Using large scale surveys to investigate seasonal variations in seabird distribution and abundance. Part II: The Bay of Biscay and the English Channel

Emeline Pettex a, *, Sophie Laran a, Matthieu Authier a, Aurélie Blanck b, Ghislain Dorémus a, Hélène Falchetto a, Charlotte Lambert c, Pascal Monestiez d, Eric Stéfan e, Olivier Van Canneyt a, Vincent Ridoux a, c

a Observatoire PELAGIS, UMS 3462 CNRS/Université de la Rochelle, 5 allées de l’océan, 17000 La Rochelle, France
b Agence des Aires Marines Protégées, 16 quai de la douane, 29229 Brest Cedex 2, France
c Centre d’Étude Biologique de Chizé, UMR 7372 CNRS - Université de La Rochelle, Institut du Littoral et de l’Environnement, 2 rue Olympe de Gouges, 17000 La Rochelle, France
d INRA, UR0546, Unité Biostatistique et Processus Spatiaux, Domaine Saint Paul, Site Agroparc, 84914 Avignon, France
e APECS, 13 rue JF Tartu, 29200 Brest, France

A B S T R A C T

Seabird distributions and the associated seasonal variations remain challenging to investigate, especially in oceanic areas. Recent advances in telemetry have provided considerable information on seabird ecology, but still exclude small species, non-breeding birds and individuals from inaccessible colonies from any scientific survey. To overcome this issue and investigate seabird distribution and abundance in the eastern North Atlantic (ENA), large-scale aerial surveys were conducted in winter 2011-12 and summer 2012 over a 375,000 km² area encompassing the English Channel (EC) and the Bay of Biscay (BoB). Seabird sightings, from 15 taxonomic groups, added up to 17,506 and 8263 sightings in winter and summer respectively, along 66,307 km. Using geostatistical methods, density maps were provided for both seasons. Abundance was estimated by strip transect sampling. Most taxa showed marked seasonal variations in their density and distribution. The highest densities were recorded during winter for most groups except shearwaters, storm-petrels, terns and large-sized gulls. Subsequently, the abundance in winter nearly reached one million individuals and was 2.5 times larger than in summer. The continental shelf and the slope in the BoB and the EC were identified as key areas for seabird conservation, especially during winter, as birds from northern Europe migrate southward after breeding. This large-scale study provided a synoptic view of the seabird community in the ENA, over two contrasting seasons. Our results highlight that oceanic areas harbour an abundant avifauna. Since most of the existing marine protected areas are restricted to the coastal fringe, the importance of oceanic areas in winter should be considered in future conservation plans. Our work will provide a baseline for the monitoring of seabird distribution at sea, and could inform the EU Marine Strategy Framework Directive.

1. Introduction

The Marine Strategy Framework Directive (2008/56/EC) requires assessing the environmental status of the European waters and to maintain or restore the “Good Environmental Status” (GES) of marine ecosystems by 2020. However, important gaps in the knowledge of marine species distribution and abundance could make difficult to achieve the evaluation of GES, especially for mobile species (Crise et al., 2015). Although the distribution of marine species is relatively well documented in most coastal waters, important gaps remain offshore. The distribution of marine species is affected by a strong spatiotemporal variation in oceanographic conditions (temperature, salinity, currents...), which locally drive productivity and the availability of prey for consumers (Bakun, 1996). Among the predictable variations, seasonality, which is regular and marked in temperate environments, has shaped the life history traits of marine predators, compelling them to commute between favourable places throughout the year. It is therefore important to consider seasonal variations in species distributions. This is particularly true for seabirds. Breeding seabirds are central place foragers, travelling between colonies where
they raise their nestlings and distant foraging areas. When their breeding is completed, most species leave colonies and migrate towards more favourable areas to spend the non-breeding season.

Knowledge of the distribution and movement of seabirds has considerably benefited from major advances in telemetry since the 1990s (Burger and Shaffer, 2008; Wilson et al., 2002). However, within the seabird population, a large proportion remains excluded from any telemetry investigations, either because of the species size, their sensitivity to handling, the status of individuals (juveniles, immatures and non-breeding adults; see Péron and Grémillet, 2013) or the inaccessibility of breeding sites. Visual surveys may offer an interesting complement when investigating the distribution in seabirds at various spatiotemporal scales, since it includes the whole community in the sampling. Generally focusing on coastal waters and associated with oceanographic surveys, small scale studies (< 10,000 km²) can be repeated at monthly or yearly intervals (Arcos et al., 2012). Investigations at a broader scale (< 10,000 km²) are limited by the cost of the dedicated platforms used and the constraints resulting from a large sampling area (Bretagnolle et al., 2004; Certain et al., 2011; Lieske et al., 2014). Ships are commonly used to study distributions at sea, but aerial surveys present multiple benefits for broad scale surveys such as lower costs, faster coverage of the sampling area and the ability to select the best weather conditions for observation (Buckland et al., 2001; Camphuysen et al., 2004; Certain and Bretagnolle, 2008).

Our study took place in a continuous area encompassing the Bay of Biscay, the English Channel and the southern Celtic Sea. This area of the eastern North Atlantic (hereafter ‘ENA’) is highly productive and is one of the most intensively exploited seas by human activities mainly through fisheries and commercial routes, but also, more specifically in the English Channel, for industrial activities like sand and gravel extraction and forthcoming wind farm projects. It is also known to be a major area for a numerous and diversified seabird population that breeds in the north of Europe on its way to southern wintering grounds or for the entire non-breeding period (Bretagnolle et al., 2004; Fort et al., 2012; Frederiksen et al., 2012; Kubetzki et al., 2009; Magnusdottir et al., 2012), and the Western English Channel has been identified as a biodiversity hotspot for megafauna (McClellan et al., 2014). During spring and summer, various species of seabirds breed in colonies spread along the British and French coasts of the Channel and the northern Bay of Biscay (Cadiou et al., 2004a; Mavor et al., 2006).

Among the seabirds dwelling in the ENA, several species are listed on Annex I of the EC Birds Directive (2009/147/EC) or the OSPAR List of Threatened and/or Declining Species list (OSPAR 2008/358) and should be monitored in order to ensure their protection. Several dedicated and opportunistic at-sea surveys documented the distribution and composition of the avian population of the shelf of the Bay of Biscay (Castège and Hémery, 2010; Certain et al., 2011; Certain and Bretagnolle, 2008), but to our knowledge, only one ferry-based survey sampled offshore waters in the western Channel and the continental slope of the Bay of Biscay, along a route linking Portsmouth to Bilbao (Brereton et al., 2003; Louzao et al., 2015). In the English Channel and the Celtic Sea, numerous ship or aircraft surveys have been conducted since 1979 and gathered in the ‘European Seabirds at Sea’ dataset, which represents a global effort of 1,240,664 km in the northwest European waters (JNCC, 2016; Dunn, 2012; Kober et al., 2010) and provide seasonal distribution maps for most seabirds (Stone et al., 1995).

In order to provide a synoptic view of seabirds distribution,
including offshore areas in the ENA, we conducted an aerial survey, covering an area of 375,000 km² during two contrasting seasons (winter 2011/2012 and summer 2012). The aim of the study was (1) to assess the distributions of all seabird species present in the area and investigate their seasonal variations, (2) to estimate the densities and abundance of seabird taxa and (3) to highlight areas of importance for seabird conservation at sea especially beyond territorial waters.

2. Material and methods

2.1. Study area

The study area was 375,000 km² in size, encompassing the English Channel (EC), the Bay of Biscay (BoB) and the southern Celtic Sea (CS) in the ENA (Fig. 1). The EC is a shallow epicontinental sea, and its dynamic is characterised by strong tidal currents and dominant westerly winds that bring oceanic waters towards the North Sea (Carpentier et al., 2009). The BoB is an open oceanic area in the ENA, characterised by a wide continental shelf in its northern part (> 260 km) narrowing to 30–40 km wide in its southern part. The continental slope delimited shallow waters of the shelf (up to 200 m deep) from abyssal plains (up to 5000 m deep) (Koutsikopoulos and Cann, 1996).

2.2. Aerial survey and data collection

The SAMM (Suivi Aérien de la MégaFaune Marine; Aerial Census of Marine Megafauna) aerial surveys were conducted from November 2011 to mid-February 2012 and from mid-May to mid-August 2012. Seabird sightings were collected within a 200 m wide strip following a standardised strip-transect protocol (assuming that all seabirds would be detected within the strip), from high-wing aircrafts equipped with bubble windows (see details in Pettex et al., 2017). A stratified survey was designed as following (Fig. 1): neritic strata (depth < 200 m) hereafter designated as N_EC and N_BoB for EC and BoB; slope S_BoB (200 m < depth < 2000 m) and oceanic O_BoB strata (> 2000 m). One additional coastal survey (C_EC and C_BoB) was conducted within a strip of about 12 nautical miles wide from the shore, to provide detailed information on seabird coastal distributions. The identification of seabirds was performed at the lowest taxonomic level, but some species could not be identified at the species level and were pooled into groups on the basis of common morphological criteria (Table 1). Environmental conditions were also recorded at the beginning of each transect and whenever a change occurred in sighting conditions.

2.3. Spatial distribution

To describe the species distribution over the study area, we used a ‘Poisson kriging’ geostatistical model to draw maps of local sightings density (De Oliveira, 2014; Monestiez et al., 2006; also used for seabirds in Mannocci et al., 2013). Geostatistics correct for spatial autocorrelation between sightings and transects as well as for heterogeneity related to zigzag transect distribution (Strindberg and Buckland, 2004; Van der Meer and Leopold, 1995). All data validation and treatments were conducted using FME Desktop 2013 SP4 (Safe Software, 2013). Transects were split in 5 km segments, to which sightings were assigned. Segments for which the seastate was > 3 or subjective conditions were < medium/good were removed and a minimum of 100 pairs of segments per class of distance was used for accurate variogram estimation using the least squares method (see details in Appendix 1). For each taxon, we tested two covariance models (exponential and Matérn; both models are relying on weak assumptions and are parsimonious) and selected the best fitting model with the lowest sum of squares. Following variogram estimation and selection, we performed spatial interpolation to predict the local density of sightings in a grid of 0.05° longitude and latitude over the study area (for details, see Appendix 1). Winter and summer surveys were treated separately; taxa with fewer than 15 observations were not considered for analysis. For each taxon, winter and summer density predictions were plotted using a common scale, fixing a threshold set at the 0.99 quantile in the colour bar to avoid visual distortions by extreme predictions. To identify areas of higher density, we summed the kriging maps of all taxa to produce a map of the cumulative density (i.e. sum of predicted densities per 0.05° cell) for each season. All geostatistical analyses were conducted using R 3.2.1 (R Core Team, 2013).

2.4. Density and abundance at sea

The strip transect protocol assumes that all seabirds are detected within the 200 m wide strip. Similarly to spatial analyses, bouts of effort with sea state > 3 and subjective conditions < medium/good were removed. All abundance analysis were conducted using the software Distance 6.0 (Thomas et al., 2010). Density of groups and mean group size were calculated by Distance 6.0 for each strata and each season separately. Density estimates, in number of individuals per square kilometres (ind km⁻²) and obtained by multiplying density of groups by mean group size, were compared between seasons using a Z-test. To avoid the overestimation of abundance in relation with aggregates of seabirds (fishing vessels), the group size was corrected by fixing a threshold set at the 0.99 quantile. The abundance and density estimates presented here did not take into account birds dwelling on land, and were uncorrected for any detection bias. They might thus be underestimated and should be considered as a minimum value. Abundance estimates in the results section were rounded to the higher ten.

3. Results

A total of 66,307 km was sampled on effort during the winter and summer surveys (Table 2). To ensure the best conditions for observation, flights were carried out only when meteorological parameters were optimal. Therefore, the percentage of effort conducted in good conditions reached 28,066 km in winter (87%) and 31,427 km in summer (93%).

During our study, a total of 18,155 and 8439 sightings of birds were recorded in winter and summer respectively (Table 3, Appendix 2). Seabirds represented 95% of the sightings and belonged to eight families: procellariids (fulmars and shearwaters), hydrobatids and oceanitids (storm petrels), phalacrocoracids (cormorants and shags), stercorarids (skuas and jaegers), sulids (northern gannet), larids (gulls and terns) and alcids (razorbill, guillemots and puffins). Although some species were pooled, 15 taxa were identified to the species level (Table 1).

In the BoB, the avian community was dominated by larids (36.8% of the total estimated abundance), sulids (29.3%) and alcids (21.8%) in winter, and in summer, by larids (50.5%) and procellariids (19.7%), followed by sulids and by hydrobatids and oceanitids (17.5% and 9.8%, Fig. 2). In the EC, larids (38.1% of the total estimated abundance), alcids (35.3%) and sulids (15.7%) were also dominant in winter, while community composition shifted to larids (51.1%) and sulids (22.7%) in summer (Fig. 2).

3.1. Procellariids

3.1.1. Northern fulmar

The northern fulmar showed a very similar distribution in both seasons (Fig. 4). The species mainly occurred in the northern EC, as well as in the northern BoB. The highest densities were observed in N_EC (0.12 ind km⁻²) and C_EC (0.07 ind km⁻²) in winter (Fig. 3). In summer, EC densities were significantly lower (p=0.01 for N_EC and p=4e−06 for C_EC). In the BoB, densities varied from 0.02 to 0.04 ind km⁻² without a
Table 1
Details of seabird groups composition: group names refer either to the English name of a species/taxonomic group, or to a descriptive term for species morphologically similar from the air.

<table>
<thead>
<tr>
<th>Family</th>
<th>Group names</th>
<th>Group composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Procellariids</td>
<td>Northern fulmar</td>
<td>Fulmarus glacialis</td>
</tr>
<tr>
<td></td>
<td>Small-sized shearwaters</td>
<td>Manx shearwater Puffinus puffinus</td>
</tr>
<tr>
<td></td>
<td>Large-sized shearwaters</td>
<td>Balearic shearwater Puffinus mauretanicus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Great shearwater Puffinus gravis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sooty shearwater Puffinus griseus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cory's shearwater Calonectris diomedea</td>
</tr>
<tr>
<td>Hydrobatids and oceanitids</td>
<td>Storm petrels</td>
<td>European storm-petrel Hydrobates pelagicus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Leach's Storm-petrel Hydrobates leucourrhous</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wilson's storm petrel Oceanites oceanicus</td>
</tr>
<tr>
<td>Sulids</td>
<td>Northern gannet</td>
<td>Morus bassanus</td>
</tr>
<tr>
<td></td>
<td>Cormorants</td>
<td>Great cormorant Phalacrocorax carbo</td>
</tr>
<tr>
<td>Phalacrocoracids</td>
<td></td>
<td>European Shag Phalacrocorax aristotelis</td>
</tr>
<tr>
<td>Stercorariids</td>
<td>Great skua</td>
<td>Colanectris skua</td>
</tr>
<tr>
<td></td>
<td>Jaegers</td>
<td>Long-tailed skua Stercorarius longicaudus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Parasitic skua Stercorarius parasitic</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pomarine skua Stercorarius pomarinus</td>
</tr>
<tr>
<td>Alcids</td>
<td>Auksp</td>
<td>Common guillemot Uria aalge</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Razorbill Alle torda</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Atlantic puffin Procella azure</td>
</tr>
<tr>
<td>Larids</td>
<td>Ternsp</td>
<td>Arctic tern Sterna paradisaea</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Little tern Sterna albifrons</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sandwich tern Thalasseus sandvicensis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hydrocoloeus minutus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Riissa tridactyla</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Black-headed gull Larus ridibundus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mediterranean gull Larus melanoccephalus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lesser black-backed gull Larus fuscus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Herring gull Larus argentatus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yellow-legged gull Larus michaellis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified/immature/immature/immature L. michaellis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>and/or L. argentatus L. fuscus L. marinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified/immature/immature/immature L. michaellis</td>
</tr>
</tbody>
</table>

Table 2
Area, total effort (in km) and effort collected in good conditions (Beaufort ≤3, Subjective conditions = medium/good) during winter 2011–12 and summer 2012.

<table>
<thead>
<tr>
<th>Bathymetric strata</th>
<th>Surface area (km²)</th>
<th>Total effort in winter (km)</th>
<th>Effort in good condition (km &amp; %)</th>
<th>Total effort in summer (km)</th>
<th>Effort in good condition (km &amp; %)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bay of Biscay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coastal (C_EA)</td>
<td>27,293</td>
<td>4459</td>
<td>3816</td>
<td>4004</td>
<td>92%</td>
</tr>
<tr>
<td>Shelf (Nhra)</td>
<td>103,374</td>
<td>7345</td>
<td>6329</td>
<td>5735</td>
<td>91%</td>
</tr>
<tr>
<td>Oceanic (Ohra)</td>
<td>91,183</td>
<td>2599</td>
<td>2365</td>
<td>5087</td>
<td>95%</td>
</tr>
<tr>
<td>Total_EA</td>
<td>282,141</td>
<td>20,814</td>
<td>17,695</td>
<td>21,675</td>
<td>94%</td>
</tr>
<tr>
<td>English Channel</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coastal (C_EE)</td>
<td>26,682</td>
<td>4467</td>
<td>4079</td>
<td>4065</td>
<td>92%</td>
</tr>
<tr>
<td>Shelf (N_EE)</td>
<td>92,875</td>
<td>7162</td>
<td>6292</td>
<td>5687</td>
<td>88%</td>
</tr>
<tr>
<td>Total_EE</td>
<td>92,875</td>
<td>11,629</td>
<td>10,371</td>
<td>9752</td>
<td>90%</td>
</tr>
<tr>
<td>Total ENA</td>
<td>375,016</td>
<td>32,443</td>
<td>28,066</td>
<td>31,427</td>
<td>93%</td>
</tr>
</tbody>
</table>

significant seasonal difference. Abundance in the ENA was estimated at 19,950 individuals (95% CI: 13,040–31,395) in winter and 8,010 (95% CI: 4,882–13,948) in summer.

3.1.2. Small-sized shearwaters
Rare observations were collected in winter, mainly in the southeastern BoB, resulting in low to null densities (Fig. 3). In summer, small-sized shearwaters occurred along the French and English coasts of the western EC, and in the north of CBoB (between Brittany and the Gironde estuary; Fig. 3). Nevertheless, few sightings were recorded offshore in the BoB. Small-sized shearwaters preferentially visited coastal and shelf strata in both subregions (densities varied from 0.05 to 0.12 ind km⁻²), although summer densities were significantly higher in N_EA (p=0.006), N_BoB (p=0.03) and in C_BoB (p=0.004). Abundance was estimated at 710 individuals (95% CI: 257–1979) in winter and 10,210 (95% CI: 4612–22,701) in summer.

3.1.3. Large-sized shearwaters
Large-sized shearwaters were only seen in summer, along the slope and in oceanic waters of the northern BoB (Fig. 4). Summer densities were significantly higher in those strata (S_BoB: p=5e⁻⁰⁷ and O_BoB: p=1e⁻⁰⁶; Fig. 5). The group was absent from the EC during both seasons. Abundance was estimated at 31,980 individuals (95% CI: 21,324–48,776) in summer.

3.2. Hydrobatids and oceanitids
Storm petrels showed contrasting patterns of distribution between seasons. In winter, they were seen in the southern BoB, with similar densities among strata (Figs. 3 and 4). In summer, they occurred in high densities in N_BoB and S_BoB (0.09 and 0.12 ind km⁻² respectively, Figs. 3 and 4) but were absent from coastal waters. Storm petrels were concentrated southwest of Brittany, but also north of Spain. The western EC was inhabited to a lesser extent. This seasonal contrast in distribution was reflected in density, with significantly higher values in summer in the EC (C_EC and N_EC: p=3e⁻⁰⁵) and in the BoB (C_BoB: p=0.04; N_BoB: p=0.001 and S_BoB: p=2e⁻¹⁰ for). Abundance was estimated at 10,640 individuals (95% CI: 5998–19,889) in winter and 23,710 (95% CI: 18,848–29,999) in summer.
3.3. Sulids

The northern gannet distribution varied markedly between seasons. In winter, gannets were present over the shelf but concentrated in the eastern EC, between the Bay of the Seine and the Dover Strait, and in the BoB, from the south of Brittany to Spain (Fig. 5). The highest density was recorded in CEC (1.44 ind km$^{-2}$), while NEC and NBoB also showed high densities (between 0.81 and 1.06 ind km$^{-2}$; Fig. 3). The summer distribution was more diffuse, although the highest densities were found in the western EC (Fig. 5). In the BoB, low densities were recorded off Brittany and to a lesser extent, southward along the coast. In both subregions, winter concentration patches had completely disappeared, resulting in a reverse distribution. Coastal and shelf densities were two to nine times lower in summer (CEC: p=8e-10 and NEC: p=8e-07; CBoB: p=9e-06 and NBoB: p=1e-14). The winter density was higher in the OBoB (p=0.003) and SBoB densities were similar for both seasons. Seasonal variations in densities mirrored estimated abundance with 210,910 individuals (95% CI: 170,024–263,389) in winter and 83,140 (95% CI: 70,318–98,780) in summer.

3.4. Phalacrocoracids

Cormorants and shags displayed a similar coastal distribution in both seasons (Fig. 5), extending from the Gironde estuary to the Dover Strait. The highest density was found in CEC (0.14 ind km$^{-2}$), similarly in winter and summer. Seasonal variations in density were not significant in the ENA, except for CBoB (p=0.02), in which the density was significantly decreased in summer (Fig. 3). Abundance estimates were similar to 612 individuals (95% CI: 3642–10,533) in winter and 6080 (95% CI: 3029–13,625) in summer.

3.5. Stercorarids

In winter, great skuas showed a marked preference for the outer edge of NBoB and SBoB (0.03 ind km$^{-2}$ and 0.02 ind km$^{-2}$; Fig. 3), where they distributed from north to south (Fig. 5). They also distributed in eastern CEC and in central western NEC. In summer, the distribution was diffuse and displayed no specific pattern. The great skua was present in all strata of the ENA, in lower densities than during winter in CEC (p=1e-04), NBoB (p=2e-05), SBoB (p=0.003) and OBoB (p=0.04). Abundance was estimated at 5430 individuals (95% CI: 3783–7868) in winter and at 2120 (95% CI: 1176–3865) in summer.

3.6. Alcids

The auk distribution varied drastically across seasons. In winter, auks showed a widespread distribution on the shelf (Fig. 5). Three high-density areas occurred: the eastern CEC between the Bay of Seine
3.7. Larids

3.7.1. Terns

In winter, terns were found in low densities in NBoB between Brittany and the Gironde estuary while scarce sightings were recorded in CEC (Fig. 6). The summer distribution was also mainly coastal; high density patches extended in CEC (especially in the Bays of the Somme and Seine rivers, as well as the Gulf of Saint-Malo) and in CBoB, from the tip of Brittany to the Gironde estuary. Rarely sighted along the Aquitaine coast, terns were nevertheless recorded in nearby Arcachon Bay. In summer, CEC showed the highest density (0.31 ind km$^{-2}$; Fig. 3), significantly higher than in winter (p=8e−16), as for NEC (p=2e−12) and CBoB (p=6e−05). Abundance was estimated at 2720 individuals (95% CI: 14,498–28,165) in winter and 20,040 (95% CI: 14,998–28,165) in summer.

3.7.2. Little gull

Little gulls mainly occurred in the EC, between the Dover Strait and the Gulf of Saint-Malo (Fig. 6), where highest densities were recorded (Fig. 3). In the BoB, sightings recorded were widespread in oceanic waters. Winter densities were significantly higher in all strata (CEC: p=2e−5; NCE: p=0.02; NBoB: p=0.002; SBoB: p=0.001 and OBoB: p=0.01) except in CBoB (p=0.18). In summer, rare sightings were recorded around Brittany. Abundance was estimated at 5050 individuals in winter (95% CI: 2850–9005) and 740 individuals (95% CI: 144–3778) in summer.

3.7.3. Black-legged kittiwake

The seasonal patterns of the distribution of black-legged kittiwakes were strongly contrasting. The highest densities of kittiwakes were recorded in the EC (0.29 and 0.33 ind km$^{-2}$ in CEC and NEC respectively, Fig. 3). They showed a preference for the coastal waters of Cornwall and Devon in the western EC, and from Sussex to the Dover Strait in the eastern EC (Fig. 6). In French waters, kittiwakes were frequently recorded along bays and coasts of the eastern EC. In the BoB, the species was concentrated in the outer NBoB and in SBoB, and to a lesser extent in OBoB. Kittiwakes were far less numerous in summer; winter densities were therefore significantly higher in all strata (CCEC: NCE: NBoB and SBoB: p=2e−16; CBoB: p=2e−10, and OBoB: p=3e−13). Abundance was estimated at 77,260 individuals in winter (95% CI: 66,523–89,908) and 2050 individuals (95% CI: 1065–4078) in summer.

3.7.4. Hooded gulls

The black-headed gull and Mediterranean gull, which could not be clearly differentiated from the air, were pooled as ‘hooded gulls’. Hooded gulls displayed a contrasting distribution between seasons (Fig. 6). In winter, they occurred in the entire ENA, with densities decreasing offshore (Fig. 3). Densities were higher in the EC, where hooded gulls were concentrated mainly along the French coast (CEC: 0.57 ind km$^{-2}$). In the BoB, a diffuse distribution occurred in the southern half of NBoB and SBoB. In summer, the distribution was more coastal with high density patches found in the Bay of Seine, the Gulf of Saint-Malo and the Dover Strait (Fig. 6). Densities were significantly lower in summer, in all strata except OBoB (CCEC: p=2e−12; NCE: p=2e−16; CBoB: p=1e−10; NBoB: p=4e−15 and SBoB: p=2e−9). Abundance was estimated at 74,790 individuals in winter (95% CI: 59,895–93,752) and 10,520 individuals (95% CI: 7102–15,947) in summer.

3.7.5. Grey-backed gulls

Adults of European herring gulls and yellow-legged gulls could not be told apart from the air and were pooled as ‘grey-backed gulls’. Grey-backed gulls displayed a contrasting distribution between seasons (Fig. 3). Adult herring gulls and yellow-legged gulls could not be told apart from the air and were pooled together as ‘grey-backed gulls’. Winter and summer distributions were similar and essentially coastal, though grey-backed gulls were sighted further offshore in NBoB, in the eastern EC and in the Gulf of Saint-Malo (Fig. 7). The highest densities were recorded in winter in CBoB (0.58 ind km$^{-2}$; Fig. 3), along the southern shore of Brittany. In summer, high densities were estimated along the shore from the Dover Strait to the Gironde estuary. The Aquitaine coast was poorly frequented at both seasons, although a high-density patch occurred in the Spanish Basque Country. Densities were higher in summer in CEC (p=4e−06), NCE (p=1e−04) and NBoB (p=0.008), and in winter in CBoB (p=0.008). Abundance was estimated at 24,740 individuals (95% CI: 17,267–36,986) in winter and 46,180 (95% CI: 34,619–62,496) in summer.

3.7.6. Black-backed gulls

Adults of lesser and greater black-backed gulls, pooled together as ‘black-backed gulls’, showed similar distributions during winter and summer. They were mostly found in neritic areas of the EC and the northern half of BoB (Fig. 7). In winter, high densities were found in the eastern EC, between the Bay of Seine and the Dover Strait, and in the BoB, between the tip of Brittany and the Gironde estuary. In summer, black-backed gulls were concentrated north of the Channel Islands and south of Brittany. Densities per strata did not differ between seasons, except in CEC (p=2e−04), where the winter density reached a maximum value (0.34 ind km$^{-2}$; Fig. 3). Abundance was
estimated at 23,640 individuals (95% CI: 16,894–33,360) in winter and 25,110 (95% CI: 17,866–35,673) in summer.

3.7.7. Unidentified larids

Within the larids, a substantial number of sightings could not be assigned to any of the four groups described above. Two categories of unidentified larid sightings were defined: 1) immature/unidentified large-sized gull, which were mostly immatures or juveniles, 2) unidentified larids, comprised mostly of birds sitting on the sea surface, making the differentiation among larid groups very difficult.
Fig. 4. Density maps (kriging) in winter 2011–2012 (left panel) and summer 2012 (right panel) for northern fulmar, small-sized and large-sized shearwaters, storm petrels in number of sightings.km$^-2$. Sightings are represented in black dots when kriging was not possible.
Fig. 5. Density maps (kriging) in winter 2011–2012 (left panel) and summer 2012 (right panel) for northern gannet, cormorants, great skua and auks in number of sightings.km$^{-2}$. 
Fig. 6. Density maps (kriging) in winter 2011–2012 (left panel) and summer 2012 (right panel) for terns, little gull, black-legged kittiwake and hooded gulls in number of sightings.km$^{-2}$. Sightings are represented with black dots when kriging was not possible.
Unidentified large-sized gulls represented 67,410 individuals (95% CI: 39,905–114,785) in winter and 56,060 individuals (95% CI: 33,825–95,319) in summer. Unidentified larids were estimated at 93,380 (95% CI: 54,078–167,978) in winter and 26,610 (95% CI: 11,310–62,943) in summer (Table 3).

3.8. Overall distribution of seabirds

The cumulative density was higher during the winter season (Fig. 8). In winter, the highest level of density was found in the continental shelf with some hotspots: the French coast of the eastern EC and the Dover Strait, the English coast of the western EC, and the BoB shelf (except the tip of Brittany). In summer, maxima occurred mainly in coastal areas, along the French coast from the south of
Brittany to the Bay of the Somme and along the English coast, from Cornwall to Lyme Bay.

4. Discussion

Based on a thorough sampling effort deployed during two contrasting seasons, the distribution and the relative abundance of seabird species were investigated at a large scale in the EC and the BoB. Our results highlight seasonal variations in the distribution and abundance of most seabird groups. Spatial analyses revealed areas of high-density in the ENA. While maximum values mainly occurred on the continental shelf (in the eastern EC and in the BoB) in winter, densities were higher in summer in the western EC, and further offshore, in the slope and oceanic strata in the BoB.

4.1. Limitations

The principal limit lies in species identification. The high flight speed and the lack of identification cues associated with aerial observation are sources of uncertainty (Camphuysen et al., 2004). Although such misidentification is unlikely for northern gannets, northern fulmars, great skuas, little gulls or kittiwakes, some species within the groups of gulls, terns, auks and shearwaters cannot be unambiguously identified from the air. Hence, the distribution maps and abundance estimates of pooled species should be interpreted cautiously.

The detection of animals, which is particularly sensitive to sighting conditions, is another issue in aerial surveys (Marsh and Sinclair, 1989). In this study, tight weather criteria in which to conduct flights were set to reduce detection bias (see Section 2.4); this resulted in optimal sighting conditions for 91% of the observation effort. Finally, strip transect sampling assumes that all animals are detected within the strip; this is likely an overestimation of actual detection and therefore leads to an underestimation of actual densities. The detection of small-sized or dark-plumaged species, such as auks and storm petrels, was probably affected by sea-state, light conditions and distance to the track line within the strip (even when sea-state was <3 and subjective conditions > medium/good). In the future, the digital methods should improve detection and identification of seabirds at sea and are expected to replace visual surveys (Buckland et al., 2012). Besides, as the surveys were conducted over a 3-months period, variations in the abundance related to migration peaks could not be detected. For all these reasons, abundance estimates represent a minimum value. Finally, because the time scale of the study covered only a single year, there is no evidence that our findings are typical. A replication of this survey would allow for the estimation of inter-annual variability. However, the size of the study area and the coverage of two contrasting seasons are strengths of this survey.

4.2. Seasonal variations in the distribution at sea

The seabird species of EC and BoB displayed various distribution patterns. While cormorants, terns and to a lesser extent grey-backed gulls clearly showed a coastal distribution, other species were found in more oceanic waters of the continental shelf (auks, black-backed gulls, hooded gulls, small-sized shearwaters and gannets), the slope (great skuas, storm petrels and black-legged kittiwakes) or the oceanic area (large-sized shearwaters). Interestingly, northern fulmars, little gulls and kittiwakes occurred in higher densities on the shelf in the EC and displayed a more oceanic distribution in the BoB.

Beyond these specific preferences, the avian community varied in its composition and its overall distribution between winter and summer, reflecting the pre- and post-breeding migrations performed by most seabirds, as breeding areas are often distant from wintering areas (Schreiber and Burger, 2001). Depending on their life history traits, seabird species were either wintering or breeding in the study area, but several groups were found year-round in the ENA and may also perform seasonal movements within the area.

4.2.1. Winter visitors

Most of the seabird groups encountered in the ENA were more abundant during winter and could therefore be considered as winter visitors. With about 300,000 individuals concentrated over the ENA shelf (the two-thirds within the EC), auks were the most represented group during winter. A previous study conducted over the shelf of the BoB estimated 94,000–102,000 individuals during winter (Bretagnolle et al., 2004), which was close to our estimate (90,183 individuals 95% CI: 78,036–105,421). Adults of common guillemots wintering in the EC originate from eastern Britain, whereas the BoB mainly shelters immature birds from Ireland and western Britain (Cadiou et al., 2004b; Grantham, 2004). Razorbills, which leave their colonies in late July, migrate southwards across a vast area from southern Norway to western Africa, hence through the ENA (Furness, 2015; Wernham et al., 2002). The high-density areas of auks observed in the EC during winter 2011–12 (Bay of the Seine, Dover Strait, Cornwall) were identified in previous studies (McClellan et al., 2014; Stone et al., 1995). In summer, the abundance of auks represented less than 5% of that of winter, which was consistent with the size of the breeding population and the known distribution in the area (Cadiou et al., 2004a; Stone et al., 1995).

The northern gannet was the second most abundant species in winter (>210,000 individuals), which could be explained by migrations from colonies in the UK or Norway (Fort et al., 2012; Kubetzki et al., 2009). However, the high densities of gannets in the eastern EC during winter 2011–12 do not occur in distribution maps of the European seabirds at sea dataset (Stone et al., 1995). As most breeders return to the colonies in northern Europe in spring, gannets were less abundant in the ENA during summer (>83,000) and mainly foraged in the western EC within the range of the breeding sites located close to the Gulf of Saint-Malo (Pettex et al., 2010; Wakefield et al., 2013).

The northern fulmar distribution varied slightly between seasons, but the abundance in the EC was five times higher during winter. Fulmars were found in the northern part of the study area, in accordance with predicted distributions by Watson et al. (2013). The population of the north Atlantic was estimated at 10 million individuals, and winter movements may lead to a small proportion (estimated at 19,950 individuals in our study) of numerous breeders migrating from northern Europe to the ENA (Furness, 2015; Stone et al., 1995). By April, most birds have returned to northern waters of UK, Faroes, Iceland and Norway to breed. The breeding population in the EC was estimated at about 4100 breeding pairs in the early 2000s (Cadiou et al., 2004a; Mitchell et al., 2004), which was consistent with our summer estimate of 8000 individuals in the ENA.

The black-legged kittiwake was the most represented species within the larids, with a minimum estimate of 77,000 individuals in winter. A recent telemetry study highlighted that 80% of the 4.5 million breeding adults might winter west of the mid-Atlantic ridge, while a lower proportion of breeders from Ireland and western Britain would stay in Europe (Frederiksen et al., 2012). Kittiwakes sighted in the EC during winter could then either be adults engaged in a transatlantic migration or wintering in the area (as shown in Stone et al., 1995), while those observed in the BoB might be juveniles, immatures and adults originating from UK (Coulson, 2011; Wernham et al., 2002). In summer, the abundance decreased to about 2000 individuals, and the distribution tended to reflect the location of colonies along the coast of the EC and Brittany (Cadiou et al., 2004a).

In our study, hooded gulls were seven times more abundant (>74,700) in winter and mostly sighted on the continental shelf of the EC and the BoB. The highest densities were recorded in large bays during this season. In summer, hooded gulls were found in low densities in the ENA (10,000 individuals). These results were consistent with the biology of both black-headed and Mediterranean gulls. Black-headed
gulls breed in a large area from Iceland to Kamchatka (including continental fresh waters), while most Mediterranean gulls breed in the Black and Azov Seas. However, both species breed in the ENA. The latest census conducted in France in 2011 indicated 2900 pairs of Mediterranean gulls (a strong increase since 2000) and 5500 pairs of black-headed gulls along the coasts of the study area (Cadiou, 2014). Ring recoveries previously showed that black-headed gulls from the northern Europe and western Russia winter in the western Europe and in northern Africa (Atkinson et al., 2007) and that Mediterranean gulls originating from eastern Europe winter in the ENA (mostly in the south of the BoB) and in the Mediterranean Sea (del Hoyo et al., 1996).

The little gull is a fully migratory species that also winters in the north Atlantic after a breeding season spent between Scandinavia and western Russia (del Hoyo et al., 1996). Little gulls are known to winter along coasts of the southern North Sea and EC (Stone et al., 1995), which is in line with our results in the EC. The global population has been estimated to be 97,000–270,000 individuals (Delany et al., 2006). Our estimates for the little gull in the ENA reached 5000 individuals (2–3% of the global population) during winter and almost 750 individuals in summer, consistent with the migratory pattern described earlier.

An important proportion of larid sightings could not be attributed to groups or species. They were mostly birds sitting on the sea, for which size and shape could not be determined. However, abundance estimates (93,373 in winter and 26,610 in summer) showed a similar trend with the three larid groups discussed above. Black-legged kittiwakes, hooded gulls and little gulls could therefore represent an important proportion (but currently unknown) of these unidentified larids.

Great skuas were also more abundant in winter (about 5400 individuals) than in summer (2100). During the winter 2011–2012, this species preferentially visited the shelf edge and the slope in the BoB, but was also present in the EC. A recent telemetry study highlighted that the EC and the BoB are preferential wintering areas of the 5700 pairs breeding in Iceland and in Norway (Magnusdottir et al., 2012). UK breeders (9000 pairs) also travel through the study area to reach western Africa, but peaks of migration usually occur earlier in autumn, i.e. between August and October (Furness, 2015).

Most of summer sightings might then correspond to non-breeders, either adults or immatures. Distribution patterns in the EC and in the southern Celtic Sea during our surveys were very similar to those of the European Seabirds at Sea dataset (Stone et al., 1995).

4.2.2. Summer visitors

Several seabird groups dwelled in the area during the summer season. This was the case of procellariid groups (except for the northern fulmar), for which abundance estimates were higher in summer. Small-sized shearwater sightings recorded along the coast of the BoB from Vendée to Brittany and along the western EC shores were probably Manx and Balearic shearwaters. Manx shearwaters observed in the western EC may be breeders from the Scillies, the Channel Islands (200 pairs, Mitchell et al., 2004; Stone et al., 1995) and the Brittany coast (200 pairs, Cadiou, 2014). Balearic shearwaters mainly breed in the Balearic Islands (Spain), but increasing numbers of individuals have been recorded in the BoB and in the western EC during summer (Boué and Dalloyau, 2013; Jones et al., 2014). For the last two decades, this species has shown a rapid range expansion northwards in relation to a shift in the anchovy and sardine distributions, attributed to climate change (Wynn et al., 2007; Yésou, 2003).

Large-sized shearwaters were apparently absent from the ENA in winter, but about 31,000 individuals were estimated beyond the shelf edge of the northern BoB in summer. Previous surveys already identified important numbers of Cory’s shearwaters and Great shearwaters (probably non-breeders) in the deep waters off the BoB and the Celtic Sea (Hobbs et al., 2003; Munilla et al., 2016; Stone et al., 1995), and telemetry revealed that breeders from Portugal visited the same area during their post-breeding migration in autumn (Catry et al., 2011).

With about 23,000 individuals, storm petrels in summer were twice as abundant as in winter. This could be explained by the return of storm petrels to their breeding sites in northern Europe. In the ENA, previous studies at sea showed that storm petrels are observed in high densities in the Celtic sea and the western Channel during the summer (Stone et al., 1995; Van der Meer and Leopold, 1995). In the north of BoB, they exploit an upwelling area, located at the shelf edge (Castége and Hémery, 2010; Van der Meer and Leopold, 1995). In our study, these areas of high density were clearly visible in the summer distribution (Fig. 4). About 850-900 pairs breed in the Atlantic French waters, mostly at the tip of Brittany (Cadiou, 2014). In winter, the storm petrels concentrated in the southern half of the BoB are of unknown origin and status (Hémery, 1991).

During summer, terns were almost ten times more abundant than in winter. They dwelled in the coastal waters of almost all study areas, with a preference for large bays. Among the species breeding along the French Atlantic coast in 2011, the sandwich tern was the most abundant with about 5850 pairs in 2010 (70% of them breeding close to Arcachon Bay), while the common terns contributed about 3000 pairs in the ENA, and little terns comprised 220 pairs (Cadiou, 2014).

4.2.3. Year-round residents

Several groups displayed no significant changes either in their distribution or abundance between the two sampled seasons. However, this does not exclude movements of these seabird groups within the area, which could have been masked by the pooling of different species or by the dates of the surveys.

Estimated numbers of large-sized gulls were relatively stable between seasons (between 115,000 and 130,000 individuals). In both seasons, approximately half of the large-sized gulls were mostly juveniles or immature birds, which could not be attributed to either black-backed or grey-backed gulls, as the plumage does not differ at the youngest stages. Grey-backed gulls doubled in number in summer, but their distribution did not vary between seasons. This group was frequently encountered all along the Atlantic shore, except along Aquitaine, where densities were lower. Most of the sightings could correspond to the herring gull, as only a limited number of yellow-legged gulls breed in this area (350 pairs, see Cadiou, 2014). In 2009-2012, the herring gull breeding population was about 55,000 breeding pairs in colonies distributed between the Gironde Estuary and the Dover Strait (Cadiou, 2014). In the EC, the observed distributions were similar to the European Seabirds at Sea data for the herring gull (Stone et al., 1995). During the post-breeding period, dispersive movements lead birds up to 150–200 km from their colony and may explain the limited changes observed between seasons in our distribution maps. As birds standing on the shore or inland were not counted, estimates for this group were probably widely underestimated.

Black-backed gulls, comprising the lesser and greater black-backed gulls, also occurred from the Gironde estuary to the Dover Strait with no significant changes in their range between seasons. Although abundance estimates barely varied, the high density patches observed in the eastern EC during winter did not occur in summer, as previously shown in Stone et al. (1995). The distribution of breeding sites is similar for both species of black-backed gull and do not differ from those of grey-backed gulls. The latest counts showed 22,000 pairs of lesser black-backed gulls and 6500 pairs of great black-backed gulls breeding along the Atlantic coast (Cadiou, 2014).

Similarly, cormorants and shags showed few changes in numbers and distributions between winter and summer. Similar to large-sized gulls, they were very coastal and were not found south of the Gironde estuary. The great cormorant and the European shag usually reach their breeding sites in January and in November, respectively, and the last breeders leave the colonies in August (Cadiou et al., 2004a). This long and poorly synchronised reproduction cycle may explain the lack...
4.3. Implications for conservation

The number of seabirds in the entire eastern North Atlantic basin is estimated to be 90-100 million, including approximately 30 million breeding pairs, 60% of them breeding in the higher latitudes of the Arctic (Barrett et al., 2006; ICES, 2003). The North Sea and the EC support an estimated number of 2.5 million breeding pairs, while the western European waters from the Faroe Islands to Ireland reach 3.5 million (ICES, 2003; Mitchell et al., 2004). In contrast, the whole breeding population from the Atlantic coast, from France to south of Portugal, represents only 100,000 pairs. Most of these seabird species undergo partial (i.e. dispersive) or total migration towards wintering grounds after the breeding period (generally occurring between August and December) before returning to their colony (between January and May). An important number of breeders from the Arctic, such as the little auk, kittiwake and guillemot, mainly follow a transatlantic route leading towards southern Greenland or Newfoundland (Fort et al., 2013a, 2013b; Frederiksen et al., 2012). A second migratory route, following the continental shelf, leads numerous seabird species to the ENA or further south up to the West African upwelling (Camphuysen and van der Meer, 2005; Grémillet et al., 2015) or to the southern Atlantic (Guilford et al., 2009). In accordance with these facts, our estimate for the seabird community of the EC and BoB in winter reached nearly a million individuals and was 2.5 times higher than in summer (364 thousands). This winter estimate, calculated for the November-February period, did not consider peaks of migration, and should therefore be considered as a minimum value. This result confirmed the importance of the ENA for seabirds during the wintering season at the European scale, as numbers of migrant birds widely exceed those of breeding birds. Simultaneously, this work highlighted the importance of oceanic areas as shelters of an abundant avian fauna, when most of the existing marine protected areas are restricted to the coastal fringe. A recent study addressed a list of priority research questions to improve seabird conservation science (Lewison et al., 2012). Among other things, the authors pointed out the necessity to increase efforts of research and conservation in oceanic areas. Even if conservation measures implemented at colonies have greatly benefited to seabird populations, they obviously do not reduce the impact of threats at sea. In accordance with the conclusions of their study, our results highlight the necessity to coordinate conservation plans beyond national jurisdictions, at least at the European scale, and to focus on processes occurring at sea, in particular during the non-breeding season. As mandated by the recent Marine Strategy Framework Directive (2008/56/EC), all European states are required to regularly monitor and report the state of the marine environment of their waters. The distributional range and the abundance of species are possible indicators to contribute assessing the achievement of GES in terms of seabirds. This study could provide a baseline of the seasonal distribution of seabirds in the ENA and their relative abundance, complementary to the monitoring of breeding sites. However, these surveys should be repeated at regular intervals in order to consider the inter-annual variability, which probably affects the distribution of seabirds.

5. Conclusion

The purpose of this study was to increase the current knowledge on seabirds in the ENA. It offers a snapshot of seabird distributions and abundances at sea during two contrasting seasons at the scale of the EC and the BoB, and highlights the occurrence of important seasonal variations for most seabird groups. Hence, abundance and diversity of seabird species were higher during the winter, when numerous breeders of northern Europe crossed the ENA to winter or to reach southern wintering grounds. To illustrate this, height of the fifteen seabird groups were identified as mostly winter visitors, four groups as summer visitors and three groups as year-round residents. Important areas were identified, but also varied across seasons. While seabirds concentrated on the continental shelf of eastern EC and BoB in winter, they were more abundant in the oceanic areas of the western EC, as well as the slope and oceanic waters of the BoB in summer.

Overall, our results emphasise and complement those of telemetry studies, but present the advantage of a larger sample size and a wider panel of species. Nevertheless, a perspective to this work is obviously to consider the inter-annual variations in the environment which strongly influence the distribution of most oceanic and mobile seabirds and may potentially lead to significant changes between years, although the comparison of our results with the long-term European Seabirds at Sea dataset supports the hypothesis of a persistency in several species distribution.

Acknowledgements

The French Ministry in charge of the environment (Ministère de l’Environnement, de l’Energie et de la Mer) and the French Marine Protected Areas Agency (Agence des aires marines protégées, AAMP) funded the SAMM survey. The PELAGIS observatory, with the help of the AAMP, designed, coordinated and conducted the survey. We thank all the observers: Thomas Barreau, Ariane Blanchard, Vincent Brettle, Alexis Chevalier, Cécile Dar, Léa David, Olivier Dian, Nathalie Di-Méglio, Emilie Durand, Marc Duville, Emmanuelle Levesque, Alessio Maglio, Marie Pellé, Morgane Perri, and Sandrine Serre. We are indebted to all aircraft crew members of Pixair Survey and the logistic partnership SINAY. We thank Veremes and Safe Software for the free use of FME Desktop 2013 SP4. We are grateful to Auriane Virgili for her help with R and her fruitful comments on the manuscript. We are grateful to the referees and to the editor for their constructive input.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2016.11.012.

References


