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# Do marine food subsidies predict large scale distribution of scavenging seabirds within the Bay of Biscay?

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A B S T R A C T

Omnivorous and opportunistic species have the potential to exploit human food subsidies. In marine ecosystem, understanding interaction between seabirds and fishery activities, particularly their scavenging behaviour on discards is crucial nowadays, in the context of EU landing obligation. The Bay of Biscay is one of the major fishing zones in Europe and a central area for the wintering of a high number of seabird species. During spring and autumn, oceanographic surveys were conducted by the R/V Thalassa with the aim to evaluate fishing resources along transects over the continental shelf, thereby providing an opportunity to study the distribution and scavenging behaviour of seabirds in this area. We investigated the influence of fishery activities (i.e. distribution of professional fishing vessels, quantity of discards) at large scale, and oceanographic conditions on the distribution of scavenging seabirds along the continental shelf. On average, large gulls (Larus spp) and northern gannets accounted for 70 % of the seabirds scavenging on discards. We compared model predictions using oceanographic variables with those using both oceanographic variables and fishery activities, in separate for spring and autumn and group of seabirds (i.e. large gulls and northern gannets). Results suggested that the distribution of scavenging seabirds was better predicted by oceanographic variables than by fishery activities. The predicted numbers of scavenging seabirds were higher in autumn than in spring, probably due to the annual cycle of seabirds (i.e. breeding versus wintering). At large scale, oceanographic variables were better predictors of suitable habitat. However, a closer evaluation of prediction differences between the two models highlighted high anomaly values for large gulls in autumn along the coast, that may indicate over predictions. These results have provided new knowledge on the ecology of scavenging seabirds, in an area with high fishery activity, especially in the context of landing obligation.

## 1. Introduction

Understanding drivers of species distribution and their foraging behaviour is central in ecology to the development of management and conservation strategies (Morris, 2003; Rhodes et al., 2005). In marine ecosystems, oceanographic conditions have often been described as drivers of highly mobile species such as seabirds. As indicator of accessibility and availability of prey (Bertrand et al., 2014; Cox et al., 2018), oceanographic conditions are used as marine derived resources (Koyama et al., 2024). These drivers influence seabirds' foraging distribution, assemblages and distance to the colonies (Hyrenbach et al., 2007; Ribic et al., 1997; Woehler et al., 2003) on different spatial and temporal scales (Hunt and Schneider, 1987). At large scale, water masses and boundary currents can be compared to terrestrial biomes (based on vegetation, Daudt et al., 2024). At smaller scale, physical structures such as fronts, continental shelf areas, and sites of upwelling can provide predictable aggregation of prey for marine predators (Bost et al., 2009; Lea et al., 2006; Lee, 2007; Weimerskirch, 2007). However, oceanographic habitats are now modified by human activities and climate change, which can alter the influence of these natural drivers on the distribution of birds (Cox et al., 2018).

Nowadays, ecosystems are altered by food supplied to animals by humans (Oro et al., 2013), which are highly spatially and temporally predictable, and easier to access compared to natural resources (Tixier et al., 2016). These predicable anthropogenic food subsidies (PAFS, Oro et al., 2013) provided by human activities such as refuse in landfills and

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discards in marine ecosystems, are impacting species at different levels: 1) at the individual through changes in foraging behaviour (Collet et al., 2017) and migration patterns (Marcelino et al., 2023); 2) at the population by influencing growth rates and dynamic (Brunk et al., 2022); and 3) at the community levels by changing their composition and diversity (Oro et al., 2013). Through cascading effect, PAFS can have direct consequences on foodwebs and on the transfer of nutrients between biomes (Caut et al., 2012; Pais de Faria et al., 2021; Polis et al., 1997); increasing in some cases wildlife-human conflicts (Newsome et al., 2015). Opportunistic species, often considered as omnivorous and feeding on more than one trophic level, such as gulls, have the potential to directly exploit most of these PAFS (Coulson and Coulson, 2009).

The exploitation of marine resources by commercial fisheries has profoundly changed marine ecosystems (de la Cruz et al., 2022). The attraction of marine megafauna to fishing vessels has modified both their foraging behaviour and their population dynamics (Mul et al., 2020; Oyarbide et al., 2021). This attraction for PAFS can have negative consequences for these predators such as bycatch (Delord et al., 2005; Wienecke and Robertson, 2002) or positive ones such as discards that provide an abundant quantity of potential preys while reducing the energetic cost of foraging (Bartumeus et al., 2010). Fishery discards are the third most important anthropogenic food resources for wildlife (Oro et al., 2013), representing an estimated annual amount of 10.3 million tons of natural available food resource worldwide (Pauly and Zeller, 2016). They can affect marine food webs (Camphuysen, 1999; Reeves and Furness, 2002) from benthic fauna (Erzini et al., 2003) to top predators (Hill and Wassenberg, 2000; Luque et al., 2006). However, eliminating discards is necessary to ensure that fisheries are economically and environmentally sustainable (Bellido et al., 2011). Since 2019, to improve fishing practices, the European community has implemented a discard ban, involving a landing obligation. This discard ban might have important consequences on the community of scavenging seabirds (Calado et al., 2021).

Seabirds include some conspicuous scavenging species with a long history of association with fisheries, worldwide. Interactions with fisheries affect 52 % seabird species (Oro et al., 2013), and two of the most noticed are gulls (Calado et al., 2021; Ouled-Cheikh et al., 2020) and gannets (Grémillet et al., 2008; Le Bot et al., 2019; Votier et al., 2013). The predictability of this anthropogenic resource (Real et al., 2018; Sherley et al., 2020) may be key to this dependence to fishery discards, which could vary according to the species, seasons and locations. Seabirds seem to be more dependent on discards during winter, when the availability of their natural preys is more limited (Mitchell et al., 2004) and during the chick rearing period, when breeding adults are constrained by their chicks to perform shorter trip duration (Phillips et al., 2021). Then, discards impact different aspects of seabirds ecology, such as their foraging behaviour (Bartumeus et al., 2010; Votier et al., 2013; Votier et al., 2010). Telemetry surveys revealed that gull and shearwater species in the Mediterranean Sea have adjusted their movement, distribution and activity pattern to the scheduled routines of fishery activities (Bartumeus et al., 2010; Ouled-Cheikh et al., 2020). In spring, interactions with fishery discards can also influence breeding success (Oro, 1996) depending on the quality of food. In the Western Mediterranean Sea, (Oro, 1996) highlighted the positive influence of discards on lesser black backed gull eggs volume, as foraging on discards improved the body condition of females. Conversely, in the Benguela current system and in the English Channel, consumption of discards of low energy densities by gannets negatively impacted their reproductive success (Grémillet et al., 2008; Le Bot et al., 2019). Population dynamics (Oro et al., 2004) and community ecology of many species are also impacted by foraging on discard (Wagner and Boersma, 2011). In the North Sea, herring and great black-backed gull numbers have decreased by more than 80 % in the absence of fishing activities (Hüppop and Wurm, 2000). Abundance of discard maintained great skua populations during the decline of sandeel resources, while other seabird species have declined (Church et al., 2019). In the Mediterranean Sea, discards negatively influenced the dispersal probability of Audouin's gulls (Oro et al., 2004).

The Northeast Atlantic ocean has been identified as a "discard hotspot" (Guillen et al., 2018). In this area, most of studies focused on the North Sea, but comparatively few focused on the Bay of Biscay (BoB, Depestele et al., 2016; Louzao et al., 2020; Zorrozua et al., 2024). The BoB is an area of particular interest for understanding the extent of interaction between seabirds and fisheries beyond coastal areas, and notably to explore the potential impact of such interactions on seabird distribution at meso-scale. The influence of numerous physical processes (eddies and stratification) and river discharge plume make it a heterogeneous environment with seasonally important fish resources (Doray et al., 2018). The BoB is one of the major fishing zones for the European Union in terms of landings (Guénette and Gascuel, 2012). In 2018, around 2000 fishing vessels were active in this area (Demaneche et al., 2019). Numerous fleets operate in here such as trawlers, seiners, gillnetters. From several European Countries (France, Ireland, Uk, Belgium, Spain, Netherlands, Demaneche et al., 2019), varying from <12 m long (French average size) to over than 100 m (e.g. Dutch average size). The BoB is a central area for many seabirds, particularly during winter. In this area, large gulls (*Larus spp*) and northern gannets (*Morus bassanus*) dominated the avian community during winter and summer (Pettex et al., 2017). Distribution between both seasons vary markedly for northern gannets but not for large gulls. Many of these seabird species are breeding in northern Europe and find enough resources to spend the entire non-breeding period (i.e. winter) in the BoB (Pettex et al., 2017). In spring, over the continental shelf, mainly immature or adult non-breeding individuals are observed, probably feeding on pelagic fish (Certain et al., 2011; Certain et al., 2007) such as: European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), European sprat (*Sprattus sprattus*), hake (*Merluccius merluccius*), Atlantic mackerel (*Scomber scombrus*) and Atlantic horse mackerel (*Trachurus trachurus*) and demersal fish from discards.

In this study, we investigated if the distribution of scavenging seabirds over the BoB continental shelf was impacted by fishing activities beyond what was expected from oceanographic conditions only. We assumed that oceanographic conditions play an important role in the distribution of seabirds in this areas, particularly in spring, where the density of pelagic fish is high. However, we also considered the importance of fishery activities as driver of their distribution, as demonstrated by Depestele et al. (2016) and Louzao et al. (2020) particularly in offshore areas, since they could offset intra- and interspecific competition on a local scale. In the BoB, oceanographic surveys designed for fish stock assessments also collected standardized data on seabird distribution over the continental shelf. Trawling operations along transects were carried out for scientific sampling purposes and followed by systematic discard events of the whole trawl. This provides a relevant context to investigate seabirds' scavenging behaviour. We used these data to study whether the oceanographic conditions or fishery activities drove the scavenging seabirds' distribution. We first modelled the distribution of scavenging seabirds using only oceanographic conditions; secondly, we fitted a model including both oceanographic variables and fishery activities; then, we compared the fit of two models. We focused on the two most abundant groups of species mainly observed scavenging on discards in the BoB: large gull species and the northern gannet.

## 2. Material and methods

### 2.1. Survey data

In the BoB, oceanographic surveys designed for fish stock assessments collected standardized data over the continental shelf. Trawling operations along transects were carried out for scientific sampling purposes and were followed by systematic discard events of the whole trawl. Data were collected on two oceanographic surveys conducted annually by IFREMER on the R/V Thalassa and covering spring and autumn respectively, PELGAS (*PELagiques GAScogne*[1]) and EVHOE (*EValuation des ressources Halieutiques de l'Ouest Europe*[2]) surveys series (Fig. 1). The PELGAS survey collects data in the major components of pelagic ecosystem (hydrology, phyto and zooplankton, fish, top predators) in the BoB, during April and May (Doray et al., 2018). We used data collected from 2014 to 2018 for this spring survey. The EVHOE groundfish survey collects data on the distribution, abundance and life-history parameters of demersal and pelagic fish and commercial invertebrates, as well as top predator sightings from October to November (Mérillet et al., 2021). This survey covered the BOB and the Celtic Sea, but we focused only on the BoB data. Furthermore, we only used data from 2015 to 2018 for this survey in autumn as only few data on scavenging seabirds were collected during discard events in 2014, making it impossible to cover the entire area.

### 2.1.1. Scavenging seabird data

Scavenging seabird data were collected during discard events following trawling operations by marine mega-fauna observers (Fig. 1). Any bird detected in the wake of ship (i.e. within a distance of 500 m), and attracted by the fishing activity was considered as scavenging. Data on bird flocks were collected: species composition, number of individuals, and when possible the stage of maturity (i.e. adults and immatures). We focused on the two main group species observed in the BoB during both surveys from 2014 to 2019: the northern gannets and large gulls: great black-back gull (*Larus marinus); lesser black-backed gull (Larus fuscus); herring gull (Larus argentatus); yellow-legged gull (Larus michahellis*). Meteorological conditions such as the sea state on the Beaufort scale (hereafter Beaufort) were also recorded for each event.

### 2.1.2. Discards data

Data on the biomass and composition of trawl hauls and their localisation, during the PELGAS and EVHOE surveys between 2014 and 2018 were provided by the *Système d'Informations Halieutiques.*[3] Three functional categories of discards following haul compositions for each season were defined according to the seabirds selectivity (based on field experiments, Table 1). This classification was based on the size and shape of the species making up 90 % of the trawl haul biomass. *Class n°1 (CLA1)* was composed by: any round fish (without backbone) and cephalopod (i.e. mantle) less than 20 cm in size; *class n°2* (CLA2): any round fish (without backbone) and cephalopod between 20 and 30 cm, as well as any round fish with backbone or flatfish smaller than 30 cm; *class n°3* (CLA3): any organism larger than 30 cm (Table 1). We used the summed biomass of each class to represent the biomass discarded.

### 2.1.3. Fishing boats data

Following a standardized line transect protocol (Thomas et al., 2010), data on the density of professional fishing boats in the vicinity of the research vessel have been collected during each survey series. Sighting effort was conducted whenever the R/V speed exceeded the 8 knots, from the sunrise to the sunset. Two marine megafauna observers scanned simultaneously the 90° of their side, covering an 180° area ahead the bow. Here, we have only used the density of fishing boats, as it was not always possible for observers to identify the metier.

## 2.2. Oceanographic variables

Based on seabirds' habitat selection (de la Cruz et al., 2021; Jessopp et al., 2020; Waggitt et al., 2020), we used different oceanographic variables as potential proxies of physical and biological drivers of the distribution of seabirds in the BoB. Chlorophyll A (Chla) were sourced from MODIS model,[4] representing near surface concentration (in mg. $m^{-3}$) with a spatial resolution of 4 km and temporal scale of a month. Other oceanographic characteristics were provided from the *Service Hydrographique et Oceanographique de la Marine* (SHOM): frontal structures of salinity (SSS, in $1e^{-3}.m^{-1}$) and Sea Surface Temperature (SST, in °C.m), stratification intensity (in kg.m-$^{1}$.s$^{-2}$), low frequency average current (current, m.s$^{-1}$), and mix layer depth (MLD, in m). All these variables had a spatial and temporal resolution of 1 nautic mile (i.e. 1.852 km) and month respectively (Tew-Kai et al., 2020). We then averaged these data over two months corresponding to spring (i.e. April and May for PELGAS survey series) and autumn (i.e. October and November for EVHOE survey series) for each year. All these variables were downloaded as netcdf files and extracted using the *netcdf4* package in R version 4.1.2 (R Core Team, 2021). We monthly average and rasterized them using *raster R package*. Bathymetry was sourced from European Marine Observation and Data Network (EMODnet, https://www.emodnet-bathymetry.eu/), with a grid size resolution of of 0.125*0.125 min. Distance from shore was calculated as the straight-line distance to the closest point along the coast using ArcGIS "*Nearest*"function. Unlike other studies, we did not to use the distance to the colony. Indeed, our study covered the entire continental shelf, where most of the birds encountered at sea are not central place constrained (i.e. immature and/or non-breeding individuals).

## 2.3. Spatial data homogenisation

A spatial homogenisation of observation data *(*i.e. scavenging seabirds, number of professional fishing boats, Beaufort) and oceanographic variables was carried out. The different datasets were averaged by block over a common grid spanning the BoB (longitude 42–55°N; latitude −11.5 W-8.5°E), following the block averaging method (Petitgas et al., 2014). The grid mesh size selected was 0.25° in latitude and 0.25° in longitude. This procedure is equivalent of a kernel interpolation (Petitgas et al., 2014) and smooth the data, thereby attenuating edge effects. The result were smoothed values: the averaging procedure yields data for which an assumption of gaussianity for further modelling is reasonable.

## 2.4. Scavenging seabird distribution modelling

Statistical analyses were performed independently for spring and autumn, and for both species groups using R version 4.1.2 (R core Team 2021). We fitted two types of model to determine the influence of fishery activities beyond the oceanographic drivers on scavenging seabirds distribution: 1) models containing only oceanographic variables (oceanographic-only models) and 2) models containing both oceanographic variables and fishery activities (oceanographic-fishery models).

Data exploration was carried out following the protocol described in (Zuur and Ieno, 2016). When outliers were observed in a variable, we log-transformed the variable. We used the oceanographic, distance from shore, Beaufort and fishery activities variables in a principal component analysis (PCA, *PCA* function FactoMine R package (Lê et al., 2008) to identify cluster of highly correlated variables. First, these variables were standardized (mean centred and unit scaled) to ensure that each variable contributes equally to the formation of the principal components. We used PCA to reduce the variables number to a maximum of 5 by pruning highly correlated variables.

For oceanographic-only models, *Generalized Additive Mixed Models* (GAMM) were used to model the distribution of seabirds with the function gam of *mgcv* R Package (Wood, 2017). These models were fitted with a *gaussian family* argument using an identity link, as smoothed data from block averaging method were used, breaking the temporal

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[1] https://doi.org/10.17600/18001265

[2] https://doi.org/10.18142/8

[3] https://sih.ifremer.fr/

[4] https://modis.gsfc.nasa.gov/

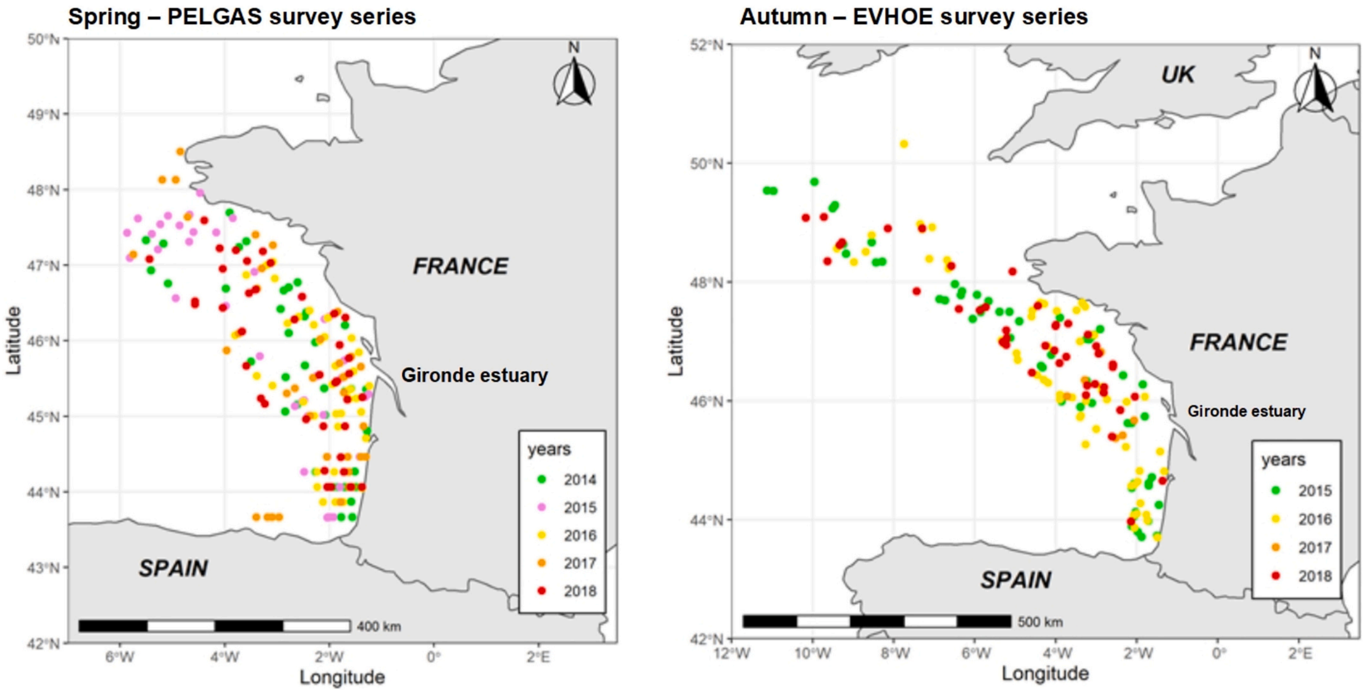

**Fig. 1.** Maps of discard operations in the Bay of Biscay for spring (i.e. PELGAS survey series, from 2014 to 2018) and autumn (i.e. EVHOE survey series, from 2015 to 2018).

**Table 1**
Discard classification – Main fish species constituting each discard class for spring (i.e. Pelgas survey series) and autumn (i.e. Evhoe survey series); Class 1 (i.e. CLA1, fish length < 20 cm); Class 2 (i.e. CLA2, fish length from 20 to 30 cm); and Class 3 (i.e. CLA3, fish length > 30 cm).

| Survey | Class 1 | Class 2 | Class 3 |
|---|---|---|---|
| Spring | *Engraulis encrasicolus* (<20 cm) | *Capros aper* (<30 cm) | *Scomber scombrus* (>30 cm) |
| | *Sardina pilchardus* (<20 cm) | *Merluccius merluccius* (20–30 cm) | |
| | *Sprattus sprattus* (<20 cm) | *Micromesistius poutassou* (20–30 cm) | |
| | *Trachurus trachurus* (<20 cm) | *Trachurus trachurus* (20–30 cm) | |
| Autumn | *Engraulis encrasicolus* (<20 cm) | *Argentina silus* (20–30 cm) | *Conger conger* (>30 cm) |
| | *Merluccius merluccius* (<20 cm) | *Capros aper* (<30 cm) | *Galeus melastomus* (>30 cm) |
| | *Micromesistius poutassou* (<20 cm) | *Melanogrammus aeglefinus* (20–30 cm) | *Leucaraja naevus* (>30 cm) |
| | *Sardina pilchardus* (<20 cm) | *Merluccius merluccius* (20–30 cm) | *Merluccius merluccius* (>30 cm) |
| | *Scomber scombrus* (<20 cm) | *Micromesistius poutassou* (20–30 cm) | *Rhizostoma pulmo* (>30 cm) |
| | *Sprattus sprattus* (<20 cm) | *Scomber scombrus* (20–30 cm) | *Scyliorhinus canicula* (>30 cm) |
| | *Trachurus trachurus* (<20 cm) | *Trisopterus luscus* (20–30 cm) | *Squalus acanthias* (>30 cm) |
| | *Trisopterus minutus* (<20 cm) | | |

correlation within the data. Numbers of scavenging individuals per grid cell were used as the response variable and were log(x + 1) transformed before model fitting. Explanatory variables selected by the PCA were treated as continuous variables, and we set the regression splines (i.e. knots number) to 4. Years were modelled as random effect using *te* argument in the *gam* function to consider the temporal autocorrelation of the data within year. Furthermore, we also used the Markov Random Field Smooth (mrf function mgcv R package) to consider spatial autocorrelation and border effects which can strongly influence spatial predictions. Different spatial effects were estimated for each year. The best model was selected using the AIC criteria (*Akaike's Information Criteria*, Akaike, 1973).

Secondly, to highlight the importance of fishery activities beyond the oceanographic conditions, oceanographic-fishery models were fitted. We followed the same statistical procedure of oceanographic-only models. Following the results of the PCA, we chose the oceanographic variables based on the selection of fishing activity variables. Then the selected variables were used as explanatory variables in the models. Following our field observations of the two groups of species, only the cumulative biomass distributions of CLA1 and, CLA1 and CLA2 were used for large gulls and northern gannets, respectively.

Thirdly, we compared oceanographic-only, oceanographic-fishery models, and a null model for each species group and each season. For each model, the AIC (Akaike Infomation Criterion, (Akaike, 1973), the difference between AIC of the specific model and of the null / best model (Δ AIC) and AIC weight (normalized weight of evidence in favour of the specific model, relative to all candidate models, Burnham and Anderson, 2002) were calculated.

We used spatial predictions of these models to compare their fit. In addition, prediction anomalies were calculated as the difference between predictions from the two models. For each cell, the fitted values of the two models were averaged; then the mean was subtracted from the prediction of the model containing only the oceanographic variables, determining the anomaly deviation. The larger the anomaly errors, the larger the prediction differences between the two models will be, indicating a difference in prediction.

## 3. Results

### *3.1. Scavenging seabird and fishery activities data*

During the period of the study, large gulls and northern gannets were the two main group species observed in the BoB compared to the others, representing 56 % and 28 % of the total individuals observed in spring; and 41 % and 39 % (Supplemental 1).

A total of 260 discard events were recorded (Table 2). One hundred and nineteen events were recorded during spring between 2014 and 2018, including 118 events with interactions with large gulls and 90 events with interactions with northern gannets. One hundred and forty-one events were recorded between autumn 2015 and 2018, including 130 events with interactions with large gulls and 149 events with interactions with northern gannets. On average, over the years, large gulls and gannets represented nearly 96 % of scavenging seabirds in spring (75 % and 22 % were respectively large gulls and northern gannets), and 71 % of scavengers in autumn (54 % and 19 % were large gulls and gannets respectively, Table 2). Total number of individuals observed per species group varies per year and season (Table 2). Scavenging seabirds were evenly distributed throughout in the BoB considering both season and species group, except in 2017 where the effort was less important as damage occurred to the oceanographic vessel during EVHOE survey (Figs. 2 and 3). In average, juvenile and immature seabirds were present in more than 90 % and 60 % of the sightings for northern gannets in spring and autumn respectively. They also represented an important part of the observations for large gulls, as they were in 90 % of the sightings and 80 % over the years, respectively for spring and autumn (Supplemental 2).

Professional fishing vessels were distributed over the continental shelf for both season and over the years with a higher density during spring (Supplemental 3). In spring, the quantity of discarded fish for CLA1 was more important than those for CLA2 and CLA3 (Supplemental 4) over the years, except for 2015, representing more than 100 tons of discards. In Autumn, discard species composition was more diversified than in spring (Table 1). The quantity of discarded fish was higher (> 200 tons) and more homogeneous between the three classes in autumn (Supplemental 4).

### 3.2. Scavenging seabird distribution modelling

For each species and seasons, variables were selected depending of their scores in the principal component axes (Table 3, Fig. 4). For the oceanographic-only model, the variables selected by PCA were the same for both species' groups in spring and autumn (i.e. Chla, stratification intensity, SSS, MLD, and distance from shore). On the opposite, the selection of variables was different for the oceanographic-fishery model between both group of species and seasons (Table 3). In spring, stratification intensity, distance from shore, the density of fishing vessels, and CLA1 were selected for large gulls, while stratification intensity, density of fishing vessels, CLA1, and CLA2 were selected for northern gannets. In autumn, bathymetry, MLD, the density of fishing vessels and CLA1 were selected for large gulls, while bathymetry, MLD, density of fishing vessels and CLA2 were selected for northern gannets.

The oceanographic-only model selected for each season and species group, was considered as the best model (i.e. lower AIC value, higher AIC weight and deviance explained in every case) compared to the null and oceanographic-fishery models (Table 4). Thus, oceanographic-only models better predicted the distribution of gannets and large gulls in spring and autumn. Explanatory variables selected, both in oceanographic-only and oceanographic-fishery models, by the model selection varied according to species group and season. Delta AIC between oceanographic-only model and oceanographic-fishery model was lower in spring (i.e. 6 and 9 for gannets and large gulls respectively) and higher in autumn (i.e. 30 and 68 for gannets and large gulls respectively). However, for large gulls in spring, the delta AIC between the oceanographic-fishery model and the null model was lower than 2 (i.e. equivalent), indicating that the null model performed better than the oceanographic-fishery model. This suggests that adding explanatory variables did not significantly improve the fit of the model. Then, we did not pursue the oceanographic-fishery predictions and their comparison with oceanographic-only model predictions for large gulls in spring.

The predicted number of individuals with oceanographic-only model in spring varied little over the BoB (i.e. 0 to 25 individuals) for both group of species (Fig. 5-A). The predicted number of large gulls was higher North of the Gironde estuary and along the Spanish coasts. Higher value of predicted number of gannets was also observed along the Spanish coasts. In autumn, predicted number of individuals were higher along the coasts, particularly for large gulls with values of prediction higher than 200 individuals (i.e. hotspots), than in more offshore waters. The predicted values with oceanographic-fishery model varied little spread over the BoB in spring (i.e. 0 to 25 individuals) with higher predicted number along the Spanish coast for northern gannets (Fig. 5-B). Predicted number of individuals was higher in autumn (25 to 75 individuals by unit cell vs 0 to 25) and less homogeneously distributed for both groups of species, particularly for large gulls.

### 3.3. Oceanographic-only model & oceanographic-fishery model comparison

#### 3.3.1. Spatial prediction comparison

Spatial predictions of oceanographic-only model were plotted against spatial predictions of oceanographic-fishery model in order to evaluate differences in predictions (Fig. 6). The more similar the spatial predictions of the two models are, the more the scatterplot will take the form of diagonal. Differences in predictions were observed between the

**Table 2**

Scavenging seabird counts during discard events. Percentage per event (mean ± standard deviation): percentage that the group represents in relation to the total number of seabirds observed; Number of individuals per event (mean ± standard deviation): number of individuals for each species group observed on average for spring (i.e. Pelgas survey series) and autumn (i.e. Evhoe survey series); Total number: total number of individuals observed for each species group and season.

| Season | Year | Group of species | Discard event | Percentage per event (mean ± SD) | Number of individuals per event (mean ± SD) | Total number |
|---|---|---|---|---|---|---|
| Spring | 2014 | Large gulls | 32 | 70 ± 40 | 39 ± 57 | 1248 |
| | | Northern gannets | | 25 ± 35 | 10 ± 30 | 319 |
| | 2015 | Large gulls | 26 | 84 ± 23 | 31 ± 44 | 800 |
| | | Northern gannets | | 9 ± 15 | 2 ± 2 | 42 |
| | 2016 | Large gulls | 17 | 80 ± 26 | 117 ± 149 | 1997 |
| | | Northern gannets | | 20 ± 26 | 28 ± 49 | 475 |
| | 2017 | Large gulls | 26 | 80 ± 31 | 87 ± 94 | 2264 |
| | | Northern gannets | | 17 ± 29 | 12 ± 25 | 314 |
| | 2018 | Large gulls | 18 | 59 ± 30 | 55 ± 41 | 992 |
| | | Northern gannets | | 37 ± 28 | 47 ± 67 | 848 |
| Autumn | 2015 | Large gulls | 48 | 53 ± 38 | 197 ± 328 | 9443 |
| | | Northern gannets | | 18 ± 24 | 68 ± 126 | 3280 |
| | 2016 | Large gulls | 53 | 58 ± 40 | 198 ± 348 | 10,489 |
| | | Northern gannets | | 22 ± 31 | 122 ± 429 | 6476 |
| | 2017 | Large gulls | 5 | 60 ± 27 | 35 ± 22 | 175 |
| | | Northern gannets | | 23 ± 12 | 14 ± 11 | 71 |
| | 2018 | Large gulls | 35 | 46 ± 38 | 153 ± 193 | 5365 |
| | | Northern gannets | | 15 ± 14 | 40 ± 57 | 1414 |

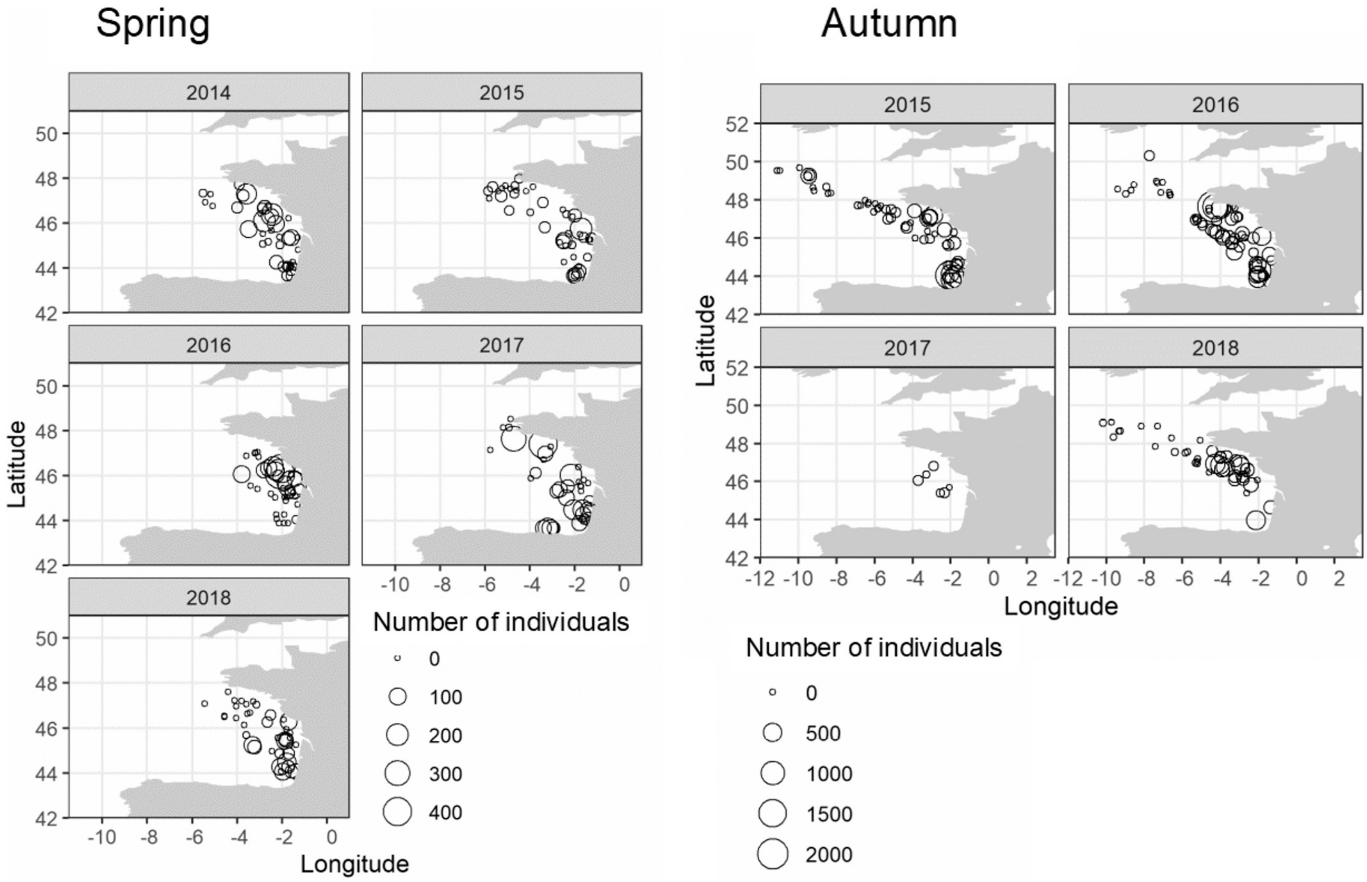

**Fig. 2.** Large gulls abundance (i.e. number of individuals) attending discard events in the Bay of Biscay in spring (i.e. Pelgas survey series from 2014 to 2018) and autumn (i.e. Evhoe survey series from 2015 to 2018).

two models for northern gannets in spring, and for large gulls and gannets in autumn. For the models including fishery variables, the highest predictions quickly reached a plateau whereas those of the oceanographic-only were unbounded. This was more marked for gannets in spring, and large gulls in autumn. Oceanographic-fishery model might underestimate the distribution of large gulls. Conversely, the oceanographic-only model could predict a larger number of individuals, and was therefore less constrained.

### 3.3.2. *Anomaly values' maps*

When the anomaly values were negative, the prediction values of oceanographic-fishery model were higher than those of oceanographic-only model. Conversely, when the anomaly values were positive, then the prediction values of oceanographic-fishery model were lower than those of oceanographic-only model. Anomaly values were generally negative in the offshore areas (varying between −30 and 0, Fig. 7), and positive near the coast (from 0 to 30), for both species in autumn. For northern gannets, in spring, the picture was more mixed with positive values in the southern part of the BoB and negative anomaly values in the northern part of the BoB. Very high positive anomaly values were observed near the coast for large gulls in the autumn (values higher to 100).

## 4. Discussion

This study highlighted that at large scale and over the continental shelf in the Bay of Biscay, the distribution of large gulls and northern gannets following trawlers and scavenging on fishery discards was better predicted by oceanographic conditions than by the discard cumulative biomass distribution and number of professional fishing vessels, both in spring and autumn. This was more pronounced in autumn and for large gulls. Consequently, the distribution of these species at a large spatial scale appeared not to be predicted by fishery activities such as the quantity of biomass discarded and the distribution of professional fishing vessels, suggesting that seabirds might not follow fishing boats outside their natural habitat in the context of the BoB during the period of this study. Nevertheless, these activities could influence fine-scale spatial aggregations in this area.

### 4.1. *Methodological aspects*

Data on the distribution of scavenging seabirds were collected over the continental shelf of the BoB from R/V Thalassa. For the first time, we investigated the drivers of scavenging seabirds' distribution in this area. Previous studies on scavenging seabirds in the European waters mainly focused on the North Sea (Darby et al., 2021; Sherley et al., 2020; Votier et al., 2013). The spatial coverage of fishery surveys allowed us to collect data over the continental shelf of the BoB including areas with contrasted fish resources, density of seabirds (García-Barón et al., 2019; Pettex et al., 2017) and fishery activities (Demaneche et al., 2019; Kroodsma et al., 2018). Sampling contrasting situations is important to understand the drivers of scavenging seabirds' distribution. The use of a research vessel represents an original aspect in the study of the distribution of scavenging seabirds to standardize the collection of data, in contrast to data collected on professional fishing boat (Hudson and Furness, 1989; Louzao et al., 2020; Valeiras, 2003; Walter and Becker, 1997), as they only collect data on a restricted part of the seabirds' distribution areas. As the R/V Thalassa is a trawler, the potential attraction of the scavenging seabirds for the boat was assumed to be constant throughout the campaign, with multiple discard events along

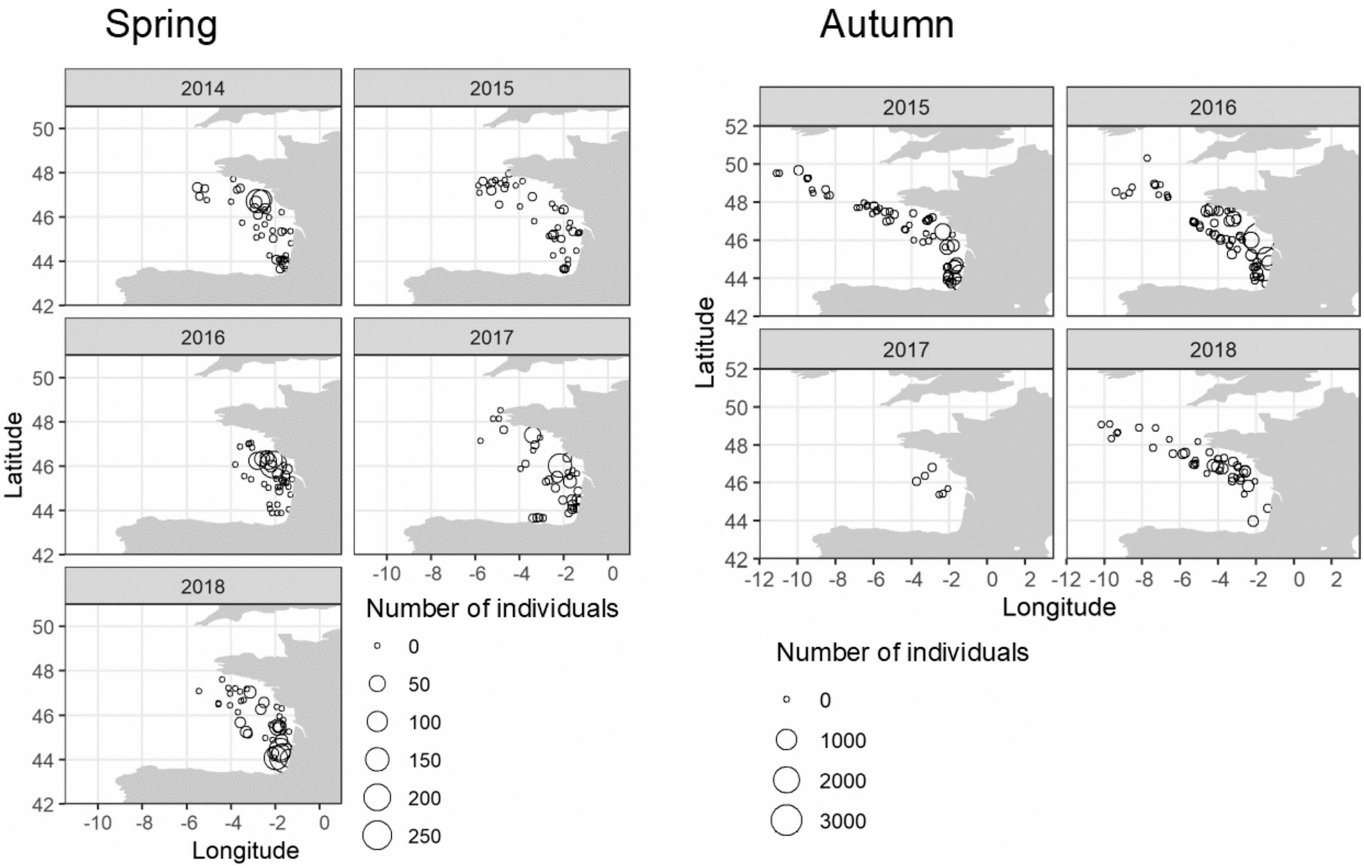

**Fig. 3.** Northern gannets abundance (i.e. number of individual) attending discard events in the Bay of Biscay in spring (i.e. Pelgas survey series from 2014 to 2018) and autumn (i.e. Evhoe survey series from 2015 to 2018).

**Table 3**

Variables selected by the principal component analysis for each group species and season. Log Chla: Chlorophyll A lograrithm; Log(SSS): sea surface salinity logarithm; MLD: mixed layer depth; Fishing vessels; number of professional fishing vessels; LogCLA1: class 1 biomass discarded logarithm; LogCLA2: class 2 biomass discarded logarithm.

| Group of species | Spring | | Autumn | |
|---|---|---|---|---|
| | Oceanographic-only model | Oceanographic-fishery model | Oceanographic-only model | Oceanographic-fishery model |
| Large gulls | Log(Chla)<br>Front intensity<br>Log(SSS)<br>Distance from shore | Stratification intensity<br>Distance from shore<br>Fishing vessels<br>Log(CLA1) | Log(Chla)<br>Stratification intensity<br>Log(SSS)<br>MLD<br>Distance from shore | Bathymetry<br>MLD<br>Fishing vessels<br>Log(CLA1) |
| Northern Gannets | Log(Chla)<br>Front intensity<br>Log(SSS)<br>Distance from shore | Stratification intensity<br>Fishing vessels<br>Log(CLA1)<br>Log(CLA2) | Log(Chla)<br>Stratification intensity<br>Log(SSS)<br>MLD<br>Distance from shore | Bathymetry<br>MLD<br>Fishing vessels<br>Log(CLA2) |

transects. However, we cannot exclude the hypothesis that the attraction to the R/V might be reduced in areas of high fishing activities with the presence of other professional vessels. This bias was difficult to quantify but was considered to be consistent throughout the study. Furthermore, as the discarded biomass for each event corresponded to the quantity of prey caught by the R/V Thalassa, we had access to the quantity and composition of each discard event. Fishing boat records along the transects also provided a good representation of fishing activities throughout the BoB during the study period and provide in-situ data. Other studies investigating the relationship between scavenging seabirds and discards have used Vessel Monitoring System (VMS) data for vessel presence (e.g. Darby et al., 2021; Granadeiro et al., 2014; Patrick et al., 2015; Votier et al., 2010). The distribution data of fishing vessels via the VMS could be used in such study. However, many fishing vessels, especially small fishing boats (i.e. <12 m), are not equipped with VMS. For this reason, we chose to use the distribution data of professional fishing vessels collected by observers during the PELGAS and EVHOE surveys, as we could account the vessels that were not detected via the VMS. The use of fronts data from SHOM models allowed us to have a good picture of the oceanographic processes at the origin of the primary production and thus a proxy of the resource availability. We averaged data into large cell grid to only detect large scale phenomenon. The use of oceanographic processes and the size of the BoB to study the distribution of scavenging seabirds is consistent with the large-scale approach chosen in this study. Our results showed a strong difference in predictions for large gulls between the two types of models in the coastal zone, indicating probably an overestimation of the model including only oceanographic variables or an underestimation of the model including

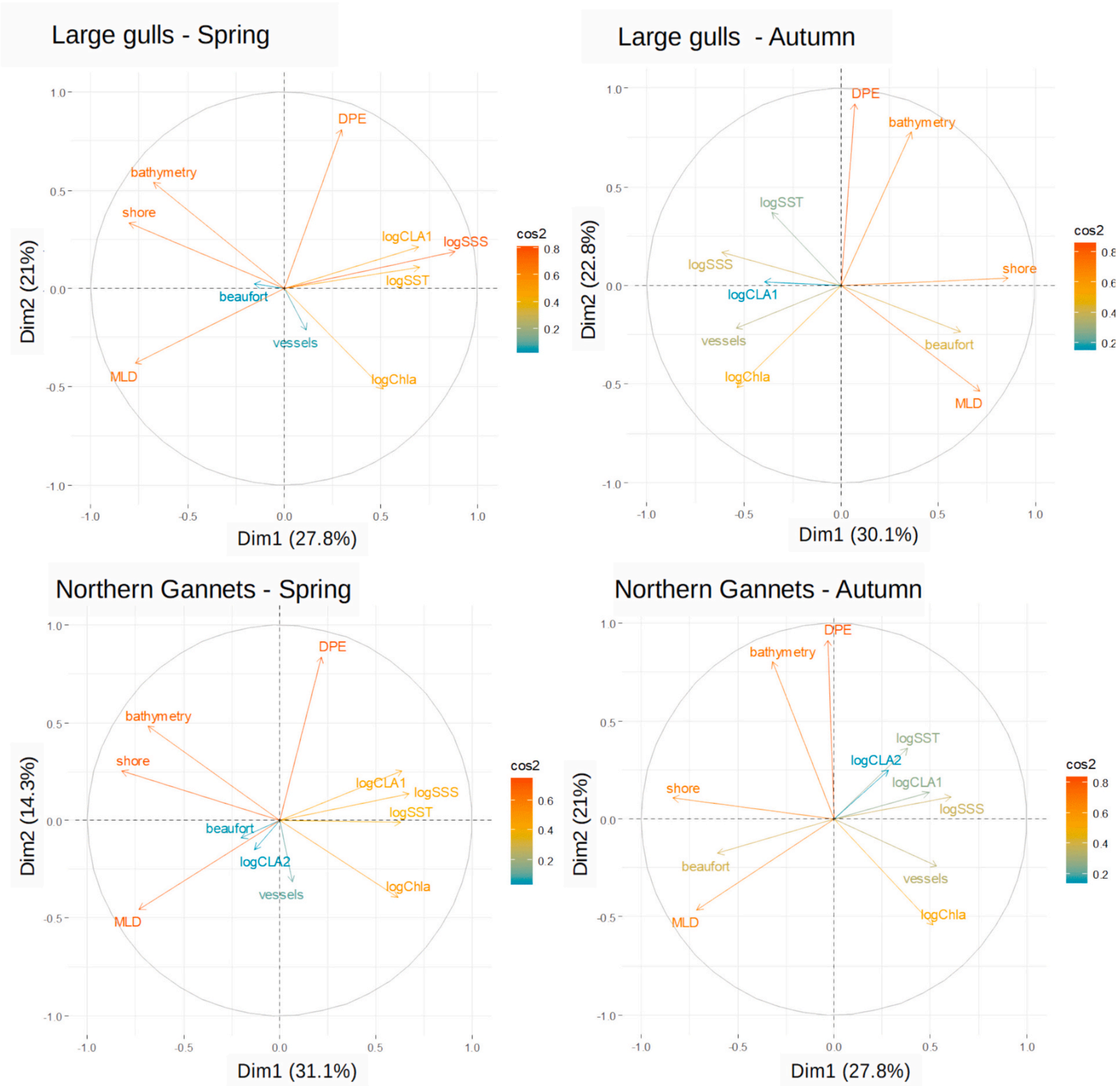

**Fig. 4.** Principal component analyses for large gulls and northern gannets in spring and autumn: Dim1: Principal component 1; Dim2: Principal component 2; DPE: stratification intensity; logChla: chlorophyll *a* logarithm; shore: distance from shore;MLD: mixed layer depth;log SST: sea surface temperature logarithm; logSSS: sea surface salinity logarithm; vessels: density of professional fishing vessels; logCLA1: class 1 of biomass discarded logarithm; logCLA2: class 2 of biomass discarded.

**Table 4**

Selected models for each group species and season. Oceanographic: oceanographic-only model; Oceanographic-fishery: Oceanographic-fishery model; Null: null model; DE: Deviance explained; AIC: Akaike Information criterion; ΔAIC: delta AIC; shore: distance from shore; log(Chla): chlorophyll *a* logarithm; MLD: mixed layer depth; Fishing vessels: number of professional fishing vessels; LogCLA1: class 1 biomass discarded logarithm; LogCLA2: class 2 biomass discarded logarithm.

| Season | Species | Model | Selected variables | DE (%) | AIC | ΔAIC | AIC weight |
|---|---|---|---|---|---|---|---|
| Spring | Northern gannets | **Oceanographic-only** | **Shore - log(Chla)** | **45.8** | **1976** | / | **0.323** |
| | | Oceanographic-fishery | Fishing vessels - log(CLA1)-log(CLA2) | 45.8 | 1982 | 6 | 0.024 |
| | | Null | / | 41.4 | 2019 | 43 | 0.00 |
| | Large gulls | **Oceanographic-only** | **log(Chla)** | **38.5** | **2570** | / | **0.980** |
| | | Oceanographic-fishery | Shore – Fishing vessels | 37.2 | 2579 | 9 | 0.01 |
| | | Null | / | 37.2 | 2579 | 9 | 0.01 |
| Autumn | Northern gannets | **Oceanographic-only** | **Shore – Stratification intensity - log(Chla)** | **45.5** | **2235** | / | **1** |
| | | Oceanographic-fishery | Bathymetry - log(CLA2) | 42.9 | 2265 | 30 | 0 |
| | | Null | / | 37.8 | 2308 | 73 | 0 |
| | Large gulls | **Oceanographic-only** | **Shore – MLD – Stratification intensity - log(Chla)** | **61.7** | **2394** | / | **1** |
| | | Oceanographic-fishery | Bathymetry - log(CLA1) | 56.6 | 2462 | 68 | 0 |
| | | Null | / | 55.3 | 2474 | 80 | 0 |

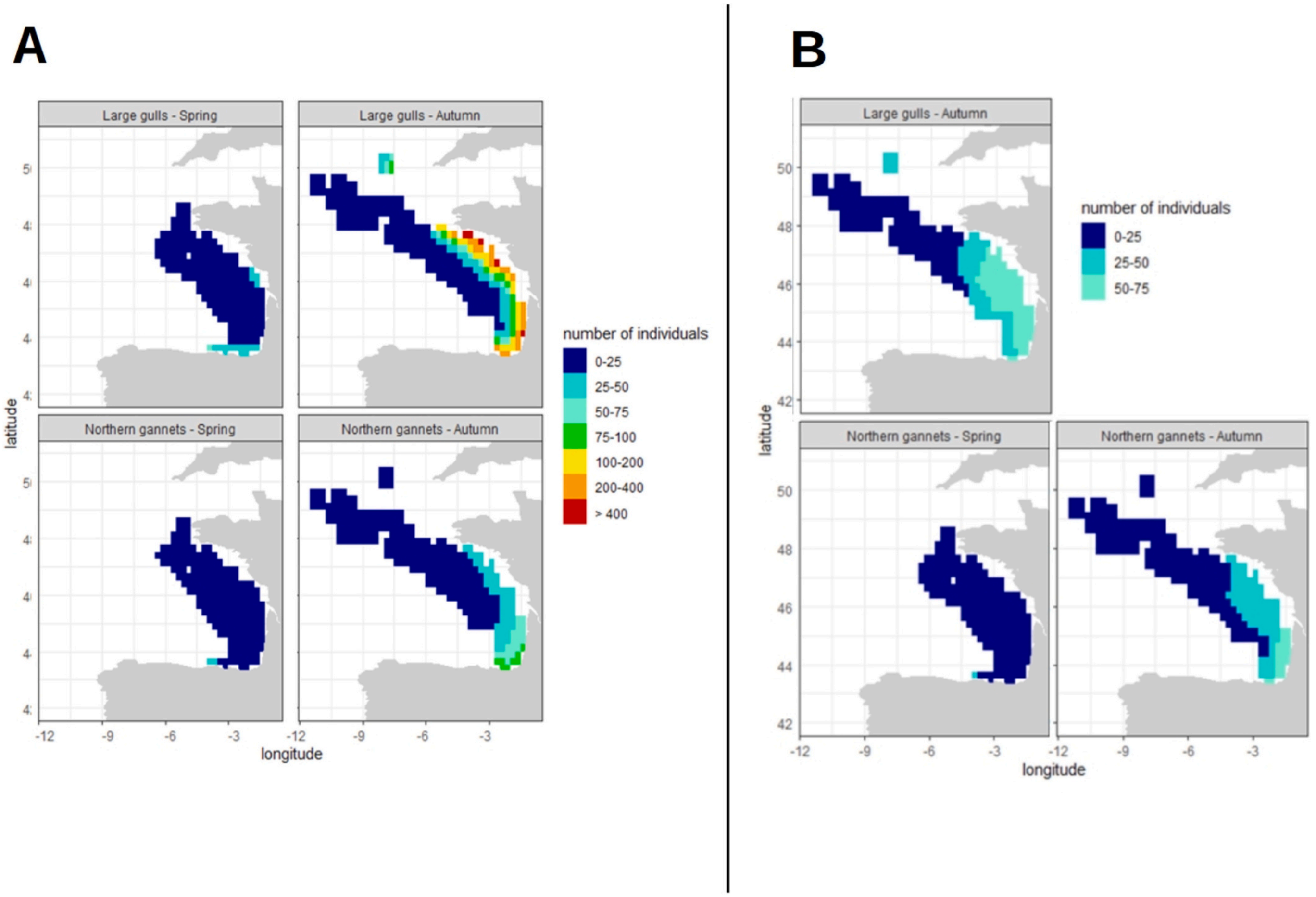

**Fig. 5.** Maps of spatial predictions (i.e. number of individuals) for oceanographic-only models (A) and for oceanographic-fishery models (B); for large gulls and northern gannets in spring and autumn.

fishery activities variables. This strong difference in prediction may be indicative of the limitations of large-scale modelling in the coastal zone where, for example, the model with fishery activity could be locally better suited than the model with environmental variable only.

### 4.2. *Scavenging northern gannet distribution*

Whether using the oceanographic-only model or the oceanographic-fishery model, the number of scavenging northern gannets was greater throughout the BoB in autumn than in spring. This difference can be explained by the annual cycle of this species (Louzao et al., 2020). In spring, an important part of gannets is concentrated around colonies, leading up to the breeding season. Northern gannet colonies are located further north in the BoB, with the closest colony being in the Rouzic Island (in the Western English Channel, Grémillet et al., 2006). Conversely, in autumn, the BoB is an important wintering ground for gannets breeding in Northern Europe to the sub-tropical Atlantic waters (Fort et al., 2012). The cumulative biomass distribution of discards and the presence of professional fishing vessels had little influence on the predicted distribution in the BoB, especially in autumn, when the AIC difference between the two types of models was the largest. At large scale, foraging on discard would be more an opportunistic behaviour instead of a driver of their distribution (De la Cruz et al., 2023). Furthermore, seabirds' discards consumption varies in time and space within species (de la Cruz et al., 2022; Sherley et al., 2018; Votier et al., 2008; Votier et al., 2004). Whether they are breeding or migrating, northern gannets are able to travel several hundred kilometres to forage in the offshore environment (Fort et al., 2012). In these areas, they use physical oceanographic features (i.e. front, eddies, tidal flow fields, stratification etc.) to forage on diverse pelagic species, representing a major habitat for this seabird (Cox et al., 2016). However, this is contrasted with the foraging behaviour of northern gannets around their colonies, which is mainly driven by fishery activities (Grémillet et al., 2020; Le Bot et al., 2019). Then, the dependence of northern gannets to fishery discards seems to be influenced more by their annual cycle. During the breeding season and close to the colonies, they use discard predictability. Outside this period, and in off-shore areas, this dependency relationship may be weakened, or even disappear in our study area. Results on northern gannets in this study are in accordance with recent studies focused on albatrosses which foraged on natural prey instead of fishery discards when natural feeding opportunities were favourable (Kuepfer et al., 2023).

### 4.3. *Scavenging large gulls distribution*

As well as gannets, the number of scavenging large gulls is greater in autumn than in spring, with much higher values for the oceanographic-only model. This seasonal difference can be explained by the annual cycle (breeding period versus wintering) of large gulls. This is particularly true for lesser black-backed gulls, which can migrate from the North to the South of Atlantic in winter, and use the BoB as a wintering area (Klaassen et al., 2012). Models with only oceanographic variables had a lower AIC than models including fishery activities variables. Moreover, the difference between the two types of models was higher for this group of species. This indicates that in the BoB oceanographic variables were better predictors than fishery activities' variables of the

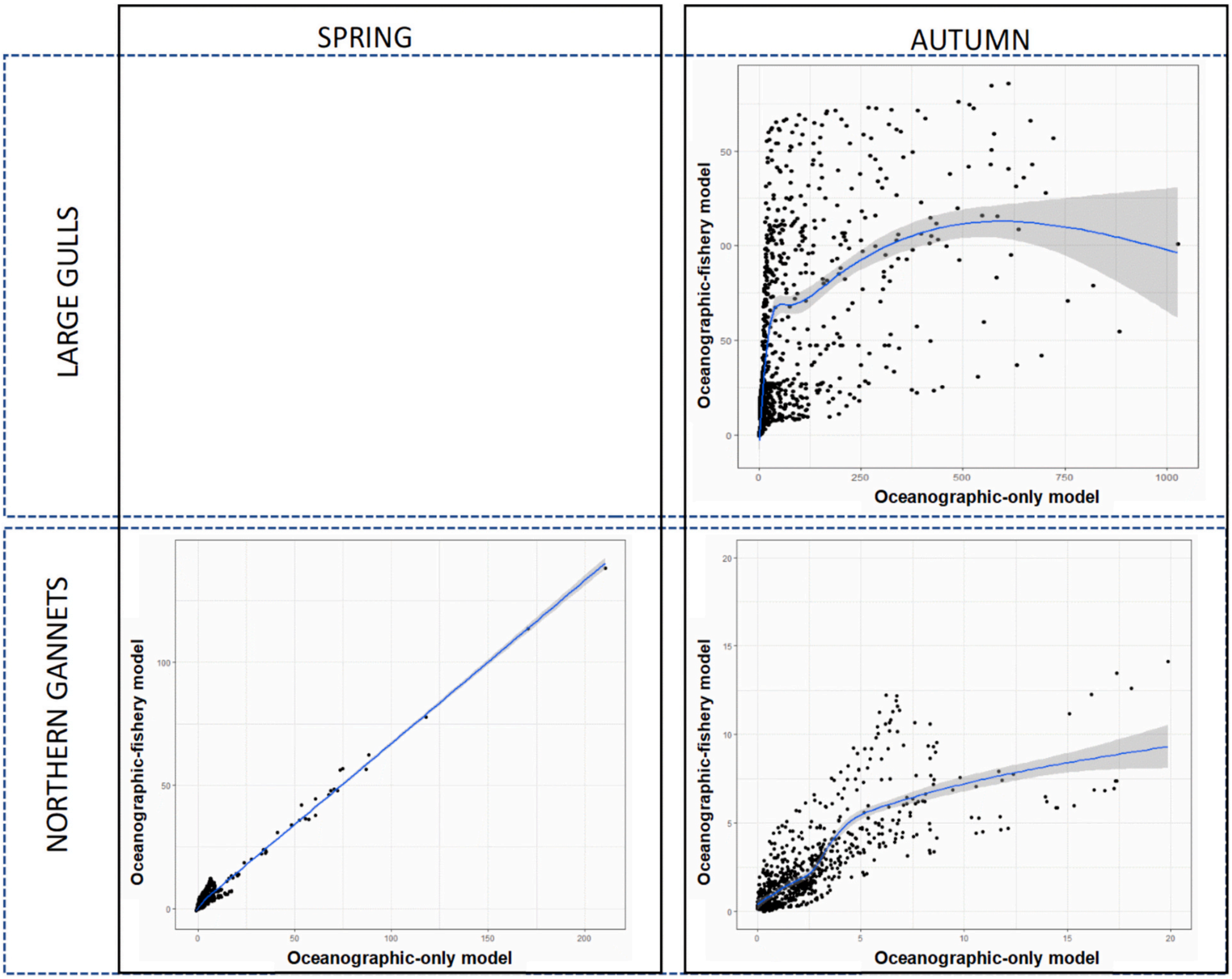

**Fig. 6.** Plot of the spatial predictions of oceanographic-only model (i.e. horizontal axis) versus oceanographic-fishery model (i.e. vertical axis) for both species groups and seasons. The more similar the spatial predictions of the two models are, the more the scatterplot will take the form of a diagonal.

large-scale distribution for scavenging large gulls in spring and autumn. However, we were expecting an influence of the presence of professional fishing vessels and the cumulative biomass of CLA1 discards on the distribution of scavenging large gulls in the BoB. Several gull species exhibit high behavioural plasticity and adaptability in their foraging strategy (Gutowsky et al., 2023), being highly opportunistic and feeding on a wide range of prey, with an important shift to anthropogenic food during the last decades (Shlepr et al., 2021). These species are highly dependent on human activities both on land and in the marine environment (Mercker et al., 2021; Shepard et al., 2016; Thaxter et al., 2015). In the Mediterranean Sea and Portugal, fishery activities and discards strongly influence foraging activities of Audouin's gull (*Larus audouinii*) and yellow-legged gull, decreasing the intra and interspecific competition (Matos et al., 2018). Gulls might benefit from the spatio-temporal predictability of fishing activities. In Netherlands, lesser black-backed gulls have adapted to the weekly and even daily rhythm of fishing boats (Tyson et al., 2015). Then, these authors demonstrated that the monitoring of certain individuals by telemetry in the Wadden Sea revealed a concordance between the gulls' journeys and those of the fishing boats during the week, and a change in habitat use at weekends (switching to terrestrial areas) when the boats stopped. However, results of a recent study on the yellow-legged gulls in the south of the BoB (Zorrozua et al., 2024), suggested that gulls do not depend strongly on scavenging discards exhibiting low overlap between fishery activities and gulls spatial usage, which are in accordance with our results.

### 4.4. *Influence of spatial scale*

Data collected on the distribution of scavenging seabirds in this study covered all the continental shelf of the BoB from coast waters to the slope. This allowed us to work at large spatial scale encompassing various environmental conditions, densities of seabirds and fishing activities. However, this may have certain limitations, such as the lost of resolution and extrapolation of results. Most of the studies carried out on scavenging seabirds focused at local scale and in coastal areas (Ouled-Cheikh et al., 2020; Tyson et al., 2015), using individuals tagged on the colonies or on professional fishing vessel. Huettmann and Diamond (2006) highlighted that the scale dependency in finding the spatial relationships of organisms that are distributed over large areas, such as seabirds is particularly important. In offshore areas and at large scale, natural food availability is more predictable for seabirds, than at small scale (Weimerskirch, 2007). At large scale, seabirds generally forage in association with oceanographic features like fronts (Cox et al., 2016), river discharges (Waggitt et al., 2020), ice edge (Tarroux et al., 2020), or shelf edge (Cox et al., 2016) that prompt prey aggregations, and thus, better foraging opportunities. The difference of spatial scale could explain the difference between our results and those obtained in other studies. Indeed, the BoB includes important oceanographic processes that take place on a large scale (Doray et al., 2018), allowing for high primary production in some places, and consequently important fishery resources. Then, the birds could take advantage at finer spatial scale of the fishery discards which may induce some local seabird aggregations

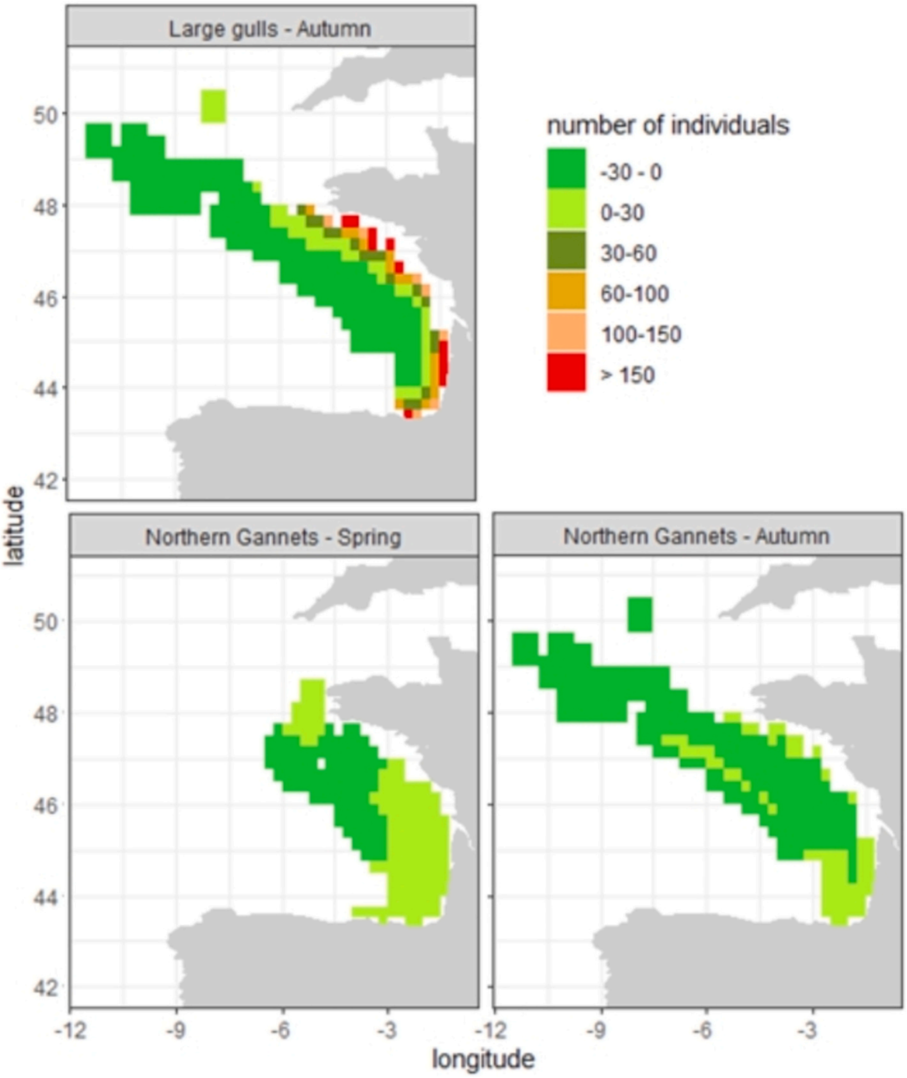

**Fig. 7.** Maps of anomaly values (i.e. number of individuals) for large gulls in autumn, and northern gannets in spring and autumn.

or shape seabird feeding areas within their natural habitat. This can be tested by using telemetry devices to collect behavioural data (i.e. foraging activity) at finer scale (Gulka et al., 2023). The influence of scale in detecting the role of fishing activities on the distribution and habitat selection of scavenging seabirds has been demonstrated (De la Cruz et al., 2023). Thus, at large scale, data collected from oceanographic vessel have shown that the distribution of northern fulmars was mostly dictated by the influence of oceanographic processes (i.e. indicators of prey distribution) rather than by fishing activities in the North Sea (Skov and Durinck, 2001). However, a recent telemetry-based study revealed that fishing activities influence the distribution of this species in the Northeast Atlantic, particularly when incorporated fishing activities alongside environmental variables in modelling exercises (Darby et al., 2021). Overall, the detection of the influence of anthropogenic activities on the distribution of biodiversity and wildlife behaviour appears to be detectable only on a fine scale (Anadón et al., 2010; Vistnes and Nellemann, 2008). The most supported factors controlling biodiversity (in terms of species richness) at large scale are energy availability and environmental heterogeneity (Davies et al., 2007). The influence of human activities is then visible as the spatial scale decreases (Anadón et al., 2010). Here, we revealed similar patterns in marine ecosystems with the distribution of scavenging seabirds at large spatial scale in the BoB (i.e. 0.25°), where the distribution of fishing vessels and quantity and degree of discards selectivity do not shape the global distribution of seabirds. Nevertheless, further telemetry studies are required to explore the influence of fishing activities on scavenging northern gannets and large gulls in the BoB at a finer scale.

### *4.5. Fishery discards ban*

In 2015, the European Union common fishery policy implemented reforms related to the fish stocks management and a ban on discarding, aiming the creation of economically and environmentally sustainable fisheries (Bicknell et al., 2013). This landing obligation may have cascading effects on scavenging seabirds. However, we still have poorly understanding how seabird communities will respond to the changing discard availability, particularly in high latitude ecosystem (Votier et al., 2023). It has been supposed that discard ban could have potential positive effects, such as the reduction of bycatch and a population reduction of large generalist species which increased by discards consumption and are currently dominate some other species communities (Garthe et al., 1999; Oro and Martínez-Abraín, 2007). Northern gannets and large gulls could respond differently to the discard ban at local scale. As generalist piscivore, northern gannets have great flexibility, suggesting that this species might be able to switch on alternative pelagic fish prey (Votier et al., 2013). For large gulls, considered as generalist omnivores, beyond the consequences on their survival rates and breeding performance, they might move to novel habitats such as inland and urban environment

(Camphuysen, 2006; Camphuysen et al., 2010; Oro et al., 1997). Then, at large scale, we could hypothesize a limited impact of the discard ban on the northern gannets and large gulls, particularly if this discard ban is implemented with a management of pelagic fish stocks. This study can potentially fill some knowledge gaps on the potential impact of fishery discards and completes previous results already obtained in the BoB (Depestele et al., 2016; Louzao et al., 2020; Zorrozua et al., 2024). This is particularly true for immatures and wintering seabirds. Future studies are needed to investigate these interactions on a finer scale (i.e. combining both biologging and isotope analyses) and to evaluate the influence of discard ban during the next decades. However, an important part of seabirds considered in this present study come from colonies located in Northern Europe. Then, it would be appropriate to develop these futures studies at a European scale, involving a synergy of countries concerned.

To conclude, our results provide important insights into the balance between the influence of fishing activities and oceanographic conditions at large scale in the BoB, which is an area with strong oceanographic processes, important fishery activities, and important wintering ground for numerous seabirds species in Europe. Despite fishery activities did not have influence on scavenging seabirds' distribution at large scale when compared to oceanographic features, this study highlighted the need to use telemetry devices to study the influence of fishery activities on seabirds' foraging at finer scale. This study was conducted as part of the bigger program (i.e. Devenir des Rejets de l'Air au fond de la Mer, DREAM project[5]) aiming to evaluate the impacts of fishery discards on marine food web, from scavenging seabirds to scavenging benthic fauna. Beyond seabirds ecology, these results could be integrated in a global context of the understanding of fishery discards on marine food web.

## Authors' contribution

MH and MA conceived the ideas and developed the methodology with the help of JS and GD. MH analysed the data and led the writing of the manuscript. All authors contributed critically to the draft and gave the final approval for publication.

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## CRediT authorship contribution statement

**M. Huon:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **G. Dorémus:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **M. Authier:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **J. Spitz:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

My co-authors and I have no conflict of interest to declare.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2024.e00367.

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