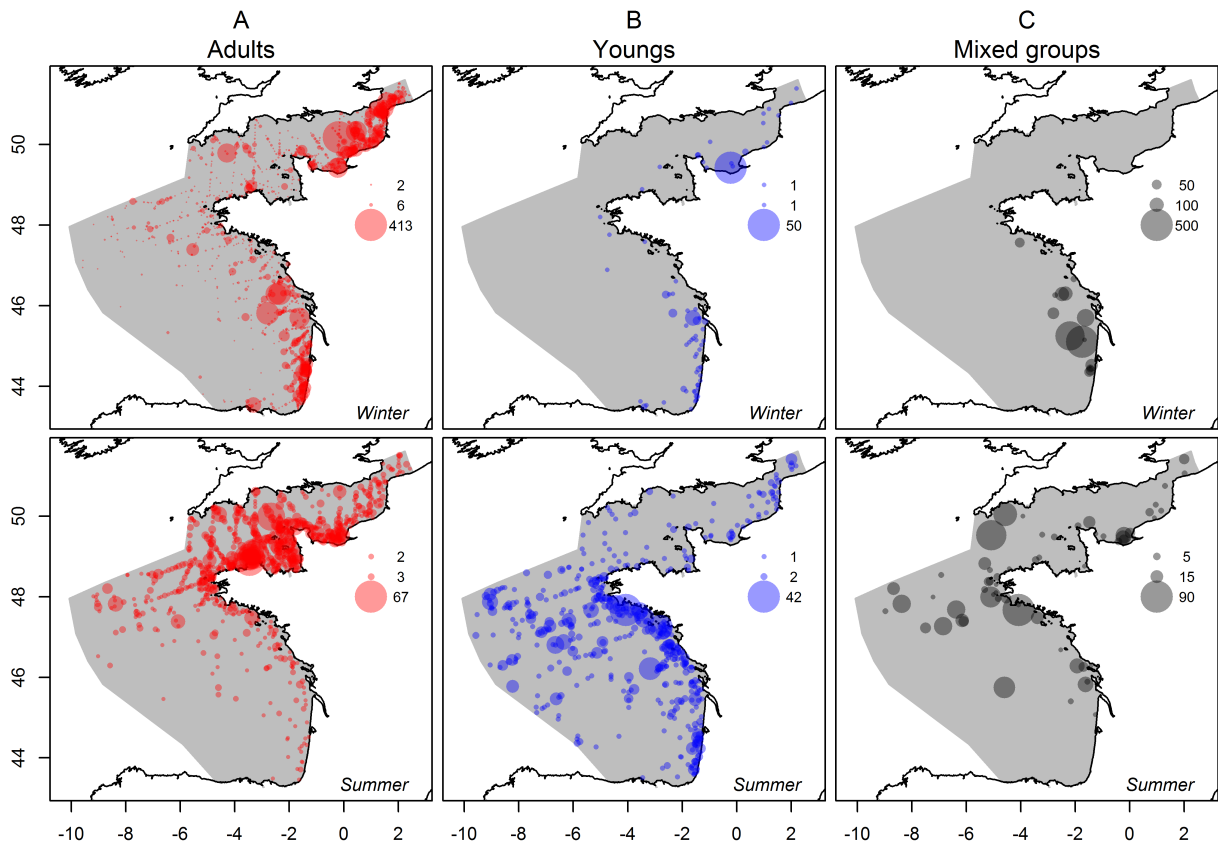


Figure 2. Sightings of adults (A), immatures (B) and mixed groups (C) of Northern Gannets in winter (upper panel) and summer (lower panel). Legend are 50, 75 and 100 percentiles of sightings size.

ship and high positive contributions in southern BoB. Concerning adults, mean SSH (7d, positive relationship) and SST_{var} (28d, overall negative relationship) were the other two selected covariates. The mean SSH had important positive contributions within eastern EC while SST_{var} had positive contributions in northern BoB, western EC and CS. For immature gannets, mean SST (28d) and SD SSH (28d) were the other two selected covariates, with overall low contributions and positive relationship to response variable.

In summer, the models explained 42.8% and 16.8% of the deviance for adults and immatures, respectively (Figure 3B). As for winter, the two groups shared three selected covariates, the distance to the closest colony, SST_{grad} (28d) and SST_{var} (7d). However, their relationships to the most contributory covariate (Supplementary Material, Figure B2), the distance to closest colony, were opposite: for adult gannets, the density of individuals decreased with distance to colony, with null density farther than about 300 km from colony; while for immatures the density was positive between about 150 and 450 km from colony. However, their relationship to SST_{grad} was similar, with an overall positive relationship. This covariate had important contributions for both groups, with positive ones mainly along the coasts and the BoB slope. For both groups, the SST_{var} (7d) had lower contributions: for adults, the covariate presented localized important contributions, in southern Cornwall and off Loire estuary, with an overall positive relationship; while for immatures, the covariate had a complex relationship with a slight mode and overall low contributions. Finally, the last selected covariate for the adults model was mean SST (7d). It presented fairly good contributions in the north of the area, and the relationship was unimodal with a maximum around 14.5°C. For immatures the last covariate was mean SSH (28d), presenting fairly good positive contributions all over the BoB and western EC, with a slight mode around -0.5 m.

3.3 Predictions

Given they had similar most contributory covariates, the predicted distributions of adult and immature & juvenile gannets in winter showed similarities, despite the tenfold higher densities of adults (Figure 4). First,

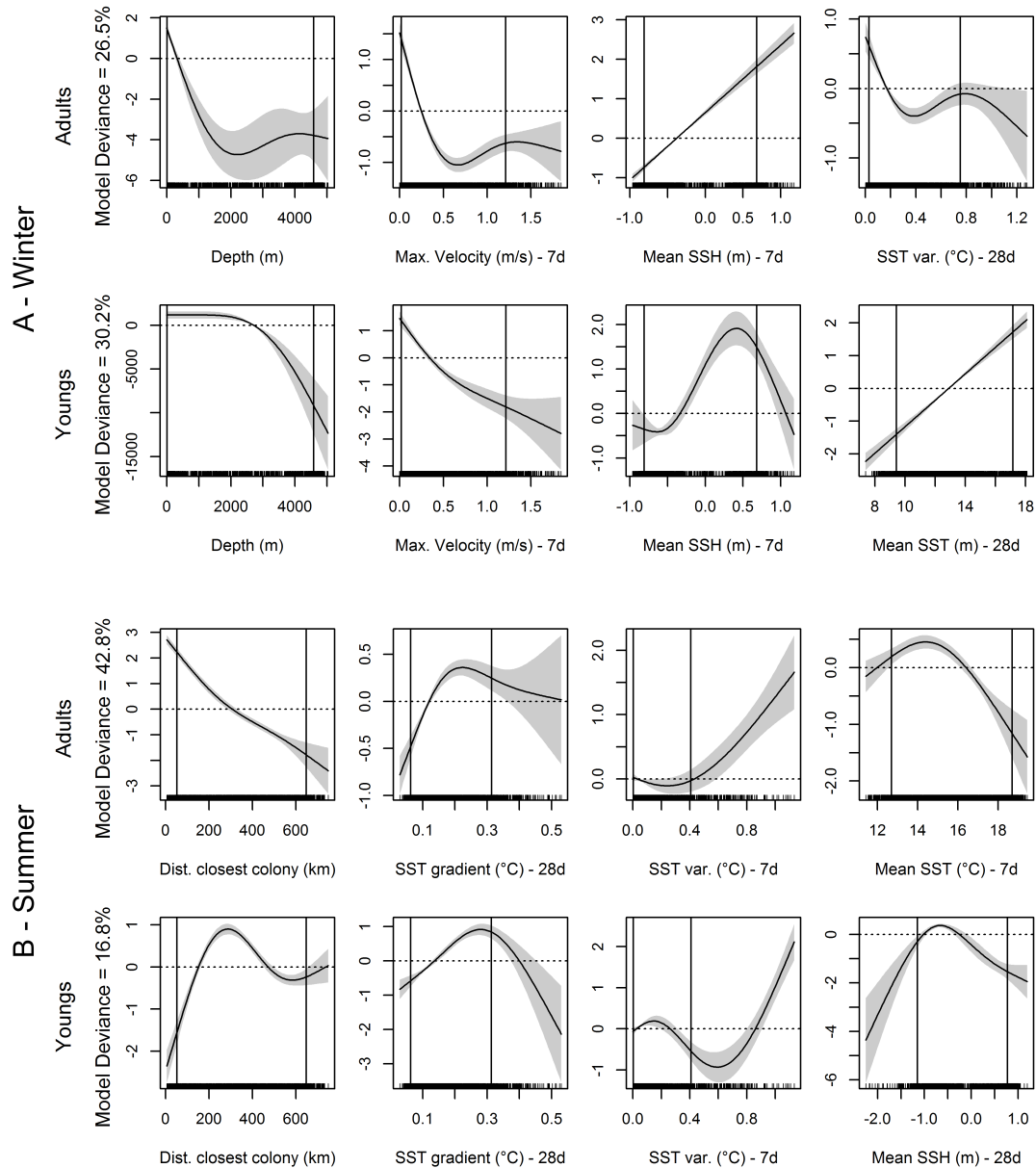


Figure 3. Habitat models selected in winter (A) and summer (B) for adult and immature gannets. Deviances of models are indicated beside. Vertical black lines indicates 5 and 95 percentiles of the covariates, while the horizontal dotted lines indicates the zero in response variables.

both presented higher densities in the southern BoB shelf, up to Galicia, and in the eastern EC, although this hotspot was less pronounced for immatures. However, adults also showed fairly high densities off Ireland, which was not the case for immatures. Both gannets groups were absent from oceanic waters.

In summer, adults were predicted in higher densities than immatures as well (Figure 4). Their distribution were interestingly opposite, due to the avoidance of colonies by immature birds. While adults concentrated within 200 km from colonies, immatures precisely avoided this area. However, once this dichotomy noted, both groups targeted long-term thermal gradient, thus leading to higher densities of immatures along the BoB coast and slope. In all cases, the highest CVs around predictions occurred were the models predicted the lowest densities (Supplementary Material, Figure C1).

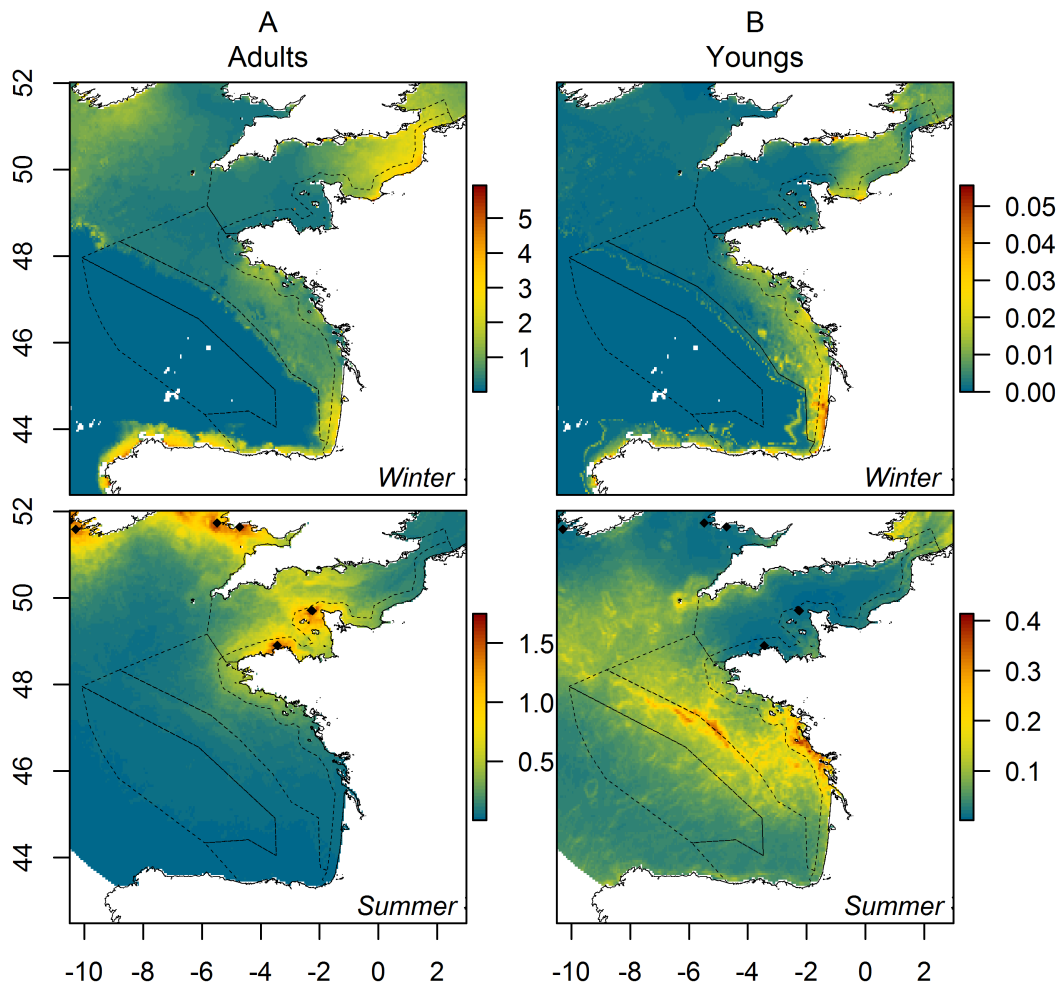


Figure 4. Habitat predictions in individuals per km² for adult (A) and immature (B) Northern Gannets in winter (upper panel) and summer (lower panel). Black dots are the colony locations.

4 Discussion

In this study, we have investigated and compared the habitat preferences and the resulting at-sea distribution of adult and immature northern gannets during two contrasting seasons across the EC, the BoB and the CS. Our results showed that adults and immatures displayed similar habitat preferences, resulting in a spatial segregation during the breeding period due to a strong intra-specific competition originating in adult birds outcompeting the younger ones from the vicinity of breeding sites. During the inter-breeding period however, the intra-specific competition relaxed as adults were no more constrained by central-place foraging, and immature and adult gannets shared both the same distribution and habitat.

During the winter 2011/2012, both age stages were predicted in higher densities over all the continental shelf of the EC, the CS and the BoB. Within this range, adult and immature gannets were concentrated in two main areas: the southern BoB shelf characterized by low tidal currents and warmer sea surface temperatures and the eastern Channel combining shallow waters and positive sea surface height (Lambert et al., In press). The distribution of both groups were similar in winter, although higher densities of adults were predicted in the CS, hence no spatial nor habitat segregation seemed to occur between the two stages during this non-breeding period. This was consistent with recent telemetry data obtained from four fledging gannets and twenty-four adults from the largest French colony in the EC (Rouzic), which showed that immature gannets were following the same migration route towards southwards to western Africa (Gremillet et al., 2015). After breeding, gannets are known to spread over the whole species range (Nelson, 2002; Fort et al., 2012) and so occur in lower densities along the migration path and wintering grounds. There is probably few, if any, intra-specific competition, so

that immature birds can share the same habitats and resources than adults.

Less experienced immatures, especially juveniles in their first months after fledging, would probably benefit from social learning or local enhancement by following adults during the wintering migration (Buckley, 1996; Davoren et al., 2003; Thiebault et al., 2014), since adults are able to anticipate or memorize favourable areas (Pettex et al., 2010) and may be more efficient to detect prey patches. The survival rate of adult gannets in UK and Ireland has been estimated at more than 90% between 1959 and 2002, while it only reached 42% for first year gannets (Wanless et al., 2006). Starvation in newly independent juvenile gannet is a major cause of death, as they may be unable to fish under harsh winter conditions like adults do (Nelson, 2002). Therefore, following experienced adults during their long migration might provide an advantage to survive for juvenile birds as long as the density level does not lead to competition. Older immature gannets (second and third year), which survived to the first year wreck and increased their fishing skills and diving capacity with age (Greig et al., 1983; Marchetti & Price, 1989), would also use aggregations of conspecifics as a proxy of feeding opportunities as it was recently shown in Cape gannets, a closely related species (Thiebault et al., 2014; Tremblay et al., 2014).

During summer 2012, the habitat models predicted two spatially segregated and complementary distributions for adult and immature gannets. Immature gannets globally behave as adults in their habitat preferences, but the most explanatory covariate was the distance to the closest colony for both groups. According to the relationships with this variable, immature birds avoided areas up to 150 km away from breeding sites, where the highest densities of adults were predicted. The underlying process of this spatial segregation certainly is a strong intra-specific competition for food, dominated by breeding adults. Gannets breed in large colonies, up to tens of thousands nest for the largest ones, and are constrained to forage within a limited range of several hundreds of kilometres, which can lead to severe prey depletion around the colony. As a result, birds are constrained to increase their foraging trip and to forage further, proportionally with the size of the colony (Lewis et al., 2001). This density-dependent competition was also shown to induce a segregation between foraging range of neighbouring colonies, where smaller colonies are constrained to smaller ranges (Wakefield et al., 2013).

If the presence of conspecifics helps gannets to identify food opportunities (Thiebault et al., 2014), kleptoparasitism and injuries due to collision (possibly fatal to birds) is the counterpart of such local enhancement (Capuska et al., 2011). In such a competitive context, the foraging success of less experienced and skilled birds, probably lower than those of adults as recently shown in shearwaters (Fayet et al., 2015), could even be directly reduced by the higher predatory skills of adults. Therefore, individuals which are not constrained by central-place foraging would logically avoid areas close to colonies to forage in similar habitats beyond the range of breeding adults. This idea was supported by the a recent study investigating the foraging trips of five immature gannets (one two years-old and four three years-old birds) aggregating in "club-sites" close to nesting areas (Votier et al., 2011). This study revealed that these immature gannets were able to prospect other colonies and to disperse further than adults, but they were overall faithful to the colony and acted as central-place foragers. Stable isotope analysis however indicated a strong segregation with breeders (Votier et al., 2011), suggesting that immature either foraged in different areas of adults or fed on different prey, maybe in order to avoid competition with breeders.

During the SAMM surveys, it is probable that birds identified as immature gannets displayed a conspicuous immature plumage from the dark post-juvenile (first year) to the most black-spotted plumage of third year gannet. These birds clearly avoided the competition with central-place forager birds, *i.e.* breeders or older immatures (3 and 4 years-old) acting as central-place foragers, although they shared similar habitat preferences. It worth noting that there was some overlap between both adult and immature distributions, with young gannet density increasing slowly as adult gannet density decreased with the distance to colony. This could reflect the behaviour of immature gannets aggregating in club-sites as described in (Votier et al., 2011), which forage further than breeders but still return regularly to the colony.

Intra-specific competition apparently affects all stages of maturity in northern gannets, from post-fledging juveniles to breeding adults. Youngest birds would cope with it by a strict avoidance of areas exploited by central-place foragers, then as birds mature, they would join clubs in colonies and find adaptive strategies

to limit the competition with breeders as long as they are not really constrained by the central-place foraging (niche segregation or use of distant areas). It has been recently suggested, that the long period of immaturity in the wandering albatross *Diomedea exulans* would be related to a learning period dedicated to integrate constraints of reproduction and central-place foraging (Riotte-Lambert & Weimerskirch, 2013). The learning of foraging skills would be an issue for survival only during the first months after fledging, but the following long period of immaturity would allow immature birds to get the necessary skills for breeding (Riotte-Lambert & Weimerskirch, 2013).

To conclude, our findings suggest that a continuum occurs in the adaptive strategies deployed by immature gannets to cope intra-specific competition along the maturation process, which can be reflected in the habitat selection and distribution. Although the fishing technic of plunge diving used by gannets necessarily imply a period of learning for fledgings in their first months, it is probably not a limiting factor after the first winter.

To our knowledge, this study brings the first evidence of intra-specific competition between adult and immature gannets during the breeding period as well as a synoptic description of the at-sea distribution and habitat preferences of immature and breeding adults at this scale and over two contrasting seasons, although there is an increasing number of studies on immature seabirds in the literature. Immature seabirds are thought to represent more than 50% of the global seabird population but the topic is relatively undocumented as immature seabirds often wander at sea during their first years. This knowledge is however of great interest to understand the processes driving the dispersion and recruitment of immature birds and to take into account the ecological needs of an important part of the population in terms of conservation.

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Appendix A

Colonies Locations

Northern gannets breed on discrete locations (Nelson, 2002), well documented and surveyed (Figure 1), with one large colony in France (Rouzic), two colonies in Channel Islands (Les Etacs and Ortacs), two colonies in Wales (Grassholm and St Margaret's Island), seven in Ireland (Bull Rock, Little Skellig, Great Saltee, Ireland's Eye, Lambay Island and two on Clare Island), one in England (Flamborough Head) and finally sixteen in Scotland (mainly in Orkney, Shetland and Western Isles). Colonies of Helgoland and Norway (not shown here) were also referenced, although too far to be involved in our summer data.

The locations were mainly extracted from Nelson (2002) and Joint Nature Conservation Committee, with additional informations from involved researchers (e.g., Pettex and colleagues for Norway colonies).

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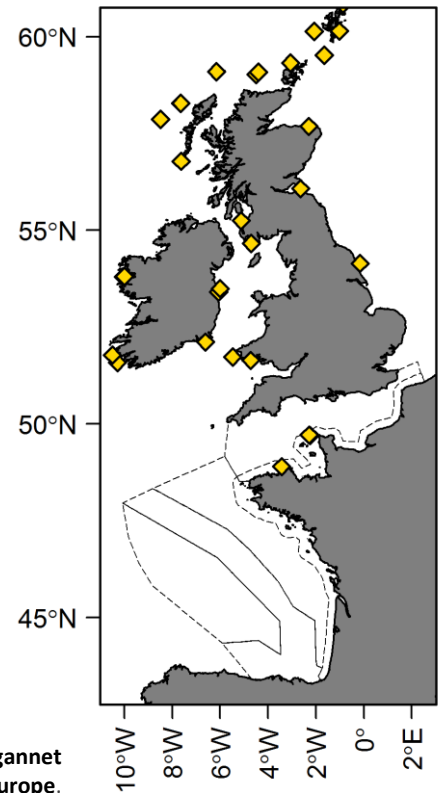


Figure A1. Northern gannet colonies on western Europe.

Appendix B

Habitat modelling

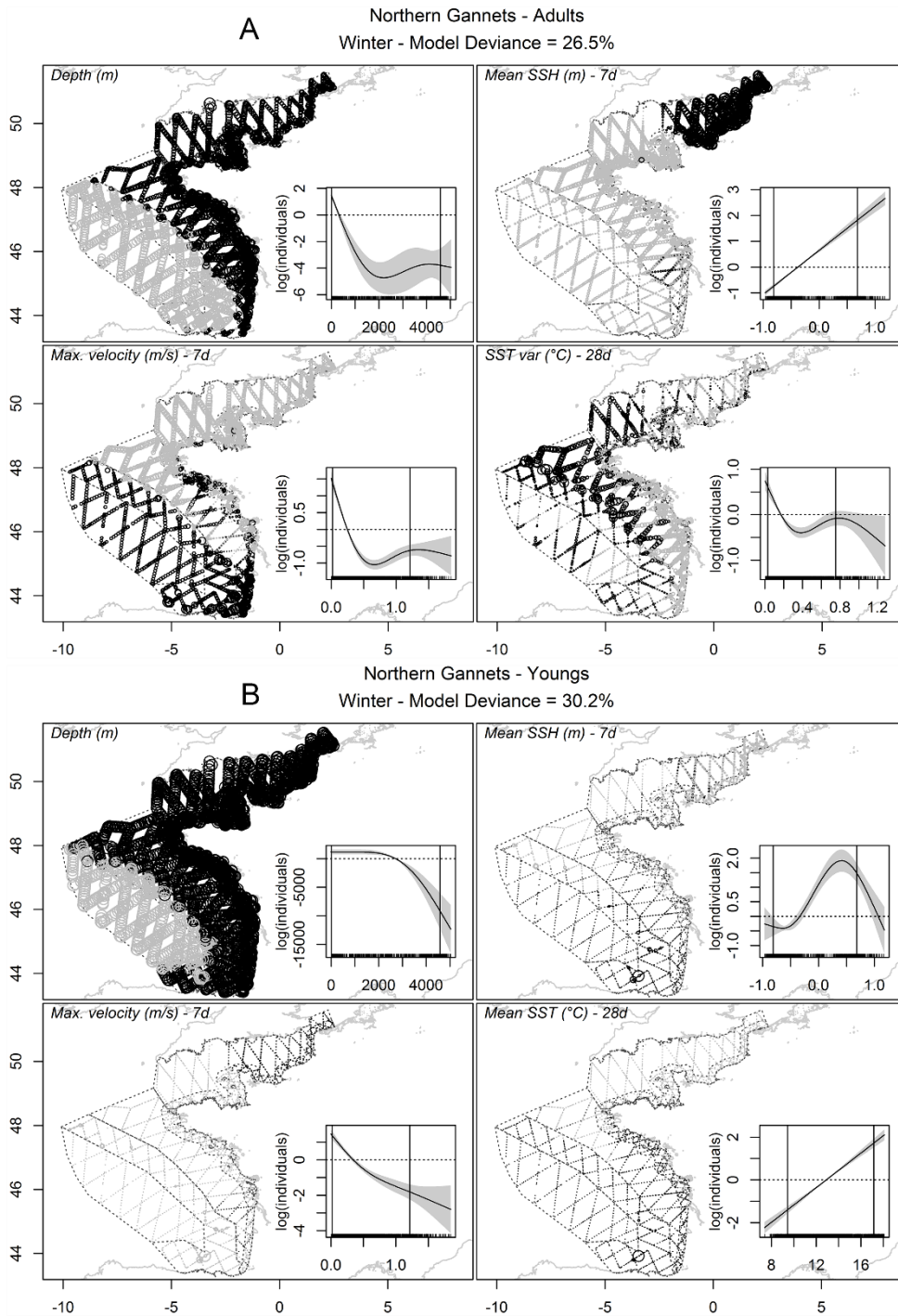


Figure B1. Winter habitat model selected for **A** – adult northern gannet (explained deviance = 22.6%), **B** – young gannets (explained deviance = 30.2%). Each panel spatially represents the contribution of the concerned covariate to the linear predictor for each sampled segment, with the dot size proportional to the covariate relative contribution regarding the three other covariates contributions in that point. Grey dots represent points with negative covariate contribution, black dots where it is positive. Corresponding GAMs curves are inserted in corresponding panels, representing the relationship between the covariate (abscissa) and the linear predictor ($\log(\text{individuals})$ ordinate). The two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range must be avoided, since the smooth splines might not be reliable.

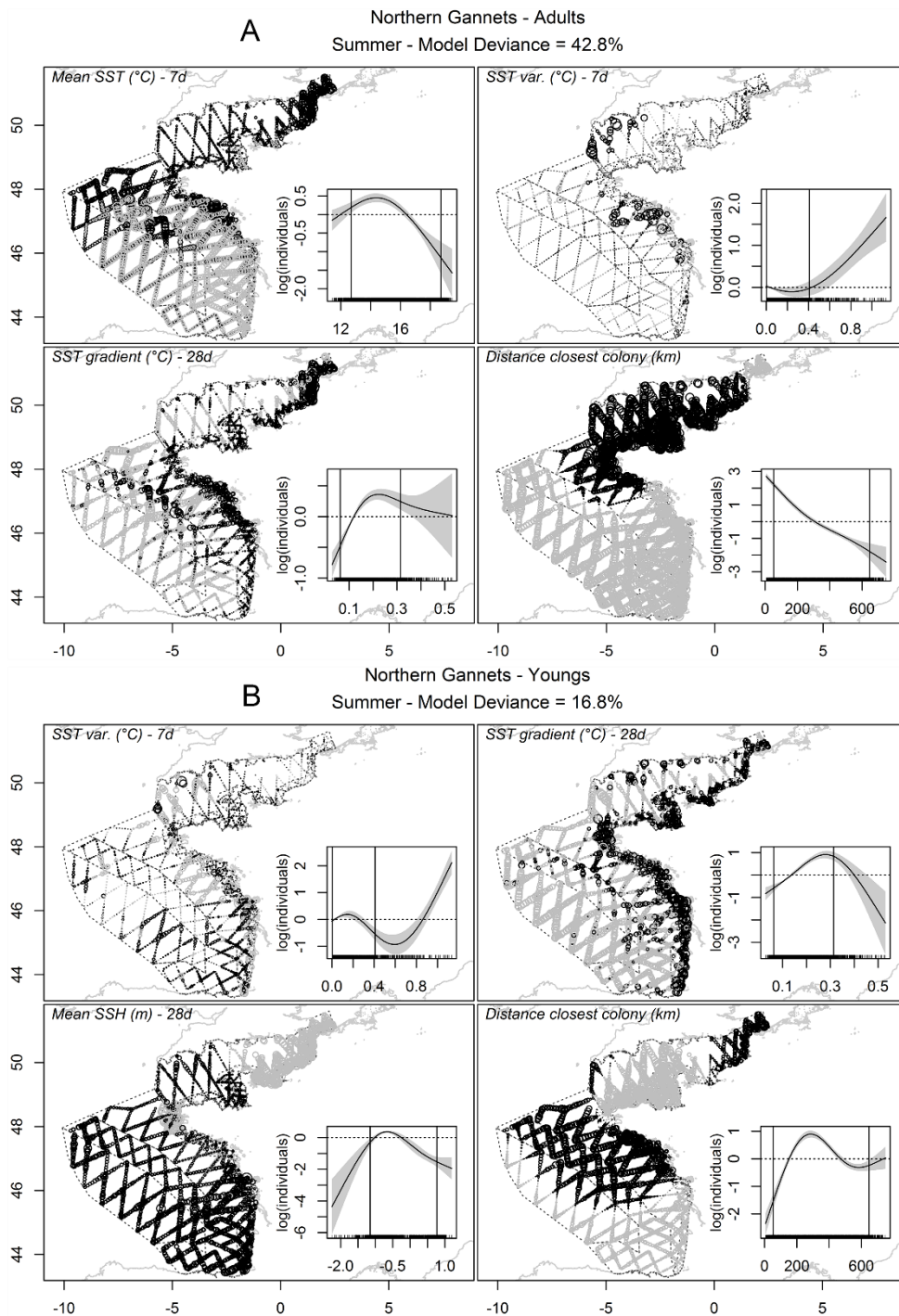


Figure B2. Summer habitat model selected for A – adult northern gannet (explained deviance = 42.8%), B – young gannets (explained deviance = 16.8%). Each panel spatially represents the contribution of the concerned covariate to the linear predictor for each sampled segment, with the dot size proportional to the covariate relative contribution regarding the three other covariates contributions in that point. Grey dots represent points with negative covariate contribution, black dots where it is positive. Corresponding GAMs curves are inserted in corresponding panels, representing the relationship between the covariate (abscissa) and the linear predictor (log(individuals) ordinate). The two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range must be avoided, since the smooth splines might not be reliable.

Appendix C

Coefficients of Variation

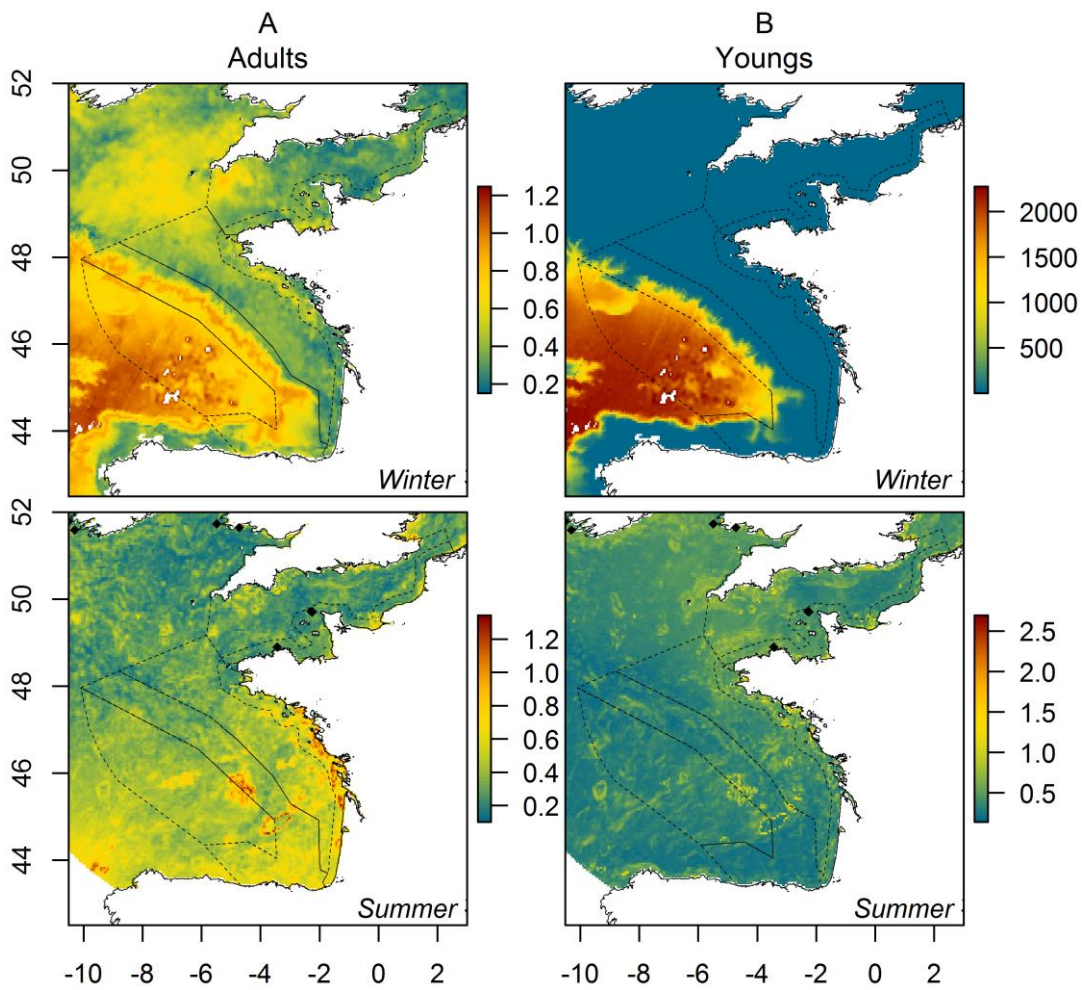


Figure C1 – Coefficient of variations around mean predictions based on habitat models for adult (A) and young (B) northern gannets, in winter (above) and summer (below). Empty cells were due to the limitation of the prediction within the range of sampled values for each selected covariates, in order to avoid extrapolation. Thick dotted lines materialized the survey area (see Figure 1).

Appendix **F**

Chapter 6 - Supporting information

Supporting information to Chapter 6

1 Distributions of the small pelagic fish acoustic detections

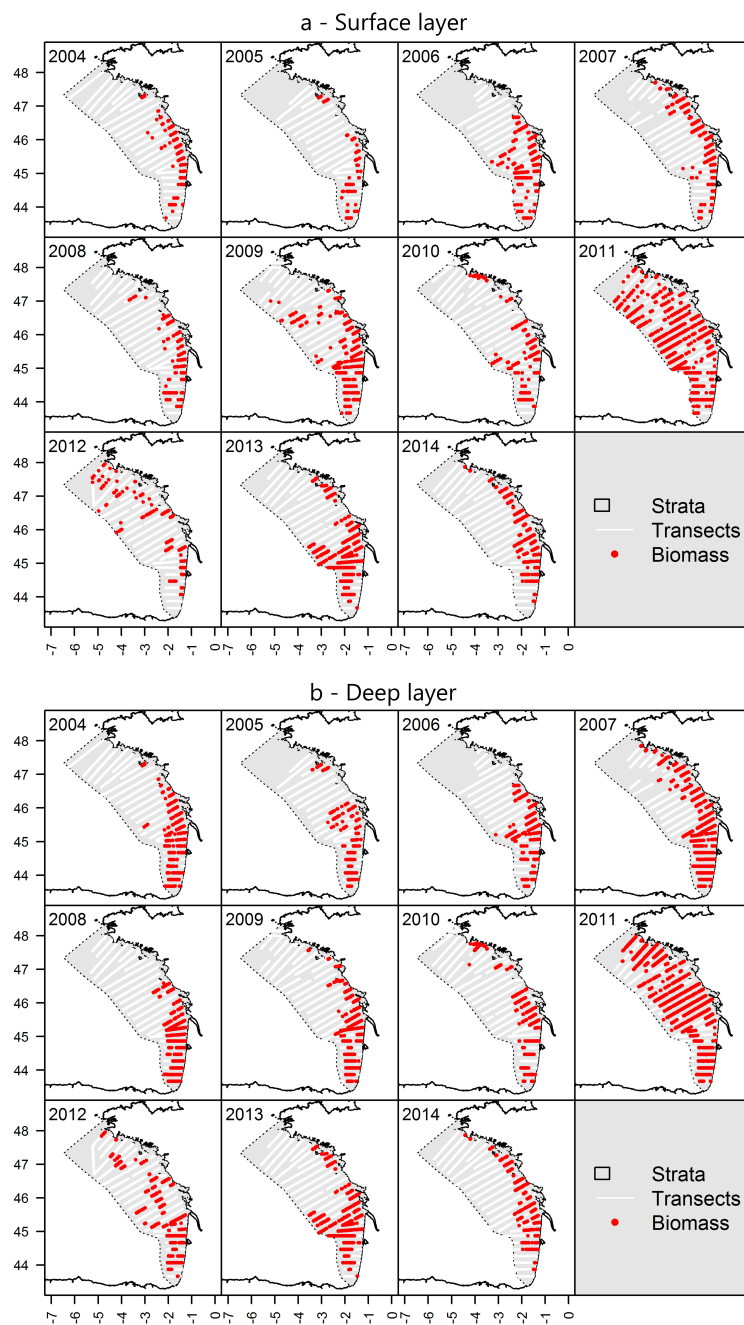


Figure 1. Distributions of acoustic detections of individuals smaller than 10 cm in the surface (a) and deep layers (b), in red. In white is indicated the acoustic sampling trace.

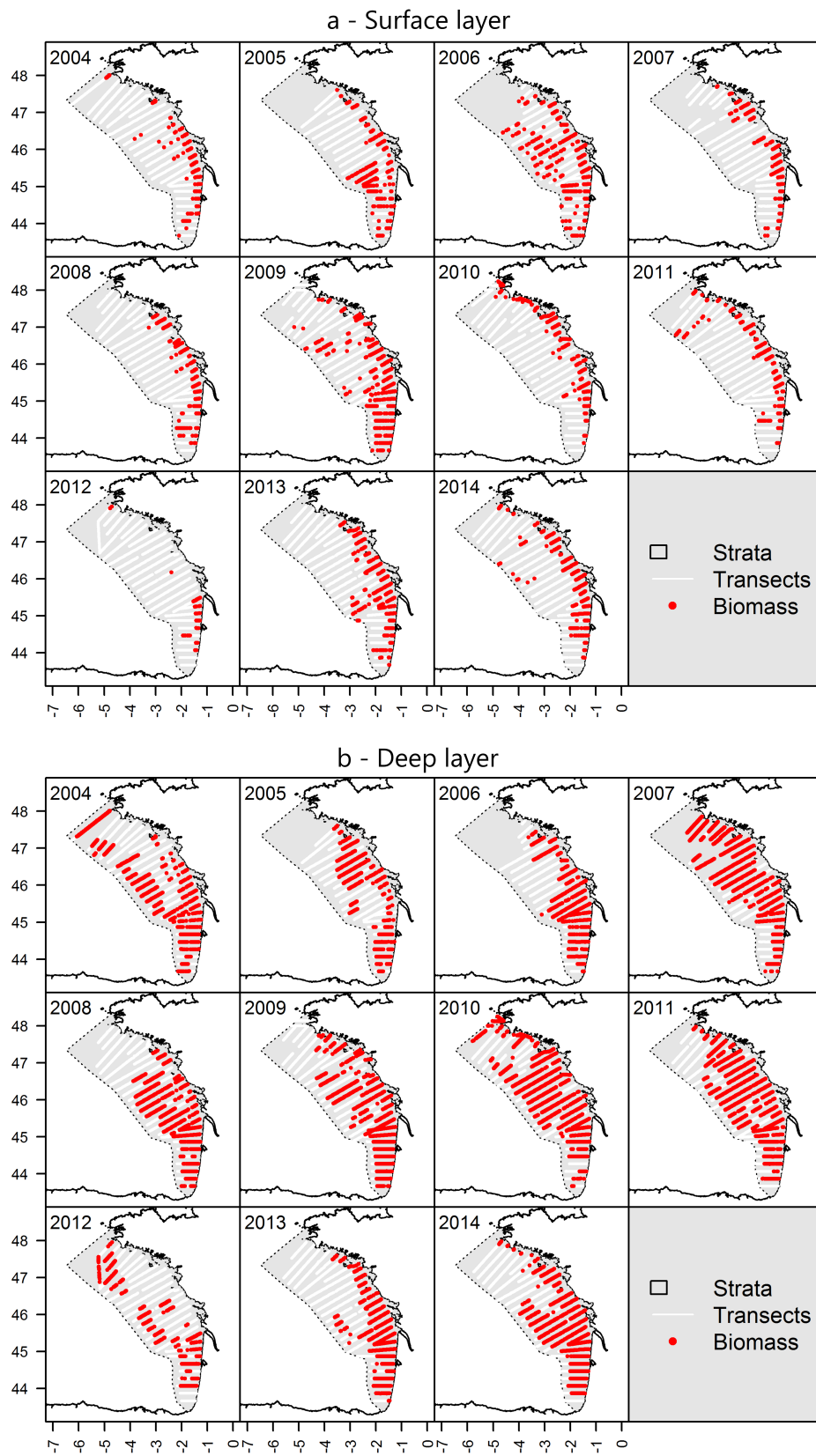


Figure 2. Distributions of acoustic detections of individuals between 10 and 20 cm in the surface (a) and deep layers (b), in red. In white is indicated the acoustic sampling trace.

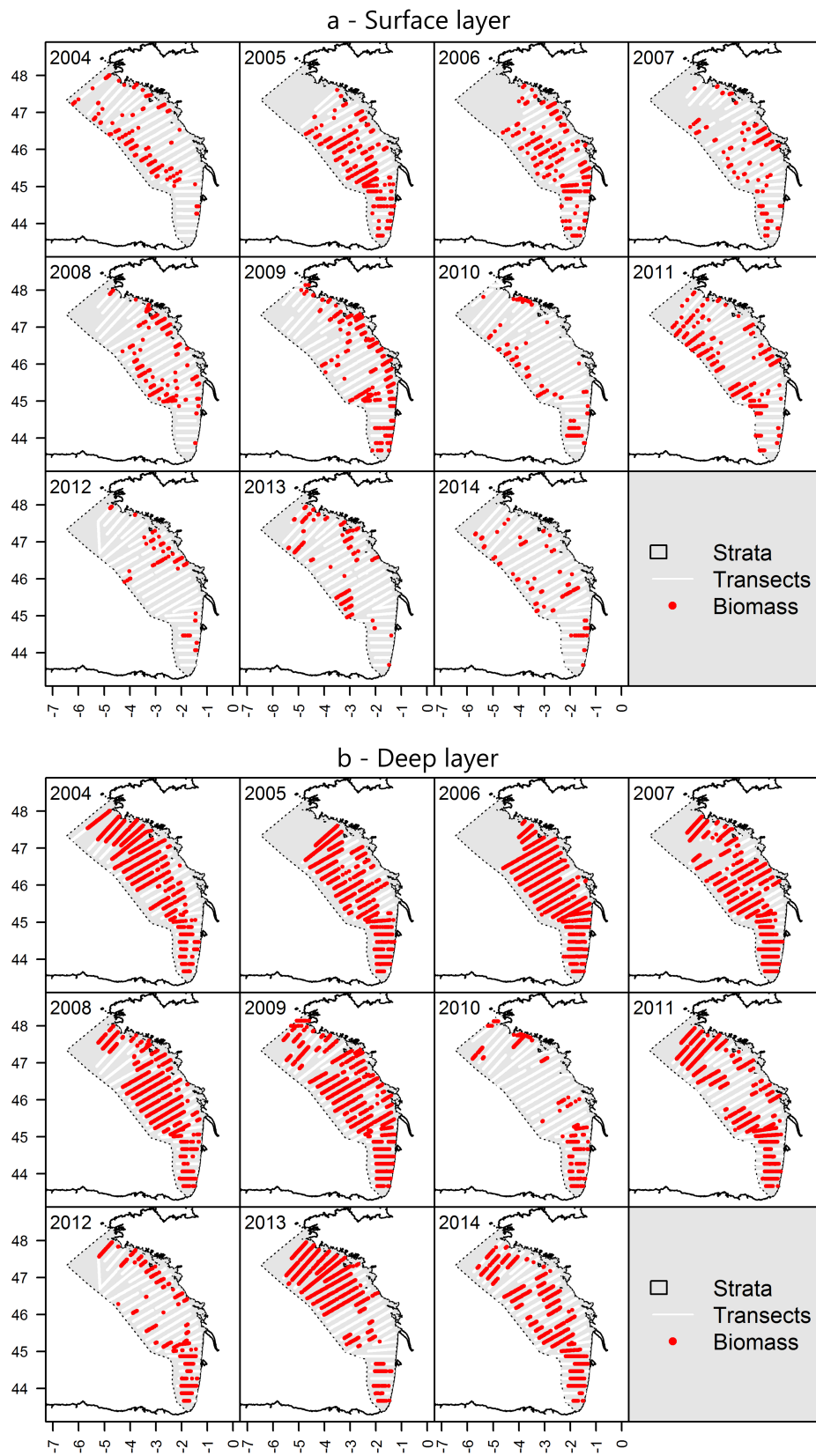


Figure 3. Distributions of acoustic detections of individuals between 20 and 30 cm in the surface (a) and deep layers (b), in red. In white is indicated the acoustic sampling trace.

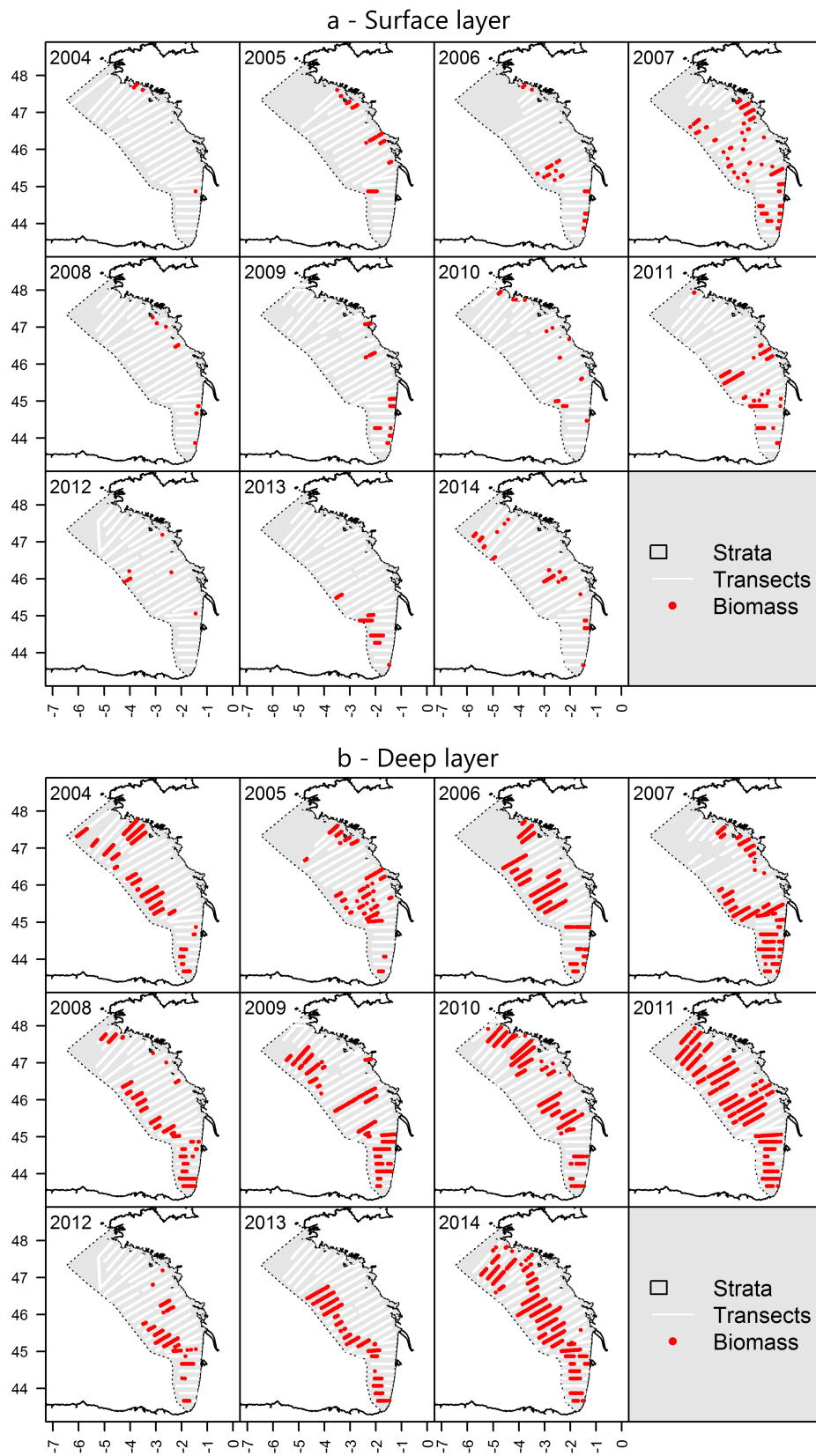


Figure 4. Distributions of acoustic detections of individuals larger than 30 cm in the surface (a) and deep layers (b), in red. In white is indicated the acoustic sampling trace.

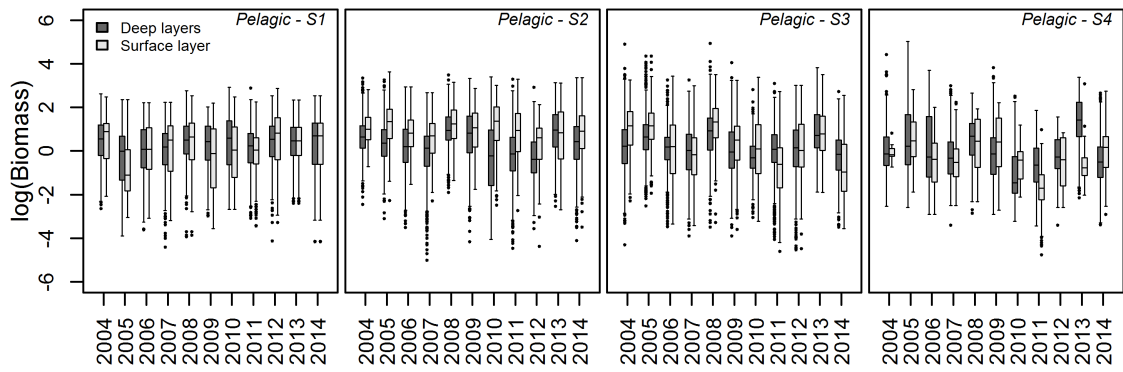


Figure 5. Biomass (log) of the four size classes of small pelagic fishes detected within the Bay of Biscay between 2004 and 2014, for the surface and deep layers. S1: < 10 cm; S2: 10–20 cm ; S3: 20–30 cm; S4: > 30 cm.

2 Distributions of the top predator sightings

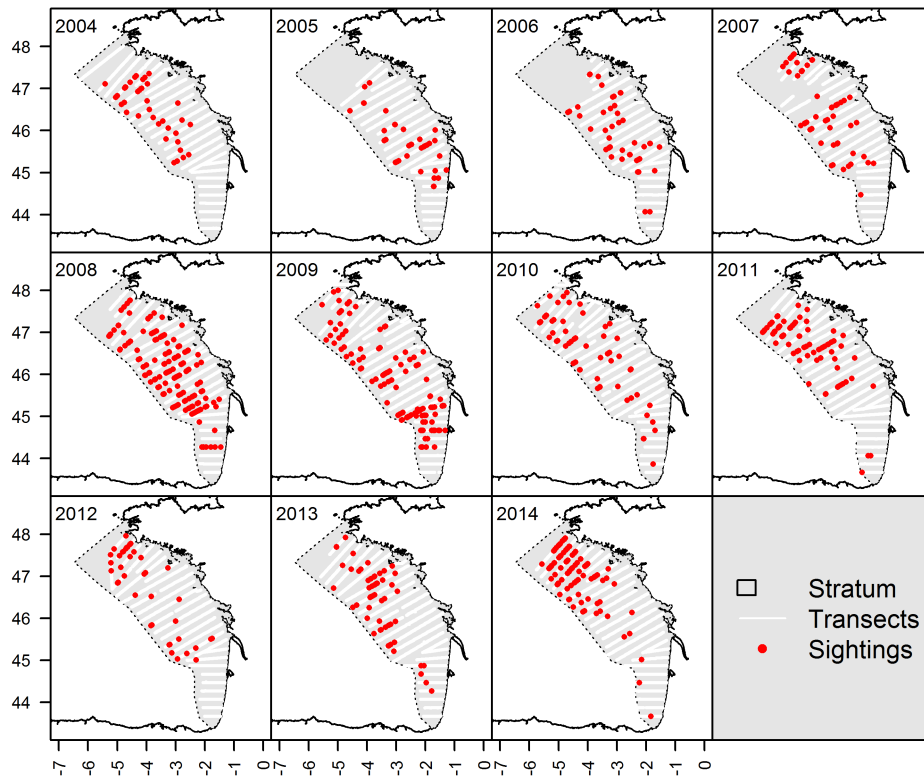


Figure 6. Northern fulmars sightings associated to acoustic detection from 2004 to 2014.

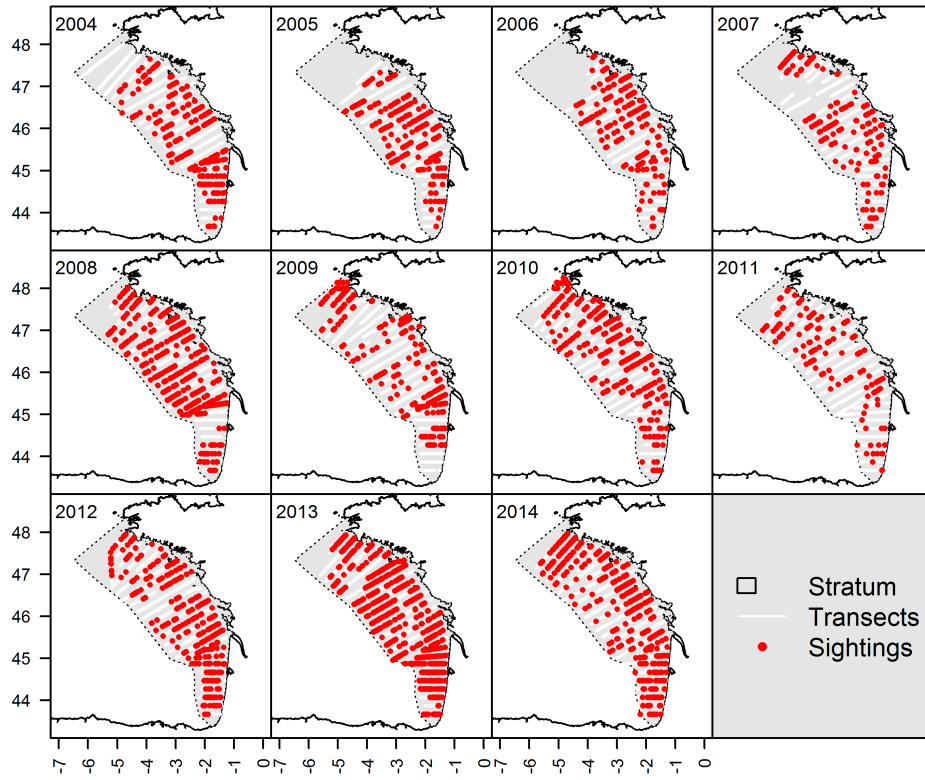


Figure 7. Northern gannets sightings associated to acoustic detection from 2004 to 2014.

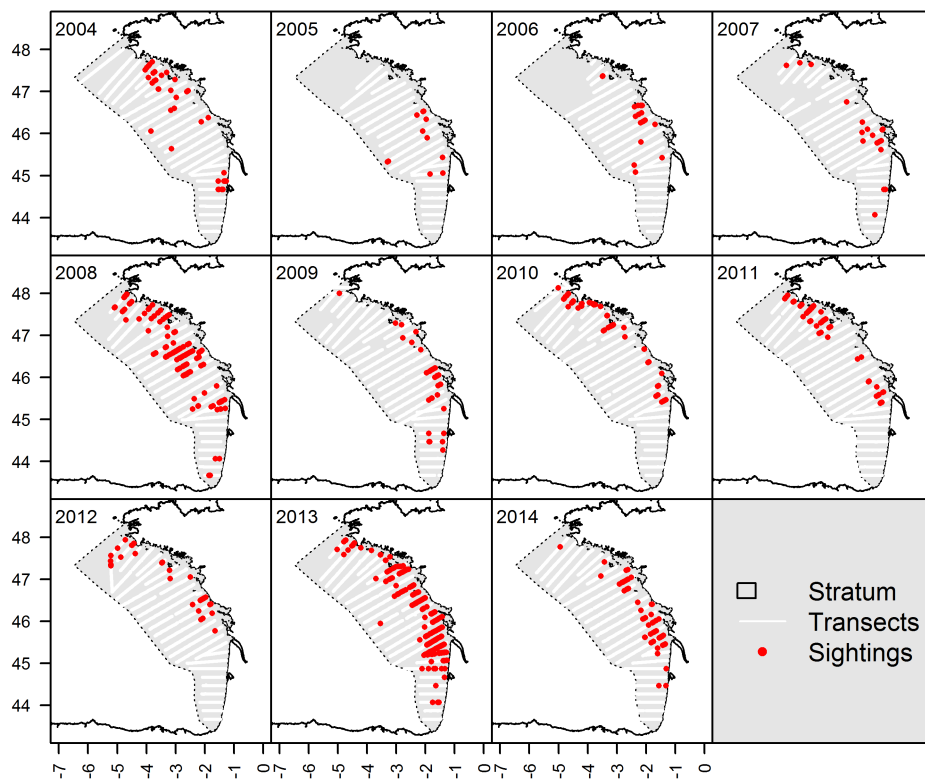


Figure 8. Auks sightings associated to acoustic detection from 2004 to 2014.

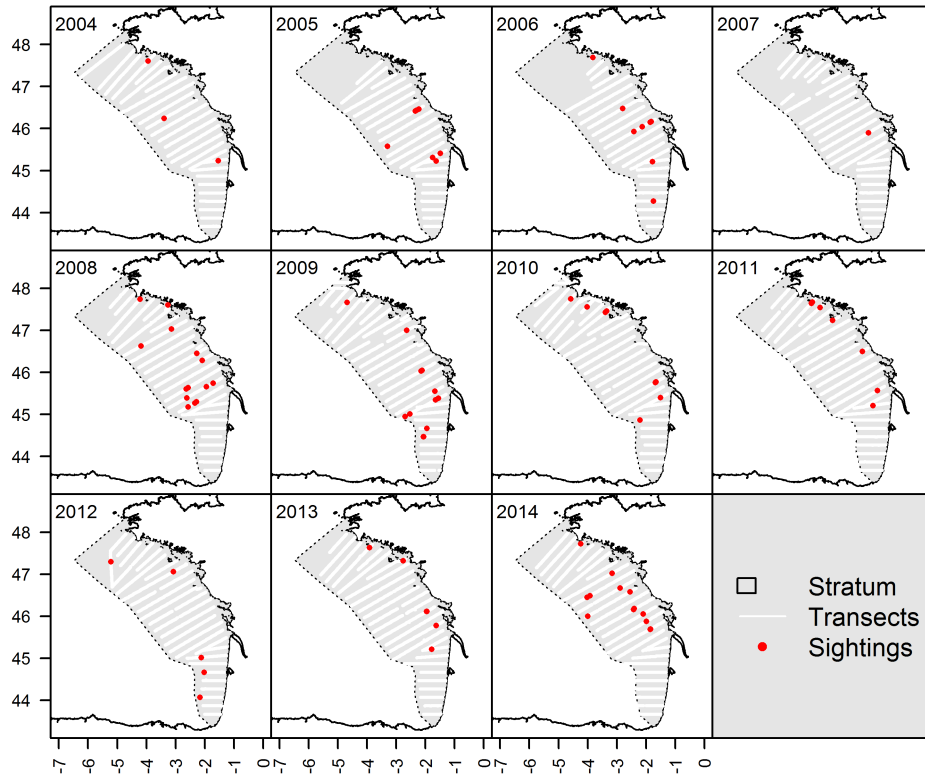


Figure 9. Common dolphins associated to acoustic detection sightings from 2004 to 2014.

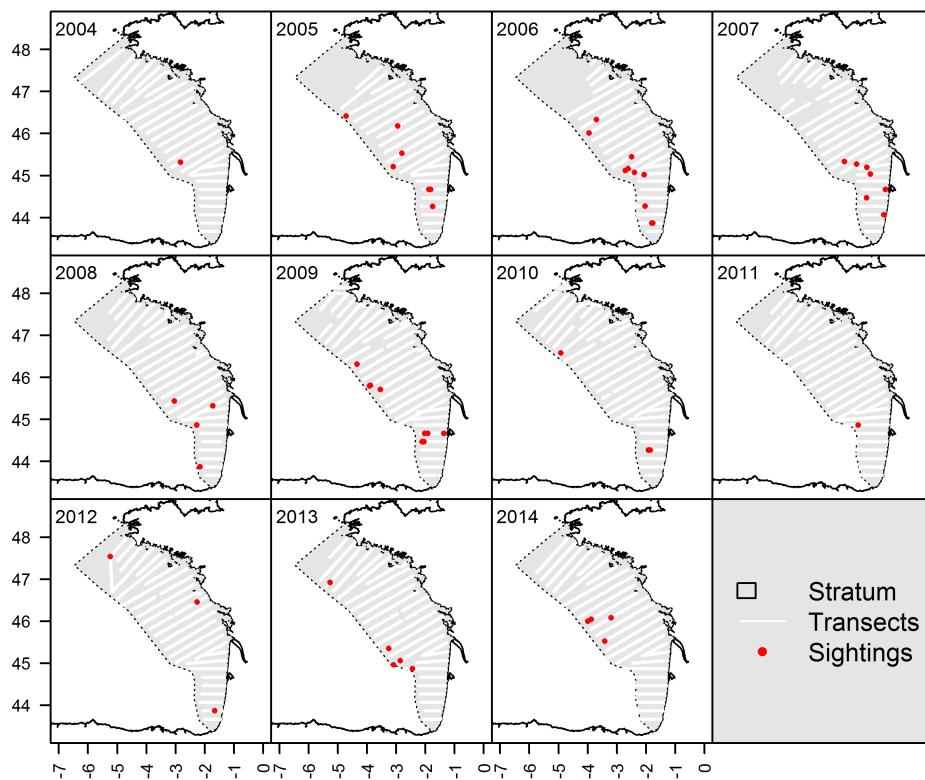


Figure 10. Bottlenose dolphins associated to acoustic detection sightings from 2004 to 2014.

3 Relationships between predators and forage fishes in the Bay of Biscay

[Figures below]

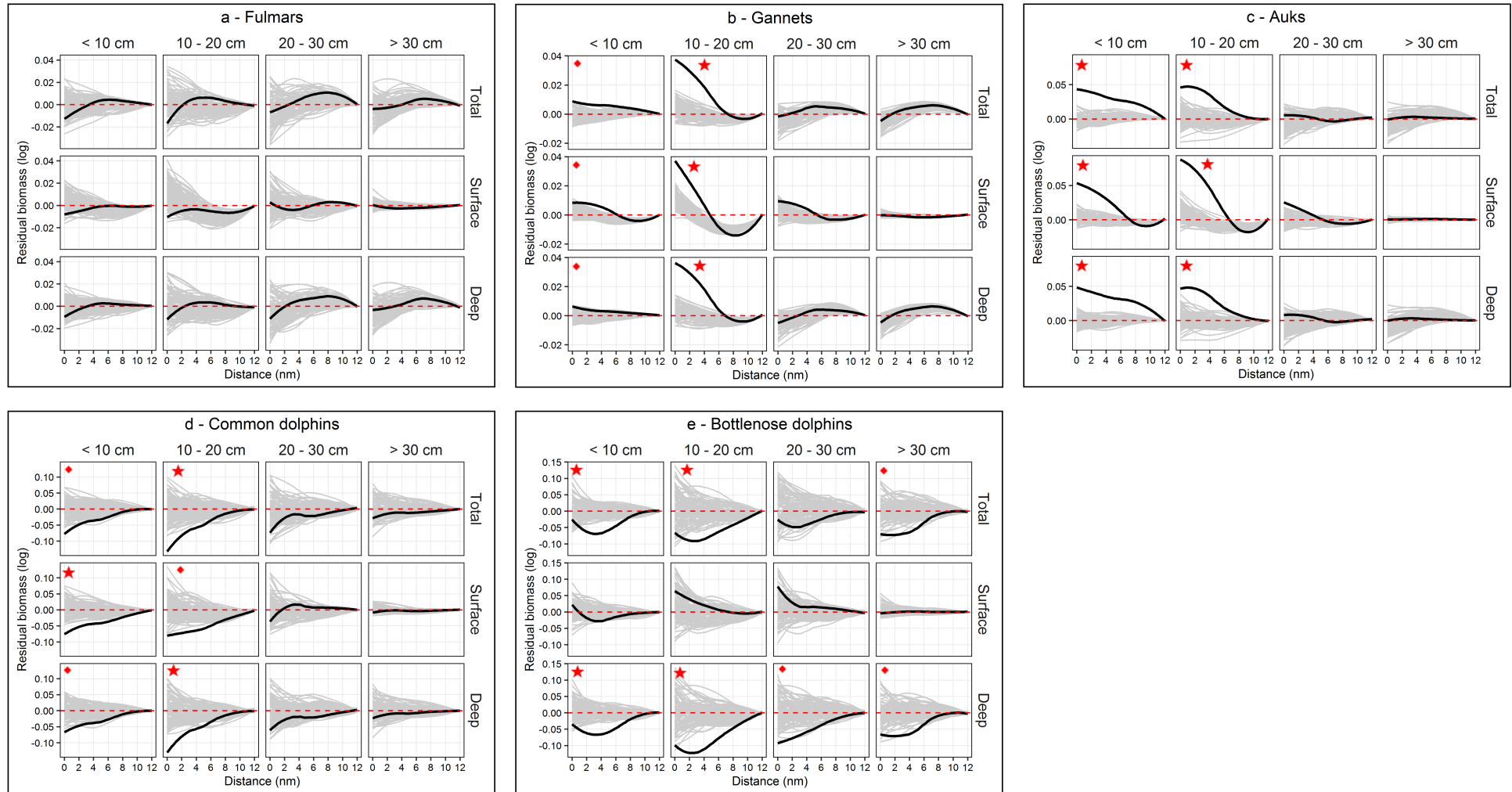


Figure 11. Simulated (grey) and observed (black) averaged relationships between the residual biomass (log) and the distance from the sighting (distance, in nautical miles) for the five studied species, the four prey size classes (columns) and depth layers (rows). The red stars indicate relationships clearly diverging from a random distribution (in grey), the red diamonds indicate marginal relationships compared to the random distribution.

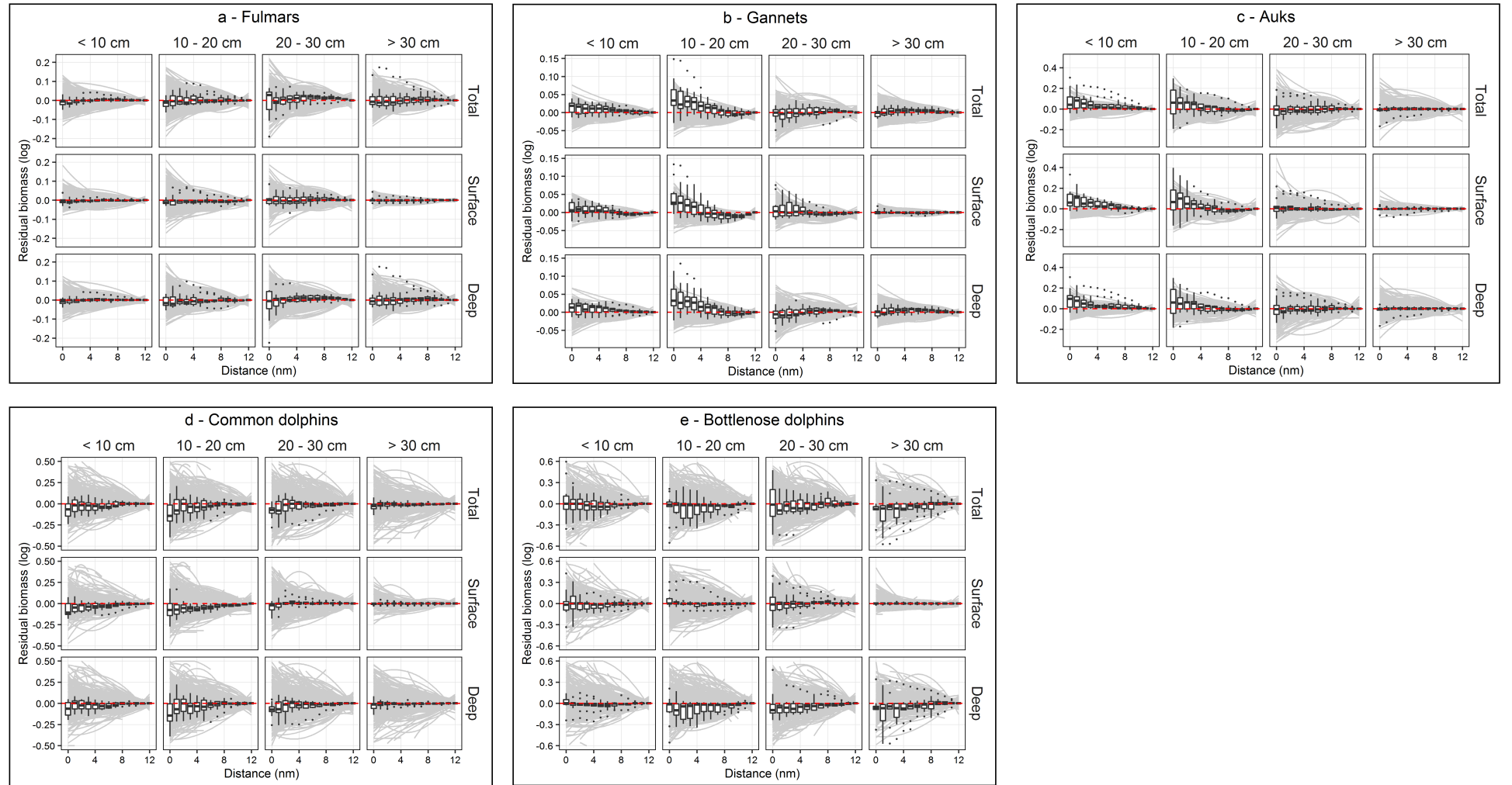


Figure 12. Boxplots of the annually averaged residual biomass (log) by distance from the sighting (distance, in nautical miles) for the five studied species, the four size classes (columns) and depth layers (rows). Each boxplot represents the distribution of annual averages of residual biomass for the considered distance (there is eleven values behind each boxplot). In grey are the simulated annually averaged relationships between residual biomass and distance.

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Les prédateurs supérieurs dans l'écosystème marin

leur réponse à la variabilité spatio-temporelle de l'océan

Résumé : Le milieu marin est un espace difficile à étudier et notre connaissance des cétacés et des oiseaux marins présente encore de nombreuses lacunes, notamment concernant leur distribution au large. Le milieu marin pélagique est caractérisé par une forte variabilité spatio-temporelle, les différents processus écologiques composant cet écosystème étant très dynamiques dans le temps et l'espace. Il est donc crucial pour ces espèces marines d'anticiper ces variations afin de se maintenir dans le milieu. Grâce à des campagnes en mer à grandes échelles réalisées en Manche, Golfe de Gascogne et Méditerranée occidentale, cette thèse vise à améliorer la connaissance de la distribution des cétacés et oiseaux marins dans ces régions, et explorer l'impact de la variabilité spatio-temporelle de l'océan sur leur écologie. Ce travail se focalise notamment sur deux échelles temporelles, les variations saisonnières et interannuelles. Dans un premier temps, nous étudierons les variations de préférences d'habitats des espèces étudiées à ces deux échelles. Les cétacés et oiseaux marins étant des espèces longévives caractérisées par de longues périodes d'apprentissage au début de leur vie, nous explorerons également comment la réponse à la saisonnalité varie en fonction de l'expérience chez une espèce commune dans la région, le fou de Bassan. Enfin, nous finirons par explorer les liens prédateurs-proies dans le Golfe de Gascogne, en considérant notamment l'accessibilité de ces proies en termes de taille et de profondeur. Ainsi, cette thèse nous permettra de discuter les implications de ce travail concernant l'écologie des cétacés et oiseaux marins, ainsi que leur conservation.

Mots clés : Niche écologique, environnement marin, hétérogénéité spatio-temporelle, cétacés, oiseaux marins, Golfe de Gascogne, Manche, Méditerranée, modélisation d'habitats

Top predators in marine ecosystem

their response to ocean spatio-temporal variability

Summary: Marine ecosystem is hard to study and several gaps remain in our understanding of cetaceans and seabirds, particularly regarding their at-sea distributions. The pelagic ecosystem is characterised by an important spatiotemporal variability, thanks to the space and time dynamics of its constituting ecological processes. Top predators thus have to anticipate this variability to sustain themselves in the ecosystem. Based on large-scale surveys across waters of the English Channel, Bay of Biscay and north-western Mediterranean Sea, this thesis aimed at improving knowledge regarding the distribution of cetaceans and seabirds in the area, and to explore the impact of ocean spatiotemporal variability on their ecology. This work focused on two temporal scales, the seasonal and interannual variability. We first explored the variations of habitat preferences of studied species at these two temporal scales. Cetaceans and seabirds being long-lived species characterised by long learning periods in their early life, the response to seasonality was investigated according to age and experience in northern gannets, the most abundant seabird species in the area. Finally, the predator-prey association within the Bay of Biscay was also explored, by contrasting prey accessibility in terms of size and depth. The implications of this work regarding the ecology of marine top predators, as well as their conservation, are finally discussed.

Keywords: Ecological niche, marine environment, spatiotemporal heterogeneity, cetaceans, seabirds, Bay of Biscay, English Channel, Mediterranean Sea, habitat modelling



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