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 processes 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 García-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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http://dx.doi.org/10.1016/j.dsr2.2016.06.011
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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., 2019, 2011) or from platforms of opportunity with yearly coverage (Castège and Hémery, 2011; Kiszka et al., 2007), as well as telemetry studies on seabirds (Petters 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., 2017), 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 Lazere, 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 within a band of 200 m on each side of the flight altitude, and the number of species encountered at the sightings was recorded. Sampling transects were flown at a mean speed of 167 km/h and an altitude of 200 m above ground 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 Globicephala melas 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
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. Procellarids were divided into two independent groups, the northern fulmars *Fulmarus glacialis* and the small-sized shearwaters, encompassing Manx *Puffinus puffinus* and Balearic *P. mauretanicus* shearwaters that are indiscernible from a plane. As for delphinids, unidentified procellarids 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., 2017, 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 (SSTvar) and gradient (SSTgrad), sea surface height (SSH) mean and standard deviation (SSHSD) 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 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 splines 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 covariate. Predictions were then produced for each day

![Fig. 1. Study area, with survey area and sampled transect (A), and geographical names (B).](image-url)
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 ($CV = \sqrt{\text{seasonal variance/seasonal mean}}$). 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 porpoise model resulted in an explained deviance of 39.6% (Table 3, Fig. 3A). The selected covariates were depth, SST\textsubscript{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\textsubscript{mean} inducing positive contributions mostly in eastern the EC and southern BoB, and a preference for null SSH. Finally, SSHSD was the least contributing covariate, with positive contributions over the whole area, but mean SSH and SSHSD were the two most contributing variables. Their relationships indicated a preference for negative SSH and lower SSHSD\textsubscript{max}, inducing negative contributions over the EC. The last two covariates showed similar relationships, with relationships highlighting 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 33.6% (Table 4, Fig. 3B), with mean SSH (7d), mean SST (28d), SSH\textsubscript{mean} (28d) and maximum velocity (28d) as 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\textsubscript{mean} 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\textsubscript{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\textsubscript{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\textsubscript{grad} (28d) and SSH\textsubscript{grad} (28d). As in winter, all covariates showed high contributions over the whole area, but mean SSH and SSH\textsubscript{grad} were the two most contributing variables. Their relationships indicated a preference for negative SSH and lower SSH\textsubscript{grad}, inducing negative contributions over the EC. The last two covariates showed similar relationships, 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\textsubscript{var} (7d), mean SST (28d) and SST\textsubscript{var} (28d). The overall most contributing

| Table 2 |
|------------------|------------------|------------------|------------------|------------------|------------------|
| Species               | Winter Number of sightings | Winter Number of individuals | Winter Encounter rate (ind./km) | Summer Number of sightings | Summer Number of individuals | Summer Encounter rate (ind./km) |
|------------------|------------------|------------------|------------------|------------------|------------------|
| Harbour Porpoise   | 279              | 481              | 0.015            | 272              | 423              | 0.012            |
| Small-sized        | 442              | 4737             | 0.146            | 680              | 16,306           | 0.482            |
| delphinids         | Bottlenose dolphins | 48              | 327              | 0.010            | 63               | 383              | 0.011            |
| Globicephalinae    | 40               | 130              | 0.004            | 57               | 241              | 0.007            |
| Northern gannets   | 3697             | 11,123           | 0.343            | 2540             | 1178             | 0.035            |
| Aukss              | 6221             | 16,841           | 0.519            | 240              | 530              | 0.016            |
| Northern fulmar    | 346              | 740              | 0.023            | 195              | 283              | 0.008            |
| Small-sized        | 16               | 31               | 0.001            | 179              | 770              | 0.023            |
| shearwaters        | Black-legged     | 2255             | 3233             | 0.1              | 73               | 93               | 0.003            |
covariate was \(\text{SST}_{\text{var}}\) (7d), followed by mean SST and \(\text{SST}_{\text{var}}\) (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, \(\text{SST}_{\text{var}}\) (7d) and \(\text{SSH}_{\text{SD}}\) (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 \(\text{SSH}_{\text{SD}}\) 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 \(\text{SST}_{\text{grad}}\) (7d) and \(\text{SSH}_{\text{SD}}\) (7d) as the two most contributory covariates, selected with slope and \(\text{SST}_{\text{var}}\) (28d). The relationships with \(\text{SST}_{\text{grad}}\) highlighted a preference for reduced weekly thermal fronts (hence negative contributions along the coasts) and for reduced \(\text{SSH}_{\text{SD}}\) (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 \(\text{SST}_{\text{var}}\) 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 \(\text{SST}_{\text{grad}}\) (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 \(\text{SST}_{\text{var}}\) (7 and 28d), \(\text{SST}_{\text{grad}}\) (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

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**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.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Harbour porpoises</th>
<th>Small-sized delphinids</th>
<th>Bottlenose dolphins</th>
<th>Globicephalinae</th>
<th>Northern gannets</th>
<th>Auks</th>
<th>Northern fulmars</th>
<th>Black-legged kittiwakes</th>
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<tr>
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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.)
northern BoB and in the east), 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 preference for areas very close to the shore, within 50 km from the closest colony. The model 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 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\(_{\text{var}}\) (28d), mean SSH (28d) and SSH\(_{\text{SD}}\) (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\(_{\text{SD}}\). 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 British 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\(_{\text{var}}\) (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.
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., 2017). 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.

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.)
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., 2017), 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 kitiwakes, 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., 2017). 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 (Caffinadas 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; Caffinadas 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., 2017).

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 shelf waters was consistent with the known diet of the two species (Cadiou et al., 2012). 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 Pierrepont 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 (Wierskirk 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.

Acknowledgements

The French ministry in charge of the environment (Ministère de l’Écologie, du Développement Durable et de l’Énergie, MEDDE) and the French Marine Protected Areas Agency (Agence des Aires Marines Protégées, AAMP) funded the SAMM survey. The PELAGIS observatory, with the help of the AAMP, designed, coordinated and conducted the survey. We thank all the observers and aircraft crew members (Pixair Survey) who participated in the survey. We are grateful to Hélène Falchetto for preparing and processing survey data for use in this study. We are indebted to PREVIMER for furnishing us with MARS-2D and MARS-3D model outputs. We also thank Auriane Virgili for her help in preparing environmental data, and Matthieu Authier for fruitful advice concerning habitat modelling analysis. Finally, we are thankful to the French ministry in charge of research (Ministère de l’Enseignement Supérieur et de la Recherche, MESR) for funding CL’s PhD grant. Finally, we thank the two reviewers for their fruitful comments on the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this paper can be found in the online version at http://dx.doi.org/10.1111/dsr2.2016.06.011.

References


