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Mismatches between the current marine Natura 2000 network and seabird distributions call for enhanced protected areas off metropolitan France

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A B S T R A C T

Seabirds are among the most threatened vertebrates, under pressure from fisheries bycatch, climate change, overfishing, and human disturbance. In France, demographic studies have highlighted adult survival as a key factor in population trends, which calls for large-scale marine conservation efforts. In this context, the Natura 2000 policy requires the designation of Special Protection Areas (SPAs) to protect seabirds under the Birds Directive. To assess the completeness of the French marine SPA network, data from aerial, boat, and coastal surveys, as well as tracking devices and distribution models, were collected for 57 seabird taxa. This data collection allowed the EU minimum criteria for a coherent SPA network to be spatially implemented, and the most ecologically valuable areas for seabirds around metropolitan France to be identified and prioritised, and overlaid with the current French SPA network and Marine Important Bird Areas (mIBAs) to identify potential inconsistencies. This analysis revealed seabird hotspots outside the existing ecological network, confirming some insufficiencies for coherent seabird conservation. Although data dependent, this analysis highlighted the limitations of using global proportion coverage to assess network coherence when coverage of biodiversity and abundance hotspots was not achieved. Furthermore, these results summarised the main target areas for policy makers to effectively improve seabird conservation around metropolitan France. In a context of increasing demands for marine spatial planning, improvements in this knowledge, the SPA network and conservation actions are required.

1. Introduction

In the context of the continuing human population growth and its demands for natural resources and energy, which reduce the natural areas and their connectivity, conservation biology has emphasized the need to link conservation with land-use planning and economic development [1]. For global effectiveness, species habitat use should be considered not only within protected areas, but also beyond their boundaries to avoid compromising conservation efforts made elsewhere [2–4]. A key operational tool is the development of ecological networks, in which core areas surrounded by buffer zones, and connected by corridors across a heterogeneous landscape, should form a coherent ecosystem that supports more biodiversity than core areas in isolation [5].

To be functional and achieve its objectives, the spatial configuration of such a network is crucial and requires a systematic approach across landscapes [6]. In Europe, this goal of long-term sustainability for wildlife and natural habitats has been translated into policy by the European Union (EU): the designation of Special Protection Areas (SPA) and Special Areas of Conservation (SAC) under the Birds (Council Directive 79/409/EEC) and Habitats (Council Directive 92/43/EEC) directives respectively, form the Natura 2000 network. This network covers 27 EU Member States and is considered to be the largest integrated ecological network in the world [7].

Initiated on land, the Natura 2000 network has been extended to the marine environment [8], which is also affected by global human threats [9]. At sea, SPA perimeters are dedicated to seabirds, one of the most threatened groups of vertebrates, with declines across taxonomic groups mainly due to the cumulation of threats such as incidental bycatch in fisheries, climate change, overfishing and disturbance [10]. Around France, demographic analysis points to adult survival as a key parameter for populations trajectories, requiring at-sea and international conservation action [11,12]. Such a large-scale effort is not without its challenges, and national approaches vary across Europe [13].

However, scientific criteria for sites designation have been established in order to ensure effectiveness of the network [8,14]. Completeness of the network, also referred to as network sufficiency, is achieved when all habitat types and species listed in the Birds and Habitats Directives in a country, are adequately represented and protected within the national network. Although considered challenging to achieve [15,16], it is a legal obligation for all EU Member States to have a national network in place and managed in accordance with these European criteria. In this context, the achievement of network completeness is being monitored by the European Commission (EC). The Birds Directive requires a scientific procedure, independent of socio-economic considerations, to designate "the most suitable territories, in number and size, as special protection areas" (Art. 4). This non-specific criterion has so far led the EC and the EU Court of Justice to assess the adequacy of SPA designations against the non-legally binding NGO inventory of Important Bird and Biodiversity Areas, and at sea, the marine Important Bird Areas (mIBA) [17].

Although the marine waters covered by SPAs in metropolitan France exceed the 30 % target set by the EU Biodiversity Strategy 2030 [18] and the UN Convention on Biological Diversity [19], the coherence of this

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national network is being questioned [20]. In particular, the EC has raised questions about the completion of the network in coastal waters (compared to mIBAs) where anthropogenic pressure is high [21]. Therefore, in the present study, a spatial implementation of the EU minimum criteria for a coherent SPA network was carried out, to 1) locate and prioritise the most ecologically valuable areas for seabirds around metropolitan France, and 2) overlay them with the current French SPA network and marine Important Bird Areas (mIBA) to identify potential inconsistencies.

2. Materials and methods

2.1. Biogeographical areas, seabird species and time-periods

The Birds Directive defines the biogeographical regions for its application in Europe. In metropolitan France, this concerns the Atlantic and Mediterranean marine environments, delimited by the boundaries of waters under French jurisdiction [22]. For the analysis, the marine environment polygons were gridded into $0.05 \times 0.05^{\circ}$ cells, for consistency with the available distribution models [23–25]. The Birds Directive also lists the bird species to be considered in SPAs, which were previously refined with seabirds regularly occurring in metropolitan France [26]. Rare vagrants or species associated with coastal lagoons were excluded from this list, resulting in 53 taxa for the Atlantic and 27 taxa for the Mediterranean (57 taxa in total including subspecies, Table A.1). The annual life cycle of seabirds can be divided into two main periods, which are associated with drastic changes in their spatial distribution: 1) the breeding period, when breeding individuals become central-place foragers during the pre-nuptial, incubation and chick-rearing stages, and 2) the non-breeding period, when individuals may disperse away from breeding colonies and/or undertake migrations to wintering areas. This temporal distinction was maintained for the distribution data, either by using the information provided by the data producers, or, when at-sea sightings did not provide information on reproductive status, by combining the Julian date with the reported breeding phenology of the species in metropolitan France [27].

2.2. Data compilation

Spatial conservation planning requires high quality information on abundance and distribution [8]. In order to include all relevant and available data, we searched for all at-sea seabird data available in 2022 among predicted distribution, tracking, density and sighting data, produced and/or held by various NGOs, universities and national institutions (Table 1, Fig. 1). Tracking studies were searched in the online platforms Seabird Tracking Database [28] and MoveBank [29],

Table 1
Types of data and datasets used to map the distribution of seabirds in French waters.

Data	Platform	Acquisition protocol	Data format	Pro(s)	Con(s)	Datasets
Predicted distribution	Plane	Aerial transects	Density predicted by habitat modelling	Basin-scale sampling covering all the study areas, enabling large-scale habitat modelling	Decadal campaigns, species identification often at taxonomic group level, low detectability of elusive species. Modelling requires sufficient sightings for robust results	SAMM 1, SAMM 2, SCANS III, ASI
	Multi-source	Boat transects + coastal repeated counts	Density predicted by habitat modelling	Regional scale sampling enables habitat modelling	In the Mediterranean, insufficient sampling leads to limited spatial predictions	Balearic shearwater National Action Plan 2018
Interpolated density	Boat	Boat transects	Densities predicted by spatial interpolation	Annual, seasonal campaigns Large scale sampling	Timed for fish studies. Coastal waters under sampled, abyssal waters not sampled.	MEGASCOPE, PELMED (PELAGIS Observatory)
				Annual, monthly campaigns	Regional-scale sampling	ERMMA (Biarritz sea centre)
Tracking	Bird	GPS, Argos	Bird locations	Fine-scale recording of trips at sea, from days to months (depending on material and settings). Ability of infer behaviour. Freedom from observer bias	Biologging impact [83]. Large sample size required for representativeness [84]. Repeated sampling over time and space for robust identification of priority areas [85,86]	Detail of the numerous studies in Annex II
Sightings	Plane	Transects	Bird numbers	Annual, seasonal campaigns, sampling of coastal and neritic waters	Local/Regional scale	SPEE, survols OFB (Bretagne Nord, PNMI), DepoBio
	Boat	Transects, repeated counts, unprotocoled sightings		Annual, seasonal campaigns, sampling of coastal and neritic waters	Local/Regional scale	PelMed (CEFE), ObsEnMer, DepoBio, RN estuaire de Seine
	Coastal	Repeated point-counts, unprotocoled sightings		Wide coverage of the coast	Spatio-temporal variation of sampling effort, coverage limited to 3 nautical miles	OFB grebes and loons survey, Trektellen
				Knowledge of bird's origin and age	Spatio-temporal variation of sampling effort, close observation only	CRBPO
				Covers the whole coast, species-level sightings, most reports of elusive species come from here	Spatio-temporal variation of sampling effort, detection distance limited to 3 nautical miles	Faune-France, SINP
		Sectoral repeated counts		Coordinated counts within assigned sectors, annual	Detection distance limited to 3 nautical miles	International waterbird census (Wetlands International)

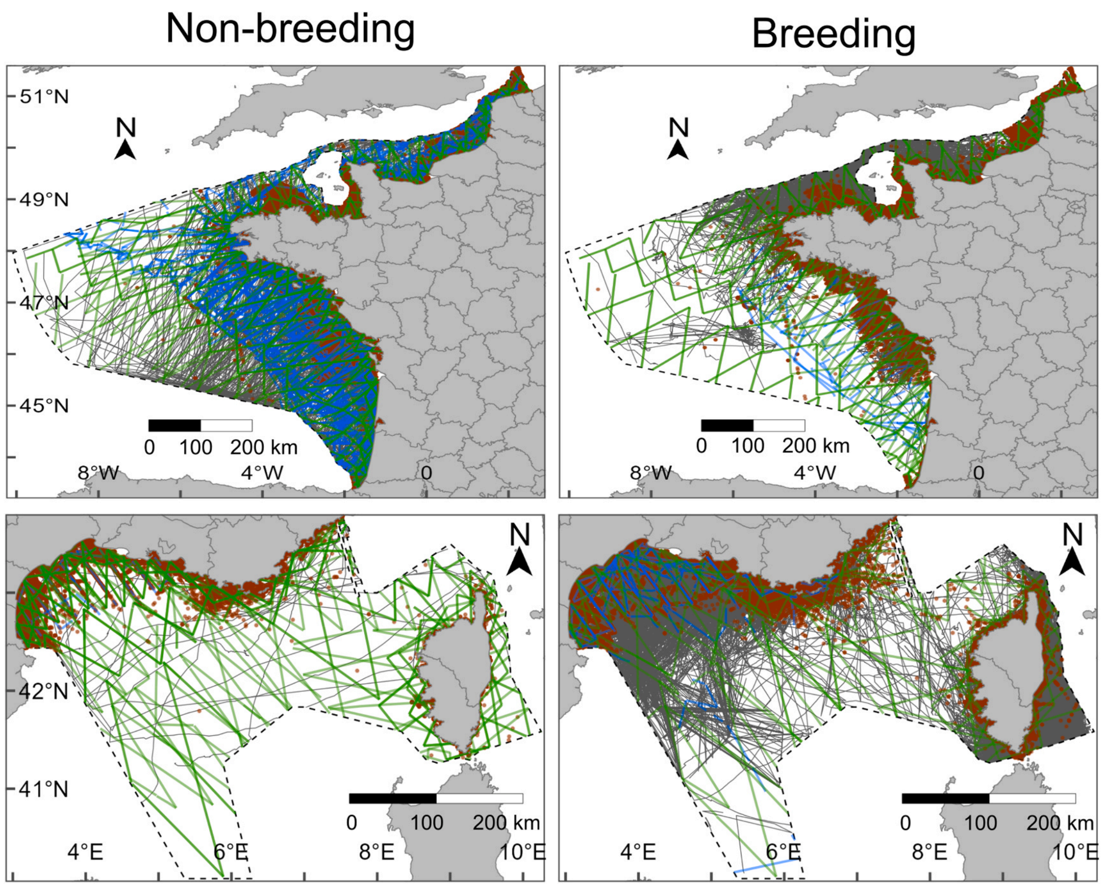

Fig. 1. Spatio-temporal distribution of seabird data and observation efforts (nautical in blue, aerial in green, tracking in grey and sightings in brown) collected in the waters under French jurisdiction in the Atlantic and Mediterranean during the period 2002–2022.

restricted to GPS or Argos tags for spatial accuracy. This included not only the studies conducted in metropolitan France, but also studies conducted abroad with seabirds using French waters (Table A.2). Only data collected during the last two decades (2002–2022) were considered, given the possible temporal evolution of population sizes and their areas of use (Table 1, Fig. 1). This choice was a compromise between obtaining a large amount of data, maximising the number of repeated observations over time (necessary for a robust selection of priority areas for mobile species, [30,31]), while remaining sufficiently recent to be representative of the current situation.

2.3. Data preparation

All data were imported into R version 4.1.3 [32], georeferenced to the WGS 84 geodetic system using the *sf* package [33], and plotted using the *ggplot2* package [34].

2.3.1. Filtering

The compilation of the various datasets required an initial filtering process, as the quality of the data may have an impact on the results. In particular, the following data were excluded: observations of stranded individuals following exceptional weather conditions [35] and oiled individuals, whose locations may reflect exhaustion rather than natural occurrence. Data from fisheries bycatch and translocation experiments were excluded as they are likely to reflect attraction to vessels and unnatural trip characteristics, respectively. Counts of breeding colonies or roosting places on land were also excluded because they do not provide accurate information on areas used at sea, as seabirds can travel tens to hundreds of kilometres per day [36–38]. Furthermore, the terrestrial colonies have already guided the first SPA designations in France, whereas seabird conservation today requires more knowledge at sea [12,39].

2.3.2. Species distribution models

Given the species-based approach recommended for Natura 2000, the density at-sea predicted by habitat models available in metropolitan French waters was used (Table 1). When available at a taxonomic group level, they were attributed to the most abundant species in the group (Table A.3). In the Mediterranean, the predicted densities of shearwaters were judged to be biased towards the coast [24], which contradicts the repeated tracking data studies [40–42]. Therefore, these were excluded in favour of the tracking data.

2.3.3. Tracking data

This heterogeneous collection of tracking data included different devices, settings, and sample sizes, so these raw data required pre-processing steps. For each species, tracking data were divided into foraging trips [43]. Anomalous locations with unrealistic speeds above 90 km/h were removed [44] prior to linear interpolation at one-minute intervals (common denominator). From these trips, the time spent within the gridded regions was extracted and transformed as a percentage of the total trip duration, averaged across individuals. This standardised time per area weighted the importance of the cells used, as areas where birds spent more time at sea are indicative of foraging behaviour [45,46]. The result was a distribution layer by species and period, including both French and foreign tracking information.

2.3.4. Interpolated density

Bird density layers from at-sea surveys were either received directly as usable layers (ERMMA dataset, Table A.2), or obtained from raw data by kriging (SAMM, SCANS dataset, Table A.2) assuming a Poisson distribution and zero nugget model [47] implemented in the *Pelakrig* package [48]. Other studies that did not provide data on prospecting effort data were treated as sightings.

2.3.5. Sightings

Sightings were derived from a variety of counting methods and mostly from citizen reports of opportunistic observations. They are heterogeneous and sensitive to observation effort [49], so they cannot be analyzed using the statistical techniques described above. However, the numbers reported all along the coasts can still provide information on some locations with high concentrations of species, and sometimes represent the majority of the available data (Table A.5, A.6). Therefore, they were integrated as another distribution layer by species and time period. To smooth out their spatio-temporal sampling bias, the sightings were aggregated within the cells of the gridded regions as the mean of the annual maxima. Such a transformation made it possible to map areas of regular and important concentrations for each species by season.

2.4. Data processing

2.4.1. Collation

The first step was to create a spatial distribution layer for each available data type, species and life cycle period, forming the basis for the network evaluation (Fig. 2). Where a layer was derived from repeated data within cells, they were summarized by keeping the average of the maximum per year. The resulting distribution layers, with different quantitative scales depending on the data type, were transformed as follows:

$$\textit{standardised data (from 0 to 1)} = \frac{(\textit{data} - \textit{minimum})}{(\textit{maximum} - \textit{minimum})}$$

This standardization of the layers into a common relative scale allowed the different distribution gradients to be used simultaneously with equal weight for a comprehensive analysis of species distribution (Fig. 2).

2.4.2. Process for identifying priority areas

Official European texts require a scientific procedure to designate “the most suitable territories, in number and size, as Special Protection Areas” (Birds Directive, Art. 4). Finding these most important areas, where management efforts would conserve biodiversity in the most cost-effective way, is the goal of systematic conservation planning [6], and is based on distribution data and predefined conservation objectives. In the case of the Natura 2000 network for highly mobile and migratory marine species such as seabirds, these objectives are translated into specific criteria published in European texts for the establishment and evaluation of Natura 2000.

2.4.2.1. European scientific criteria relevant to highly mobile species. For a given species, the adequacy of a Natura 2000 network is assessed on the basis of by two main criteria: the natural range and the sufficiency. These two criteria are broken down into several sub-criteria. Natural range is assessed by the distribution variability and habitat/genetic variability. Sufficiency is assessed by the proportion, the conservation status and the proportionality (Table 2).

For seabird species in metropolitan French waters, the conservation status, population trend and proportionality sub-criteria have already been integrated into a Responsibility Index (RI) for each species [50], established in the French context of the Marine Strategy Framework Directive (Directive 2008/56/EC) (Table A.5, A.6). This recent index, available by marine sub-region, allowed a geographical refinement of the Atlantic region: Greater North Sea, Celtic Sea, Bay of Biscay and Iberian coast. Therefore, these categorical sub-criteria (natural range) and quantitative sub-criteria (network sufficiency) were applied to the compiled data in order to assess the potential presence of remaining gaps as defined by the EC recommendations.

2.4.2.2. Identification and prioritization of the areas of concentration. Several decision support tools that use an algorithmic approach to species distribution data have been developed to identify areas of high conservation value [51–53], and have been used in the context of national ecological network assessments [16,54,55]. The performance and results of these decision support tools are not necessarily consistent with

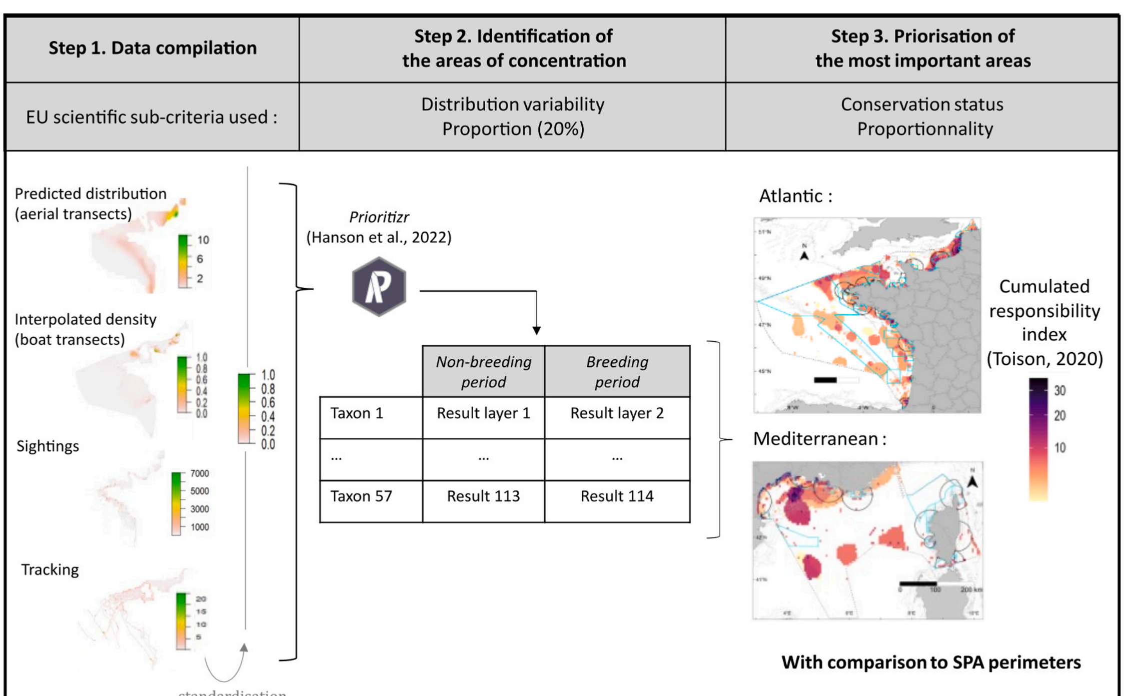

Fig. 2. Data processing for the evaluation of the SPA network for seabirds, applying the EU criteria.

Table 2
European scientific criteria used to evaluate the Special Protection Areas network for seabirds.

Criteria	Sub-criteria	Implementation principle	Reference
Natural range	Distribution variability	Variability in spatio-temporal distribution	HD art 3.1
	Habitat/Genetic variability	Natural variability of the habitat itself and species genetic variability (Sub-species and local population with specific ecology/behaviour)	BD art 4,1–2 ETC/BD 2010
Network sufficiency	Proportion	"Insufficient" when proportion of the species population is ≤ 20 % within the network	EC 1997
	Conservation status	Higher priority if species evaluated with population in decline or threatened	ETC/BD 2010
	Proportionality	Proportion of the species population within network must be equivalent to European proportion	HD art 3.2 Evans 2012

one-another, and the choice of software depends on the objective of the analysis [56,57].

Given our objective to localize priority areas for comparison with the existing networks, we used the open-source package *Prioritizr* [53]. Within the $0.05 \times 0.05^{\circ}$ gridded marine environment, our spatial problem was to extract from the available standardized distribution layers the minimum number of cells necessary (*add_min_set_objective* and *add_binary_decision* functions) to represent a network of areas meeting the minimum EC proportion criteria (20 %, set with the *add_relative_target* function). For each species, the algorithm identified the cells that fall within the optimal mathematical solution, representing the areas with the highest population concentrations. These selected cells are weighted with the corresponding Responsibility Index (RI) (as a reminder, depending on the species, the marine sub-region and the life cycle period [50]), or cumulative RI when multiple species were encountered in the same cell. By summing the weighted solutions, areas with the highest conservation values are distinguished (Fig. 2). In addition, all available standardized layers for a species were combined into a single averaged layer, to assess the global proportion of the species population covered by the current SPA network.

Within the biogeographical regions, the failure to cover the minimum proportion threshold and/or important(s) area(s) outside the existing SPA perimeters were used to assess the presence of remaining gap(s).

3. Results

3.1. Data collation

A total of 3 855 346 data observations were collected in the waters under French jurisdiction, 2 857 590 in the Atlantic and 997 756 in the Mediterranean (Fig. 1). In the Atlantic, these raw numbers were mainly derived from direct observations (54.4 %) and tracking data (45.6 %), while in the Mediterranean the opposite was true, with more data coming from tracking studies (71.3 %) and less from direct observations (28.7 %). Detailed regional data contributions are available by dataset (Table A.4) and by species (Table A.5, A.6).

3.2. Minimum network and priority areas

In the Atlantic, the algorithm identified 5 034 cells as areas of highest species concentration, covering 38.6 % of the region, in all oceanographic domains (Fig. 3). Within this minimum network, 2 566 cells were located within the existing SPA network, representing a general agreement of 50.9 %. With respect to the mIBAs, 1 313 cells were located within it, representing a general agreement of 26.0 %. Considering the yearly period, the highest cumulative RI values distinguished three main areas: (*A1*) the plume front of the Picardy estuaries (35.6), (*A2*) around the head of the submarine canyon off Capbreton (24.8), and (*A3*) on a tidal coastal front between the islands of Houat and Dumet (19.1) (Fig. 3). These areas corresponded to the non-breeding period hotspots where the cumulative Responsibility Index (RI) was found to be the highest (28.8, 24.8 and 16.1 respectively). Interestingly, areas *A1* and *A3* were partially covered by existing SPA perimeters, while *A2* was completely outside (Fig. 3). During the breeding season, the highest cumulative RI values were found on other areas: (*A4*) around the Sept-îles archipelago (22.9), (*A5*) Cape Fréhel (14.3) and (*A6*) the Loire estuary (12.3) (Fig. 3). On the other hand, these areas (*A4–6*) were located within existing SPA perimeters (Fig. 3) designated for nearby seabird colonies of national importance.

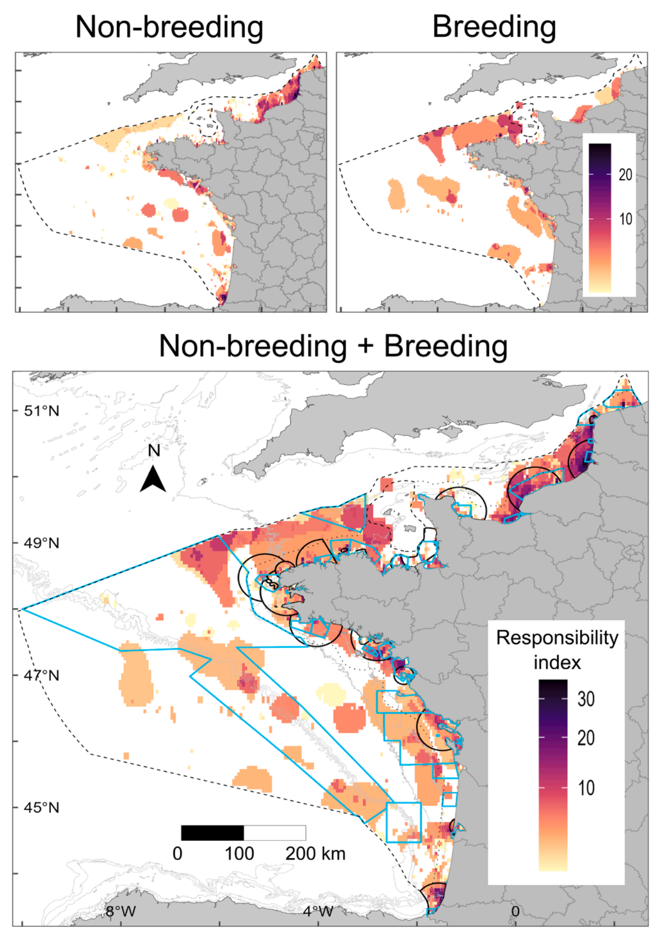

Fig. 3. Theoretical minimum network for 53 seabird taxa meeting the representativeness criteria in the Atlantic under French jurisdiction, coloured by the cumulative Responsibility Index (RI). The outer limits of waters under French jurisdiction and territorial waters are shown as dashed and dotted lines respectively. The existing French networks of SPAs and mIBAs are shown in blue and black, respectively. The grey lines represent the −50, −100, −200, −500 and −1000 m isobaths.

In the Mediterranean, the algorithm identified 1 275 cells as areas of highest species concentration, covering 25.9 % of the region in all oceanographic domains (Fig. 4). Within this minimum network, 199 cells were located within the existing SPA network, representing a general agreement of 15.6 %. For the mIBAs, 367 cells were located within it, representing a general agreement of 28.7 %. Considering the yearly periods, the highest cumulative RI values distinguished six main areas: (*M1*) the eastern part of the Languedoc coast, off the Thau lagoon (28), (*M2*) offshore towards the centre of the Gulf of Lion (22.5), (*M3*) the Cape Béar (22), (*M4*) the Gulf of Marseille (20.7), (*M5*) the Rhône estuary / Gulf of Fos-sur-Mer (16.2) and (*M6*) the western part of the Languedoc coast (15.2) (Fig. 4). The highest cumulative RI values were found mainly during the breeding season (*M1*=17.7, *M4*=15.2, *M3*=14.7 and *M2*=13.2) and to a lesser extent during the non-breeding season (*M6*=11.7, *M5*=10.5). Of these seabird hotspots, only *M3* was within a SPA. The rest were located either partially (*M1*) or completely (*M4*, *M2, M5*) outside the existing SPA network (Fig. 4), as well as outside mIBA boundaries when offshore (*M2*).

The spatial analysis of the seabird species distributions in regard to the current protection network also revealed that the proportion of the species population with the SPA network was above the critical threshold for all species in the Atlantic, but below that threshold in the Mediterranean for 6 coastal affinity species and 3 pelagic affinity species (Fig. 5).

4. Discussion

4.1. Contribution of the study

This study integrated available and relevant datasets on seabird at sea data to provide a comprehensive synthesis of the most important areas for seabirds in the Atlantic and Mediterranean waters under metropolitan French jurisdiction. This data-driven work allowed a scientific assessment of the completeness of the French marine Natura 2000 network for seabirds and showed contrasted results between the Atlantic and the Mediterranean regions.

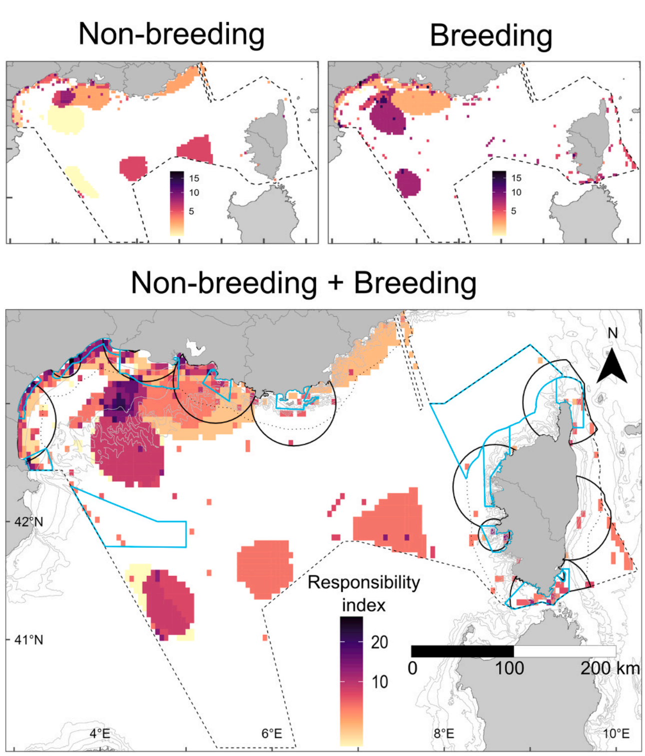

Fig. 4. Theoretical minimum network for 27 seabird taxa meeting the representativeness criteria in the Mediterranean under French jurisdiction, coloured by the cumulative Responsibility Index (RI). The outer limits of waters under French jurisdiction and territorial waters are shown as dashed and dotted lines respectively. The existing French networks of SPAs and mIBAs are shown in blue and black, respectively. The grey lines represent the −50, −100, −200, −500 and −1000 m isobaths.

4.1.1. Priority areas and gaps identified

In the Atlantic, the SPA network met the minimum population proportion and, unlike the mIBA network, covered most of the seabird concentration areas. However, some priority areas remained outside the SPA network, in coastal and territorial waters. In the Mediterranean, the SPA network failed to meet the minimum population proportion for a third of the species, as it covered only a minority of the seabird concentration areas, and even fewer than the mIBA network. Although some priority areas remained outside the SPA network in coastal waters, the largest were found in offshore waters.

The presence of remaining gaps in the French SPA network has already been suggested based on area comparisons [17,20], spatial prioritization using pooled mammal and seabird aerial surveys [58–60] or expert opinion (EU Pilot 8347/16/ENVI). Our novel approach, objectively based on at-sea seabird data only, explained why the present results were not fully consistent with previous criticisms. For example, some low coverage of mIBA by SPA in the absence of concentration areas did not seem problematic, because of their different methodologies [61]. The current French validated mIBA were determined by applying the theoretical foraging radius (2001 data) around breeding colonies [62]. This type of mIBA failed to distinguish fine-scale [63] or colony-specific habitat use [41], but more importantly, failed to cover important areas further offshore [64] and during the non-breeding season. Therefore, their crude use of surface area to assess the sufficiency of an ecological network raises concerns. On the other hand, the present results refined previous offshore areas reported for SPA designation in the Atlantic (GS7, Capbreton) and Mediterranean (GS8, Gulf of Lion) [59,60], which were confirmed for seabirds around the submarine canyon head off Capbreton, and in the central part of the Gulf of Lion, respectively. In addition, the current study identified two new priority areas outside the current SPA network in the Atlantic (Picardy estuaries and between the islands of Houat and Dumet), although they had previously been reported for taxon concentrations by aerial [23,25] or nautical [31] surveys. Overall, our analysis revealed remaining gaps and calls for improvement of the SPA network in both regions, with priority in the Mediterranean.

4.2. Limitations and prospects

4.2.1. Data collection

The large amount of data collected in the present study (> 3.8 million) must be placed in relation to the vast marine areas considered. In the Atlantic and the Mediterranean, the average number of bird locations per km^2 was 11 and 9, respectively. This scarcity of at-sea data for seabirds in metropolitan France has already been reported since the seaward extension of the Natura 2000 network [67], prompting the creation of a national marine data acquisition plan. Although this resource-intensive plan has improved the understanding of the general distribution [23,25] and foraging areas of certain seabird species [42], the data available for metropolitan France remain uneven between species and sometimes insufficient (Table A.5, A.6), potentially weakening the results for species with low distributional precision. The reliance on data quantity and quality in the spatial prioritization process is a recognized challenge, but the growing body of knowledge on seabird distribution and at-sea behaviour [65] offers hope for improvement.

In the current national context of offshore wind farm planning, new aerial, nautical transect and/or tracking studies at both basin and regional scales have been initiated in recent years, while long-term studies continue. In addition, local impact studies are now feeding data into the French DepoBio platform. All these projects will significantly increase the amount of data and knowledge in metropolitan French waters in the coming years. Furthermore, statistical development to combine different data sources in distribution modelling [66] (aerial surveys, boat transects, sightings) is underway throughout France. Together with accurate correction factors accounting for the species detection [67], these developments will improve the robustness of

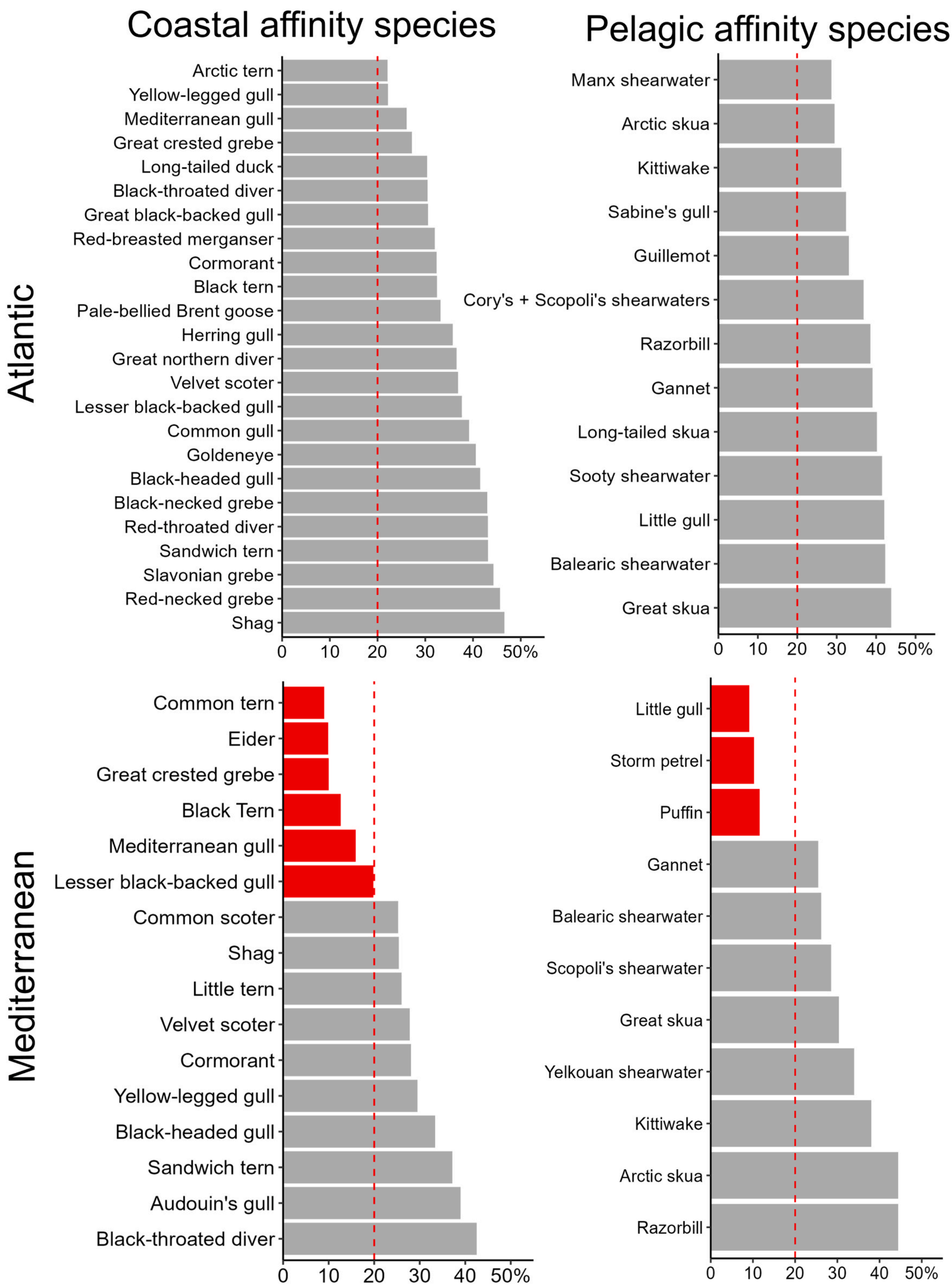

Fig. 5. Assessment of the proportion of species population within the French network of SPAs. The red dashed line represents the critical threshold below which it is recognised as insufficient (red bars).

distribution models.

The present data collection revealed the need for complementary at-sea data for several species of high conservation value: Storm petrel, Balearic and Manx shearwaters, Black and Roseate terns, Razorbill, Velvet scoter, Puffin, Greater scaup, Fulmar and Little gull. Although the present study provided a readily applicable starting point towards the goal of completing the Natura 2000 network at sea, a future reassessment of the French SPA network should be undertaken once such data improvements are achieved.

4.2.2. Arbitrary quantitative criteria and qualitative criteria requiring expert opinion

The use of European quantitative criteria (i.e. the proportion of the seabird population to be included in the Natura 2000 network) also implies the use of an arbitrary threshold (i.e. the minimum 20 % threshold), which drives the results. Obviously, the use of a higher threshold would increase the number of concentration areas and the size of the optimal network. The application of this minimum threshold at the biogeographic scale was responsible for the selection of the most important hotspots and the potential to neglect less important ones. For this reason, some areas may appear blank ('white') on the results maps, either inside or outside the SPAs, but this did not mean that birds were not present in these areas. It simply meant that such data did not pass the threshold, despite the potential presence of a breeding colony or a known foraging area. Therefore, our results represented a relative prioritization of the most concentrated areas for seabirds and should only be considered in the present context of network evaluation.

Moreover, this application of quantitative criteria was an important first step in the process of designating concentration and priority areas, but should not be considered in isolation. Indeed, the other European qualitative criteria (i.e. network distribution within the species range, physical and biological essential factors) must also be considered prior to SPA designation, according to the available literature and expert opinion [68]. For example, the inclusion of essential habitat has supported the designation of the large SPA along the Atlantic shelf break (SPA n°FR5212016), where data are very limited.

4.2.3. National vs. pan-European networks

Establishing coherent and functional ecological networks for highly mobile species remains a scientific challenge [18]. The site-based Natura 2000 approach recommends appropriate siting of protected areas around seasonal aggregations in order to benefit conservation and optimize efforts [73]. This approach has been criticized for limited effectiveness for highly mobile species that require large-scale, coordinated international action [69,70]. National designations are limited to administrative boundaries that seabirds regularly cross [71]. Following the need for transboundary marine spatial planning and management [72,73], SPA and mIBA network assessment could be based on pooled European distribution data and common workflow, to facilitate gap analysis and final network completion at the pan-European level.

4.2.4. A fixed network in a changing world

To date, the complex, interconnected and spatio-temporally variable marine environment has been protected by fixed SPA boundaries. As environmental variability and climate change impacts on marine ecosystems, among others, have contrasting effects on seabird demography and distribution [74], the fixed boundaries of protected areas have become an issue for sustainable seabird conservation. In the long term, the conservation contribution of current boundaries may be compromised. One proposed solution is to incorporate predicted future distributions into network design and evaluation [75]. Such predictions would allow potential range shifts to be identified and refugia to be pre-emptively secured, thus creating a network that allows for seabird adaptation and resilience [76,77]. However, accurately predicting the future distribution of marine species and ecosystems is another major challenge [78]. Another more practical option, less sensitive to uncertainty by adapting to environmental variability in near real time, has also been developed with dynamic management [79]. In any case, the sustainability of the seabird populations and their adequate coverage by the Natura 2000 network will always depend on strong scientific knowledge integrated into policy [20] and effective management [80].

5. Conclusion

The inherently challenging marine environment has slowed down the establishment of protected areas within it, as has the time-consuming and resource-intensive task of collecting data at sea repetitive. Despite the efforts made to monitor seabirds throughout the maritime zone of metropolitan France, it is not surprising that information on their spatio-temporal distribution and ecology still needs to be improved. The valuable data already collected have shown the importance of certain areas that have been repeatedly identified by various studies. Again, their identification in this study as seabird hotspots outside the French Natura 2000 network of SPAs gave confidence to confirm the existence of remaining gaps in the network. This national example illustrated the challenge of establishing a coherent, complete and functional ecological network for seabirds at the pan-European level. While additional marine data are being collected, the SPA network still needs scientific progress to be completed and to meet its conservation objectives. Continuing pressures on marine ecosystems make this imperative.

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Credit authorship contribution statement

Timothée Poupart: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thibaut de Bettignies**: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Matthieu Authier**: Writing – review & editing, Data curation. **Nicola Baccetti**: Writing – review & editing, Data curation. **Luca Börger**: Writing – review & editing, Data curation. **Iker Castège**: Writing – review & editing, Data curation. **Jacopo G. Cecere**: Writing – review & editing, Data curation. **Nicolas Courbin**: Writing – review & editing, Data curation. **Jamie Darby**: Writing – review & editing, Data curation. **Karine Delord**: Writing – review & editing, Data curation. **Ghislain Doremus**: Writing – review & editing, Data curation. **Hayley A. Douglas**: Writing – review & editing, Data curation. **Gilles Faggio**: Writing – review & editing, Data curation. **Giorgia Gaibani**: Writing – review & editing, Data curation. **Fabrice Gallien**: Writing – review & editing, Data curation. **Cécile Gicquel**: Writing – review & editing, Data curation. **Jacob González-Solís**: Writing – review & editing, Data curation. **David Grémillet**: Writing – review & editing, Data curation. **Simona Imperio**: Writing – review & editing, Data curation. **Jude Lane**: Writing – review & editing, Data curation. **Amélie Lescroël**: Writing – review & editing, Data curation. **Maite Louzao**: Writing – review & editing, Data curation. **Jeanne de Mazières**: Writing – review & editing, Data curation. **Noëmie Michez**: Writing – review & editing, Data curation. **Emilie Milon**: Writing – review & editing, Data curation. **Ellie Owen**: Writing – review & editing, Data curation. **Vitor H. Paiva**: Writing – review & editing, Data curation. **Federico De Pascalis**: Writing – review & editing, Data curation. **Clara Péron**: Writing – review & editing, Data curation. **Francesco Pezzo**: Writing – review & editing, Data curation. **Pascal Provost**: Writing – review & editing, Data curation. **Raül Ramos**: Writing – review & editing, Data curation. **Jaime A. Ramos**: Writing – review & editing, Data curation. **Solène Robert**: Writing – review & editing, Data curation. **Diego Rubolini**: Writing – review & editing, Data curation. **Olivier Scher**: Writing – review & editing, Data curation. **Lorenzo Serra**: Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors have no competing interests to declare.

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Appendices

Table A.1
Seabird taxa by biogeographical region (ATL= Atlantic Ocean, MED= Mediterranean Sea)

English name	Latin name	Region		IUCN Conservation status	
		ATL	MED	Europe	France
Red-throated diver	*Gavia stellata*	✓	✗	LC	na
Black-throated diver	*Gavia arctica*	✓	✓	LC	na
Great northern diver	*Gavia immer*	✓	✗	LC	VU
Great crested grebe	*Podiceps cristatus*	✓	✓	LC	LC
Red-necked grebe	*Podiceps grisegena*	✓	✗	VU	CR
Slavonian grebe	*Podiceps auritus*	✓	✗	VU	VU
Black-necked grebe	*Podiceps nigricollis*	✓	✗	VU	LC
Fulmar	*Fulmarus glacialis*	✓	✗	VU	NT
Scopoli's shearwater	*Calonectris diomedea*	✓	✓	LC	VU
Cory's shearwater	*Calonectris borealis*	✓	✗	LC	-
Great shearwater	*Puffinus gravis*	✓	✗	LC	na
Sooty shearwater	*Puffinus griseus*	✓	✗	NT	na
Manx shearwater	*Puffinus puffinus*	✓	✗	LC	EN
Balearic shearwater	*Puffinus mauretanicus*	✓	✓	CR	VU
Yelkouan shearwater	*Puffinus yelkouan*	✗	✓	VU	EN
Storm petrel (Atlantic ssp.)	*Hydrobates pelagicus pelagicus*	✓	✗	LC	VU
Storm petrel (Mediterranean ssp.)	*Hydrobates pelagicus melitensis*	✗	✓	LC	VU
Leach's storm petrel	*Oceanodroma leucorhoa*	✓	✗	NT	na
Gannet	*Morus bassanus*	✓	✓	LC	NT
Cormorant	*Phalacrocorax carbo carbo*	✓	✓	LC	LC
Shag (Atlantic ssp)	*Phalacrocorax aristotelis aristotelis*	✓	✗	LC	LC
Shag (Mediterranean ss.)	*Phalacrocorax aristotelis desmarestii*	✗	✓	LC	LC
Dark-bellied brent goose	*Branta bernicla bernicla*	✓	✗	LC	LC
Light-bellied brent goose	*Branta bernicla hrota*	✓	✗	LC	LC
Common shelduck	*Tadorna tadorna*	✓	✗	LC	LC
Greater scaup	*Aythya marila*	✓	✗	LC	NT
Eider	*Somateria mollissima*	✓	✓	EN	CR
Long-tailed duck	*Clangula hyemalis*	✓	✗	LC	na
Common scoter	*Melanitta nigra*	✓	✓	LC	LC

(continued on next page)

Table A.1 (*continued*)

Velvet scoter	*Melanitta fusca*	☑	☑	VU	EN
Goldeneye	*Bucephala clangula*	☑	☒	LC	na
Red-breasted merganser	*Mergus serrator*	☑	☒	NT	CR
Red phalarope	*Phalaropus fulicarius*	☑	☒	LC	na
Pomarine skua	*Stercorarius pomarinus*	☑	☒	LC	na
Arctic skua	*Stercorarius parasitus*	☑	☑	EN	na
Long-tailed skua	*Stercorarius longicaudus*	☑	☒	LC	VU
Great skua	*Catharacta skua*	☑	☑	LC	na
Mediterranean gull	*Ichthyaetus melanocephalus*	☑	☑	LC	LC
Little gull	*Hydrocoloeus minutus*	☑	☑	LC	na
Sabine's gull	*Xema sabini*	☑	☒	LC	na
Black-headed gull	*Chroicocephalus ridibundus*	☑	☑	LC	NT
Audouin's gull	*Ichthyaetus audouinii*	☒	☑	VU	EN
Common gull	*Larus canus*	☑	☒	LC	EN
Lesser black-backed gull	*Larus fuscus*	☑	☑	LC	LC
Herring gull	*Larus argentatus*	☑	☒	LC	NT
Yellow-legged gull	*Larus michahellis*	☑	☑	LC	LC
Great black-backed gull	*Larus marinus*	☑	☒	LC	LC
Kittiwake	*Rissa tridactyla*	☑	☑	VU	VU
Sandwich tern	*Thalasseus sandvicensis*	☑	☑	LC	NT
Roseate tern	*Sterna dougallii*	☑	☒	LC	CR
Common tern	*Sterna hirundo*	☑	☑	LC	LC
Arctic tern	*Sterna paradisaea*	☑	☒	LC	CR
Little tern	*Sternula albifrons*	☑	☑	LC	LC
Black tern	*Chlidonias niger*	☑	☑	LC	EN
Guillemot	*Uria aalge*	☑	☒	LC	EN
Razorbill	*Alca torda*	☑	☑	LC	CR
Puffin	*Fratercula arctica*	☑	☑	EN	CR
TOTAL : 57		53	27		

Table A.2
Datasets compiled for waters under French jurisdiction in the Atlantic Ocean (ATL) and the Mediterranean Sea (MED)

Dataset name	Region	Producer(s)	Diffusion platform	Access	Linked publication	URL giving access or contact
Argos_Macreuse noire Mont St Michel_2011_2012	ATL	P. Provost S. Provost	-	request	-	pascal.provost@lpo.fr
Argos_Plongeon catmarin Lithuanie_2013_2017	ATL	R. Žydelis	Movebank	request	-	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study5636685 zydelis@ornitela.eu
Argos_Puffin des Baléares Mor braz_2012_2013	ATL, MED	FAME program	-	request	-	henri.weimerskirch@cebc.cnrs.fr
Comptages Wetlands	ATL, MED	Wetlands International	LPO, INPN	request	-	https://www.wetlands.org/ gwenael.quaintenne@lpo.fr
DepoBio transects aérien	ATL	Impact assessment studies	Depobio	harvest (SINP)	-	https://depot-legal-biodiversite.naturefrance.fr/
Enquête OFB Grèbes-Plongeons	ATL	OFB	-	request	-	sonia.carrier@ofb.gouv.fr
GPS Goéland brun 2010_2019	ATL, MED	UVA	Zenodo	public	[81]	https://zenodo.org/records/3565706#.Yz1U-oTP02x
Faune France 2002_2022	ATL, MED	Faune France	Faune France	request	-	http://www.faune-france.org/ philippe.jourde@lpo.fr
GPS_Cormoran huppé Chausey_2011_2018	ATL	D. Grémillet	-	request	[82]	https://doi.org/10.1007/s00227-020-3655-5 david.gremillet@cefe.cnrs.fr
GPS_Cormoran huppé Saint Marcouf_2018	ATL	D. Grémillet	-	request	[82]	https://doi.org/10.1007/s00227-020-3655-5 david.gremillet@cefe.cnrs.fr
GPS_Fou de Bassan Bass Rock_2018_2019	ATL	K. Hamer, J. Lane	Seabird Tracking Database	request	[83]	https://data.seabirdtracking.org/dataset/1815
GPS_Fou de Bassan Great Saltee_2017_2018	ATL	M. Jessopp, A. Bennison	Seabird Tracking Database	request		https://data.seabirdtracking.org/dataset/1543 m.jessop@ucc.ie
GPS_Fou de Bassan Les Etacs_2011_2015	ATL	V. Warwick-Evans	Movebank	public	[84]	https://www.datarepository.movebank.org/handle/10255/move.697
GPS_Fou de Bassan Sept Îles_2005_2017	ATL	D. Grémillet	Seabird Tracking Database	request		https://data.seabirdtracking.org/dataset/734 and 1793,1794,1795,1796 david.gremillet@cefe.cnrs.fr
GPS_Fulmar boréal 2010_2019	ATL	UCC	-	request	[85]	https://doi.org/10.3354/meps13887 jamie.darby@ucc.ie
GPS_Fulmar boreal St Martins_2011	ATL	RSPB, FameStar-NOFU-STM	Seabird Tracking Database	request	[85]	https://data.seabirdtracking.org/dataset/1237eowen@nts.org.uk
GPS_Goéland argenté Oostende_2013_2018	ATL	UVA	Zenodo	public	[86]	https://zenodo.org/record/3541812#.Yz1niITP02x
GPS_Goéland brun Clyde Muirshiel_2017_2018	ATL	H. Douglas	Movebank	request		https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study261292168 h.a.douglas@hotmail.co.uk
GPS_Goéland d'Audouin Aspretto_2014_2016	MED	B. Recorbet, G. Faggio	Movebank	public		http://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study277815715 gilles.faggio@oec.fr
GPS_Goéland d'Audouin Pianosa_2015_2020	MED	N. Bacetti, M. Zenatello	Movebank	request		https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study297847376 nicola.baccetti@isprambiente.it
GPS_LARUS_LPO Ré_2017_2022	ATL	LPO	Movebank	request	-	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study603876591 frederic.robin@lpo.fr
GPS_Mouette mélanocéphale Cervia_2016_2017	ATL, MED	J.G.Cecere, L.Serra, F.De Pascalis	Movebank	request		https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1131915461 lorenzo.serra@isprambiente.it
GPS_Mouette tridactyle Boulogne_2014	ATL	D. Grémillet	-	request	[87]	https://doi.org/10.1007/s00227-017-3151-8 david.gremillet@cefe.cnrs.fr
GPS_Mouette tridactyle Fécamp_2014	ATL	D. Grémillet	-	request	[87]	https://doi.org/10.1007/s00227-017-3151-8 david.gremillet@cefe.cnrs.fr
GPS_Mouette tridactyle St Pierre du Mont_2014	ATL	D. Grémillet	-	request	[87]	https://doi.org/10.1007/s00227-017-3151-8 david.gremillet@cefe.cnrs.fr
GPS_Océanite tempête Banneg_2020_2021	ATL	B. Cadiou	Movebank	request	-	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1401942981 bernard.cadiou@bretagne-vivante.org
GPS_Océanite tempête Capo Caccia_2019_2021	MED	J.G. Cecere, D. Rubolini, F. De Pascalis	Seabird Tracking Database	request	[88]	https://data.seabirdtracking.org/dataset/1556 and 1617, 1853 federico.depascalis@unimi.it
GPS_Puffin cendré Cima islet_2011_2015	ATL	V. Paiva, J. Ramos	Seabird Tracking Database	request		https://data.seabirdtracking.org/dataset/1033
GPS_Puffin de Scopoli LaMaddalena_(inc) _2011_2019	MED	J.G. Cecere, G. Gaibani, S. Imperio	Seabird Tracking Database	request	[89]	https://data.seabirdtracking.org/dataset/785 iacopo.cecere@isprambiente.it
GPS_Puffin de Scopoli Cala Morell_2014_2020	MED	J. Gonzalez-Solis	Seabird Tracking Database	request		https://data.seabirdtracking.org/dataset/1618 and 1619, 1623, 1624, 1643,1644 jgsolis@ub.edu
GPS_Puffin de Scopoli Frioul_2011	MED	D. Grémillet C. Péron	Seabird Tracking Database	request	[40]	https://data.seabirdtracking.org/dataset/1803 david.gremillet@cefe.cnrs.fr

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Table A.2 (*continued*)

GPS_Puffin de Scopoli Giraglia_2011_2012	MED	D. Grémillet C. Péron	Seabird Tracking Database	request	[41]	http://seabirdtracking.org/mapper/index.php david.gremillet@cefe.cnrs.fr
GPS_Puffin de Scopoli LaMaddalena_ (chick-rear) _2013	MED	J. G. Cecere, S. Imperio, D. Rubolini, F. De Pascalis	Seabird Tracking Database	request	[90]	https://data.seabirdtracking.org/dataset/1554 and 1555 iacopo.cecere@isprambiente.it
GPS_Puffin de Scopoli LaScola_2010_2011	MED	J. G. Cecere, G. Gaibani, S. Imperio N. Bacetti	Seabird Tracking Database	request	[91]	https://data.seabirdtracking.org/dataset/786 iacopo.cecere@isprambiente.it
GPS_Puffin de Scopoli Lavezzi_2011_2012	MED	D. Grémillet C. Péron	Seabird Tracking Database	request	[41]	http://seabirdtracking.org/mapper/index.php david.gremillet@cefe.cnrs.fr
S_Puffin de Scopoli Riou_2011_2020	MED	D. Grémillet C. Péron	Seabird Tracking Database	request	[40,41]	https://data.seabirdtracking.org/dataset/1804 and 1805, 1806 david.gremillet@cefe.cnrs.fr
GPS_Puffin de Scopoli Spargiotto_2013_2019	MED	J. Cecere, G. Gaibani, S. Imperio N. Baccetti	Seabird Tracking Database	request	[91]	https://data.seabirdtracking.org/dataset/784 iacopo.cecere@isprambiente.it
GPS_Puffin des Anglais 2008_2016	ATL	T. Guilford	Movebank	public	[92]	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study961039869
GPS_Puffin yelkouan Montecristo_2021_2022	MED	M. Zenatello, N. Baccetti	Movebank	request	-	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1958889088 nicola.baccetti@isprambiente.it
GPS_Puffin yelkouan Port-Cros_2011_2012	MED	D. Grémillet, C. Péron	Seabird Tracking Database	request	[42]	http://seabirdtracking.org/mapper/index.php david.gremillet@cefe.cnrs.fr
GPS_Puffin yelkouan Tavolara_2011_2015	MED	M. Zenatello, N. Baccetti	Movebank	public	[93]	https://www.datarepository.movebank.org/handle/10255/move.1326
GPS_Sterne caugek EFGL/EolMed_2021	MED	O. Scher, CEN Occitanie	Movebank	request	-	http://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1546386720 olivier.scher@cen-occitanie.org
ObsEnMer	ATL, MED	GECC	ObsEnMer	request	-	https://www.obsenmer.org/ obsenmer@gecc-normandie.org
PNM Golfe du Lion	MED	OFB	-	request	-	noemie.michez@ofb.gouv.fr
RN estuaire de la Seine	ATL	Natural reserve of the Seine estuary	-	request	-	https://www.maisondelestuaire.org/ simon.guilbaud@maisondelestuaire.org
SINP	ATL, MED	PatriNat	SINP	request	-	https://inpn.mnhn.fr/informations/sinp/presentation solene.robert@mnhn.fr
Survols OFB Bretagne Nord	ATL	OFB	-	request	-	elodie.giacomini@ofb.gouv.fr
Survols OFB PNMI	ATL	OFB	-	request	-	cecile.gicquel@ofb.gouv.fr
Transects aériens SAMM, SCANS	ATL, MED	PELAGIS Observatory	PelaObs	request	[23,24]	https://www.observatoire-pelagis.cnrs.fr/ ghislain.doremus@univ-lr.fr
Transects aériens SPEE	ATL	PELAGIS Observatory	PelaObs	request	-	http://www.observatoire-pelagis.cnrs.fr/ ghislain.doremus@univ-lr.fr
Transects nautiques DepoBio	ATL	Impact assessment studies	Depobio	harvest (SINP)	-	https://depot-legal-biodiversite.naturefrance.fr/
Transects nautiques ERMMA	ATL	Biarritz Sea centre	-	request	[94]	https://www.centredelamer.fr/ iker.castege@centredelamer.fr
Transects nautiques MEGASCOPE 2003_2020 (CGFS, EVHOE, IBTS, PELGAS)	ATL	PELAGIS Observatory	PelaObs	request	-	https://www.observatoire-pelagis.cnrs.fr/ ghislain.doremus@univ-lr.fr
Transects nautiques PELMED 2002_2016	MED	Ifremer, CEFE	-	request	-	https://campagnes.flotteoceanographique.fr/series/19/fr/ david.gremillet@cefe.cnrs.fr
Transects nautiques PELMED, MOOSE	MED	PELAGIS Observatory	PelaObs	request	-	https://www.observatoire-pelagis.cnrs.fr/ ghislain.doremus@univ-lr.fr
Trektellen	ATL, MED	Trektellen	Trektellen	request	-	https://www.trektellen.nl/?language=french gerard.troost@sovon.nl

Table A.3
Assignment of species to predicted distribution layers

Predicted distribution layers on taxonomic groups from PELAGIS	Attributed species	
	Atlantic Ocean	Mediterranean Sea
Alcidae	Guillemot	NA
CATSKU	Great skua	NA
Grey gulls	Herring gull	Yellow-legged gull
Black gulls	Lesser black-backed gull	NA
LARMIN	Little gull	Little gull
LARMEL	NA	Mediterranean gull
LARSPP	Black-headed gull	NA

(*continued on next page*)

Table A.3 (*continued*)

Predicted distribution layers on taxonomic groups from PELAGIS	Attributed species	
	Atlantic Ocean	Mediterranean Sea
Hydrobatidae	Atlantic Storm petrel	Mediterranean Storm petrel
Procellaridae	Manx shearwater	NA
Small procellariforms	NA	Not used
Large procellariforms	NA	Not used
Sternidae	Sandwich tern	Sandwich tern
SULBAS	Gannet	Gannet
RISTRI	Kittiwake	NA

Table A.4
Datasets compiled in this study

Dataset	Producer(s)	Number of data		Remarks
		ATL	MED	
National citizen science database Faune-France	LPO and contributors	1 274 954	250 750	Marine environment + 500 m coastal strip to include all land-based observations
Tracking in France	see Annex II	872 908	635 786	GPS, Argos
Tracking abroad	see Annex II	432 607	75 909	GPS
Trektellen	Trektellen	7427	8 437	Stationnary birds only
SINP	SINP	54 466	3 405	Duplicates removal
MEGASCOPE (CGFS, EVHOE, IBTS, PELGAS)	PELAGIS Observatory	52 785	-	-
Natural reserve of the Seine estuary	Natural reserve of the Seine estuary	58 632	-	-
Aerial transects (SAMM, SCANS, SPEE)	PELAGIS Observatory	20 427	3 222	-
National citizen science database ObsEnMer	GECC	16 277	4 360	-
ERMMA	Biarritz Sea Centre	23 771	-	-
Nautical transects (DepoBio)	DepoBio	29 636	-	-
Wetlands census	LPO and contributors	14 553	1 733	Mediterranean Sea: 2002–2021 Atlantic Ocean: sub-sectors accuracy, 2019–2022
Aerial transects (DepoBio)	DepoBio	7 993	-	-
Nautical transects PELMED	Ifremer - CEFE	-	9 867	2002–2016
Aerial transects OFB Bretagne Nord	OFB	2 202	-	-
Aerial transects OFB PNMI	OFB	1 923	-	-
Ring controls	CRBPO	2 911	88	-
Nautical transects (PELMED, MOOSE)	PELAGIS Observatory	-	2 357	2017–2020
National marine parc of the Gulf of Lion	National marine parc of the Gulf of Lion	-	1 842	-
Census OFB Grebes and Loons	OFB	108	-	-
TOTAL		2 857 590	997 756	-

Table A.5
At-sea data by species for the French Atlantic

Species	Maximum Responsibility Index [50]	Sighting	Tracking (France)	Tracking (abroad)	Interpolated density (nautical transects)	Predicted density (aerial transects)	TOTAL
Herring gull	3.3	131 749	192 629	176 158	4 181	1 377	506 094
Gannet	4.3	71 997	256 452	103 421	32 931	16 995	481 796
Lesser black-backed gull	2.8	67 314	95 062	143 097	6 474	1 230	313 177
Great black-backed gull	2.5	95 721	181 730	0	3 668	1 238	282 357
Black-headed gull	3	155 772	0	0	222	290	156 284
Shag	3	28 549	125 792	0	1 293	494	156 128
Common shelduck	3.3	123 659	0	0	29	47	123 735
Dark-bellied brent goose	5	92 605	0	0	111	162	92 878
Cormorant	2	87 060	0	0	739	178	87 977
Sandwich tern	3.3	74 387	0	0	1 290	503	76 180
Mediterranean gull	2.3	66 501	0	5 160	674	528	72 863
Great crested grebe	2.3	55 278	0	0	42	12	55 332
Kittiwake	5	16 197	15 698	0	4 399	5 737	42 031
Yellow-legged gull	1.3	40 294	0	0	155	5	40 454
Common gull	4.3	39 040	0	0	234	155	39 429

(continued on next page)

Table A.5 (*continued*)

Common tern	1.5	35 427	0	0	425	86	35938
Black scoter	2	26 704	4 350	0	245	123	31 422
Guillemot	6.5	21 073	0	0	10 096	36	31 205
Black-necked grebe	1.3	28 876	0	0	19	0	28 895
Balearic shearwater	8	19867	411	0	1 813	86	22 177
Great northern diver	5	16944	0	0	288	0	17 232
Great skua	3.3	11585	0	0	2 380	658	14 623
Razorbill	7.8	10 467	0	0	3 254	4	13 725
Fulmar	5.8	6 966	0	2 645	2 863	707	13 181
Little gull	3.8	10 612	0	0	542	1 616	12 770
Red-throated diver	5	11 403	0	106	149	1	11 659
Arctic skua	5.3	9 290	0	0	127	0	9 417
Manx shearwater	6.5	7 859	0	309	638	18	8 824
Slavonian grebe	4.3	8 625	0	0	0	0	8 625
Little tern	1	7 039	0	0	4	5	7 048
Storm petrel	5.3	4 444	784	0	1 722	6	6 956
Eider	5	6 416	0	0	16	5	6 437
Black-throated diver	5	5 487	0	0	126	0	5 613
Black tern	6.5	5 370	0	0	49	0	5 419
Sooty shearwater	1	4 563	0	0	314	0	4 877
Long-tailed duck	1	2 969	0	0	1	0	2 970
Velvet scoter	6.3	2 962	0	0	0	6	2 968
Light-bellied brent goose	5	2 965	0	0	0	0	2 965
Red phalarope	1	2 571	0	0	28	0	2 599
Roseate tern	7	2 518	0	0	3	0	2 521
Pomarine skua	5.3	2 387	0	0	94	0	2 481
Sabine's gull	1	2 002	0	0	86	3	2 091
Cory's/Scopoli's shearwater	3.5	1 741	0	0	18	221	1 980
Arctic tern	1	1 815	0	0	12	0	1 827
Goldeneye	1.8	1 714	0	0	0	0	1 714
Cory's shearwater	3.5	0	0	1 711	0	0	1 711
Great shearwater	1	1 297	0	0	386	11	1 694
Puffin	7.8	1 327	0	0	255	0	1 582
Greater scaup	6	1 525	0	0	0	0	1 525
Red-breaster merganser	2.5	1 467	0	0	4	2	1 473
Leah's storm petrel	1	1 372	0	0	16	0	1 388
Red-necked grebe	1	1 062	0	0	1	0	1 063
Long-tailed skua	5.3	275	0	0	5	0	280
TOTAL		1 437 109	872 908	432 607	82 421	32 545	2 857 590

Table A.6
At-sea data by species for the French Mediterranean

Species	Maximum Responsibility Index [50]	Sighting	Tracking (France)	Tracking (abroad)	Interpolated density (nautical transects)	Predicted density (aerial transects)	TOTAL
Scopoli shearwater	5.3	5 874	521 261	45 501	2 226	202	575 064
Sandwich tern	2.5	23 263	59 731	0	683	184	83 861
Yellow-legged gull	3.5	76 117	0	0	6 163	600	82 880
Black-headed gull	3.3	57 137	0	0	36	52	57 225
Yelkouan shearwater	6.5	2 661	17 748	24 226	896	0	45 531
Audouin's gull	6.5	1 808	37 046	3 153	127	0	42 134
Cormorant	2	34 176	0	0	3	9	34 188
Mediterranean gull	2.8	10 547	0	2 569	287	462	13 865
Great crested grebe	1.5	12 464	0	0	0	0	12 464
Common tern	1.5	10 032	0	0	823	0	10 855
Little tern	2	9 003	0	0	12	16	9 031
Gannet	1.8	7 058	0	0	399	156	7 613
Shag	3.5	6 168	0	0	6	18	6 192
Little gull	5.5	1 753	0	0	0	1 328	3 081
Lesser black-backed gull	1	2 646	0	70	4	0	2 720
Black-throated diver	3	1 704	0	0	0	0	1 704
Balearic shearwater	7	1 008	0	0	376	0	1 384
Black tern	4.3	1 257	0	0	19	0	1 276
Storm petrel	7.8	593	0	390	90	97	1170
Arctic skua	3	1 114	0	0	14	0	1 128
Razorbill	4.3	985	0	0	1	89	1 075
Eider	3	906	0	0	0	0	906
Velvet scoter	4.3	802	0	0	0	0	802

(*continued on next page*)

Table A.6 (*continued*)

Kittiwake	3	602	0	0	1	1	604
Black scoter	1.3	392	0	0	0	0	392
Great skua	1	311	0	0	36	8	355
Puffin	4.3	234	0	0	22	0	256
TOTAL		270 615	635 786	75 909	12 224	3 222	997 756

Data availability

The authors do not have permission to share all the data, but available data are shown in Table A.2.

References

[1] J.G. Nelson, National parks and protected areas, national conservation strategies and sustainable development, Geoforum 18 (3) (1987) 291–319, https://doi.org/10.1016/0016-7185(87)90013-3.

[2] G.W. Allison, J. Lubchenco, M.H. Carr, Marine reserves are necessary but not sufficient for marine conservation, Ecol. Appl. 8 (sp1) (1998) S79–S92, https://doi.org/10.1890/1051-0761(1998)8[S79:MRANBN]2.0.CO;2.

[3] P.D. Boersma, J.K. Parrish, Limiting abuse: marine protected areas, a limited solution, Ecol. Econ. 31 (2) (1999) 287–304, https://doi.org/10.1016/S0921-8009(99)00085-3.

[4] C.M. Roberts, Selecting marine reserve locations: optimality versus opportunism, Bull. Mar. Sci. 66 (3) (2000) 581–592.

[5] R.H.G. Jongman, Nature conservation planning in Europe: developing ecological networks, Landsc. Urban Plan. 32 (3) (1995) 169–183, https://doi.org/10.1016/0169-2046(95)00197-O.

[6] C.R. Margules, R.L. Pressey, Systematic conservation planning, Nature 405 (2000) 243–253, https://doi.org/10.1038/35012251.

[7] EEA. The Natura 2000 protected areas network. [Page] 2023 [cited 2025 9 March]; Available from: 〈https://www.eea.europa.eu/themes/biodiversity/natura-2000〉.

[8] EC, Guidelines for the establishment of the Natura 2000 network in the marine environment. 2007. p. 79.

[9] B.S. Halpern, S. Walbridge, K.A. Selkoe, C.V. Kappel, F. Micheli, C. d'Agrosa, J. F. Bruno, K.S. Casey, C. Ebert, H.E. Fox, A global map of human impact on marine ecosystems, science 319 (5865) (2008) 948–952, https://doi.org/10.1126/science.1149345.

[10] R.A. Phillips, J. Fort, M.P. Dias, Conservation status and overview of threats to seabirds. Conservation of marine birds, Academic Press, 2023, pp. 33–56, https://doi.org/10.1016/B978-0-323-88539-3.00015-7.

[11] N. Courbin, A. Besnard, D. Grémillet, Transnational mortality from Spanish longline fisheries bycatch is shaping the decline of a vulnerable French seabird, Biol. Conserv. 293 (2024) 110597, https://doi.org/10.1016/j.biocon.2024.110597.

[12] N. Courbin, E. Dortel, D. Grémillet, Jd Lebreton, A. Besnard, Note on demography to assist in the management and conservation of breeding seabird populations along the French mainland coast, Naturae 2022 (16) (2022) 285–296, https://doi.org/10.5852/naturae2022a16.

[13] R.H.G. Jongman, M. Külvik, I. Kristiansen, European ecological networks and greenways, Landsc. Urban Plan. 68 (2-3) (2004) 305–319, https://doi.org/10.1016/S0169-2046(03)00163-4.

[14] ETC/BD, Additional guidelines for assessing sufficiency of Natura 2000 proposals (SCIs) for marine habitats and species. 2010: Paris. p. 17.

[15] V. Kati, T. Hovardas, M. Dieterich, P.L. Ibisch, B. Mihok, N. Selva, The challenge of implementing the European network of protected areas Natura 2000, Conserv. Biol. 29 (1) (2015) 260–270, https://doi.org/10.1111/cobi.12366.

[16] E.A. Virtanen, M. Viitasalo, J. Lappalainen, A. Moilanen, Evaluation, gap analysis, and potential expansion of the Finnish marine protected area network, Front. Mar. Sci. 5 (2018), https://doi.org/10.3389/fmars.2018.00402.

[17] Mitchell, D., Vulcano, A. & Dias, M., Assessment of the protection of Important Bird and Biodiversity Areas for seabirds by Special Protection Areas of the Natura 2000 network. How well are EU Member States protecting seabirds?, B. International, Editor. 2022. p. 39.

[18] EC, Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions - EU Biodiversity Strategy for 2030. Bringing nature back into our lives, E. Commission, Editor. 2020: Brussels. p. 22.

[19] CBD, Decision adopted by the Conference of the Parties to the Convention on Biological Diversity - 15/4. Kunming-Montreal Global Biodiversity Framework., C. o.B. Diversity, Editor. 2022: Montreal, Canada. p. 20.

[20] J. Claudet, C. Loiseau, A. Pebayle, Critical gaps in the protection of the second largest exclusive economic zone in the world, Mar. Policy 124 (2021) 104379, https://doi.org/10.1016/j.marpol.2020.104379.

[21] R. Devillers, R.L. Pressey, A. Grech, J.N. Kittinger, G.J. Edgar, T. Ward, R. Watson, Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? Aquat. Conserv.: Mar. Freshw. Ecosyst. 25 (4) (2015) 480–504, https://doi.org/10.1002/aqc.2445.

[22] OFB, 2018, DCSMM - Sous-régions marines (France), O.f.d.l. biodiversité, Editor.

[23] Laran, S., Genu, M., Authier, M., Blanchard, A., Dorémus, G., Sanchez, T., Spitz, J. & Van Canneyt, O., Distribution et abondance de la mégafaune marine en France métropolitaine. Rapport final de la campagne SAMM II Atlantique-Manche - Hiver 2021. 2022, Observatoire Pelagis (UAR 3462, La Rochelle Université / CNRS). p. 72.

[24] Laran, S., Nivière, M., Genu, M., Dorémus, G., Serre, S., Spitz, J., Van Canneyt, O. & Authier, M., Distribution et abondance de la mégafaune marine lors des campagnes SAMM cycle I et II en Méditerranée. Rapport final. 2021, Observatoire Pelagis (UMS 3462, La Rochelle Université / CNRS) & OFB. p. 76.

[25] Pettex, E., Lambert, C., Laran, S., Ricart, A., Virgili, A., Falchetto, H., Authier, M., Monestiez, P., Van Canneyt, O., Dorémus, G., Blanck, A., Toison, V. & Ridoux, V., Suivi aérien de la mégafaune marine en France métropolitaine. Rapport final. 2014, Observatoire Pelagis (UMS 3462, La Rochelle Université / CNRS) & Agence des aires marines protégées. p. 123.

[26] Comolet-Tirman, J., Hindermeyer, X. & Siblet, J.P., Liste des oiseaux marins susceptibles de justifier la création de Zone de Protection Spéciale. 2007, SPN/MEDD: Paris, France. p. 11.

[27] Cadiou, B., Méthodes de suivi des colonies d'oiseaux marins: dénombrement de l'effectif nicheur et suivi de la population en jeunes. 2022, GISOM (groupement d'intérêt scientifique oiseaux marins). p. 107.

[28] BirdLife International, Seabird Tracking Database - a platform for seabird researchers to share their tracking data with the research and conservation communities, B. International, Editor. 2023.

[29] Wikelski, M., Davidson, S.C. & Kays, R., Movebank: archive, analysis and sharing of animal movement data. 2023, Max Planck Institute of Animal Behavior, the North Carolina Museum of Natural Sciences, and the University of Konstanz.

[30] I. García-Barón, S. Giakoumi, M.B. Santos, I. Granado, M. Louzao, The value of time-series data for conservation planning, J. Appl. Ecol. 58 (3) (2021) 608–619, https://doi.org/10.1111/1365-2664.13790.

[31] C. Lambert, G. Dorémus, V. Ridoux, The persistence in time of distributional patterns in marine megafauna impacts zonal conservation strategies, Peer Community J. 1 (2021) e39, https://doi.org/10.24072/pcjournal.46.

[32] R Core Team, R: a language and environment for statistical computing. 2022: Vienna, Austria.

[33] E. Pebesma, Simple features for R: standardized support for spatial vector data, R. J. 10 (1) (2018) 439–446, https://doi.org/10.32614/RJ-2018-009.

[34] H. Wickham, ggplot2: elegant graphics for data analysis (ed. Use R!), Springer-Verlag New York, 2016.

[35] P. Yésou, Tempêtes hivernales et échouages d'oiseaux marins en février 2014, OrnithoScience 26 (5) (2019) 244–255.

[36] R.H.G. Klaassen, B.J. Ens, J. Shamoun-Baranes, K.-M. Exo, F. Bairlein, Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*, Behav. Ecol. 23 (1) (2012) 58–68, https://doi.org/10.1093/beheco/arr150.

[37] C. Péron, D. Grémillet, Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird, PloS One 8 (8) (2013) e72713, https://doi.org/10.1371/journal.pone.0072713.

[38] B. Dean, H. Kirk, A. Fayet, A. Shoji, R. Freeman, K. Leonard, C.M. Perrins, T. Guilford, Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area, Mar. Ecol. Prog. Ser. 538 (2015) 239–248, https://doi.org/10.3354/meps11443.

[39] R. Lewison, D. Oro, B.J. Godley, L. Underhill, S. Bearhop, R.P. Wilson, D. Ainley, J. M. Arcos, P.D. Boersma, P.G. Borboroglu, Research priorities for seabirds: improving conservation and management in the 21st century, Endanger. Species Res. 17 (2) (2012) 93–121, https://doi.org/10.3354/esr00419.

[40] N. Courbin, A. Besnard, C. Péron, C. Saraux, J. Fort, S. Perret, J. Tornos, D. Grémillet, Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator, Ecol. Lett. 21 (7) (2018) 1043–1054, https://doi.org/10.1111/ele.12970.

[41] C. Péron, M. Authier, D. Grémillet, Testing the transferability of track-based habitat models for sound marine spatial planning, Divers. Distrib. 24 (12) (2018) 1772–1787, https://doi.org/10.1111/ddi.12832.

[42] C. Péron, D. Grémillet, A. Prudor, E. Pettex, C. Saraux, A. Soriano-Redondo, M. Authier, J. Fort, Importance of coastal marine protected areas for the conservation of pelagic seabirds: the case of vulnerable yelkouan shearwaters in the Mediterranean Sea, Biol. Conserv. 168 (2013) 210–221, https://doi.org/10.1016/j.biocon.2013.09.006.

[43] M. Beal, S. Oppel, J. Handley, E.J. Pearmain, V. Morera-Pujol, A.P.B. Carneiro, T. E. Davies, R.A. Phillips, P.R. Taylor, M.G.R. Miller, A.M.A. Franco, I. Catry, A. R. Patrício, A. Regalla, I. Staniland, C. Boyd, P. Catry, M.P. Dias, track2KBA: an R package for identifying important sites for biodiversity from tracking data, Methods Ecol. Evol. 12 (12) (2021) 2372–2378, https://doi.org/10.1111/2041-210X.13713.

[44] M.I.D. Carter, S.L. Cox, K.L. Scales, A.W.J. Bicknell, M.D. Nicholson, K.M. Atkins, G. Morgan, L. Morgan, W.J. Grecian, S.C. Patrick, GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): implications for foraging ecology and conservation, Bird. Study 63 (1) (2016) 83–95, https://doi.org/10.1080/00063657.2015.1134441.

[45] C. Péron, H. Weimerskirch, C.-A. Bost, Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet islands, Southern Indian Ocean, Proc. R. Soc. B: Biol. Sci. 279 (1738) (2012) 2515–2523, https://doi.org/10.1098/rspb.2011.2705.

[46] A. Bennison, J.L. Quinn, A. Debney, M. Jessopp, Tidal drift removes the need for area-restricted search in foraging Atlantic puffins, Biol. Lett. 15 (7) (2019) 20190208, https://doi.org/10.1098/rsbl.2019.0208.

[47] P. Monestiez, L. Dubroca, E. Bonnin, J.-P. Durbec, C. Guinet, Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts, Ecol. Model. 193 (3–4) (2006) 615–628, https://doi.org/10.1016/j.ecolmodel.2005.08.042.

[48] Genu, M. & Authier, M., pelaKrig: poisson kriging with segmented line-transect data. R package version 0.0.0.9004. 2021.

[49] S.S. Rosenstock, D.R. Anderson, K.M. Giesen, T. Leukering, M.F. Carter, Landbird counting techniques: current practices and an alternative, Auk 119 (1) (2002) 46–53, https://doi.org/10.1093/auk/119.1.46.

[50] Toison, V., Identification et priorisation de la responsabilité de chaque sous-région marine pour les enjeux ornithologiques. 2020, Office français de la biodiversité - GISOM (Groupement d'intérêt scientifique oiseaux marins). p. 16.

[51] A. Moilanen, A.M.A. Franco, R.I. Early, R. Fox, B. Wintle, C.D. Thomas, Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems, Proc. R. Soc. B: Biol. Sci. 272 (1575) (2005) 1885–1891, https://doi.org/10.1098/rspb.2005.3164.

[52] A. Moilanen, K.A. Wilson, H. Possingham, Marxan and relatives: software for spatial conservation prioritization, in: I.R. Ball, H.P. Possingham (Eds.), Spatial conservation prioritisation: quantitative methods and computational tools, Oxford, New York, 2009.

[53] J.O. Hanson, R. Schuster, M. Strimas-Mackey, N. Morrell, B.P. Edwards, P. Arcese, J.R. Bennett, H.P. Possingham, Systematic conservation prioritization with the prioritizr R package, Conserv. Biol. 39 (1) (2025) e14376, https://doi.org/10.1111/cobi.14376.

[54] S. Giakoumi, S. Katsanevakis, V. Vassilopoulou, P. Panayotidis, S. Kavadas, Y. Issaris, A. Kokkali, A. Frantzis, A. Panou, G. Mavrommati, Could European marine conservation policy benefit from systematic conservation planning? Aquat. Conserv.: Mar. Freshw. Ecosyst. 22 (6) (2012) 762–775, https://doi.org/10.1002/aqc.2273.

[55] M. Friedrichs, V. Hermoso, V. Bremerich, S.D. Langhans, Evaluation of habitat protection under the European Natura 2000 conservation network – the example for Germany, PloS One 13 (12) (2018) e0208264, https://doi.org/10.1371/journal.pone.0208264.

[56] J. Delavenne, K. Metcalfe, R.J. Smith, S. Vaz, C.S. Martin, L. Dupuis, F. Coppin, A. Carpentier, Systematic conservation planning in the eastern English Channel: comparing the Marxan and Zonation decision-support tools, ICES J. Mar. Sci. 69 (1) (2012) 75–83, https://doi.org/10.1093/icesjms/fsr180.

[57] D. Silvestro, S. Goria, T. Sterner, A. Antonelli, Improving biodiversity protection through artificial intelligence, Nat. Sustain. 5 (5) (2022) 415–424, https://doi.org/10.1038/s41893-022-00851-6.

[58] Delavenne, J., Lepareur, F., Pettex, E., Touroult, J. & Siblet, J.-P., Extension du réseau Natura 2000 au-delà de la mer territoriale pour les oiseaux et mammifères marins. 2014, Muséum national d'Histoire naturelle/Service du Patrimoine Naturel: Paris. p. 53.

[59] de Bettignies, T. & Aish, A.., Évaluation de la cohérence du réseau Natura 2000 français pour les Oiseaux marins: Façade Atlantique. 2017, PatriNat (AFB-CNRS-MNHN): Paris. p. 27.

[60] de Bettignies, T. & Aish, A., Évaluation de la cohérence du réseau Natura 2000 français pour les Oiseaux marins: Façade Méditerranée. 2017, PatriNat (AFB-CNRS-MNHN): Paris. p. 16.

[61] Poupart, T. & de Bettignies, T., Natura 2000 et mIBAs en France métropolitaine: comparaison des méthodologies de création des réseaux pour la conservation des oiseaux marins. 2021, PatriNat (OFB-CNRS-MNHN): Paris. p. 26.

[62] Deceuninck, B. & Micol, T., Identification des sites marins prioritaires pour les oiseaux marins et les oiseaux d'eaux. 2007, Ligue pour la Protection des Oiseaux: Rochefort. p. 21.

[63] C. Michelot, D. Pinaud, M. Fortin, P. Maes, B. Callard, M. Leicher, C. Barbraud, Seasonal variation in coastal marine habitat use by the European shag: insights from fine scale habitat selection modeling and diet, Deep Sea Res. Part II: Top. Stud. Oceanogr. 141 (2017) 224–236, https://doi.org/10.1016/j.dsr2.2017.04.001.

[64] E. Correia, M. Beal, N. Gomes, N. Diop, F. Wambar, M.P. Dias, A. Hernandez-Rios, T. Catry, Foraging movements and important sites for conservation of the West African Crested tern *Thalasseus albididorsalis* breeding in Guinea-Bissau, Mar. Biol. 171 (2024) 15, https://doi.org/10.1007/s00227-023-04338-6.

[65] A. Bernard, A.S.L. Rodrigues, V. Cazalis, D. Grémillet, Toward a global strategy for seabird tracking, Conserv. Lett. 14 (3) (2021) e12804, https://doi.org/10.1111/conl.12804.

[66] J.J. Waggitt, P.G. Evans, J. Andrade, A.N. Banks, O. Boisseau, M. Bolton, G. Bradbury, T. Brereton, C.J. Camphuysen, J. Durinck, Distribution maps of cetacean and seabird populations in the North-East Atlantic, J. Appl. Ecol. 57 (2) (2020) 253–269, https://doi.org/10.1111/1365-2664.13525.

[67] R.E. Dunn, J. Duckworth, S. O'Brien, R.W. Furness, L. Buckingham, F. Daunt, M. Bogdanova, J.A. Green, Temporal and spatial variability in availability bias has consequences for marine bird abundance estimates during the non-breeding season, Ecol. Solut. Evid. 5 (4) (2024) e12373, https://doi.org/10.1101/2024.03.13.584773.

[68] L.M.J. Kuismanen, E.A. Virtanen, J. Lappalainen, L. Kurvinen, P. Blankett, M. Viitasalo, Identifying ecologically valuable marine areas to support conservation and spatial planning at scales relevant for decision making, Mar. Policy 158 (2023) 105890, https://doi.org/10.1016/j.marpol.2023.105890.

[69] C.M. Fortuna, A. Cañadas, D. Holcer, B. Brecciaroli, G.P. Donovan, B. Lazar, G. Mo, L. Tunesi, P.C. Mackelworth, The coherence of the European Union marine Natura 2000 network for wide-ranging charismatic species: a Mediterranean case study, Front. Mar. Sci. 5 (2018) 356, https://doi.org/10.3389/fmars.2018.00356.

[70] M.P. Dias, R. Martin, E.J. Pearmain, I.J. Burfield, C. Small, R.A. Phillips, O. Yates, B. Lascelles, P.G. Borboroglu, J.P. Croxall, Threats to seabirds: a global assessment, Biol. Conserv. 237 (2019) 525–537, https://doi.org/10.1016/j.biocon.2019.06.033.

[71] A. Lescroël, R. Mathevet, C. Péron, M. Authier, P. Provost, A. Takahashi, D. Grémillet, Seeing the ocean through the eyes of seabirds: a new path for marine conservation? Mar. Policy 68 (2016) 212–220, https://doi.org/10.1016/j.marpol.2016.02.015.

[72] M. Kull, J.R. Moodie, H.L. Thomas, S. Mendez-Roldan, A. Giacometti, A. Morf, I. Isaksson, International good practices for facilitating transboundary collaboration in marine spatial planning, Mar. Policy 132 (2021) 103492, https://doi.org/10.1016/j.marpol.2019.03.005.

[73] S. Li, S. Jay, Transboundary marine spatial planning across Europe: trends and priorities in nearly two decades of project work, Mar. Policy 118 (2020) 104012, https://doi.org/10.1016/j.marpol.2020.104012.

[74] A. Rodríguez, J.M. Arcos, V. Bretagnolle, M.P. Dias, N.D. Holmes, M. Louzao, J. Provencher, A.F. Raine, F. Ramírez, B. Rodríguez, R.A. Ronconi, R.S. Taylor, E. Bonnaud, S.B. Borrelle, V. Cortés, S. Descamps, V.L. Friesen, M. Genovart, A. Hedd, P. Hodum, G.R.W. Humphries, M. Le Corre, C. Lebarbenchon, R. Martin, E.F. Melvin, W.A. Montevecchi, P. Pinet, I.L. Pollet, R. Ramos, J.C. Russell, P. G. Ryan, A. Sanz-Aguilar, D.R. Spatz, M. Travers, S.C. Votier, R.M. Wanless, E. Woehler, A. Chiaradia, Future directions in conservation research on petrels and shearwaters, Front. Mar. Sci. 6 (2019) 94, https://doi.org/10.3389/fmars.2019.00094.

[75] D. Grémillet, T. Boulinier, Spatial ecology and conservation of seabirds facing global climate change: a review, Mar. Ecol. Prog. Ser. 391 (2009) 121–137, https://doi.org/10.3354/meps08212.

[76] E. McLeod, R. Salm, A. Green, J. Almany, Designing marine protected area networks to address the impacts of climate change, Front. Ecol. Environ. 7 (7) (2009) 362–370, https://doi.org/10.1890/070211.

[77] A.D. Mazaris, A.D. Papanikolaou, M. Barbet-Massin, A.S. Kallimanis, F. Jiguet, D. S. Schmeller, J.D. Pantis, Evaluating the connectivity of a protected areas' network under the prism of global change: the efficiency of the European Natura 2000 network for four birds of prey, PloS One 8 (3) (2013) e59640, https://doi.org/10.1371/journal.pone.0059640.

[78] M.L. Pinsky, R.L. Selden, Z.J. Kitchel, Climate-driven shifts in marine species ranges: scaling from organisms to communities, Annu. Rev. Mar. Sci. 12 (2020) 153–179, https://doi.org/10.1146/annurev-marine-010419-010916.

[79] S.M. Maxwell, E.L. Hazen, R.L. Lewison, D.C. Dunn, H. Bailey, S.J. Bograd, D. K. Briscoe, S. Fossette, A.J. Hobday, M. Bennett, S. Benson, M.R. Caldwell, D. P. Costa, H. Dewar, T. Eguchi, L. Hazen, S. Kohin, T. Sippel, L.B. Crowder, Dynamic ocean management: defining and conceptualizing real-time management of the ocean, Mar. Policy 58 (2015) 42–50, https://doi.org/10.1016/j.marpol.2015.03.014.

[80] J.E.M. Watson, N. Dudley, D.B. Segan, M. Hockings, The performance and potential of protected areas, Nature 515 (7525) (2014) 67–73, https://doi.org/10.1038/nature13947.

[81] Brown, J.M., van Loon, E.E., Bouten, W., Camphuysen, C.J., Lens, L., Müller, W., Thaxter, C.B. & Shamoun-Baranes, J., Data for: Does migration distance influence intra-individual variation in migratory behaviour in a seabird species with diverse migration strategies? 2019, Zenodo.

[82] D. Grémillet, F. Gallien, N. El Ksabi, N. Courbin, Sentinels of coastal ecosystems: the spatial ecology of European shags breeding in Normandy, Mar. Biol. 167 (2020) 43, https://doi.org/10.1007/s00227-020-3655-5.

[83] J.V. Lane, C.J. Pollock, R. Jeavons, M. Sheddan, R.W. Furness, K.C. Hamer, Post-fledging movements, mortality and migration of juvenile northern gannets, Mar. Ecol. Prog. Ser. 671 (2021) 207–218, https://doi.org/10.3354/meps13804.

[84] V. Warwick-Evans, L.M. Soanes, R.D. Gauvain, P.W. Atkinson, J.P.Y. Arnould, J. A. Green, Changes in behaviour drive inter-annual variability in the at-sea distribution of northern gannets, Mar. Biol. 163 (2016) 156, https://doi.org/10.1007/s00227-016-2922-y.

[85] J. Darby, de, S. Grissac, G. Arneill, E. Pirotta, J. Waggitt, L. Börger, E. Shepard, D. Cabot, E. Owen, M. Bolton, Foraging distribution of breeding northern fulmars is predicted by commercial fisheries, Mar. Ecol. Prog. Ser. 679 (2021) 181–194, https://doi.org/10.3354/meps13887.

[86] Stienen, E.W.M., Desmet, P., Milotic, T., Hernandez, F., Deneudt, K., Matheve, H. & Bouten, W., HG_OOSTENDE - Herring gulls (*Larus argentatus*, Laridae) breeding at the southern North Sea coast (Belgium), R.I.f.N.a.F. (INBO), Editor. 2019, Zenodo.

[87] A. Ponchon, C. Aulert, G. Le Guillou, F. Gallien, C. Péron, D. Grémillet, Spatial overlaps of foraging and resting areas of black-legged kittiwakes breeding in the English Channel with existing marine protected areas, Mar. Biol. 164 (5) (2017) 119, https://doi.org/10.1007/s00227-017-3151-8.

[88] F. De Pascalis, D. Pala, D. Pisu, J. Morinay, A. Benvenuti, C. Spano, A. Ruiu, L. Serra, D. Rubolini, J.G. Cecere, Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird, Mar. Ecol. Prog. Ser. 668 (2021) 121–132, https://doi.org/10.3354/meps13726.
[89] A.M. Reynolds, J.G. Cecere, V.H. Paiva, J.A. Ramos, S. Focardi, Pelagic seabird flight patterns are consistent with a reliance on olfactory maps for oceanic navigation, Proc. R. Soc. B: Biol. Sci. 282 (1811) (2015) 20150468, https://doi.org/10.1098/rspb.2015.0468.
[90] F. De Pascalis, S. Imperio, A. Benvenuti, C. Catoni, D. Rubolini, J.G. Cecere, Sex-specific foraging behaviour is affected by wind conditions in a sexually size dimorphic seabird, Anim. Behav. 166 (2020) 207–218, https://doi.org/10.1016/j.anbehav.2020.05.014.
[91] J.G. Cecere, G. Gaibani, S. Imperio, Effects of environmental variability and offspring growth on the movement ecology of breeding scopoli's shearwater *Calonectris diomedea.* Curr. Zool. 60 (5) (2014) 622–630, https://doi.org/10.1093/czoolo/60.5.622.
[92] O. Padget, G. Stanley, J.K. Willis, A.L. Fayet, S. Bond, L. Maurice, A. Shoji, B. Dean, H. Kirk, I. Juarez-Martinez, R. Freeman, M. Bolton, T. Guilford, Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips, Proc. Natl. Acad. Sci. 116 (43) (2019) 21629–21633, https://doi.org/10.1073/pnas.1903829116.
[93] F. Pezzo, M. Zenatello, C. Giulia, A. Navone, G. Dimitri, S. Giovanna, E. Pollonara, A. Massolo, A. Gagliardo, B. Nicola, Productivity changes in the Mediterranean Sea drive foraging movements of yelkouan shearwater *Puffinus yelkouan* from the core of its global breeding range, Mar. Ecol. 42 (4) (2021) e12668, https://doi.org/10.1111/maec.12668.
[94] I. Castège, E. Milon, Atlas des oiseaux marins et cétacés du Sud Gascogne: de l'estuaire de la Gironde à la Bidassoa, in: Patrimoines naturels, 78, Muséum national d'Histoire naturelle, Paris, 2018, p. 280.