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## Decadal stability in top predator habitat preferences in the Bay of Biscay

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### Abstract :

Most oceanographic systems, especially shelf ecosystems, are characterised by interannual variability in the timing, extent and intensity of their seasonal patterns. Such interannual variations have important consequences on top predator habitat preferences. Capitalising on oceanographic surveys performed every spring since 2004 in the Bay of Biscay (BoB), this study explored interannual variations in habitat preferences exhibited by five mobile top predator species: bottlenose and common dolphins, auks, fulmars and northern gannets. We expected to find species with similar habitat preferences every year or species exhibiting important variability in their habitat preferences. First, we identified with a Principal Component Analysis (PCA) three different habitats of varying extent depending on year: river plumes, central shelf waters and shelf edge. Second, the Principal Components were used to explore the habitat preferences of predators through Generalized Additive Models. We fitted two kinds of models, using and not using the year as an interaction term, to test whether habitat preferences changed across years. Our results showed a range of habitat strategies based on the specificity and stability of species preferences. Species exhibiting narrower habitat preferences also exhibited stronger stability in their preferences among years while the species with wider habitat preferences exhibited higher variability among years. The target habitats differed across studied species, with bottlenose dolphins targeting the shelf edge exclusively, auks preferring river plumes, fulmars exhibiting a gradual preference from the shelf edge to river plumes and gannets being present in any of the three habitats. In contrast, the habitat preferences of common dolphins, the most sighted cetacean species in the BoB, could not be reliably inferred.

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## Highlights

► Concurrent sampling of predators and habitat unveiled their relationships in time. ► PCA on environmental variables identified 3 main habitats used by predators. ► Predators exhibited various habitat preferences specificity and stability in time. ► Narrower habitat preferences paired with stronger stability among years. ► Wider habitat preferences paired with higher variability among years.

**Keywords** : Habitat preference, Temporal variability, Cetaceans, Seabirds, North Atlantic, Bay of Biscay

# 1 Introduction

2 The marine environment, and especially pelagic ecosystems, is highly dynamic due to complex interactions  
3 between physical and biological processes. The resulting heterogeneous and dynamic structures vary in timing,  
4 extent and intensity at many scales (Barry & Dayton, 1991; Longhurst, 2007). Over continental shelves, for  
5 example, annual variations in river discharge determine nutrient inputs (Simpson, 1997), while the localisation  
6 and intensity of eddies associated with either currents or slope can fluctuate from year to year (Longhurst,  
7 2007).

8 Heterogeneity is a challenge for species, as they must make accommodation for spatio-temporal variability  
9 in resources to ensure survival. Many species have evolved to target discrete and predictable oceanographic  
10 features (Ballance et al., 2006; Weimerskirch, 2007). This is the case of homeotherm top predators (cetaceans,  
11 seabirds and pinnipeds) which are associated with specific coarse and meso-scale habitats such as eddies and  
12 filaments (Tew-Kai et al., 2009; Cotté et al., 2011), tidal or river plume fronts (Jahncke et al., 2005; Skov &  
13 Thomsen, 2008) or shelf edges (Cañadas et al., 2002; Azzelino et al., 2008; Guilford et al., 2012). In addition to  
14 their sensory skills, most of these predators can rely on memories or social learning to locate these favourable  
15 habitats (Davoren et al., 2003) and they are highly dependent on spatial and temporal repetitiveness to find  
16 them.

17 Homeotherm top predator species exhibit a wide range of biological traits (Gaston, 2004; Perrin et al., 2009):  
18 from plankton- to marine mammal-eating species, from tropical to polar regions, from species foraging at the  
19 sea surface to those hunting over a thousand metres deep and from resident to migrating species. The main  
20 difference between cetaceans and either seabirds or pinnipeds relates to reproductive strategies; the latter two  
21 require land to breed or moult (Gaston, 2004; Perrin et al., 2009), while cetaceans have evolved a completely  
22 marine lifestyle (Chivers, 2009). Terrestrial reproduction and moulting have major consequences for seabirds  
23 and pinnipeds as they induce central-place foraging constraints, by which these species must rely on food  
24 available within a short distance from colonies and resting sites, whereas they can range freely the rest of the  
25 year (Gaston, 2004; Perrin et al., 2009).

26 Although studies on the habitat of homeotherm marine predators are now common, especially over shelf  
27 areas, they often focus on short temporal scales due to methodological constraints (but see Ballance et al., 2006;  
28 Forney et al., 2015; Becker et al., 2016), which results in only a few investigations addressing the consistency  
29 of habitat preferences over time. However, some species may be expected to use several habitats depending on  
30 their availability and quality, while other species might be specialised towards a specific habitat type year after  
31 year.

32 Since 2004, the PELGAS ("PELagique GAScogne") oceanographic survey has been conducted in May in the  
33 Bay of Biscay (BoB; eastern North Atlantic) to study the ecosystem from physical oceanography to top predator  
34 ecology (Doray et al., 2018, ; this issue). This survey represents a unique opportunity to explore the temporal  
35 variability of species relationships to their habitats in a diversified top predator community, composed of species  
36 with contrasted lifestyles. The BoB is located at the intersection of cold and warm temperate biogeographic  
37 regions and is characterised by the occurrence of species with warm water as well as cold water affinities.

38 In this study, we focused on five cetacean and seabird taxa frequently encountered in the BoB (the sighting  
39 surveys were not appropriate for spotting pinnipeds). Bottlenose (*Tursiops truncatus*) and common dolphins  
40 (*Delphinus delphis*) are two species that are widely distributed, from estuaries to offshore waters. In the BoB,  
41 we know from previous studies in spring that bottlenose dolphins are aggregated over the slope, while common  
42 dolphins can also be encountered over the shelf (Certain et al., 2011). At the western Europe scale, bottlenose  
43 dolphins mostly occur over the slope in both winter and summer while common dolphins are abundant over the  
44 shelf in winter but are more widespread from shelf to oceanic waters in summer (Lambert et al., 2017, which  
45 focused on one-year seasonal ecological preferences of cetaceans and seabirds in the eastern North-Atlantic).  
46 Northern fulmars (*Fulmarus glacialis*) and auks (common guillemot *Uria aalge* and razorbill *Alca torda*) are two  
47 taxa with cold water affinities. The BoB represents the southern part of their range during both breeding and  
48 wintering periods (Lambert et al., 2017), and despite we know auks are more aggregated along the coast while

fulmars are widespread over the shelf but avoid coastal waters (Certain et al., 2011; Lambert et al., 2017), information on their at-sea ecology remains poor. The northern gannet (*Morus bassanus*) is a more widely distributed species, breeding in northern Europe but wintering from the North Sea to western Africa (Nelson, 2002; Fort et al., 2012; Lambert et al., 2017). Although the species must face strong intra-specific competition during the breeding season, leading to sharp habitat preferences, during the wintering period gannets exhibit some flexibility with wintering grounds having different characteristics (for example, the Canary Current or the English Channel; Fort et al., 2012; Lambert et al., 2017).

In the BoB and during the PELGAS surveys, which occur during their breeding period, most of sighted auks and gannets are supposed to be non-breeders, the number of breeding auks being very low in the area (Cadiou et al., 2014) and the closest colony of gannets being in the English Channel (Nelson, 2002). Thus, the present study will provide valuable information on a poorly-known fraction of seabird populations, the non-breeding individuals (either juveniles or non-breeding adults).

Previous studies explored the averaged spatial distribution of predators over the 2003-2008 time period in the BoB (Certain et al., 2011) or unveiled the ecological preferences at the western Europe scale by contrasting winter and summer seasons (Lambert et al., 2017), but none focus on the long-term temporal variability of ecological preferences of predators. Thus, this study complements the knowledge brought by Certain et al. (2011); Lambert et al. (2017) on the habitat preferences of predators in the BoB by explicitly investigating the temporal variability of their springtime habitat preferences, thanks to the long time period of the PELGAS surveys. As suggested above, we expected two main patterns: (i) specialist species using the same pelagic habitat year after year, spatial variations of distribution reflecting spatial variations in habitat availability and (ii) species exhibiting a great variability in habitat preferences over time, either because generalist species are made up of specialist individuals with different habitat preferences, or because all individuals are generalists and remain within the same area irrespective of whether the corresponding habitat had changed.

We used in-situ environmental variables and top predator observational data collected during the decadal oceanographic surveys conducted in May every year from 2004 to 2013 within the BoB. We first characterised the habitats available in the study area in May. Given their dynamic nature, pelagic habitats are often difficult to define and distinguish (Barry & Dayton, 1991; Longhurst, 2007), but we chose to identify the different habitats available as well as their interannual variations, using a Principal Component Analysis (PCA). Springtime habitat preferences were explored with habitat modelling (generalized additive models (GAMs); Guisan & Zimmermann, 2000), highlighting potential associations to specific environmental conditions and their variation over time.

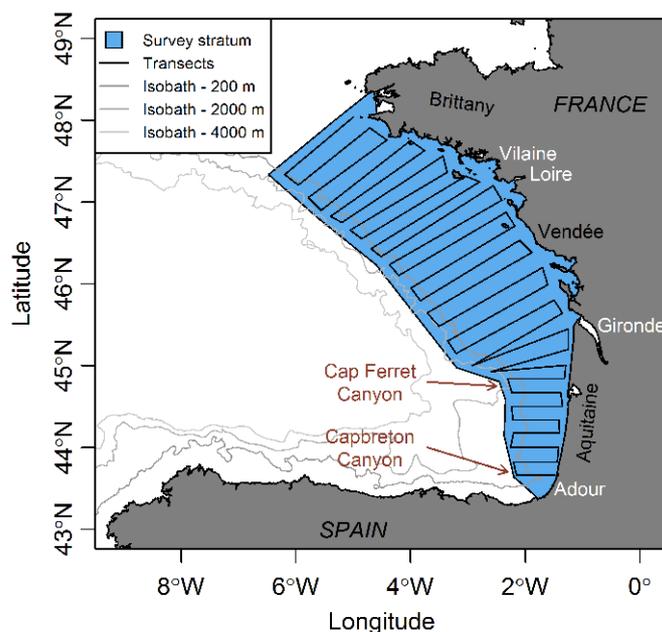
## 2 Material & Methods

### 2.1 Study area

The BoB is a large bay in the eastern North Atlantic, spanning from France to Spain (Figure 1). This bay is characterised by a broad continental shelf, which extends from 180 km in the northern part of the BoB, to 20 km in the southern part (Capbreton Canyon) and approximately 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. In the southern BoB, the interaction between the slope current flowing from Iberian Peninsula to the northern BoB and the shelf break topography 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 (Koutsikopoulos & Le Cann, 1996). Seasonality is well marked, with a thermal stratification establishing during spring from south to north (Koutsikopoulos & Le Cann, 1996) and phytoplankton blooms occurring during the same period (Pingree & Garcia-Soto, 2014).

## 92 2.2 Survey data

93 The study was based on the PELGAS pelagic oceanographic surveys, conducted by Ifremer onboard the R/V  
 94 *Thalassa*, to study the abundance and distribution of small pelagic fish and monitor the BoB pelagic ecosystem.  
 95 These surveys have been conducted every spring since 2000, along fixed parallel transects from the coast to the  
 96 shelf break, orthogonal to the main isobaths (Figure 1, Doray et al., 2018). Effective sampling design and total  
 97 survey effort vary each year depending on the annual extent of the survey, sometimes extending farther than  
 98 the shelf edge. However, in the present study, we conducted the analyses on the area commonly sampled every  
 99 year to determine variability in the same area.



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

100 Standardised top predator observations were collected from 2004 to 2013 following a line transect protocol  
 101 (Buckland et al., 2001). Effort spanned from sunrise to sunset whenever the vessel was moving at  $\geq 8$  knots  
 102 and stopped during trawling. The main observation platform was the upper deck of the R/V *Thalassa* (16 m  
 103 above sea level), but when weather deteriorated (strong winds or rain), the observation platform was changed  
 104 to the ship bridge (14 m above sea level). Two trained observers scanned with naked eyes 180° ahead of  
 105 the bow, with each observer scanning 90° on each side of the bow. The period of observation was no longer  
 106 than two hours. Observation conditions (Beaufort sea-state, swell, glare, cloud cover, platform) were recorded  
 107 every hour, or whenever observation conditions changed. For each sighting, species composition, number of  
 108 individuals, behaviour, distance and angle to the observer were recorded. Individuals attending either the  
 109 vessel or fishing vessels operating nearby were not recorded. In situ environmental variables, such as surface  
 110 and bottom temperature, salinity, mixed layer depth and surface chlorophyll a concentration were routinely  
 111 collected along transects (Doray et al., 2014).

## 112 2.3 Habitats characterisation

113 To explore the different habitats available and variations of their spatial extent over the decade, we performed  
 114 a PCA on environmental data (Figure 2). This technique allows environmental conditions to be summarised  
 115 to identify environmental structure by maximising data variance. In situ variables available for all years were  
 116 compiled over a 0.25° grid (Appendix A). They include sea surface temperature (SST), temperature near  
 117 seabed (SBT), mixed layer depth (MLD) and sea surface salinity (SSS). SST gradient (SSTg) was computed

118 over the same grid as the largest difference between each cell and its neighbours. Depth and slope aspect were  
119 summarised in the same way from the GEBCO database. Surface chlorophyll concentrations measured in situ  
120 were not available over the whole area for the whole decade. Instead, we used MODIS monthly composite  
121 surface chlorophyll a (CHL) concentration (in May, <http://oceancolor.gsfc.nasa.gov>), and Eppley-VGPM  
122 net primary productivity (NPP) at the same temporal resolution ([http://www.science.oregonstate.edu/  
123 ocean.productivity](http://www.science.oregonstate.edu/ocean.productivity)). These two variables were summarised over the PELGAS grid. These grid cells were  
124 used as samples for the PCA, and the environmental variables were scaled to unit variance for standardisation.  
125 Although the standard NASA algorithm, designed to derive chlorophyll-a in the open ocean, is not fully adapted  
126 to the continental shelf of th BoB (Tilstone et al., 2017), it has been used here as a proxy.

127 We performed a hierarchical cluster analysis on the PCA result to identify habitats available in the BoB.  
128 The number of clusters was determined based on the tree constructed from the previously estimated Principal  
129 Components (PC). The inferred clusters were plotted each year to visually assess their spatial variations. PCA  
130 was carried out in R version 3.2.3 (R Core Team, 2015) with the package FactoMineR (Husson et al., 2016),  
131 and the hierarchical cluster analysis was carried out with the function `hclust` using the "ward.D" method.

## 132 2.4 Species habitat preference per year

133 Habitat preferences over the decade were analysed for five taxa frequently encountered in the BoB during  
134 PELGAS surveys. These taxa included two cetaceans and three seabirds: bottlenose dolphin, common dolphin,  
135 guillemot and razorbill, northern fulmar, and northern gannet.

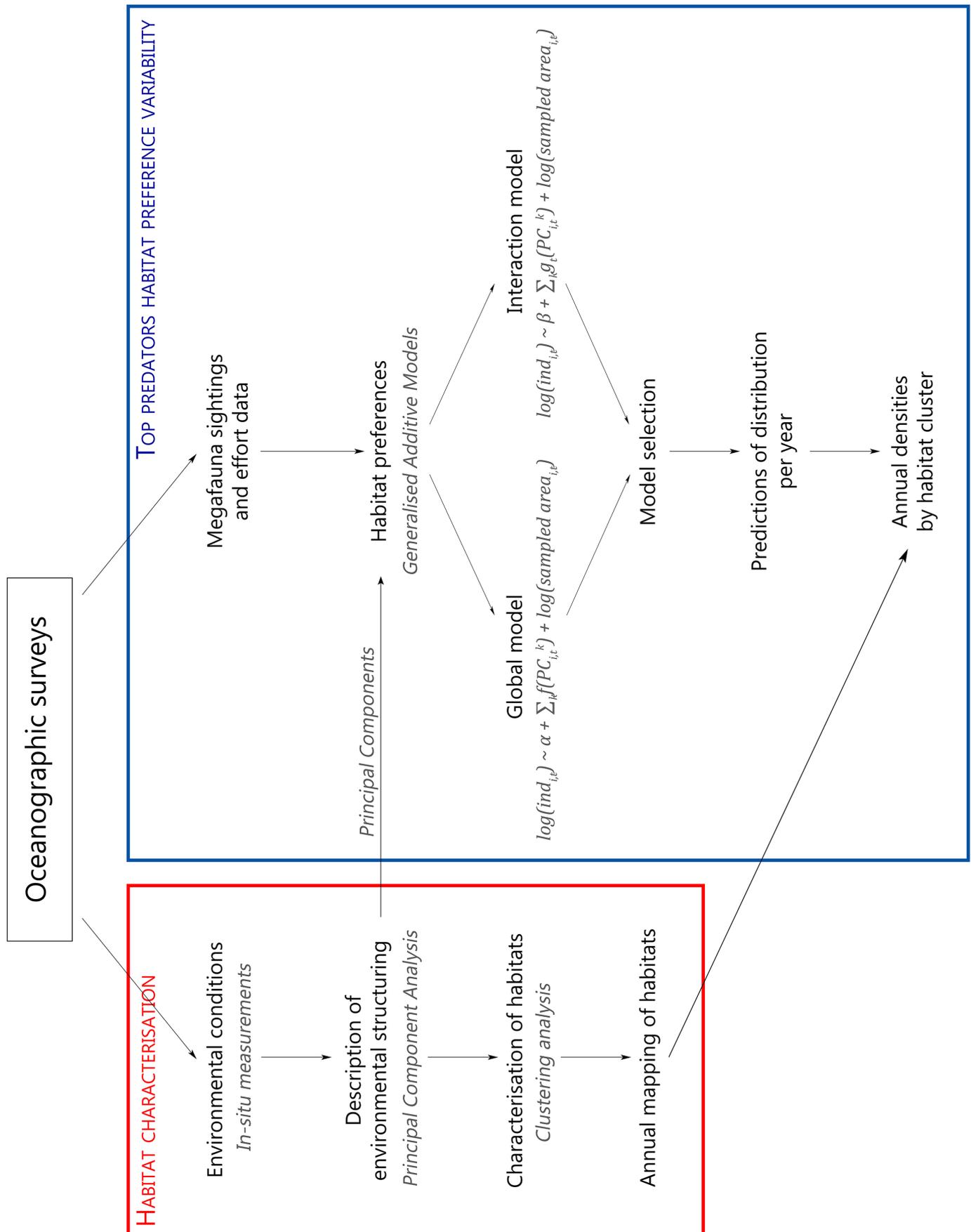
136 Sighting data were aggregated to match the 0.25° grid format of environmental covariates. We summed the  
137 numbers of observed individuals per cell as well as the effort deployed in each cell by multiplying the lengths of  
138 all segments falling within a cell by twice the effective strip width (ESW) of each species (see Appendix B for  
139 details about distance sampling analyses). Habitat preference analyses were performed only with effort realised  
140 under Beaufort sea-state lower than 4 and subjective conditions excellent to medium. All sightings of individuals  
141 attracted or repelled from the boat were removed, as well as individuals coming to the bow, scavenging behind  
142 fishing vessels or coming from the back of the observation platform.

143 To explore springtime habitat preferences, habitat modelling was performed using GAMs (Figure 2, Wood,  
144 2011) relating the number of individuals (response variables) to environmental predictors through a logarithmic  
145 link function with the Tweedie error distribution, and the sampled area as an offset.

146 Two types of models were used (Figure 2). First, a global model (*i.e.* a baseline model supposing no  
147 variation across years, providing "mean" preferences) included the three main PCs as well as the distance to  
148 the closest colony for seabirds (see Appendix A; using thin plate regression splines as smoothers). Second,  
149 an interaction model included the same four variables but with year as an interaction term (using full tensor  
150 product smooths). The inclusion of year as an interaction term allowed the relationships between response  
151 variable and covariates to differ for each year. The maximum degree of freedom for smoothers was constrained  
152 to 3 to avoid over-fitting the data. The R code for the two types of models is shown in Appendix C. Explained  
153 deviances and Akaike information criterion (AIC) as well as p-values were examined to identify the best models.  
154 From the best-performing model, predictions were made for each year.

155 To explore whether the identified environmental preferences resulted in preferential associations to any of  
156 the three habitats identified in the BoB, we extracted the abundance within each habitat cluster and related it  
157 to its respective surface for each year. These predicted densities were scaled by the maximum density that was  
158 predicted within the BoB for each year, providing annual predicted relative densities by habitat cluster.

159 The model fitting process and the predictions were done with R 3.2.3 (R Core Team, 2015), using the `mgcv`  
160 package (Wood, 2011), while the extraction of relative density within available habitats were calculated in R  
161 2.15.3, using the `raster` package (Hijmans et al., 2014).

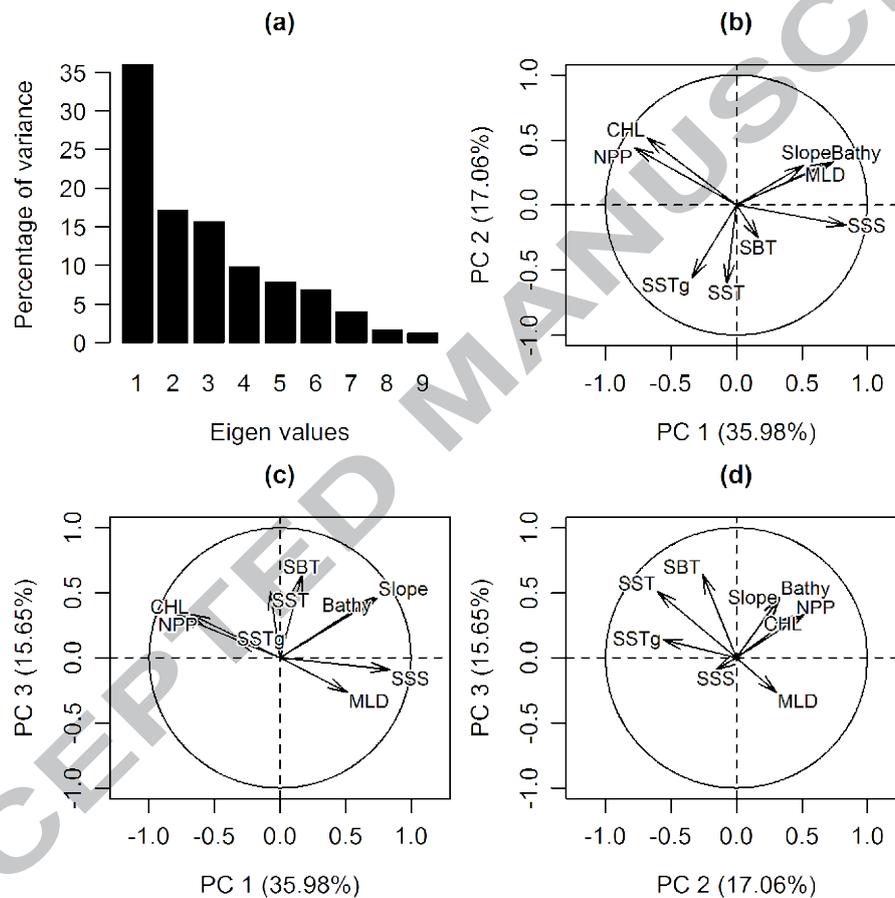


**Figure 2.** Flowchart of the several methodological steps used within this study. The equations are the formulations of the two tested generalized additive models, with  $\log(ind_{i,t})$  the response variable,  $\alpha$  and  $\beta$  the intercept values for global and interaction models (respectively),  $\sum_k f(PC_{i,t}^k)$  and  $\sum_k g_t(PC_{i,t}^k)$  the additive functions of environmental parameters (here, the Principal Components (PC) and distance to the closest colony) for global and interaction models (respectively), and  $\log(sampled\ area_{i,t})$  the offset; with  $i$  the grid cell,  $t$  the year and  $k$  the PC.  $f()$  is a thin plate regression spline,  $g()$  a full tensor product smooth; only  $g()$  explicitly includes time, as an interaction term on environmental variables.

## 162 3 Results

### 163 3.1 Habitats characterisation

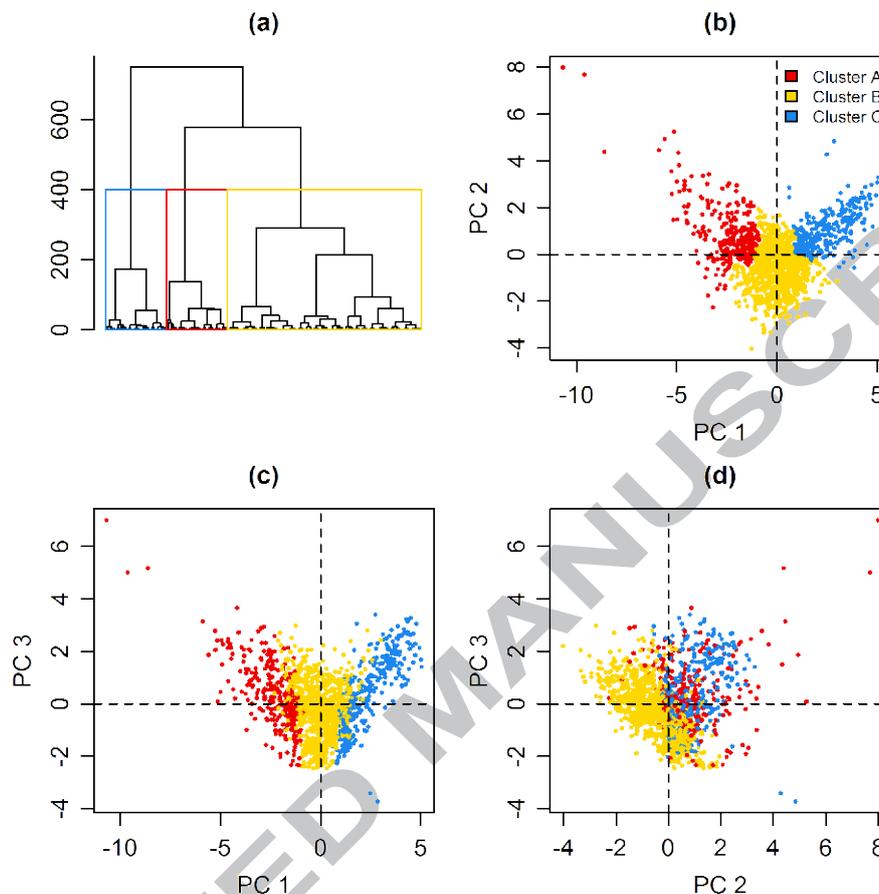
164 The first three PCs accounted for 68.7% of the variance of the data. The first PC explained 36.0% of the  
 165 variance, the second PC 17.1% and the third PC 15.7% (Figure 3a). The first PC (PC 1, Figure 3b, c) was  
 166 mainly related to SSS, bathymetry and slope with higher values to the right end of the axis, as well as to CHL  
 167 and NPP with higher values to the left end of the axis, indicating that shallow waters with low salinity were  
 168 more productive than deep waters with high salinity. The second PC (PC 2, Figure 3b, d) was mainly related  
 169 to temperature (SST, SSTg and SBT). The MLD was similarly important over the two PCs, with negative  
 170 correlation to CHL/NPP for the first PC, and negative correlation to temperature for the second PC. For the  
 171 third PC (PC 3, Figure 3c, d), all variables loaded positively, except MLD and SSS.



**Figure 3.** Results of the Principal Component Analysis (PCA): (a) percentage of variance explained by each of the nine eigen values; (b) PCA correlation circle for the first and second Principal Components (PCs); (c) PCA correlation circle for the first and third PCs; (d) PCA correlation circle for the second and third PCs. 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.

172 The hierarchical cluster analysis of the PCA suggested three main clusters (Figure 4a). These clusters were  
 173 mostly separated on the first PC (Figure 4b–d): (A) shallowest waters with lowest salinities, and highest NPP  
 174 and CHL; (B) waters with shallower depth, lower slope/CHL/NPP and higher SST compared to the averaged  
 175 situation and (C) deepest waters associated with steep slope and high salinities, as well as lower CHL/NPP.  
 176 Clusters A and B corresponded to the BoB shelf area, the former being related to coastal and productive habitats  
 177 mainly associated with river plumes, the latter corresponding to central shelf waters with lower CHL/NPP. The  
 178 third cluster corresponded to the shelf break (Figure 4), as indicated by the steep slope, high depth and salinity.  
 179 Overall, these three habitats were distributed from east to west in the area, but their spatial extent varied

180 depending on the year. For example, the habitat 1 was almost absent in 2011, but extended widely across the  
 181 shelf in 2004, while habitat 3 spread farther over the shelf in 2004, 2005 and 2010 compared to the other years  
 182 (Figure 5). On the second axis, driven by the SST, clusters A and C were both colder than cluster B.



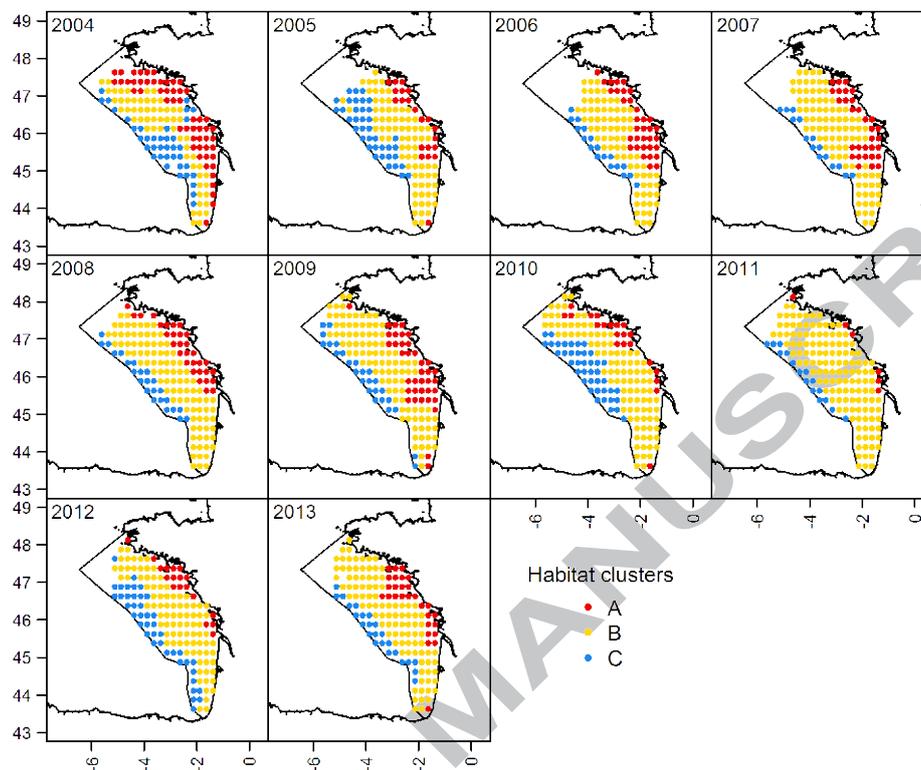
**Figure 4.** Hierarchical cluster analysis results using the three first Principal Components (PCs): (a) dendrogram and the three clusters identified; (b) clusters in the plane (PC1, PC2); (c) clusters in the plane (PC1, PC3); (d) clusters in the plane (PC2, PC3). Cluster A: river plumes; cluster B: shelf; cluster C: shelf edge.

### 183 3.2 Sighting data

184 Over the PELGAS surveys, yearly encounter rates (number of individuals sighted per 100 km of effort) were  
 185 relatively low for most species (Table 1), except for the northern gannet, which was the most sighted species  
 186 with up to 4 individuals sighted per sampled 100 km. However, the distributions of sightings showed strong  
 187 spatial patterns (Figure 6), with some variations among years (see Appendix D for sightings and density maps  
 188 per year). Overall, fulmars were mostly found over the outer shelf in the northern BoB; gannets were widely  
 189 dispersed over the entire BoB; auks were concentrated along the coast; common dolphins were found over the  
 190 whole shelf, especially in the central part; and bottlenose dolphins were mostly encountered along the southern  
 191 shelf edge (Figure 6).

### 192 3.3 Species habitat preference per year

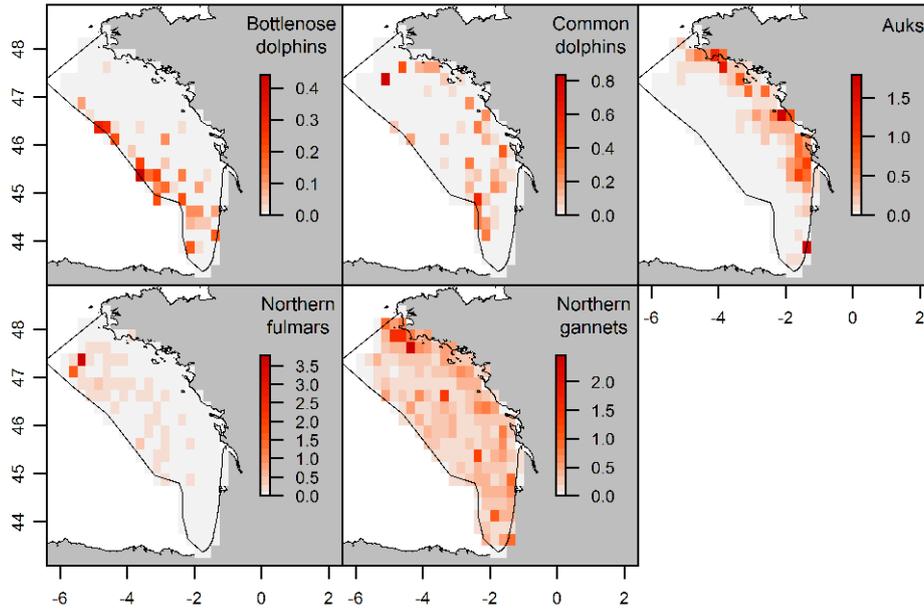
193 There is one average value per year per group for each variable allowing the inter-annual variability to be  
 194 represented in boxplots



**Figure 5.** Yearly variations of the spatial extent of the three habitats available over the Bay of Biscay from 2004 to 2013. Cluster A: river plumes; cluster B: shelf; cluster C: shelf edge.

**Table 1.** Encounter rates from 2004 to 2013, in individuals per 100 km of effort.

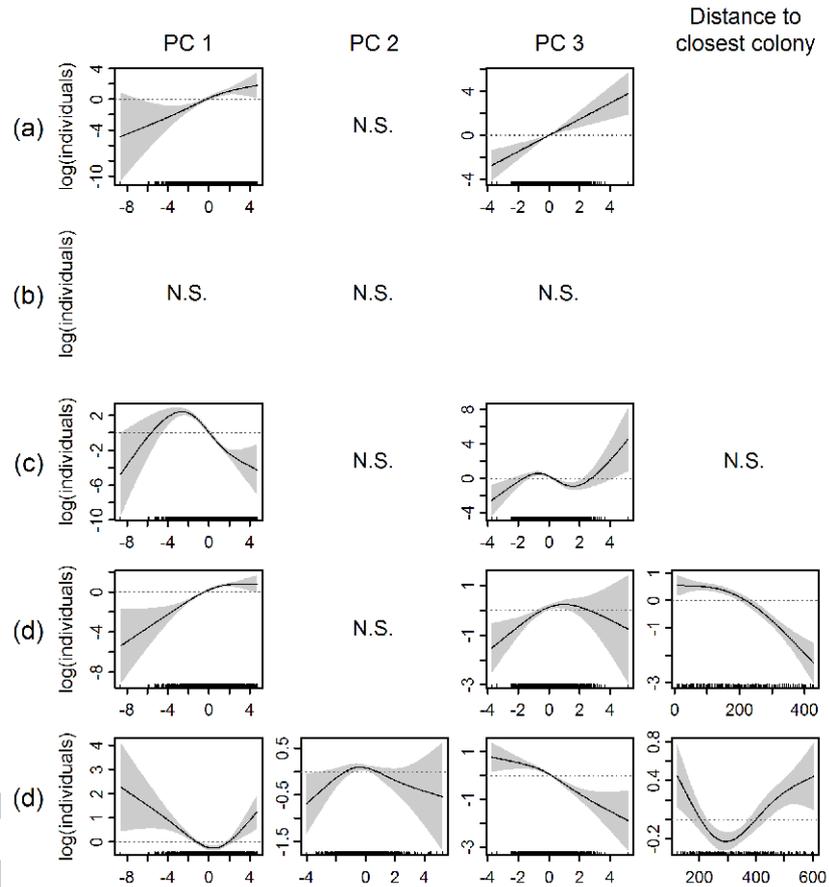
Year	Bottlenose dolphin	Common dolphin	Auks	Northern fulmar	Northern gannet
2004	0.011	0.200	0.139	0.149	1.229
2005	0.605	0.573	0.096	0.213	1.599
2006	0.413	0.467	0.101	0.200	2.596
2007	0.525	0.019	0.189	0.320	0.757
2008	0.453	1.951	0.693	0.661	4.145
2009	1.250	1.426	0.285	0.360	1.312
2010	0.440	0.733	0.336	0.515	1.591
2011	0.157	0.597	1.002	0.219	0.520
2012	0.080	0.672	0.291	0.160	1.618
2013	0.307	0.573	1.778	0.133	4.239



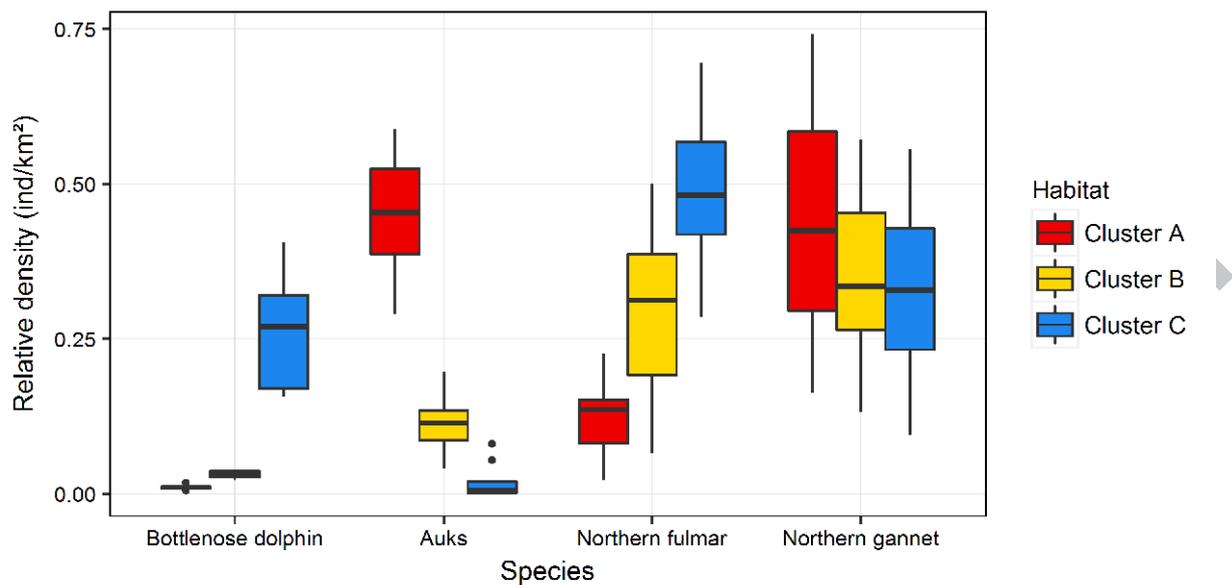
**Figure 6.** Mean sighted densities (individuals per sampled km<sup>2</sup>, with effort corrected for detection) for the studied groups of species from 2004 to 2013.

**Table 2.** Generalised Additive Model results for the five studied species. The explained deviances (in %) and the significance levels for the four covariates are given, as well as the model AICs for the global model and the interaction model. PC: Principal Component. \*\*\*: p-value  $\leq 0.001$ ; \*\*: p-value  $\leq 0.01$ ; \*: p-value  $\leq 0.05$ .

	Bottlenose dolphin	Common dolphin	Auks	Northern fulmar	Northern gannet
Global model					
Explained deviance (%)	32.9	11.0	35.0	21.8	18.2
PC 1	***		***	***	***
PC 2					*
PC 3	***		***	**	***
Distance to closest colony				***	***
AIC	1586.8	1739.3	2469.3	2783.0	6408.4
Interaction model					
Explained deviance (%)	37.9	13.0	54.1	34.5	34.9
PC 1	***		***	***	***
PC 2			***	***	***
PC 3	***		***	***	***
Distance to closest colony			***	***	***
AIC	1588.5	1737.1	2335.0	2657.0	6149.8
AIC(global model) - AIC(interaction model)	-1.7	2.2	134.3	126.0	258.6



**Figure 7.** Generalised Additive Models (global models) for (a) bottlenose dolphins, (b) common dolphins, (c) auks, (d) northern fulmars and (e) northern gannets. The curves are given for significant variables (N.S. = non significant) and represent the relationship between the covariate (abscissa) and the linear predictor ( $\log(\text{individuals})$ , ordinate). The covariates are the three first Principal Components (PC) of the Principal Component Analysis, and the distance to closest colony for seabirds.



**Figure 8.** Annual relative densities by habitat cluster for bottlenose dolphins, auks, northern fulmars and northern gannets. There is one density value per year by cluster by species, so that box-plots represent the inter-annual variability of density by habitat cluster. The differences of densities and dispersion across the three clusters by species summarise the degree of specificity in their habitat preferences (non-overlapping box-plots: strong specificity of habitat preference; overlapping box-plots: low specificity of habitat preference). Cluster A: river plumes; cluster B: shelf; cluster C: shelf edge.

### 3.3.1 Bottlenose dolphins

The global model for bottlenose dolphins reached 32.9% of explained deviance ( $AIC = 1586.8$ ), with PCs 1 and 3 as significant variables (Table 2). The relationships to these two PCs were increasing, with positive densities of dolphins associated with positive values of both PCs. (Figure 7a).

The interaction model exhibited the same significant variables, for an explained deviance of 37.9% ( $AIC = 1588.5$ ; Table 2). According to the difference in AIC, the interaction model was slightly less parsimonious than the global one, despite the improvement of explained deviance. In addition, as the AIC difference was negligible, we favoured the simplest model and chose the global model as the best model. According to the predicted distribution and the predicted densities by cluster, the bottlenose dolphins were clearly associated with habitat cluster C, with almost no variations among years (Figure 8; Appendix E1). In 2007–2008 and 2011 however, substantially high relative densities were also predicted over the shelf (cluster B).

### 3.3.2 Common dolphins

The global model explained 11% of deviance ( $AIC = 1739.3$ ) but none of the three covariates was statistically significant (Table 2). Indeed, all estimated relationships were flat (Figure 7b). The interaction model did not improve model fit, with only 13% of explained deviance ( $AIC = 1737.1$ ), and none of the variables were statistically significant (Table 2, Figure 7). Both models failed to provide reliable predictions compared to observations and no further inferences were carried out on common dolphins (see Appendix E2).

### 3.3.3 Auks

The global model for auks explained 35% of the deviance ( $AIC = 2469.3$ ), with PCs 1 and 3 significant (Table 2). Positive densities of auks were associated with negative values of the PC 1, and positive values of the PC 3 (Figure 7c). The explained deviance of the interaction model reached 54.1% ( $AIC = 2335.0$ ), and all variables were significant (Table 2). Given the increase in explained deviance, the reduction of the AIC and the significance of all variables, the interaction model was selected as best model.

218 Although the selection of the interaction model implied some variations across years, the predicted distri-  
219 butions were similar across years, as was the preferential association to identified habitats (Figure 8), with an  
220 increase in auk density over the decade (Appendix E3). Overall, auks were consistently associated with habitat  
221 cluster A, and their yearly distributions closely matched the spatio-temporal variations of this habitat. Spatial  
222 variations were associated with river plumes, where auks were most often sighted. For example, in 2009, higher  
223 relative densities were associated with the Loire river plume and in 2013, they were associated with the Gironde  
224 river plume.

### 225 3.3.4 Northern fulmars

226 The global model resulted in an explained deviance of 21.8% (AIC = 2783.0), with PCs 1 and 3 as well as  
227 distance to the closest colonies as significant variables (Table 2). The relationship to the PC 1 increased with  
228 positive densities of fulmars being associated with positive values of this PC. The relationship to the PC 3 was  
229 unimodal, with a maximum at null values of the PC. The relationship to distance to the closest colony was  
230 decreasing, with positive densities of fulmars for distance to the colony  $\leq 200$  km (Figure 7d).

231 In the interaction model, the four interaction terms were significant and the model explained 34.5% of the  
232 deviance (AIC = 2657.0; Table 2). The significance of the interaction terms and the higher explained deviance  
233 indicated that the relationship described above varied among years. Given this result and the clear improvement  
234 of the AIC, the interaction model was selected as best model, and predictions were computed annually.

235 Consistent with the significant year effect, differences among years were predicted in distribution (Appendix  
236 E4). Fulmar predicted densities increased while going offshore: densities were higher along the shelf edge and  
237 fulmars were absent from river plumes and from the southern part of the BoB. Some variations occurred among  
238 years, for example the species was more widespread towards the south in 2005–2007 and more restricted to the  
239 northern BoB in 2011–2013. This difference may be linked to annual variations in the relationship to distance  
240 to the closest colony.

241 The results from predicted distributions were mirrored by the predicted densities by habitat clusters (Fig-  
242 ure 8), which showed a preferential association to the habitat cluster C, with gradually decreasing densities  
243 from habitat cluster C to A.

### 244 3.3.5 Northern gannets

245 The global model for northern gannets explained 18.2% of the deviance (AIC = 6408.4), with all terms being  
246 significant (Table 2). The relationships to PCs 1 and 2 were both unimodals, with a minimum at null values for  
247 the PC 1 and a maximum at null values for PC 2. The relationship was decreasing for the PC 3, with gannet  
248 positive densities being associated with negative values of PC 3. The relationship to distance to closest colony  
249 was also unimodal, with negative densities of gannets associated with distances of 200–400 km from colonies  
250 (Figure 7e).

251 The inclusion of the year as an interaction term clearly improved the model, with 34.9% of explained  
252 deviance, which was an improvement of the AIC of 258.6 points (AIC = 6149.8), and all terms were significant  
253 (Table 2). Thus, this model was selected as the best model. Predicted distributions and densities by habitat  
254 (Appendix E5) clearly showed the strong year effect. Overall, a slight preference for habitat cluster A to C  
255 emerged, but with extensive yearly variations (Figure 8, Appendix E5); for example, in 2007, gannet habitat  
256 preference went from habitat cluster C to A, while in 2012 there was no difference between the three habitats.  
257 In all cases, the difference in densities between habitats was low, and the species was present everywhere.

## 258 4 Discussion

### 259 4.1 Methodological considerations

260 To explore the variations in springtime habitat preferences of five mobile top predator species over a decade  
261 (2004–2013), we first described the habitats available within the BoB with a PCA, which is a conventional  
262 method to describe and highlight relationships between a set of variables (Jongman et al., 1995). Second, we  
263 inferred the habitat preference of studied predators and focused on the stability with which predators were  
264 associated with specific habitat over the decade.

265 In this study, the use of PCA as an input of habitat modelling resulted in higher quality models and  
266 predictions than more "traditional" habitat models that use raw environmental variables (not shown). PCA  
267 is a data reduction technique, where raw data are projected onto new orthogonal axes called PCs that are  
268 uncorrelated and with maximum variance. These PCs are linear combinations of the raw variables and provide  
269 two main advantages for habitat modelling: (i) the number of variables included in models is reduced (here,  
270 from nine to three); (ii) using PCs removes collinearity issues between environmental covariates (*e.g.*, between  
271 CHL and NPP, or depth and slope).

272 A drawback of this method is that the interpretation of PCs in terms of environmental variables may be  
273 difficult (large number of variables). Fortunately, in our study, the interpretation of PCs was facilitated by  
274 considering the habitats identified on each PC by the cluster analysis, rather than the raw environmental  
275 variables combinations. For example, the first PC can be interpreted more easily as corresponding to the shelf  
276 edge at one side and river plumes at the other, rather than high depth, steep slopes and low salinity versus high  
277 CHL, NPP and salinity.

278 Moreover, as for the PCA we used only environmental variables to which the studied predators are known  
279 to be linked (based on literature), all the covariates available were used when fitting habitat models with GAMs  
280 (the three PCs and the distance to the closest colony), without implementing any selection procedure.

### 281 4.2 Pelagic habitat availability

282 Based on the PCA, we identified three main pelagic habitats in the BoB and visualized year-to-year variability  
283 in habitat spatial extent, that is their availability (Figures 4 and 5). PCA highlighted two independent environ-  
284 mental gradients in the BoB (PCs 1 and 2), accounting for 53% of data variance and separating pelagic waters  
285 into three main habitats. The first gradient separated river plumes (habitat cluster A), characterised by high  
286 values of CHL/NPP and low SSS, from the shelf edge (habitat cluster C), characterised by high depth, steep  
287 slopes and high SSS.

288 The second gradient was independent from the previous gradient and was mainly driven by temperature-  
289 related variables. This second gradient did not separate the first two habitats, which were both characterised by  
290 cold waters, but isolated a third habitat, corresponding to the central shelf (habitat cluster B) with relatively  
291 warmer temperature and intermediate values of CHL/NPP and depth/slope. Habitat clusters A and C were  
292 both characterised by low SST. River plumes had low SST due to freshwater inputs (Jegou & Lazure, 1995),  
293 and slope was associated with upwelling of colder deep oceanic water because of internal waves (Green et al.,  
294 2008).

295 Habitat cluster C, because it was mostly associated with a topographic feature, showed little spatial variation  
296 between years, although it spread farther over the shelf in particular years (2004–2005, 2010). Habitat cluster  
297 A was associated with a more dynamic feature, and its extent varied extensively among years. The extent of  
298 river plumes depends on freshwater run-off, *i.e.* on the rainfall over drainage basins during previous months, as  
299 well as on wind patterns. For example, habitat cluster A was almost absent in 2011, when river plumes were  
300 reduced due to severe rainfall shortage in April that year, while in 2009, strong winds contributed to extend  
301 river plumes offshore.

### 302 4.3 Top predator response to decadal spatio-temporal variability of available habi- 303 tats

304 Comparing models with year as an interaction term and without year as an interaction term allowed for an  
305 assessment of whether springtime habitat preferences of species varied among years. Our results showed a range  
306 of patterns depending on the specificity and stability of species preferences, which highlighted species-specific  
307 habitat flexibility. The species exhibiting the narrower habitat preferences also exhibited stronger stability in  
308 their preferences among years (bottlenose dolphins and auks) while the species with wider habitat preferences  
309 exhibited higher variability among years (gannets).

310 The most extreme case of habitat preference variability was for the bottlenose dolphin, which was confined to  
311 the shelf edge during all years, with densities one order of magnitude higher within habitat cluster C compared  
312 to the other two habitats. This preference was in line with the known distribution of the species in the area from  
313 large-scale surveys (Certain et al., 2011; Lambert et al., 2017), which all showed a clear preference of bottlenose  
314 dolphins for the shelf edge in the area, whatever the season and year. Nevertheless, the model predicted some  
315 bottlenose dolphin expansion over the shelf, especially in 2007–2008 and 2011, which was also in line with  
316 previous results, as some intrusions over neritic waters was also demonstrated in 2011 and 2012 (Lambert et al.,  
317 2017).

318 Auks also exhibited a sharp preference for habitat cluster A, corresponding to river plumes. However, unlike  
319 bottlenose dolphins, some differences occurred among years. Although the inclusion of year in the model was  
320 compatible with the increase in overall abundance over the decade, auks also exhibited year-to-year differences  
321 in their use of river plumes (some years, highest densities were in the Gironde estuary, in other years highest  
322 densities were in the Loire estuary). Despite these small variations, the distribution of auks was mostly linked to  
323 spatial variations of habitat A, but when this habitat was reduced or particularly contracted, as in 2010–2012,  
324 the species occurred in surrounding habitat B as well.

325 As much as 91.6% auk sightings were of common guillemots, while only 2.0% were of razorbills and 6.4%  
326 sightings were unidentified alcids. The number of breeding pairs of common guillemots in local colonies is very  
327 low, with only 14 individuals on average between 2000 and 2011 (Cadiou et al., 2014); thus most auks sighted  
328 within the BoB during the survey period were likely non-breeders. The presence of non-breeders is consistent  
329 with the low relevance of the distance to closest colony covariate in models, as breeding auks are known to be  
330 tightly linked to their colony during the breeding season (del Hoyo et al., 2010; Wright & Begg, 1997).

331 Our results are a valuable complement to previous study of auks habitat preferences in the area (Lambert  
332 et al., 2017), which demonstrated the strong link of auks to their colonies during the breeding season. Springtime  
333 non-breeding auks therefore seemed to exhibit habitat preferences close to those they exhibited during the winter  
334 season (tightly linked to shallow depths, Lambert et al., 2017).

335 Northern fulmars exhibited increasing densities from habitat cluster A to C. However, this preference was  
336 more gradual than in the case of auks and bottlenose dolphins, with some annual variations. If the overall  
337 preference gradient remained stable through the decade, variations occurred in the amplitude of differences in  
338 predicted density between habitats. For example, in 2010 and 2011 the northern fulmar habitat preference was  
339 clearly for habitat C, while in 2004–2006 its preference was equal for habitats C and B. If the species clearly  
340 avoided coastal waters associated with river plumes, as is consistent with the known ecology of the species  
341 during its breeding period in the area (Weimerskirch et al., 2001; Mallory, 2006; Edwards et al., 2013; Lambert  
342 et al., 2017), the southward extension of the species distribution compared to the shelf edge varied across years.  
343 This may be indicative of fulmar flexibility at the southern limit of its distribution (Brittany; Cadiou et al.,  
344 2004; del Hoyo et al., 2010).

345 Finally, gannets had the most pronounced annual variations in habitat preferences. This result was consis-  
346 tent with the known flexibility of northern gannets (Nelson, 2002). Overall, the data suggested a gradient of  
347 preference from habitat cluster A to C, but the amplitude among these three habitats varied substantially from  
348 year to year. Despite these variations, a distribution with higher densities off southern Brittany and along the  
349 entire coastline, with occurrences along the shelf edge in some years, was a recurring pattern.

350 Gannets breeding in the English Channel and the Irish Sea are known to target predictable features such  
351 as tidal fronts in the English Channel and Irish Sea, or the slope upwelling in the Celtic Sea (Pettex et al.,  
352 2010; Scales et al., 2014; Lambert et al., 2017). The consistency of such a result between studies from different  
353 colonies, different years and different methodologies (telemetry and aerial surveys) suggests a low interannual  
354 variability in habitat preference for breeding gannets in the English Channel and the Irish Sea. This is consistent  
355 with the overall preference for the productive habitat cluster A highlighted here, but not with the variability  
356 among years shown in our results.

357 The higher variability exhibited by gannets in the BoB during the PELGAS survey compared to the literature  
358 may be due to their reproductive status. Most sighted gannets were likely non-breeders since most of the sighted  
359 gannets were identified as immature or juvenile birds (not shown). Although there was also a sizeable proportion  
360 of adults, these were likely non-breeders, since, to our knowledge, no tagged breeding gannets from French, Irish  
361 or Welsh colonies have ever been shown to forage into the BoB. Thus, sighted adults could be either sabbatical  
362 birds or early failed breeders.

363 Since non-breeders are less energy-demanding and not central-place constrained, individuals may be more  
364 flexible in their foraging habitats compared to breeding gannets, explaining the higher habitat preference vari-  
365 ability in BoB compared to habitat preferences of breeding adult gannets within the English Channel and Irish  
366 Sea (Pettex et al., 2010; Scales et al., 2014; Lambert et al., 2017). This higher interannual variability in habitat  
367 preferences for non-breeders compared to breeders would be consistent with the known flexibility of the species  
368 once breeding season is over (Nelson, 2002).

369 The habitat preferences of common dolphin could not be resolved as both models failed to account for the  
370 observed variations in its distribution. The small variations predicted by the models did not correspond to the  
371 observed ones, which was consistent with the non-significance of the three covariates. This result suggests that  
372 environmental variables used in the PCA were uninformative for common dolphin habitat preferences, which  
373 may be driven by other parameters than those used during this study. Another hypothesis may be that the  
374 common dolphin responds to oceanographic processes at a smaller scale than the studied scale (0.25° cells).

375 Habitat covariates in top predator habitat modelling are generally selected because they can be considered as  
376 proxies for distribution and habitat preferences of prey. Thus, the stability in top predator habitat preferences  
377 in this study could reflect the strength of the relationships between the distribution of the targeted prey and  
378 habitat characteristics. Bottlenose dolphins and auks exhibited a stronger stability in habitat preferences. The  
379 highest densities of their preferred prey are relatively stable and predictable, with bottlenose dolphins feeding  
380 on large hakes distributed mainly in the upper slope (Spitz et al., 2006) and auks feeding on copepods (Harding  
381 et al., 2009) which are particularly abundant in river plumes during spring phytoplankton blooms (Vandromme  
382 et al., 2014). Common dolphins and gannets, with looser habitat preferences, forage mostly on small pelagic  
383 fishes (Nelson, 2002; Meynier et al., 2008), which are widely distributed in the BoB and can exhibit important  
384 interspecific and intraspecific changes in abundance and distribution among years. Therefore, it seems that the  
385 degree of habitat predictability of the targeted prey could also partly explain the degree of decadal stability  
386 observed in habitat preferences among top predators in the BoB.

## 387 5 Conclusion

388 The purpose of this study was to explore the variations of springtime habitat preferences exhibited by five  
389 mobile top predator species within the BoB over an entire decade (2004–2013). Our results showed that  
390 predators exhibited a range of responses to springtime interannual variability of pelagic habitats, from bottlenose  
391 dolphins and auks with a narrow habitat preference particularly stable over the decade to northern gannets with  
392 wider habitat preferences varying among years. There was no relationship between the type of habitat and the  
393 stability of predator preferences, as the two species with the most stable preferences targeted opposite habitats.  
394 Bottlenose dolphins targeted the habitat associated with the shelf edge, which was highly stable across time  
395 since it is associated with a topographic structure, while auks were tightly associated with river plumes, which

396 was the most spatially variable habitat identified here. A continuation of this work could include performing  
 397 similar analyses during the three other seasons to explore whether the trends identified here would evolve,  
 398 depending on the seasons or the population breeding status (breeding versus wintering period for seabirds).

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- Concurrent sampling of predators and habitat unveiled their relationships in time
- PCA on environmental variables identified 3 main habitats used by predators
- Predators exhibited various habitat preferences specificity and stability in time
- Narrower habitat preferences paired with stronger stability among years
- Wider habitat preferences paired with higher variability among years

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