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European Seabirds Show Stable Contemporary Biogeography

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Abstract.—The geographic distribution and populations of cliff-nesting seabirds are essential elements in the assessment of their ecological roles and status. Here, a geographic mapping approach was used to visualize the biogeography of European seabirds. This approach was conducted at two temporally separated time intervals: 2004-2010 was compared to 1982-1988. Three biogeographic regions were identified: Arctic, Boreal and Ibero-Atlantic. The data show that species richness has remained stable over the approximately 20-year interval, as have, in general, population numbers and geographic distribution. Such stability, compared to recent declining trends worldwide, may be due to earlier human-driven declines in the European Atlantic, followed by effective conservation measures for the remaining populations. The species richness of cliff-nesting seabirds may not be principally determined by island area and distance from a large land mass, but rather by the extent of vertical cliff façade and distance from fishing areas. The stable species richness of each European Atlantic geographical sub-unit suggests that not only individual islands and mainland but rather the entire European Atlantic functions as a single large "cliff seabird island" in determining biogeographic seabird equilibrium. *Received 17 May 2017, accepted 10 July 2017.*

Key words.—Atlantic, biogeography, cliffs, history, population, seabirds.

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The ecological influence of seabirds extends far beyond their nesting areas, both through wide-ranging foraging and over the course of large-scale migrations (Shealer 2001; Beninger *et al.* 2011). Seabirds are considered sensitive monitors of the global marine environment (Furness and Camphuysen 1997; Frederiksen *et al.* 2007; Parsons *et al.* 2008; Paleczny *et al.* 2015). Their geographical distribution has been studied for centuries, with quantitative research beginning in the early 1900s (Buturlin 1906a, 1906b, 1906c; Gurney 1913; Salmon and Lockley 1933; Edwards *et al.* 1936). Such work continued throughout the latter half of the 20th century and up to the present (Nelson 1966, 1980; Nettleship and Evans 1985; Gaston 2004). Seabirds, especially pelagic seabirds, not only change their geographic distribution in the course of reproductive migrations, but also change their habitat type depending on the stage of the life and migratory cycles (Nelson 1980; Schreiber and Burger 2001).

Nesting ranges have been intensively studied due to their role in the reproduction and subsequent population dynamics of pelagic seabirds (reviewed by Nelson 1980; Coulson 2001; Gaston 2004). Reports of declines in seabird populations worldwide over the previous two decades (Birdlife International 2004; Hasebe *et al.* 2012; Paleczny *et al.* 2015) underscore the need to probe ecological changes as far as possible into the past to understand temporal trends (Jackson *et al.* 2001; Connell *et al.* 2008). For the purposes of this study, "population" refers to monospecific assemblages at discrete geographic scales, with no arbitrary "cut-off" level of genetic exchange. The scant data on this subject indicate that there is weak genetic exchange between nesting sites (Nelson 2001).

Nesting seabirds are typical and emblematic organisms of cliff sea coasts. Nesting range information is critical to evaluation of seabird numbers and breeding success (Mitchell *et al.* 2004; Gaston *et al.* 2006). For the Atlantic coasts of Europe, the body of nesting data is large relative to other regions, encompassing both the most extensive chronological interval of any region in the world and many Northern Hemisphere breeding seabird species (Nelson 1980; Tuck and Heinzel 1985; Nettleship 1996; Birdlife International 2004). The European seabird distributions are also of particular interest because this region has been precociously, and increasingly, human-impacted over the course of human history (Palmer *et al.* 2007).

Although there are extensive data concerning cliff-nesting seabird populations and their distributions in the Northeast Atlantic, the sources are fragmented and localized, such that no coherent picture has been available at the European Atlantic geographical scale. The present study draws together data from the disparate local European Atlantic sources to provide a large-scale biogeographic synthesis, with emphasis not only on the geographic distributions but also on population sizes and the evolution of these fundamental characteristics over recent history.

METHODS

Study Area

The European Atlantic coastal region is characterized by temperate-cold waters and an extensive continental shelf (Trenhaile 1987; Gomez-Pujol *et al.* 2014; Moses 2014). Our study encompassed all regions where seabirds are historically known to nest, extending from 39° N (Berlengas archipelago) to 80° N (Spitsbergen and Franz-Josef Land) (Table 1). The area includes all rocky shore habitats along the European Atlantic coast and offshore islands.

Species

There is no universally accepted definition of "seabird" (Nelson 1980; Schreiber and Burger 2001). For this study, a seabird was defined as being a truly pelagic bird that has a wholly marine diet (thus excluding Phalacrocoracidae (Great Cormorant and European Shag; scientific names are given in Table 1), Laridae (gulls, terns), and Ardeidae (herons, egrets), and nests on cliffs (i.e., variably inclined rock faces, including ledges and associated crevices/burrows) (Nelson 1980; Gaston 2004). Thirteen species belonging to five families fulfilled these criteria (Table 1). All 13 species are indigenous to the Northern Hemisphere; some are distributed across the entire longitudinal range, while others have a more limited longitudinal distribution (North Atlantic or Northeast Atlantic). Nevertheless, all 13 of these boreal seabird species nest on European Atlantic cliff coasts.

Sources and Map Construction

Forty-four sources and 13 species were used for map construction (Table 1; Appendix). Due to the great degree of temporal and spatial heterogeneity in the data, map construction was only possible by combining them into two chronological intervals of 7 years: 1982-1988 and 2004-2010. In addition, the diversity of sources and observers necessarily resulted in an unmeasurable and unavoidable degree of heterogeneity in precision.

Three types of maps were constructed. The first map presents the species and the nesting distributions. Individual species were assigned colors: red to yellow for species whose nesting ranges extend the furthest south, blue to green for species whose nesting ranges extend the furthest north, and black to gray for species whose nesting ranges extend simultaneously the furthest north and south. A finer spatial scale was incorporated using convenient geographic units (i.e., countries and large archipelagos) (Fig. 1).

The information from the first map served as a basis for the second map, delimiting broad European Atlantic (including Azores) seabird biogeographical regions (Fig. 2). On the third map, the nesting seabird population size for each geographical unit was incorporated. Due to the heterogeneity of population sizes, population class sizes were created to distinguish between small and large nesting groups, which may comprise several colonies.

The mapping procedure described above was repeated for sources dating from 1982-1988 (the earliest dates for which quantitative data are available for the complete species set). After comparison of the maps for the two time periods (1982-1988 and 2004-2010), specific maps were constructed to highlight the temporal dynamics of species that had shown marked changes in abundance.

It was not possible to apply quantitative, comparative statistical tests to the data for the following fundamental reasons: 1) heterogeneity of counting methods and efficiencies; 2) cumulative error if data are combined from different studies; 3) inadequacy of classical statistics in a non-experimental, non-randomized context (Beninger *et al.* 2012); 4) lack of replication (historical data); and 5) temporal and spatial autocorrelation. Moreover, statistical significance is likely to be of limited meaning in a study in which status report and effect size are the primary considerations.

RESULTS

Contemporary Nesting Distributions

The contemporary nesting distributions of the 13 seabird species are shown in Fig. 1. Iceland hosted the greatest number of spe-

Table 1. Reference sources for data on geographic distribution and nesting population numbers of cliff-nesting pelagic seabirds. Reference numbers correspond to those indicated in the Appendix.

			References																																											
Family	English Name	Scientific Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Alcidae	Little Auk	*Alle alle*	o	o		o	o	o			o				o				o		o	o			o	o	o	o						o	o							o			o	
	Brünnich's Guillemot	*Uria lomvia*	o	o		o	o	o			o				o				o		o	o			o	o	o							o	o							o			o	
	Black Guillemot	*Cepphus grylle*	o	o		o	o	o			o			o	o				o		o	o			o	o	o			o	o			o	o							o		o	o	
	Common Guillemot	*Uria aalge*	o	o		o	o	o			o	o	o	o	o				o		o	o			o	o	o			o	o			o	o		o	o		o	o	o		o	o	
	Atlantic Puffin	*Fratercula arctica*	o	o		o	o	o			o	o	o	o	o				o		o	o		o	o	o	o			o	o			o	o							o		o	o	
	Razorbill	*Alca torda*	o	o		o	o	o			o	o	o	o	o				o		o	o			o	o	o			o	o			o	o			o				o		o	o	
Laridae	Ivory Gull	*Pagophila eburnea*	o	o		o	o	o			o				o				o						o	o	o															o			o	o
	Black-legged Kittiwake	*Rissa tridactyla*	o	o		o	o	o			o	o	o	o	o				o			o			o	o	o		o	o	o							o		o	o	o		o	o	
Sulidae	Northern Gannet	*Morus bassanus*		o	o	o	o	o				o	o	o	o	o	o		o	o		o			o	o	o			o	o	o	o					o	o			o	o	o		
Procellariidae	Northern Fulmar	*Fulmarus glacialis*	o	o		o	o	o		o	o	o	o	o	o			o	o			o	o		o	o	o			o	o					o		o				o		o	o	
	Manx Shearwater	*Puffinus Puffinus*		o		o	o	o	o	o		o	o	o	o				o			o			o	o	o			o	o					o						o		o		
Hydrobatidae	Leach's Storm Petrel	*Hydrobates leucorhous*		o		o	o	o		o				o	o				o			o			o	o	o			o						o						o		o		
	European Storm Petrel	*Hydrobates pelagicus*		o		o	o	o		o		o	o	o	o				o			o			o	o	o			o	o					o				o		o		o		

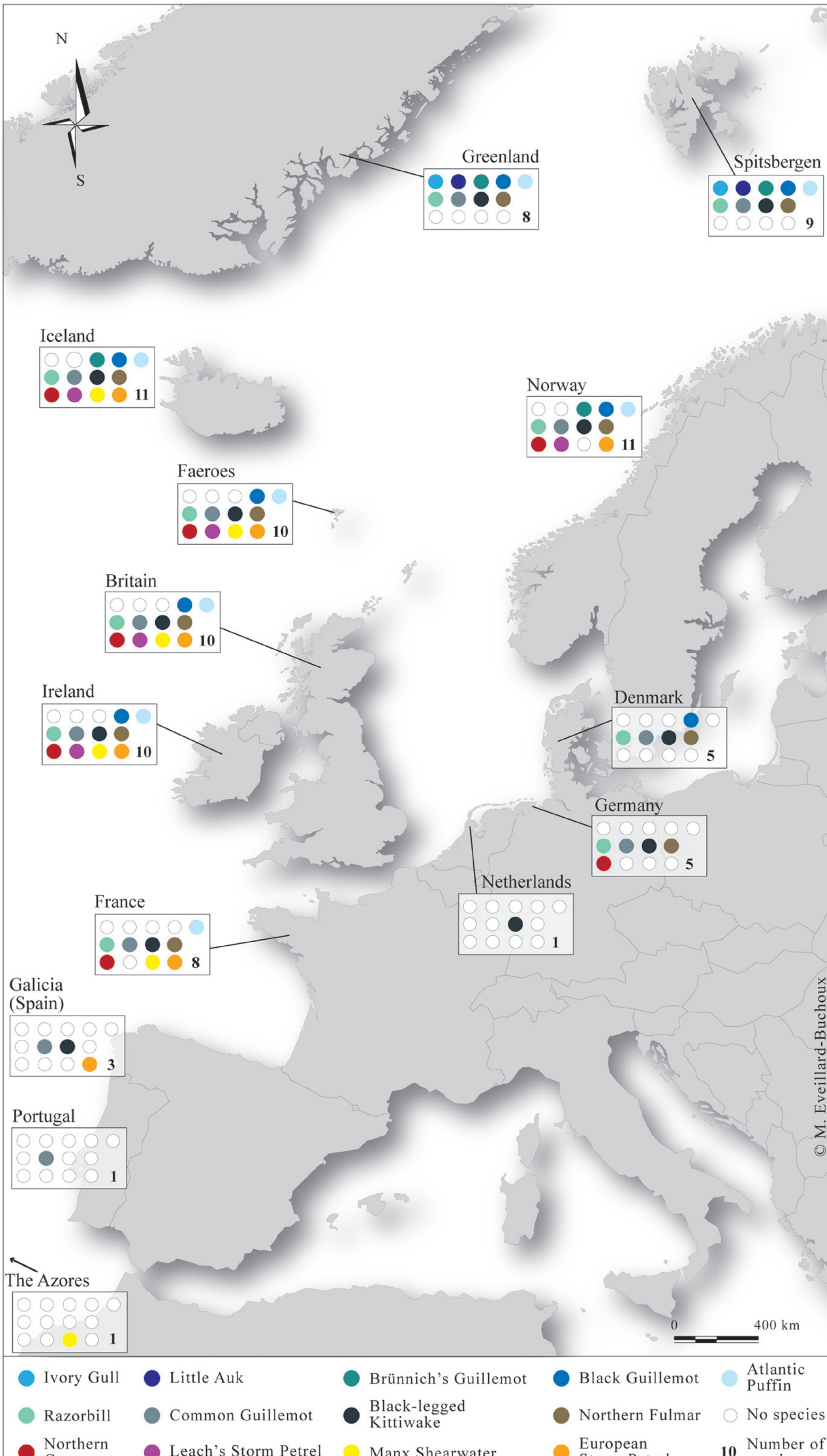

Figure 1. European Atlantic cliff-nesting pelagic seabird nesting ranges. Individual species' nesting distributions are represented by colored dots. Nesting distributions are grouped by countries or regions.

cies (11), while Norway, The Faeroes, and the British Isles each harbored 10 nesting species, followed by Greenland and Spitsbergen (9), France (8), and Iberian coasts (≤ 5).

Iceland and Norway constituted the northern distributional limit for Leach's Storm Petrel, European Storm Petrel, Manx Shearwater and Northern Gannet, while Spitsbergen was the northern distributional limit for the Atlantic Puffin, Razorbill and Common Guillemot. The remaining six species nested on cliffs up to the Arctic ice cap.

Southern distributional limits varied among the seabird species: Greenland and Spitsbergen for the Ivory Gull and Little Auk; Iceland and Norway for Brünnich's Guillemot; the British Isles for the Black Guillemot and Leach's Storm Petrel; France for the Atlantic Puffin, Razorbill, Northern Fulmar and Northern Gannet; Spain for the Black-legged Kittiwake; and Portugal for the Common Guillemot.

We distinguished three cliff-nesting seabird biogeographical regions with a clear latitudinal gradation (Fig. 2). Three seabird species (Ivory Gull, Little Auk and Brünnich's Guillemot) were limited to the northern extremity of the study area, above Iceland and northern Norway, between 66° N and the highest-latitude cliffs, in what we term the "Arctic seabird biogeographical region". Proceeding southward, we can distinguish a "Boreal region" from 43° N to the northern limits of Greenland and Spitsbergen, and an "Ibero-Atlantic region" from 36° N (Gibraltar) to 43° N.

Ten of the 13 seabird species nested within the "Boreal" region, which constitutes 80% of the total geographic area described above. Thus, these were the most characteristic seabird species of the European Atlantic coast. The three other species (Ivory Gull, Little Auk and Brünnich's Guillemot) may be considered marginal, given their Arctic geographic locations (Fig. 2); they will not be considered in detail. Within the biogeographic regions outlined above, the 10 truly northern European species presented partially overlapping latitudinal ranges, while the Common Guillemot and Black-legged Kittiwake were the most cosmopolitan nesting species, extending from the cliffs of the Iberian Peninsula to the Arctic.

Nesting Population Sizes

Nesting population numbers allowed for the construction of a numerical ranking or hierarchy for the seabirds of the European Atlantic coast (Fig. 3). The Little Auk clearly dominated in numerical terms, followed by the Atlantic Puffin, a group of four moderately present species (Common Guillemot, Brünnich's Guillemot, Black-legged Kittiwake and Northern Fulmar), and seven very minor nesting species (Razorbill, Black Guillemot, Ivory Gull, European Storm Petrel, Leach's Storm Petrel, Manx Shearwater and Northern Gannet).

The contemporary nesting populations of the 13 seabird species are shown in Fig. 3A. The U.K., Iceland and Faeroes constituted the main nesting areas of the European Atlantic continental shelf, totaling more than 100,000 nesting pairs. Therefore, the Boreal region hosted both the greatest number of species (11) and the largest nesting populations. However, within this region, Norway presented only two large contemporary nesting populations: Atlantic Puffins and Black-legged Kittiwakes, with no Manx Shearwaters. French cliffs presented only small contemporary nesting populations with much smaller populations of the Boreal species, with no Leach's Storm Petrels or Black Guillemots. The Arctic seabird biogeographical region was the next most important in terms of population numbers, with five mega-nesting groups (> 100,000 nesting pairs) of Arctic and cosmopolitan species. More southern species, such as Razorbill and Atlantic Puffin, had small nesting populations in this region (< 10,000 pairs). Seabird populations were smallest in the Ibero-Atlantic region, with less than 5,000 nesting pairs of Black-legged Kittiwake, Common Guillemot and European Storm Petrel.

Comparison of 1982-1988 and 2004-2010

The global picture of nesting species distributions and corresponding nesting popu-

Figure 2. European Atlantic cliff-nesting pelagic seabird regions. Four biogeographic regions are distinguished: Arctic, Boreal and Ibero-Atlantic.

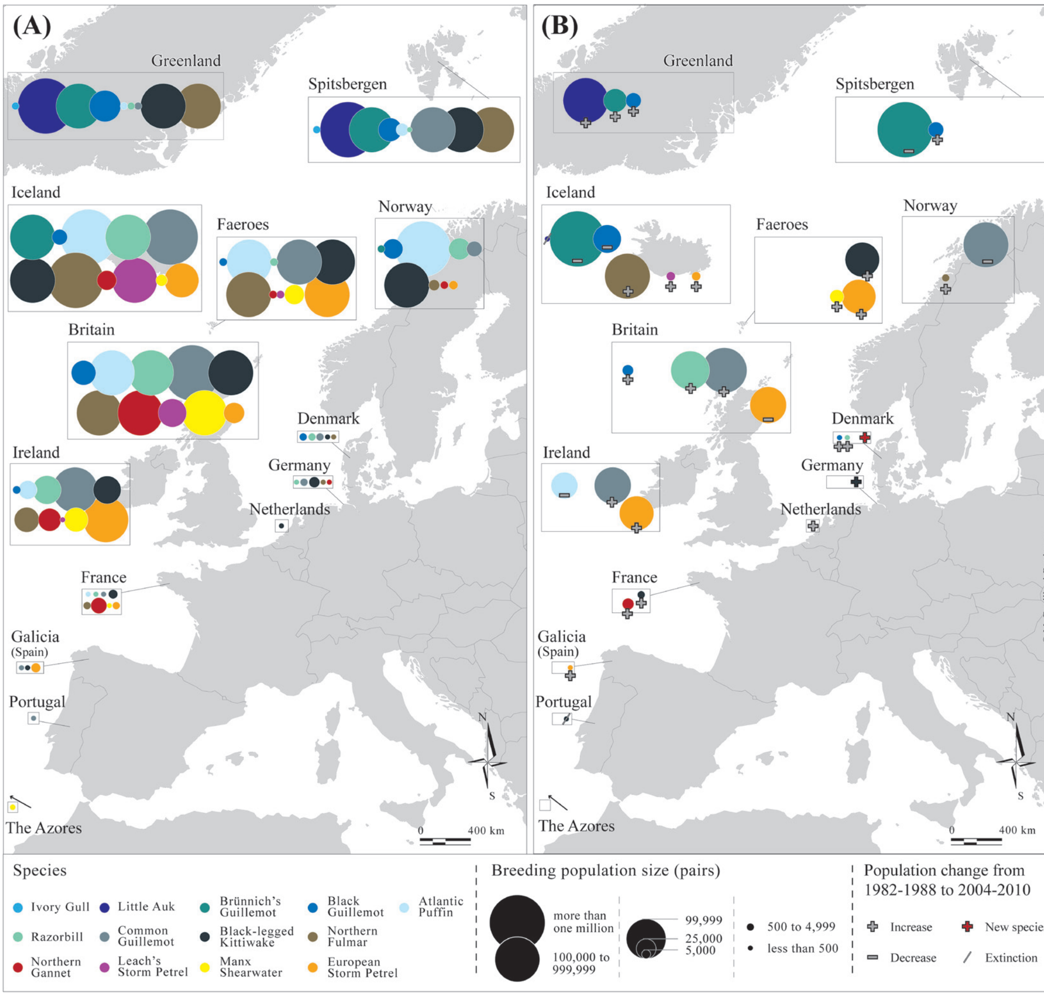

Figure 3. European Atlantic cliff-nesting pelagic seabird nesting ranges and population sizes. Each species is color-coded, with a circle corresponding to population size class. (A) 2004-2010. (B) 1982-1988. Major population changes (increase, decrease, new species and extinction) between the periods 1982-1988 and 2004-2010 are shown in (B) by +, - or /; otherwise, the data are similar to those of (A).

lation sizes remained relatively stable over the period 1982-1988, compared to the similar interval in 2004-2010, as is evident from Fig. 4B).

DISCUSSION

The present study proposes biogeographic regions for nesting European Atlantic seabirds based on their geographic distributions. This division is supported by the data concerning population sizes (Fig. 3A, B). Taken together, these results demonstrate that the Boreal region had the largest species richness and the largest population sizes, and therefore the greatest seabird biodiversity of the European continental shelf, followed by the Arctic and Ibero-Atlantic regions.

At this global scale, most significant variations in nesting population sizes concerned specific populations at their distributional limits (Barrett *et al.* 2006; Munilla *et al.* 2007; Labassen *et al.* 2010; Cadiou *et al.* 2013). The most striking population change was the decrease in Common Guillemot in continental Norway and its close islands, from > 100,000 pairs in the 1980s to ≈15,000 pairs today (Birdlife International 2004; Barrett *et al.* 2006). This contrasts with the situation on the far northern island of Bjørnøya, in which the 245,000 pairs present in 1986 were reduced to 36,000 pairs in 1987, presumably due to the collapse of the Barents Sea capelin (*Mallotus villosus*) stock. The number of breeding pairs subsequently recovered to the 1986 level by 2013 (Norwegian Polar Institute 2013).

In contrast to the situation described above, both the Storm Petrel and the Manx Shearwater counts increased significantly in Iceland. A small but distinct positive population trend was evident for Northern Gannets on the French and German coasts (where a new nesting group has appeared). Black-legged Kittiwake and Little Auk populations have decreased on their southern nesting range limits, while the Black-legged Kittiwake has disappeared from Portugal and decreased on the Spanish coasts. Similarly, the Little Auk population has disappeared from Iceland (Sociedad Espanola de Ornitologia 1997; Birdlife International 2004).

Our data on nesting population sizes can be compared to the total estimated world populations of each species (Table 1). The most abundant European seabird, the Little Auk, accounted for less than 25% of the world population, whereas the next most abundant European nesting species, the Atlantic Puffin, constituted greater than 75% of the corresponding world population. The comparatively smaller European Storm Petrel and Manx Shearwater populations represented greater than 95% of their world populations. The moderately represented Common Guillemot, Brünnich's Guillemot, Black-legged Kittiwake and Northern Fulmar each accounted for less than 25% to 50% of their corresponding world populations. Thus, the conservation importance of the 13 European seabird species varied according to the scale (European or world) considered. Although they represented small fractions of their corresponding world populations (Fig. 4), the Manx Shearwater, European Storm Petrel, Leach's Storm Petrel and Ivory Gull populations are crucial European conservation concerns.

Large year-to-year variations in specific seabird population numbers are common, being related to episodic events such as oil spills, exceptional weather conditions, or epidemics. Similarly, structural changes in the environment may induce significant population changes, such as in the abundances of

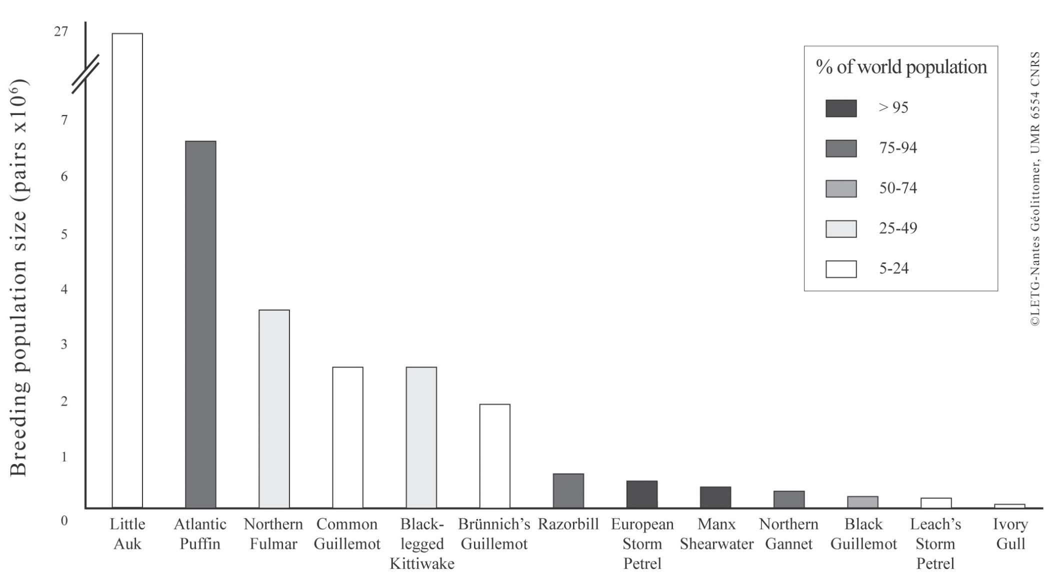

Figure 4. European Atlantic cliff-nesting pelagic seabird absolute population sizes (2004-2010) and percentages of the corresponding world populations.

plankton and prey species, predator behavior and fishing pressure (Votier *et al.* 2004; Wanless *et al.* 2005; Käkelä *et al.* 2007; Norwegian Polar Institute 2013). The striking decline in the continental Norway population of Common Guillemot should be placed in context with the considerable variations in herring (*Clupea harengus*) and capelin populations, and compared with the estimated North Atlantic population of 2.8-2.9 million pairs (Barrett *et al.* 2006; Norwegian Polar Institute 2013). The increases in the European Storm Petrel and the Manx Shearwater populations were also noteworthy, but may also be due to improved census methods for these largely nocturnal, burrow- and crevice-nesting, cliff-dwelling species (Brooke 1990, 2004; Coulson 2001).

The small but distinctly positive population trend for Northern Gannets on the French and German coasts was due to the appearance of a new colony, which echoes similar reports at the turn of the 21st century with the appearance of small new "overspill" colonies, especially on the southern nesting range margins (Nelson 2001, 2005). Inversely, Black-legged Kittiwake geographic distribution shows a general northward shift. The corresponding populations have disappeared from the Ibero-Atlantic region; within the Boreal region, they have vanished from the southern Brittany coasts, while increasing on the northern Brittany and Normandy coasts. The recent up-ticks in localized Northern Gannet and Black-legged Kittiwake populations were contemporaneous with the establishment of new protected areas (Natural Reserves of Archipel des Sept-Iles, Cap Fréhel, Cap Sizun, and Pointe du Hoc in France; Cadiou *et al.* 2004).

The biogeographic data presented in the maps of the present study (Table 1; Appendix) indicate overall stability not only in European Atlantic seabird species numbers, but also in their population numbers. This conclusion may seem at odds with the general declines observed worldwide (Birdlife International 2004; Croxall *et al.* 2013; Paleczny *et al.* 2015). Although geographic up-scaling may reveal broader patterns not apparent at the lower levels, three additional factors may help to explain this apparent contradiction. First, the data of the present study represent a contemporary time window of European seabird biogeography. Due to the recent nature of reliable, quantitative data, reconstructions of the more distant past biogeography are lacking. Because Western Europe was the first intensively human-impacted geographic region in the world, it is possible that most of the seabird declines now being observed in other parts of the world had already occurred prior to the first reliable census studies. Investigating the trends of the more distant past will have to rely on proxies, as in the approaches used to assess historical marine ecosystem changes (Jackson *et al.* 2001; Connell *et al.* 2008). Secondly, the present study focuses specifically on cliff-nesting seabirds, whose habitats have been subject to less human colonization and disturbance than other types of topography. This point is illustrated in the recent local population evolutions of cliff-nesting and ground-nesting seabirds in Scotland, where the former increased in numbers, while the latter decreased between 1986 and 2004 (Parsons *et al.* 2008). Thirdly, seabird conservation may be particularly effective in the European Atlantic. Of the 16 countries worldwide with the highest proportion of their seabird Important Bird Areas protected, eight are European Atlantic, with the United Kingdom ranking first (Croxall *et al.* 2012).

The overall recent stability of European seabird species numbers is a striking aspect of the data presented here. The theory of island biogeography relates species equilibria to two fundamental parameters: island area and distance from a large land mass (Wilson and MacArthur 1967; Brown and Dinsmore 1988; Whittaker and Fernandez-Palacios 2007; Losos and Ricklefs 2010). We hypothesize that for cliff-nesting seabirds, island area is largely irrelevant, being replaced by a more perimeter-related parameter: extent of cliff-face. Similarly, distance from a large land mass is irrelevant since seabirds can travel great distances, and land masses *per se* do not provide their vital needs. Thus, the "distance from a large land mass" parameter is replaced by "distance from a stable food source" (fishing grounds). With these fundamental modifications, not only each of the geographical sub-units (countries, islands) but also the entire European Atlantic shelf system were characterized by relatively stable seabird species numbers from the 1980s to 2010, mirroring the equilibrium species richness in island biogeography theory.

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APPENDIX

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