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Research Papers

MONITORING ABUNDANCE AND DISTRIBUTION OF NORTHERN GANNETS *MORUS BASSANUS* IN WESTERN IBERIAN WATERS IN AUTUMN BY AERIAL SURVEYS

SEGUIMIENTO DE LA ABUNDANCIA Y DISTRIBUCIÓN DE ALCATRAZ ATLÁNTICO *MORUS BASSANUS* EN AGUAS IBÉRICAS OCCIDENTALES EN OTOÑO MEDIANTE MUESTREOS AÉREOS

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Summary.—Several North Atlantic breeding seabirds, such as the Northern Gannet *Morus bassanus*, use Western Iberian Waters for wintering and migration. In this study, we aimed at producing absolute population estimates of post-breeding Gannets and evaluating the importance of the study area within the species' migration range. We performed six aerial surveys in September and/or October each year between 2010 and 2015, covering 74,840 km^2 in total. Using line transect methodology, 3,672 Gannet sightings were recorded along 10,496.3 nautical miles (nm). Immature individuals and adults comprised approximately 87% of all sightings. Using Distance sampling, overall abundance was estimated at 89,930 birds, ranging from 58,010 individuals in 2014 to 128,140 in 2015. The highest densities per sector areas were recorded in the North and Centre sectors whereas the lowest densities were registered in the Galicia sector, the Spanish region within the study area. Gannets were mostly present in shallow shelf waters of the continental shelf, particularly between 3 and 20 nautical miles offshore. Habitat

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suitability models for Gannets in the study area were tested using several eco-geographical variables and chlorophyll concentrations were found to contribute most to explaining annual Gannet occurrence probabilities. A global interannual spatial analysis demonstrated the core areas for conservation of the Northern Gannet in Western Iberian Waters. Moreover, our results demonstrate that Western Iberian waters are used by almost 10% of the global Northern Gannet population, corroborating the existence of seabird hotspots during the non-breeding period, along migration corridors and at their wintering grounds.—Araújo, H., Correia Rodrigues, P., Bastos-Santos, J., Ferreira, M., Pereira, A., Martínez-Cedeira, J., Vingada, J. & Eira, C. (2022). Monitoring abundance and distribution of Northern Gannets *Morus bassanus* in Western Iberian Waters in autumn by aerial surveys. *Ardeola*, 69: 179-202.

Key words: distance sampling, Maxent, *Morus bassanus*, Portugal, Spain.

RESUMEN.—Varias especies de aves marinas reproductoras en el Atlántico norte, como el alcatraz atlántico, utilizan las aguas ibéricas occidentales como áreas migratorias y de invernada. En este estudio, nuestro objetivo consistió en obtener estimas absolutas posreproductoras de la población de alcatraz atlántico, y evaluar la importancia del área de estudio dentro del rango de migración de la especie. Entre 2010 y 2015, realizamos seis muestreos aéreos en septiembre u octubre de cada año, cubriendo 74.840 km^2. Utilizando la metodología *Distance Sampling* (Muestreo a distancia), se registraron 3.672 avistamientos de alcatraz atlántico a lo largo de 10.496,3 millas náuticas. Teniendo en cuenta el número total de avistamientos de alcatraces, los individuos inmaduros y los adultos correspondieron aproximadamente al 87% de todos los avistamientos. Mediante *Distance Sampling*, se estimó una abundancia total de 89.930 aves, variando entre 58.010 individuos en 2014 y 128.140 individuos en 2015. Las densidades más altas se registraron en los bloques Norte y Centro, mientras que las más bajas fueron registradas en Galicia, la región española incluida dentro del área de estudio. El alcatraz atlántico estuvo presente principalmente en aguas poco profundas de la plataforma, particularmente entre las 3 y 20 millas náuticas de la costa. Los modelos de idoneidad de hábitat para alcatraz atlántico en el área de estudio se evaluaron utilizando diferentes variables ecogeográficas y se determinó que las concentraciones de clorofila son las que más contribuyen a explicar la probabilidad anual de presencia de alcatraz atlántico. Un análisis espacial interanual global demostró la importancia de las áreas centrales para la conservación del alcatraz atlántico en las aguas ibéricas occidentales. Además, nuestros resultados demuestran que las aguas ibéricas occidentales son utilizadas por casi el 10% de la población mundial de alcatraz atlántico, lo que corrobora la existencia de áreas clave de aves marinas durante el período no reproductivo a lo largo de los corredores de migración y en sus zonas de invernada.—Araújo, H., Correia Rodrigues, P., Bastos-Santos, J., Ferreira, M., Pereira, A., Martínez-Cedeira, J., Vingada, J. y Eira, C. (2022). Seguimiento de la abundancia y distribución de alcatraz atlántico *Morus bassanus* en aguas ibéricas occidentales en otoño mediante muestreos aéreos. *Ardeola*, 69: 179-202.

Palabras clave: España, Maxent, *Morus bassanus*, muestreo a distancia, Portugal.

INTRODUCTION

Studying seabird populations provides a unique perspective on ecological processes, environmental health and change in the oceans (Ballance, 2007). Monitoring seabird abundance changes within both the breeding and non-breeding periods (i.e. use of migratory corridors and wintering areas) is necessary to understanding the current demographic status of a population (Lewison *et al.*, 2012; Egunez *et al.*, 2018) and the factors affecting the annual life cycles of seabirds (Magnusdottir *et al.*, 2012). Furthermore, evaluating the conservation status of seabird populations across their geographical range is required to meet international regulations and agreements, including the European Union Birds Directive (2009/147/EC) and Marine Strategy Framework Directive (2008/56/EC).

The continental waters off Portugal and western Spain (hereafter Western Iberian Waters, WIW) are strategically important to the migratory behaviour of many seabird species. In fact, the importance of WIW as wintering and migratory areas has been previously documented for several North Atlantic breeding seabirds (Fort *et al*., 2012; SEO/BirdLife, 2012; Santos *et al*., 2013; Meirinho *et al*., 2014; de Juana & Garcia, 2015). The WIW represent important flyway, stop-over or wintering areas and offer migratory seabirds a rich prey community (e.g. ICES, 2016).

Among wintering seabird species, the Northern Gannet *Morus bassanus* is one of the most abundant pelagic predators in the WIW (Arcos *et al*., 2009; Fort *et al*., 2012; Meirinho *et al*., 2014). It is the largest pelagic seabird breeding on both sides of the North Atlantic, in latitudes ranging between 46.5ºN and 70.4ºN (Mowbray, 2020). The European population reproduces in northern France, Ireland, Iceland and Norway as well as in the United Kingdom, where the largest colonies have been recorded (del Hoyo *et al*., 1992). Throughout winter, the European population occurs over large areas, from the European Atlantic to West African coastal waters and in the Mediterranean (Veron & Lawlor, 2009; Fort *et al*., 2012; Grémillet *et al*., 2015). The European Northern Gannet breeding population is estimated to be increasing (BirdLife International, 2018). Nonetheless, further information is needed concerning the population's migratory or wintering ranges (Louzao *et al*., 2020).

Post-breeding southward passage of Gannets in WIW is prolonged, extending from late July to early December (de Juana & Garcia, 2015). In the WIW, as in all wintering areas and migration corridors, the species has been associated with highly productive areas (Meirinho *et al.,* 2014; Mann & Lazier, 2016) feeding on relatively large pelagic fish (e.g. Nelson, 2002) and fishery discards (e.g. Kubetzki *et al*., 2009).

Abundance estimates of migratory species with transnational ranges are complex, involving a large amount of resources. Aerial surveys have been used to access abundance, distribution and/or migration patterns of several wide-ranging marine animals (e.g. Bretagnolle *et al*., 2004; Camphuysen *et al*., 2004; Certain & Bretagnolle, 2008; Ridgway, 2010; Buckland *et al*., 2012; Winiarski *et al*., 2013; Péron *et al*., 2013; Araújo *et al*., 2017; Pettex *et al*., 2017; Merkel *et al*., 2019). Aerial surveys have proved effective in providing unbiased Northern Gannet abundance estimates and probability distribution maps (e.g. Pettex *et al*., 2017, 2019; Rogan *et al*., 2018). This type of survey is essential to assess abundance and demographic trends outside breeding grounds and their relation to the breeding population. Also, data obtained through aerial surveys can be used to build seabird Species Distribution Models (SDMs) (Pettex e*t al*., 2017; Rogan *et al*., 2018). SDMs are useful to identify areas of high and low occurrence probability, enabling the prioritisation of conservation actions and planning in protected areas (Hyrenbach *et al*., 2000; Cleasby *et al*., 2020).

The present study primarily aimed at evaluating the importance of WIW for Northern Gannets, by estimating their abundance in this sector of their migration range, while also evaluating their distribution and habitat preferences in the study area.

Methods

Study area

The study area comprised a 50 nautical mile (nm) strip following the Western Iberian coastline from Cape Finisterre to Vila Real de Santo Antonio (latitudes ranging from 36.5ºN to 42.9ºN) (Figure 1). The area (74,870 km^2) represents 19.0% of the Portuguese Continental EEZ and 5.4% of the Spanish Atlantic Northwest EEZ. The study area offers highly variable seabed topography and a coastline with estuaries, rias and wetlands which support extremely productive ecosystems (Valdés, 1999). The study area was divided into five sectors: Galicia, North, Centre, Alentejo and Algarve (Figure 1a).

Recently, six large marine Special Protection Areas (SPAs) have been created or expanded under the Birds Directive in continental Portugal taking into account the occurrence, distribution and reproduction of several seabird species (Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel and Sudoeste Alentejano), totalling a marine area of 6,188 km^2 (26% of the Portuguese continental shelf area). In Spain 39 large marine SPAs have also been designated recently (www.indemares.es), three of which in the Northwest Atlantic (Costa da Morte, Rias Baixas de Galicia and Banco de Galicia) adding up to an area of 14,104 km^2 (Figure 1b).

a) **b)**

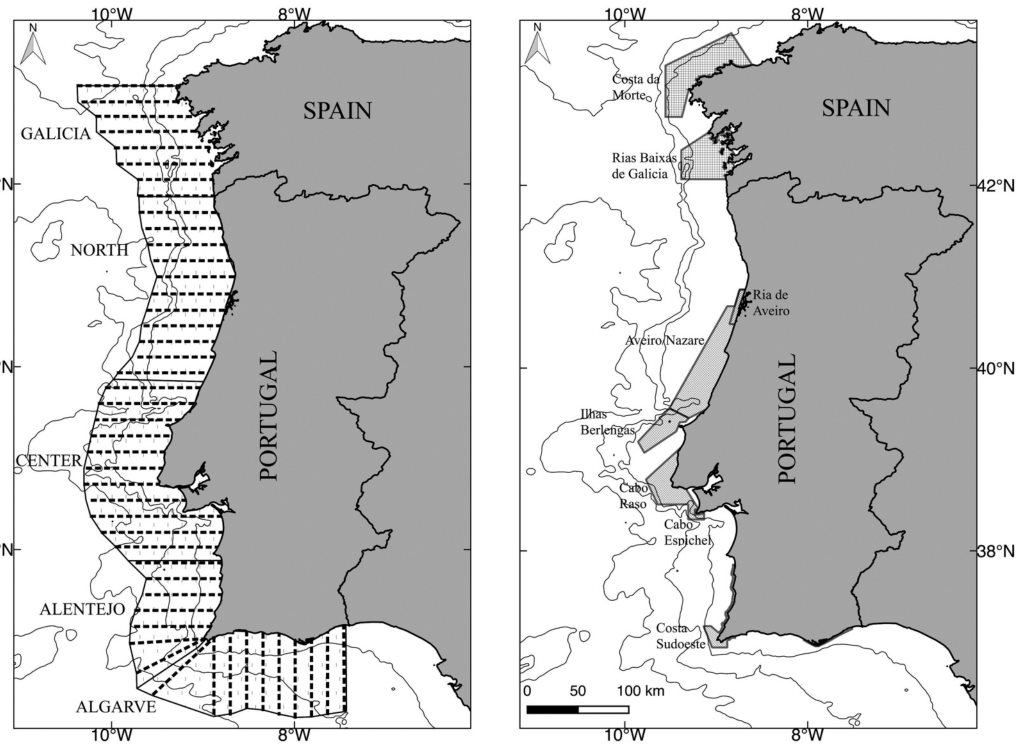

FIG. 1.—a) Overview of the study area showing the Galicia, North, Centre, Alentejo and Algarve sectors; theoretical line transects (dashed black line); b) Spanish (cross lines) and Portuguese marine SPAs (diagonal lines) in the study area. Bathymetric profile of the area showing the 200m, 1,000m and 3,000m isobaths.

[a) Representación del área de estudio mostrando los bloques de Galicia, Norte, Centro, Alentejo y Algarve; transectos teóricos (línea negra discontínua); b) ZEPA españolas (líneas cruzadas) y portuguesas (líneas diagonal) presentes en el área de estudio. Perfil batimétrico del área mostrando las isobaras de 200 m, 1.000 m y 3.000 m.]

Aerial surveys

The methodology was based on standard line-transect Distance Sampling techniques (Buckland *et al*., 2001; Thomas *et al*., 2010), which allow for interannual replication. Aerial surveys were carried out in all five sectors of the study area in September 2011 and September 2012. In September and October 2010, October 2013, September 2014 and September 2015 aerial surveys were carried out in the four Portuguese sectors only (Table 1). Flights followed a set of parallel 50nm-long transects (approximately) separated from each other by a distance of 10nm (Figure 1a). Transects were perpendicular to the coast and to the isobathymetric lines, in order to minimize variance in encounter rate (Buckland *et al*., 2001). All inflight procedures and optimal flight conditions were based on internationally tested methodologies for line transect surveys (Bretagnolle *et al*., 2004; Camphuysen *et al*., 2004; Certain & Bretagnolle, 2008). Flight surveys were performed at an average flight speed of 100 knots (185km/h) with an altitude of 500 ft (150.4m), whenever conditions allowed for a visibility range >5km and a Beaufort sea state <3. In all surveys, twin engine, high-wing aircraft were used. Aircraft were equipped with two bubble windows, to allow direct scanning below the fuselage.

For all gannet observations, the perpendicular angle from the track line to the location of sitting or flying birds was measured using a hand-held clinometer and the individual/flock position was registered using three handheld GPS units in redundancy. The survey team consisted of two trained observers, one data recorder and a pilot (Trenkel *et al*., 1997; Noer *et al*., 2000; Perkins *et al*., 2005). When possible, age class was also registered: gannets were either aged according to their plumage characteristics (adult,

TABLE 1

Aerial survey characterisation. Survey duration, total survey time each year; Area, total area covered annually; Transect length, total transect length surveyed annually; and average Beaufort windspeed scale value per campaign.
[Caracterización del muestreo aéreo. Duración del muestreo: tiempo empleado en cada muestreo. Área: superficie total muestreada anualmente. Longitud del transecto: longitud total del transecto muestreado anualmente. Condiciones Beaufort promedio por campaña.]

Campaign	Flight dates	Survey duration	Area (km^2)	Transect length (nm)	Number of transects	Average Beaufort
2010	27, 28 September, 20, 21 October	12h 38m	62 716	1 398.3	36	1.70
2011	21-24, 26-27 September	18h 47m	74 870	1 972.2	46	2.03
2012	6-10 September	18h 56m	74 870	2 000.4	47	1.32
2013	7-10 October	17h 07m	62 716	1 793.9	42	2.07
2014	2-5 September	14h 33m	62 716	1 546.2	41	2.09
2015	24-26, 28 September	17h 03m	62 716	1 785.3	40	2.40

immature, juvenile) (Armistead & Sullivan, 2015) or considered a 'mixed group' whenever a flock included both immature and/or juvenile and adult individuals in an unknown proportion (Pettex *et al*., 2019).

Environmental data

We considered several abiotic and biotic variables (available at ecologically relevant spatial and temporal scales), which are known important predictors of seabird distribution (Wakefield *et al*., 2009; Tremblay *et al*., 2009; Pettex *et al*., 2019; de la Cruz *et al*., 2021). Preliminary modelling trials were conducted (see Supplementary Material, Appendix 1, Table A1 and the Data Analysis section below). The following eco-geographical variables (EGV) were selected: Sea Surface Temperature (SST), assumed as a proxy for physical processes or features driving prey distribution; Chlorophyll Concentration (Chl), an index of marine productivity (Afán *et al*., 2014); Slope, assumed as a proxy for upwelling and known to influence seabird distributions (Nishizawa *et al*., 2017); Distance to ports, as a proxy for fishing boat presence (Correia-Rodrigues, 2017); Wind speed, an important factor influencing seabird distribution at global (Davies *et al*., 2010) and regional scales (Weimerskirch *et al*., 2012).

Monthly averages of the respective surveyed month of all dynamic EGV were extracted (for 2010, an average was calculated for September and October), and if necessary resampled, to a spatial resolution of $4km^2$. Sea Surface Temperature and Chlorophyll Concentration were obtained from Aqua-MODIS satellite imagery, using Marine Geospatial Ecology Tools (MGET) for ArcGIS 10.3 to access data available from http://ocean-color.gsfc.nasa.gov/ (assessed on the 8th of July 2020). Wind speed was obtained from the Copernicus Marine Environment Monitoring Service (CMEMS) on the 9th July 2020. We used SDMtoolbox for ArcGIS 10.3, to extract netCDF files and resampled them to $4km^2$ (spatial resolution selected for the construction of the species distribution models; see data analyses section for more detail). Slope percentage rise was calculated in ArcGIS 10.3 using the Digital Elevation Model (DEM), provided by National Geographical Data Center from U.S.A. (ETOPO2; http://www.ngdc.noaa.gov/mgg/image/2minrelief.html). Distance to ports was calculated as Cost Distance in ArcGIS. Distances of locations at sea were assigned a positive value and inland locations a negative value. The port locations and sizes were obtained from http://www.worldportsource.com/ports/MAR.php.

Data analyses

Distance sampling allows estimating density and/or abundance of objects using distances from a line transect to the location of the detected object (Buckland *et al*., 2001; Thomas *et al*., 2010). Line transects allow for a proportion of objects to be missed leading to unbiased density estimates and also allowing for a more efficient use of data (larger sample sizes, same effort), especially at relatively low object densities (Camphuysen *et al*., 2004).

Distance sampling makes several assumptions about the collected data, namely: (1) the probability of detecting an animal on the transect is certain ($g(0) = 1$) and it falls off smoothly from unity as a function of distance from the track line, (2) there is no responsive movement prior to detection, (3) distances are measured accurately, (4) cluster sizes are recorded without error and (5) the sampled plots are representative of the entire survey region (Buckland *et al*., 2001, 2008).

In the present study we used the line transect method, assuming that all individuals on the line were detected (the detection probability is 1 at zero perpendicular distance, g(0) = 1) and that the probability of detection falls off smoothly from unity as a function of distance from the track line. This function is known as the detection function (Buckland *et al.*, 2012). The assumption that all animals in the line are detected may not be met for two main reasons: (1) animals are missed because they are submerged (availability bias) and (2) observers fail to detect animals on the surface (perception bias). The availability bias should be minimal for seabird species, such as gannets, that spend most of their time on the surface (Ronconi & Burger, 2009). The abundance and density estimates obtained were not corrected for both biases.

Seabird abundances were estimated using Conventional Distance Sampling (CDS) (Buckland *et al.*, 2001) in DISTANCE software. To fit the detection functions better, we removed 5% of the longest perpendicular distances (Buckland *et al.*, 2001). Several detection model combinations (half-normal key with cosine adjustments, half-normal key with Hermite polynomial adjustments and hazard-rate key with simple polynomial adjustments) were tested in order to obtain the detection function with the best fit-lower Akaike Information Criterion (AIC) (Marques *et al.*, 2007; Thomas *et al.*, 2010). Estimates of encounter rates and expected group sizes were stratified by year and sector. The bias effect of group size on detection probability was tested by fitting a regression of log group size against detection probability. When estimating abundance, the regression mean value was used instead of the observed mean group size if significant at $\alpha = 0.15$. The coefficient of variation (CV) and 95% confidence intervals (CI) were estimated by bootstrapping (999 replicates) within strata, using transects as sampling units (Buckland *et al.*, 2001).

In order to obtain gannet habitat suitability maps and their uncertainty maps, six model scenarios (relating to each annual campaign) were considered. The gannet habitat predictor models were obtained in MaxEnt 3.4.4 and habitat suitability maps were based on occurrence probability. MaxEnt is a machine-learning algorithm that estimates the probability distribution of maximum entropy (i.e., the most spread out or closest to uniform) given a set of environmental characteristics at known occurrence sites that represent the incomplete information about the distribution of the species (Phillips *et al.*, 2006). MaxEnt provides effective model fits, even with small sample sizes (Phillips *et al.*, 2006; Wisz *et al.*, 2008; Kumar & Stohlgren, 2009), being well suited to temporarily absent species, with few observations over a large area of suitable habitat (Thaxter *et al.*, 2011). Detailed descriptions of MaxEnt and its mathematical computations are given in Phillips *et al.* (2004, 2006). Model performance was compared using different sets of predictive variables (data acquisition described in the Environmental data section). To avoid the inclusion of strongly correlated variables, we conducted a Pearson pairwise correlation test using ENMtools software (Warren *et al.,* 2010). For every highly correlated pair of variables ($|r| > 0.7$), the least relevant variable was excluded from further analyses (see Supplementary Material, Appendix 1, Table A1).

Datasets were subsampled by randomly selecting 75% of the sample points (occurrence locations) as training data and 25% as test data. MaxEnt was set to remove duplicate presence records from the same grid cell to minimise autocorrelation biases and the 'Auto-Features' default option was used to select the functional forms. MaxEnt relies on a spatially unbiased sample and therefore a 'bias file' of survey transects was used in order to reduce the sample bias (Meghan, 2018; de la Cruz *et al.*, 2021). Ten replicate models were conducted for each of the six scenario datasets. The area under the receiver operating characteristic curve (AUC) was used to assess each model's discriminative ability (Peterson *et al.*, 2007). Trial analyses included building models with different delay periods for SST and Chl (average monthly values for two and one month before the campaign month, respectively lag-2 and lag-1). Overall, these models presented worse AUCs (Appendix 1, Table A2) and were not considered in the subsequent analysis. The relative importance of each variable in the model was evaluated by means of a heuristic estimation (Phillips *et al.*, 2006). Response curves generated for each environmental variable show how the cloglog prediction changes with the fluctuation of each environmental variable, i.e. the marginal effect of changing one variable in the model, by keeping the remaining variables at their average sampled value (Phillips *et al.*, 2006, 2017). The threshold value for the minimum training presence (MTP), derived from all ten Maxent model runs, was selected to determine areas of suitable habitat. All pixels with threshold values greater than or equal to the MTP threshold (Beane *et al.*, 2013) served as areas of Northern Gannet suitable habitat.

Using the habitat suitability maps and the uncertainty maps generated by MaxEnt, a global interannual spatial analysis was carried out using Zonation software (Moilanen *et al.*, 2005, 2011; Lehtomäki *et al.*, 2016). In terms of parameterisation, an analysis with the Core-Area Zonation (CAZ) meta-algorithm was used, as it was considered the most suitable with single-species data. The CAZ algorithm is able to identify high-priority areas, which have a high occurrence level for a single rare and/or highly weighted feature (di Minin *et al.*, 2014). Finally, the Proportion of Remaining Distribution Area (graph from Zonation) was used to determine the threshold corresponding to the identification of the top 5% fraction, which represents the core areas for conservation of the Northern Gannet in WIW.

Results

Abundance estimates

We completed 25 survey days, covering a total of 10,496.3 nm. Due to weather conditions and logistic constraints, the Galicia sector was only surveyed in 2011 and 2012. As a result, an area of 62,716 km^2 was covered in 2010, 2013, 2014 and 2015 and an area of 74,870 km^2 was covered in 2011 and 2012 (Table 1). The survey effort amounted to 99.5 flight hours (only Beaufort ≤ 3 periods were considered).

During the survey, 3,678 Northern Gannet sightings were detected, corresponding to 3,536 sightings within the 5% truncation distance. The resulting estimate of the Effective strip (half-)width (ESW) was 101.47m (95% CI: 92.71m-111.05m). Due to the lower AIC value (39,601.93), the Hazard-rate key with simple polynomial adjustments was the best model combination using data from all sampled years (Supplementary Material, Appendix 2, Figure B1), when compared to models using the half-normal key with cosine adjustments (AIC = 39 672.20) and the half-normal key with Hermite polynomial adjustments (AIC = 39 673.76).

The lowest values of gannet sightings were recorded in 2014 (9.50% of total sightings) and the highest values were in 2015 (24.24%) (Table 2a and Figure 2). The lowest encounter rate value was obtained in 2014, with 0.217 sightings per nm, and the highest value was in 2015, with 0.480 sightings per nm (Table 2a). The overall mean flock size was 1.34 individuals (Table 2a, Figure 2). The annual mean flock size varied from 1.21 individuals in 2014 to 1.53 individuals in 2010. In all analysed data frames, the observed group size value was always chosen over the expected value. Gannet abundance varied between 58,010 individuals (CV = 12.83%) in 2014 and 128,140 individuals (CV = 10.92%) in 2015, whereas densities

TABLE 2

Northern Gannet flock sightings (n), encounter rate (ER), average flock size, abundance (n) and density (n/km^2). Coefficient of Variation (CV) and 95% Abundance and Density Confidence Interval (CI) calculated using bootstrapping (999 replicates) per surveyed year (a) and per surveyed area (considering the six-year dataset) (b).
[Avistamientos de grupos de alcatraz atlántico (n), tasa de encuentro (ER), tamaño medio de grupo, abundancia y densidad (n/km^2). Coeficiente de variación (CV) e intervalo de confianza 95% de la Abundancia y Densidad calculado mediante bootstrap *(999 réplicas) por año muestreado (a) y por área muestreada (considerando el conjunto de datos de seis años) (b).]*

	Number of flock sightings	ER (CV%)	Average Flock Size (CV%)	Abundance (95% CI)	Density (95% CI)	CV (%)
a) Survey year						
2010	433	0.310 (9.50)	1.53 (3.06)	82,664 (66,917-102,120)	1.104 (0.894-1.364)	10.61
2011	550	0.279 (10.18)	1.38 (2.30)	74,446 (59,558-93,056)	0.994 (0.795-1.243)	11.21
2012	639	0.319 (9.00)	1.35 (2.03)	85,273 (69,696-104,330)	1.139 (0.931-1.393)	10.15
2013	721	0.402 (9.61)	1.36 (2.13)	107,290 (86,694-132,780)	1.433 (1.158-1.773)	10.70
2014	336	0.217 (11.94)	1.21 (2.72)	58,010 (44,894-74,958)	0.775 (0.599-1.001)	12.83
2015	857	0.480 (9.85)	1.27 (1.79)	128,140 (103,060-159,330)	1.711 (1.377-2.128)	10.92
Overall	3 536		1.34 (0.90)	89,930 (79,518-101,700)	1.201 (1.062-1.358)	6.28
b) Survey sector						
Galicia	223	0.166 (10.65)	1.36 (5.30)	7,525 (5 749-9,775)	0.619 (0.477-0.804)	12.79
North	1 149	0.398 (7.20)	1.31 (1.55)	23,516 (19,793-27,940)	1.430 (1.204-1.699)	8.74
Centre	978	0.349 (9.07)	1.32 (1.69)	25,447 (20,733-31,233)	1.261 (1.027-1.547)	10.36
Alentejo	444	0.306 (9.33)	1.48 (2.68)	12,150 (9,803-15,059)	1.243 (1.003-1.541)	10.79
Algarve	742	0.312 (10.33)	1.34 (2.03)	17,534 (13,972-22,003)	1.074 (0.856-1.348)	11.45

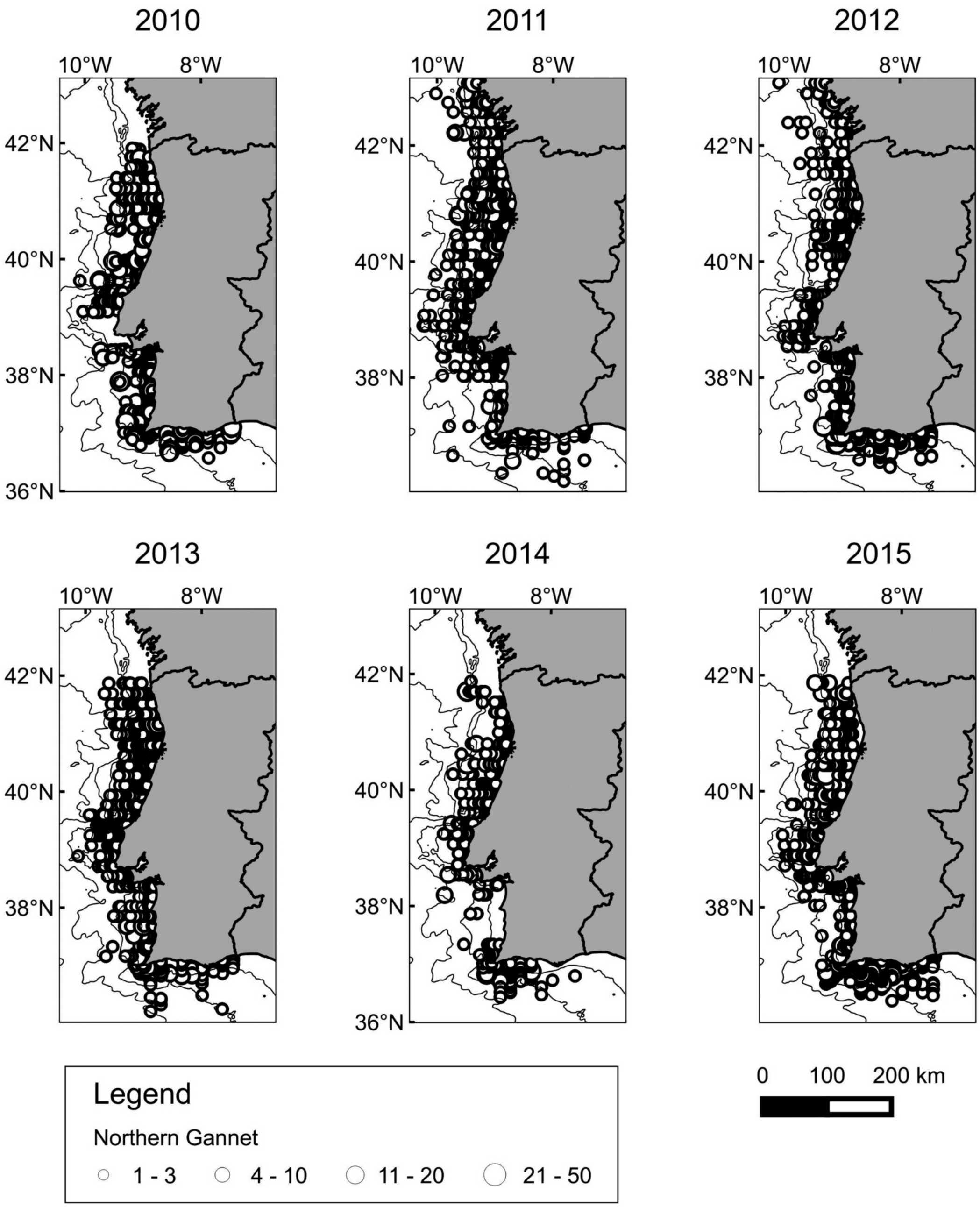

FIG. 2.—Northern Gannet sightings during aerial surveys in 2010, 2011, 2012, 2013, 2014 and 2015. Circle size indicates number of individuals per flock. The survey included the Galicia sector in 2011 and 2012.

[Avistamientos de alcatraz atlántico durante los muestreos aéreos realizados en 2010, 2011, 2012, 2013, 2014 y 2015. El tamaño del círculo indica el número de individuos por grupo. El muestreo incluyó el bloque Galicia en 2011 y 2012.]

ranged between 0.775 individuals/km^2 in 2014 and 1.711 individuals/km^2 in 2015. The overall abundance estimate (considering the six-year period) was 89,930 (CV = 6.28%) and the overall density amounted to 1.201 individuals/km^2 (Table 2a).

Most gannet sightings were recorded in the North sector of the survey area (1,149 sightings) representing 32.49% of all sightings (Table 2b). The North sector also showed the highest encounter rate value, with 0.398 sightings per nm in the sector. However, species abundance was higher in the Centre sector (an average of 25,447 individuals; CV = 10.36%) (Table 2b). In all surveyed years and sectors, the variance in gannet density (Supplementary Material, Appendix 1, Table B1) was primarily affected by the encounter rate, followed by the detection probability and group size.

Considering the total number of gannet sightings (Figure 3), immature individuals and adults corresponded to 46.70% and 40.96% of all sightings, respectively. On the other hand, juveniles, individuals of undetermined age and mixed groups corresponded to 6.60%, 2.94% and 2.80% of all sightings, respectively. Adult sightings were predominant in 2010, 2011 and 2013, while in the other years most sightings corresponded to immature individuals. Juveniles varied between 4.79% and 13.45% of all sightings, respectively in 2012 and 2011. Mixed groups (adult and immature and/or juvenile individuals) were more prevalent in 2013 with 7.21% of all sightings.

Distribution models

The predictive distribution models for the Northern Gannet reached fairly good performances with AUC values varying between 0.814 in 2011 and 0.881 in 2014 (Table 3). The suitable habitat areas, based on the MTP threshold, varied between 21,596km^2 in 2010 and 24,376km^2 in 2012. Considering the relative contribution estimates of predictor variables, Chlorophyll concentrations contributed the most to explaining annual Northern Gannet occurrence probabilities (ranging from 46.2% in 2010 to 65.5% in 2012). The

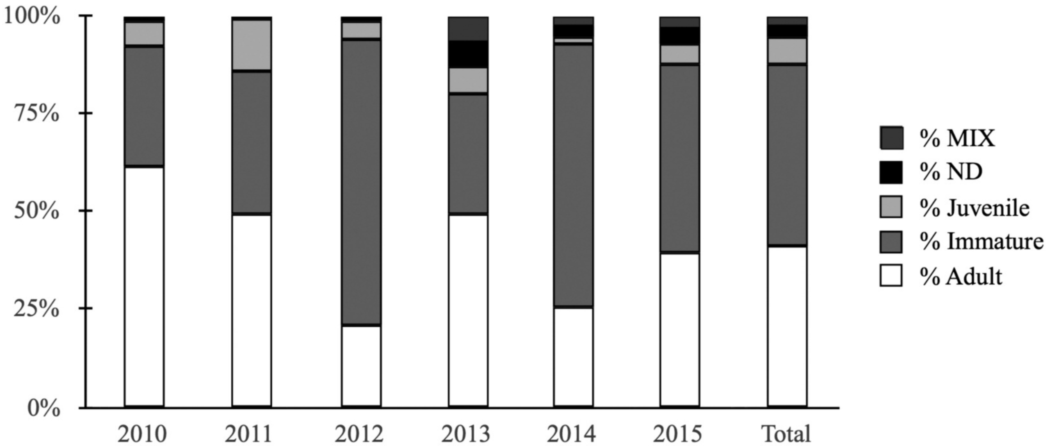

FIG. 3.—Global and annual age-class composition of Northern Gannets in the study area between 2010 and 2015. ND: non determined; MIX: Mixed Group.
[Composición total y anual de las clases de edad de alcatraz atlántico en el área de estudio entre 2010 y 2015. ND: no determinado. MIX: grupo mixto.]

remaining variables (distance to ports, Wind, SST and Slope) presented much lower contributions over the years (Table 3).

Chlorophyll concentration (Chl) response curves indicate an optimum occurrence probability at Chl around 1mg/m^3 in all years (see Figures 4 and Supplementary Material, Appendix 2, Figure B2). Concerning SST, the response curve shows some fluctuation with optimum occurrence probabilities between 18°C and 20°C in all years except for 2010 and 2012, when the optimum value occurred at 24.31°C and 15.84°C, respectively (Figures 4 and Supplementary Material, Appendix 2, Figure B3). Regarding wind speed, the response curves show optimum occurrence probabilities at speeds of 4-6m/s in all years (Figure 4, Supplementary Material, Appendix 2, Figure B4). According to the suitability distribution maps, gannet occurrence probability decreased with distance to ports and was mostly associated with smooth slope areas (Figures 4, Supplementary Material, Appendix 2, Figure B5 and B6).

Overall, models indicate that gannets are distributed throughout the Portuguese continental shelf, and preferred areas are located 3-20nm offshore (Figures 5 and 6).

TABLE 3

Average test AUCs and standard deviations (SD) of bootstrap replicate runs (10 replicates), heuristic estimate of EGVs (Chl, Distance to ports, Wind, SST and Slope) relative contributions (%) to annual models, threshold value for the minimum training presence (MTP), derived from all 10 Maxent model runs, and suitable habitat area predicted by this threshold.
[Promedio de test AUC y desviaciones estándar (SD) de las ejecuciones de réplicas de bootstrap *(10 réplicas), contribuciones relativas (%) de la estimación heurística de EGV (Chl, Distancia a puertos, Viento, SST y Pendiente) a los modelos anuales, valor de umbral para la presencia mínima de entrenamiento (MTP), derivado de las 10 réplicas del modelo Maxent y el área de idoneidad de hábitat predicha por este umbral.]*

Campaign	AUC (SD)	EGVs relative contributions (%)					Suitable Habitat	
		Chl	Distance to ports	Wind	SST	Slope	Threshold (MTP)	Area (km^2)
2010	0.839 (0.008)	46.2	37.6	12.4	2.0	1.8	0.499	21 596
2011	0.814 (0.007)	58.6	26.9	6.6	5.1	2.8	0.725	24 324
2012	0.855 (0.010)	65.5	18.8	10.4	3.8	1.5	0.646	24 376
2013	0.844 (0.014)	59.6	31.0	2.6	2.5	4.3	0.634	22 640
2014	0.881 (0.010)	57.7	22.7	14.9	2.4	2.3	0.554	23 624
2015	0.835 (0.005)	52.2	37.8	4.8	2.0	3.2	0.559	22 424

Discussion

The importance of Western Iberian Waters for the Northern Gannet

The overall abundance of Northern Gannets in WIW was estimated at 89,930 individuals. The species is therefore very abundant in WIW during late summer/early autumn. The highest annual abundance (recorded in 2015) was 128,140 individuals (CV = 10.92%), which represents 7.12-8.54% of the Northern Gannet global population (1,500,000-1,800,000 individuals, BirdLife International, 2018).

Previous studies on local gannet abundance within the WIW (Table 4) reported over 6,000 birds passing Cape Carvoeiro in mid-October 2014 (Elmberg *et al*., 2016) and around 165,000 birds passing Cape St. Vincent annually between late summer and autumn (Leitão *et al*., 2014). Arcos *et al.*

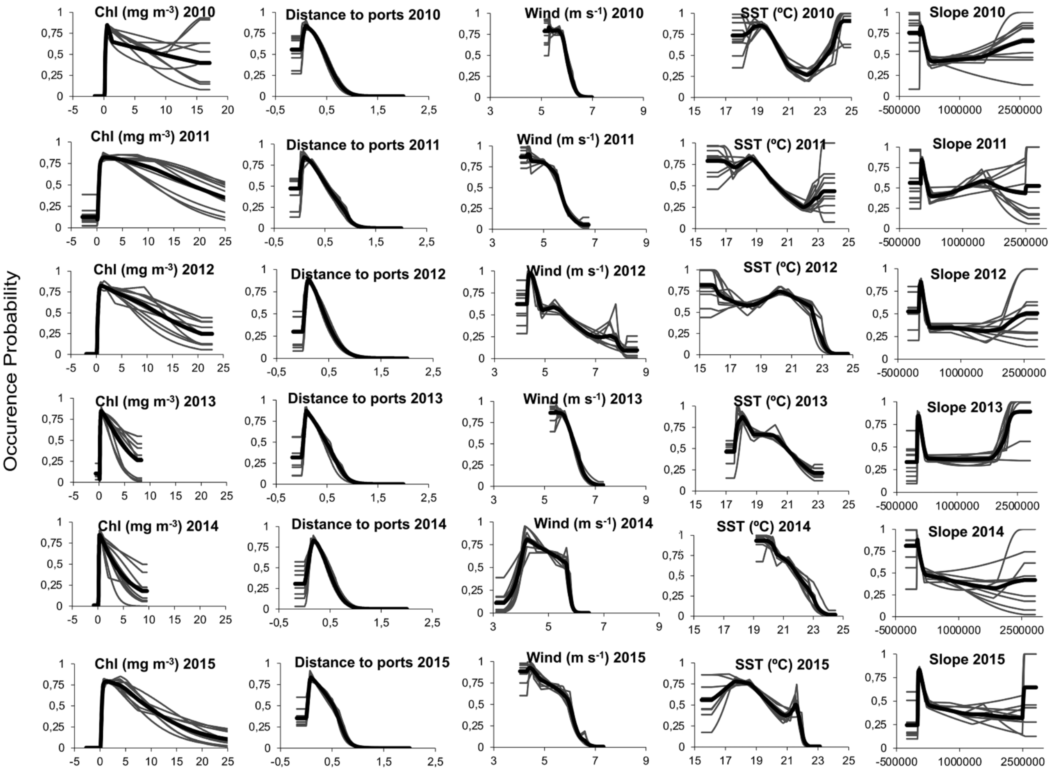

Fig. 4.—Northern Gannet occurrence probability response curves (grey lines show the output of 10 replicates, while the black line represents the mean value) to EGVs variation (Chl, Distance to ports, SST, Slope and Wind). Curves show the cloglog prediction of occurrence probability using a particular variable while keeping other environmental variables at their average sample value.

[Curvas de respuesta de probabilidad de presencia de alcatraces atlánticos (las líneas grises muestran la salida de 10 réplicas, mientras que la línea negra representa el valor medio) a la variación de EGV (Chl, Distancia a los puertos, SST, Pendiente y Viento). Las curvas muestran la predicción cloglog *de la probabilidad de ocurrencia usando una variable particular mientras se mantienen otras variables ambientales en su valor muestral promedio.]*

(2009) reported approximately 400,000 gannets off Costa da Morte IBA (IBA ES004) (near the northern border of the study area) in the post-breeding period and Ramírez *et al*. (2008) reported 12,750 gannets wintering in Berlenga IBA. These results from other studies represent direct counts by land-based or ship-based surveys using ESAS methodologies. We used distance sampling methodologies, allowing for coefficient of variation and

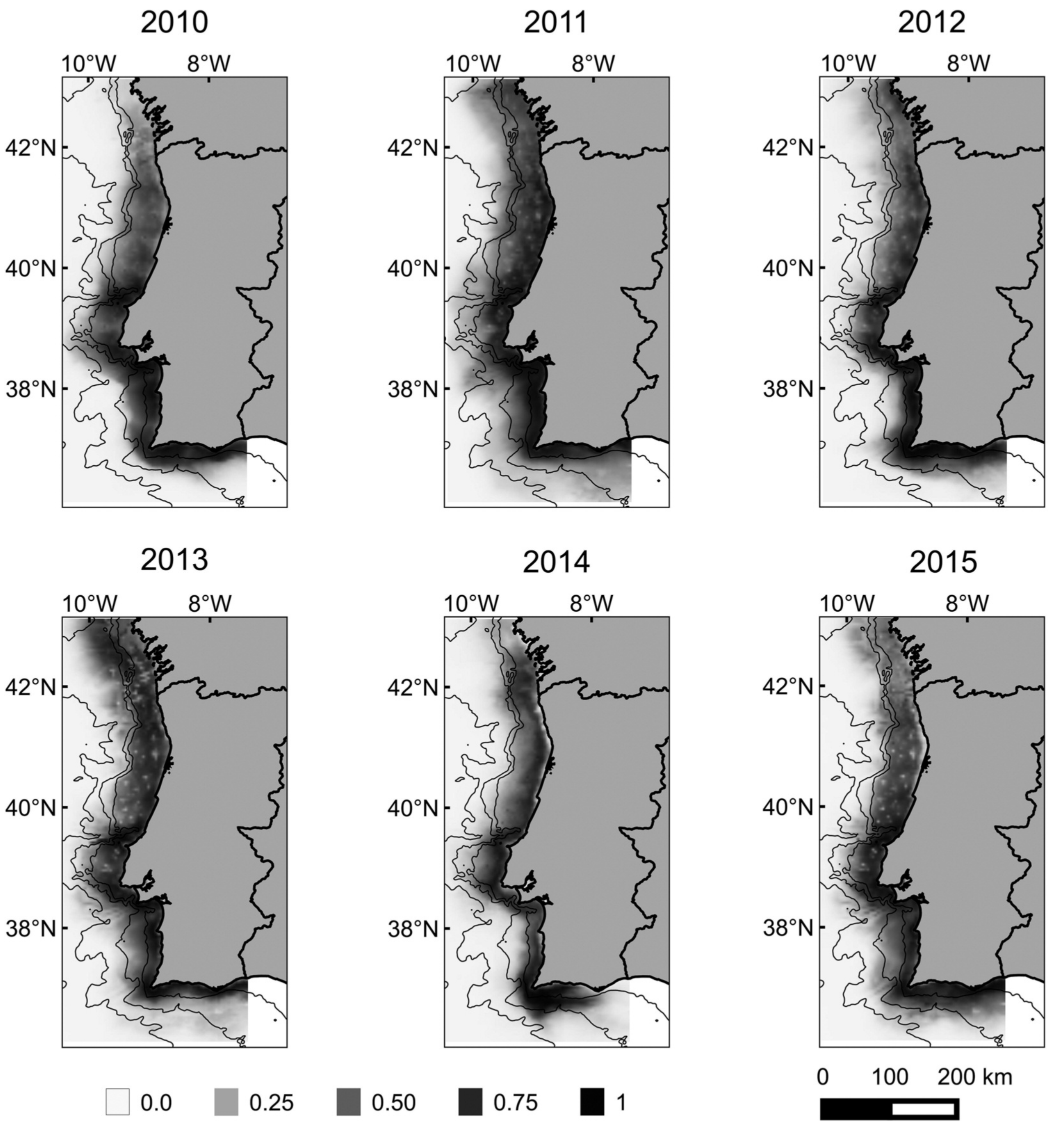

FIG. 5.—Annual (2010-2015) habitat suitability maps for Northern Gannet. Bathymetric profile of the area showing the 200m, 1,000m and 3,000m isobaths.
[Mapas anuales (2010-2015) de idoneidad de hábitat para alcatraz atlántico. Perfil batimétrico del área que muestra las isobatas de 200 m, 1.000 m y 3.000 m.]

confidence interval estimates. Therefore, our results cannot be directly compared with previous estimates for the transient population in WIW. Our approach, based on a six-year snapshot, provides the first gannet abundance estimates in WIW using a standardised method. Our estimates can be compared with those obtained in the Bay of Biscay and the English Channel in 2011/2012 (Pettex *et al*., 2017). For this neighbouring area, there was a gannet abundance of 83,138 individuals in summer and 210,910 individuals in winter, with densities varying between 0.81 and 1.44 individuals/km^2, and an average flock size of 1.5 in summer. The summer estimates in this area are similar those we estimate if compared to the overall period and to the similar period (2012). Our estimates can also be compared with those obtained in the Central Cantabrian sea between 2007 and 2012 (Louzao *et al*., 2020). The latter reports a mean density of 2.05 individuals/km^2 for the pre-winter period (September and October) with some annual fluctuation (i.e. 0.34 in 2010, 1.13 in 2011 and 6.54 birds/km^2 in 2012).

In our study, the annual abundance values show some fluctuations, particularly between 2013 and 2015. These could be associated with the fact that the survey is covering just a part of the migration period and also be

TABLE 4

Northern Gannet abundance and density in neighbouring areas. ND: Non-determined.
[Abundancia y densidad de alcatraz atlántico en áreas próximas. ND: no determinado.]

Area	Period	Abundance	Density	Method	Study
Cape Carvoeiro	Mid-October 2014	6,000	ND	Coastal counts	Elmberg *et al*. (2016)
Cape St. Vincent	Late summer until Autumn 2011-2013	165,000	ND	Coastal counts	Leitão *et al*. (2014)
Costa da Morte IBA	Post breeding 1999-2004	400,000	ND	ESAS - Boat survey	Arcos *et al*. (2009)
Berlengas IBA	Wintering 2005-2007	12,750	ND	ESAS - Boat survey	Ramírez *et al*. (2008)
Bay of Biscay and English Channel	Summer 2011/2012	83,138	0.81	Strip transect - aerial survey	Pettex *et al*. (2017)
Bay of Biscay and English Channel	Winter 2011/2012	210,910	1.44	Strip transect - aerial survey	Pettex *et al*. (2017)
Central Cantabrian Sea	September and October 2007-2012	ND	2.05	Strip transect - Boat survey	Louzão *et al*. (2020)
WIW	September and October 2010-2015	89,930	1.20	Line transect - aerial survey	Present study

associated with the weather conditions in the breeding zones and/or along the wintering areas that can affect migratory movements (Kubetzki *et al*., 2009; Fifield *et al*., 2014) leading to different arrival times at the study area. Also, seasonal movements to North-West African waters, where the species is severely affected by bycatch and intentional capture (Hagen & Wanless, 2014; Grémillet *et al*., 2015), may contribute to explaining the detected annual differences in the years after the mortality events.

The relatively high count in 2015 (128,140 individuals, CV = 10.92%) contrasts with the lowest, in 2014 (58,010 individuals, CV = 12.83%). A significant number of gannets moving south was recorded in mid-october 2014 at Cape Carvoeiro on the central Portuguese coast (Elmberg *et al*., 2016). A later arrival at WIW could explain the lower value recorded in the present study in 2014.

Considering Northern Gannet estimates per sampling sector, values confirm a preference for the North and Centre sectors of the Portuguese coast where several SPAs were already designated (SPAs Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel). In addition, the SPA Costa Sudoeste was recently enlarged to include Cape St. Vincent, where Northern Gannets can be observed in large numbers on passage.

Between 2010 and 2015, all age groups (adult, immature and juvenile individuals) and mixed groups were registered in the survey area. These results are in agreement with previous studies that show that adults and non-adults migrate southwards, along the flyway path along the Western European and West African coasts (Fort *et al*., 2012; Grémillet *et al*., 2015; Louzao *et al*., 2020). Sightings of non-adults exceeded those of adults. This is probably related to the fact that non-adults remain in the area throughout the year, as recently reported from the Berlenga SPA (Calado *et al*., 2021). The year-round presence of subadults in the area emphasises the importance of WIW for the species.

Northern Gannet distribution models

The correlation between gannet probability distributions and physiographic, oceanographic and remotely sensed data has been the subject of several studies in the species wintering or crossing grounds with different analytical techniques (e.g. Meirinho *et al*., 2014; Pettex *et al*., 2019; García-Baron *et al*., 2020). We used the maximum entropy algorithm (MaxEnt) to assess late summer/autumn gannet habitat preferences based exclusively on aerial survey data. MaxEnt outputs, as with any heuristic model result, should be considered as proxies for reality. For a more accurate model evaluation, results must be validated with future studies providing data from opportunist platforms, individual tracking or dedicated surveys.

Our modelling results indicate that the gannet is mostly present in shallow shelf waters, particularly in the strip between 3 and 20nm from the shore. A preference for shallow waters during winter was also identified in the Bay of Biscay through habitat modelling using Generalized Additive Models (GAMs) (Lambert *et al*., 2017). The shallow shelf waters of western Iberia are also an important fisheries ground (https://globalfishingwatch.force.com) where gannets may feed on discards, a common behaviour reported both from the breeding and migratory ranges (Kubetzki *et al*., 2009; Sherley *et al*., 2020). However, gannets are found quite close inshore in the Cape St, Vincent area (the most southwesterly point of continental Europe). This is a well-known hotspot for seabirds crossing over to African waters (Leitão *et al*., 2014). Other nearby areas, such as the gulf of Cádiz and the Strait of Gibraltar, are also recognised as important within the gannet migratory range (Veron & Lawlor, 2009; Lane *et al*., 2021).

Several areas were consistently selected as preferential habitats in all models including the north/central region of Portugal (i.e. between Porto and Nazaré), around Berlenga island, Cape Raso, around of Cape Espichel, Cape St. Vincent, off Algarve and, to some extent, off the Cies Islands in Galicia, Spain (Figure 6). This distribution pattern is coincident with areas already designated as SPAs and others previously known as stopover and foraging grounds (ICNF, 2014; Meirinho *et al.*, 2014). The obtained distribution pattern is supported by the coherent distribution sustained among years. Nonetheless, counts in winter should be useful to further assess the importance of western Iberian waters to the wintering gannet population that is reliant on local resources.

a) **b)**

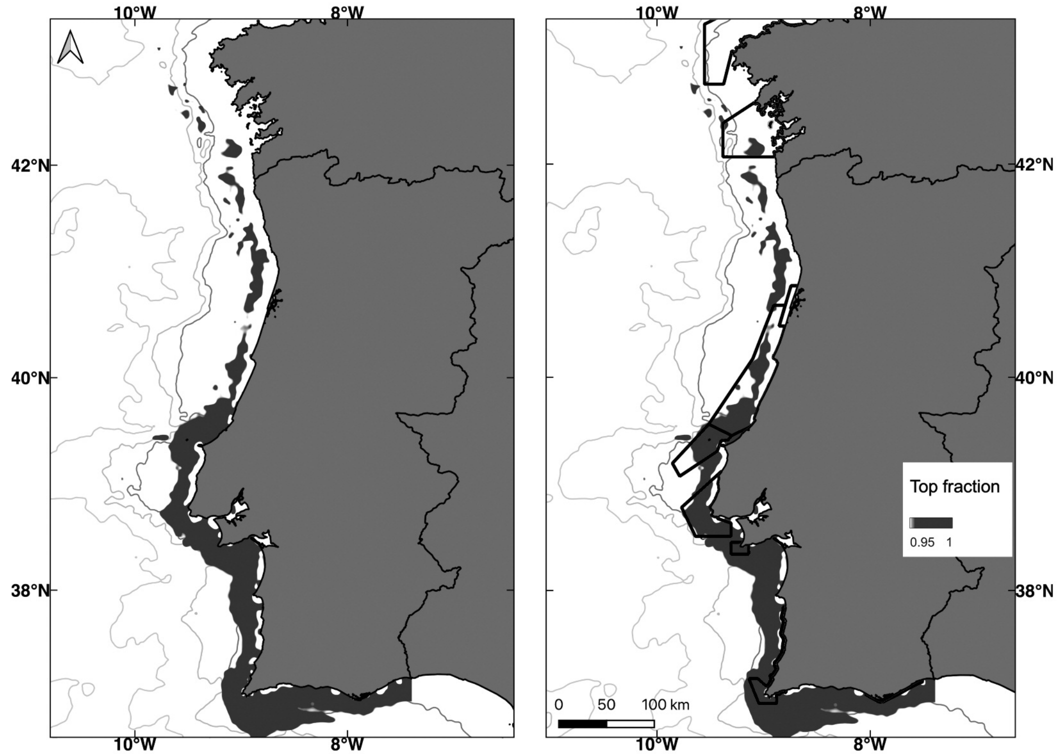

FIG. 6.—a) Proportion of Remaining Distribution Area (5% top fraction, core area for conservation of the Northern Gannet in WIW, graph from Zonation); b) Overlay of the Proportion of Remaining Distribution Area with the Portuguese and Spanish SPAs. Spanish Marine SPAs: Costa da Morte, Rias-Baixas de Galicia; Portuguese Marine SPAs: Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel, Costa Sudoeste. Bathymetric profile of the area showing the 200m, 1,000m and 3,000m isobaths.

[a) Proporción del Área de Distribución Remanente (fracción superior del 5%, área central para la conservación del alcatraz norteño en las aguas occidentales ibéricas, gráfico de Zonation); b) Superposición de la proporción del Área de Distribución Remanente con las ZEPA portuguesas y españolas. ZEPA Marinas Españolas: Costa da Morte, Rías-Baixas de Galicia; ZEPA portuguesas: Ría de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel, Costa Sudoeste. Perfil batimétrico del área que muestra las isóbatas de 200 m, 1.000 m y 3.000 m.]

In all models, the species distribution was best predicted by chlorophyll concentration. Available distribution models in the Cantabrian region also identified chlorophyll as the most important environmental variable concerning oceanographic features in the characterisation of key gannet habitats (García-Baron *et al*., 2020). The importance of chlorophyll concentration in gannet distribution was expected since it may provide a proxy for prey distribution as well as other biological factors (Solanki *et al*., 2005).

Monitoring strategy and limitations

We present Northern Gannet abundance estimates and predictive distribution maps in WIW, based on data acquired through a long term monitoring scheme using aerial surveys and standardised sampling designs. The major advantage of this method is that a large sea area can be covered in a short period of time, using a standardised, unbiased and cost-effective seabird census technique (Vingada & Eira, 2018). Therefore, this is a reliable and well-suited method for long-term surveillance schemes.

An important dataset on Northern Gannets in WIW was gathered, which allows for absolute abundance estimates. However, we emphasise that our abundance values may be underestimated. Although the method relies on the assumption that all birds are detected along the transect line, this may not always have occurred throughout the survey. If so, this could have led to an overestimation of the detection function and an underestimation of abundance values. The use of the dual-observer methodology could reduce this possible bias although aircraft logistical constraints do not usually allow this. Although the perception bias was not estimated, it can be considered constant throughout the whole survey given that the same plane, observers and field protocol were used (Panigada *et al*., 2011). In future campaigns, image acquisition by digital cameras could be used to improve seabird detection (Kemper *et al*., 2016; Žydelis *et al*., 2019). Also, simultaneous use of digital cameras and observers in line transect aerial surveys (in a dual-observer platform design) could be useful to improve detection parameters further.

Conclusions

In our study, we evaluated the importance of WIW for the Northern Gannet by estimating its abundance in the area, which was almost 10% of the global population of the species. Our results also corroborate the existence of seabird hotspots during the non-breeding period, along migration corridors or at wintering grounds (Fort *et al*., 2012). Within the study area, the most important post-breeding grounds for Northern Gannets were in Portuguese continental shelf waters, particularly 3-20nm offshore.

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Author contributions.—Study conception HA and CE; Investigation HA, PCR, JBS, MF, ATP, JMC, JV and CE; Methodology HA, PCR, JBS, JV and CE; Resources HA, JBS, JV and CE; Data curation HA, PCR, JBS, JV; Writing initial draft HA; Writing critical review and commentary of revision HA, PCR, JBS, MF, ATP, JMC and CE; Supervision PCR, JV and CE; Project Administration JV and CE.

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Supplementary Electronic Material

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Appendix 1:

Table A1. Pearson's correlations values.
[Valores de las correlaciones de Pearson.]

Table A2. AUC values for models without Chl and SST lag, with lag-1 and lag-2.
[Valores de AUC de los modelos con Chl y SST de los meses de muestreo, para los meses de muestreo –1 y –2).]

Appendix 2:

Table B1. Variance in Northern Gannet density for all survey years and sectors.
[Variación en la densidad de alcatraces para los años y bloques muestreados.]

Figure B1. Detection function.
[Función de detección.]

Figures B2, B3, B4, B5 and B6. EGV maps.
[Mapas de las variables ambientales.]

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