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Resilience of the British and Irish seabird community in the twentieth century

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ABSTRACT: We studied the British and Irish seabird community in the 20th century, a period of great anthropogenic impact. We determined the average body mass of community members and analysed population sizes, phylogenetic and spatial structures. We also quantified the total predation exerted by seabirds around Britain and Ireland and the spatial distribution of this predation in the North Sea. To achieve these aims we used (1) presence or absence of the seabird species in the different counties of Britain and Ireland between 1875 to 1900 and 1968 to 1972, (2) seabird breeding censuses of Britain and Ireland from 1969 to 1970, 1985 to 1988 and 1998 to 2002, (3) at-sea abundance and distribution surveys of seabirds in the North Sea from 1980 to 1985 and 1990 to 1995, and (4) a bioenergetics model to estimate energy expenditures for 40 seabird species. Our analyses suggest a marked expansion in the breeding range of seabirds in Britain and Ireland between 1875 and 1972. Total seabird numbers also increased at an average rate of 1% per annum between 1969 and 2002, with a related increase of 115% in predicted total seabird predation. Only terns Sternidae declined during this second period. Some characteristics of the community (geographical and phylogenetic structure, body mass) showed minor and non-significant variability between 1969 and 2002. Finally, seabird predation in the North Sea showed a slight north-eastward shift between 1980 to 1985 and 1990 to 1995. Overall, our study indicates that the seabird community of Britain and Ireland has prospered during the 20th century. These results contrast with extensive breeding failures recorded during the first years of the 21st century, which indicate that certain species within the community are now being critically disturbed.

KEY WORDS: Bird phylogeny · Population census · Bioenergetics · Predation · Regime shift · Spatial analysis · Marine environment

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INTRODUCTION

Disturbance is defined as 'any relatively discrete event in time that disrupts an ecosystem, a community, or the structure of a population and changes resource pools, substrate availability, or the physical environment' (White & Pickett 1985). Such disturbance may have natural or anthropogenic origins (Turner et al. 2003) and is one of the dominant forces that shape the structure of biological systems (e.g. Wootton 1998).

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Conversely, resilience is defined as the capacity of these systems to face natural or man-made environmental change (and their positive or negative impact) without degrading or shifting to alternate states (Holling 1973, Hughes et al. 2005).

After centuries of use of marine resources by humans, there is now compelling evidence that marine ecosystems are critically disturbed by pollution (Thompson et al. 1992), overfishing (Jackson et al. 2001) and climate change (Pinnegar et al. 2002, Frederiksen et al. 2004). Seabirds also suffer from the impact of human activities, and they are the most threatened bird group (Butchart et al. 2004). Numerous studies have assessed the impact of global climate change and consequences of overfishing on seabird populations (e.g. Croxall et al. 2002, Barbraud & Weimerskirch 2003). However, to our best knowledge, no study has so far examined the effects of disturbances at the community level. This is an important handicap in management terms, since responses to disturbance can vary substantially across species, taxonomic groups and trophic levels (Wootton 1998).

In the present study, we examined the seabird community of Britain and Ireland, which currently comprises about 8 million birds belonging to 25 different breeding species (Mitchell et al. 2004); these live in some of the most perturbed marine habitats on the planet (Halpern et al. 2008). We defined this 'community' in a taxonomic and functional sense, i.e. a group of species belonging to specific bird families sharing a wide range of life-history traits.

This seabird community has been affected by 4 main factors: (1) fisheries, (2) exploitation for food, (3) species invasions and habitat destruction, and (4) climate change.

(1) The seas around Britain and Ireland have been influenced by industrial fishing since the 19th century (Pauly & Maclean 2003), with overfishing of many stocks taking place throughout the 20th century as a result of improved fishing technology (e.g. Pauly et al. 1998, Hutchinson et al. 2003, Barrett et al. 2004). Fisheries initially removed large predatory fish such as Atlantic cod *Gadus morhua* from the system, which were potentially competing with seabirds for resources. Subsequently, mid-trophic forage fish such as Norway pout *Trisopterus esmarkii* and sandeels *Ammodytes* spp., which are important seabird prey, were intensively fished and used for fish oil or fishmeal in the agriculture and aquaculture industries (Jennings & Kaiser 1998). Intensification of industrial fishing also generated vast amounts of discards and offal, a potentially important food source for some seabird species (Garthe et al. 1996, Furness 2003). Fishery activities may, therefore, have positively (removal of competitors, higher availability of fishery refuses) or negatively (removal of seabird live prey, lethal interactions with fishing gear) impacted seabird populations, and it seems likely that the overall balance has fluctuated from positive to negative through time (Tasker et al. 2000).

(2) Enhanced adult mortality and poor breeding performance was initially caused by hunting and egg collection at breeding sites (Ratcliffe 2004).

(3) Breeding seabirds have also been facing alien species of animals and plants, as well as habitat destruction, which can critically affect their breeding performance (Blackburn 2004).

(4) Finally, a seabird community may be structured by global disturbances impacting its environment and often causing changes in prey availability (e.g. Clarke et al. 2003). The regime shift observed in the North Atlantic and adjacent seas during the mid-1980s (Beaugrand 2004, Alheit et al. 2005, Weijerman et al. 2005) is a good example of this. It is thought that this abrupt shift was the result of higher sea temperatures, which caused a northward latitudinal shift in plankton and fish communities (Beaugrand et al. 2002, Perry et al. 2005). Such modifications might have affected the Britain and Ireland seabird community, which is largely constituted of boreal species at the southern edge of their range (Mitchell et al. 2004).

In this study we used published accounts of the spatial distribution of breeding seabirds around Britain and Ireland in 1875 to 1900 and 1968 to 1972 (Holloway 1996); distribution and abundance data from 3 breeding seabird censuses in Britain and Ireland in 1969 to 1970, 1985 to 1988 and 1998 to 2002 (Mitchell et al. 2004); and a bioenergetics model to determine population and distributional trends, as well as body mass trends and overall energy requirements. We also used at-sea distributions of seabirds (extracts from the European Seabirds at Sea database [ESAS] from 1979 to 2002) and a bioenergetics model to explore the spatial distribution of seabird predation on marine resources of the North Sea and surrounding waters (English Channel, Baltic Sea and the zones of contact with the North Atlantic), comparing patterns between the breeding and non-breeding seasons for 1979 to 1985 and 1990 to 1995 (before and after the 1983 to 1988 regime shift; Beaugrand 2004).

The overall aim of our study was to investigate the characteristics of the seabird community from Britain and Ireland during a period of great anthropogenic impact, the 20th century. We hypothesized that if major changes occurred within this community, they affected: (1) the species composition, (2) global population and distribution trends, (3) trophic status, (4) predation pressure of the community upon marine resources, and (5) the spatial distribution of this predation pressure.

MATERIALS AND METHODS

Study area. The geographic zones considered are: (1) Britain and Ireland and (2) the North Sea and adjacent waters, i.e. the English Channel, the western Baltic Sea and the zone of contact with the North Atlantic, corresponding to the Zones VIIh, VIIe, VIId, IVc, IVb, IVa and IIIa of the International Council for the Exploration of the Seas (ICES).

Seabird populations of Britain and Ireland between 1875 and 1972. This analysis focused on 25 seabird species (Category 1 in Table 1) using data from Holloway (1996), that details the presence or absence of breeding seabirds by counties and by species of Britain and Ireland in 1875 to 1900 and 1968 to 1972. We calculated changes in numbers of counties occupied between the 2 periods (e.g. positive values correspond to an increase in the number of occupied counties).

Seabird populations of Britain and Ireland between 1969 and 2002. This analysis concerned 22 species of seabirds (Category 2 in Table 1) that breed in Britain and Ireland, and used data from Mitchell et al. (2004), who summarize 3 population censuses: Operation Seafarer (1969 to 1970), Seabird Colony Register (SCR) census (1985 to 1988) and Seabird 2000 (1998 to 2002).

Spatial coverage increased with each subsequent survey, with almost complete coverage in the Seabird 2000 census (in Operation Seafarer, coverage was confined to coastal colonies and a part of inland colonies was recorded in the SCR census; more details in

Table 1. Britain and Ireland seabird community species considered in our study. Categories: 1, Seabird population trends in Britain and Ireland between 1875 and 1972; 2, seabird population trends in Britain and Ireland between 1969 and 2002; 3 and 3′, predation exerted by seabirds in the North Sea (3 corresponding to breeding species and 3′ to non-breeding species)

Order	Family	Species	Common name	Body mass (g)	Category
Charadriiformes	Alcidae	*Cepphus grylle*	Black guillemot	385	1, 2, 3
		Uria aalge	Common guillemot	836	1, 2, 3
		Fratercula acrtica	Atlantic puffin	415	1, 2, 3
		Alca torda	Razorbill	677	1, 2, 3
		Alle alle	Little auk	155	3′
	Laridae	*Larus argentatus*	Herring gull	988	1, 2, 3
		Larus fuscus	Lesser black-backed gull	814	1, 2, 3
		Larus canus	Mew gull	410	1, 2, 3
		Larus melanocephalus	Mediterranean gull	796	2
		Larus marinus	Great black-backed gull	1622	1, 2, 3
		Larus ridibundus	Black-headed gull	265	1, 2, 3
		Rissa tridactyla	Black-legged kittiwake	393	1, 2, 3
		Larus minutus	Little gull	120	3
		Larus hyperboreus	Glaucous gull	1326	3′
	Stercorariidae	*Catharacta skua*	Great skua	1431	1, 2, 3
		Stercorarius longicaudus	Long-tailed skua	350	3′
		Stercorarius pomarinus	Pomarine skua	725	3′
		Stercorarius parasiticus	Arctic skua	465	1, 2, 3
	Sternidae	*Sterna paradisaea*	Arctic tern	102	1, 2, 3
		Sterna sandvicensis	Sandwich tern	249	1, 2, 3
		Sterna dougallii	Roseate tern	115	1, 2
		Sterna hirundo	Common tern	125	1, 2, 3
		Sterna albifrons	Little tern	49	1, 2
Pelecaniformes	Phalacrocoracidae	*Phalacrocorax carbo*	Great cormorant	2300	1, 2, 3
		Phalacrocorax aristotelis	European shag	1763	1, 2, 3
	Sulidae	*Morus bassanus*	Northern gannet	3015	1,2, 3
Procellariiformes	Hydrobatidae	*Oceanodroma leucorhoa*	Leach's storm-petrel	44	1, 3
		Hydrobates pelagicus	European storm-petrel	25	1, 3
	Procellariidae	*Fulmarus glacialis*	Northern fulmar	758	1, 2, 3
		Calonectris diomedea	Cory's shearwater	750	3′
		Puffinus puffinus	Manx shearwater	419	1,3
		Puffinus gravis	Great shearwater	850	3′
		Puffinus griseus	Sooty shearwater	819	3′
Gaviiformes	Gaviidae	*Gavia arctica*	Black-throated diver	3000	3′
		Gavia immer	Great Northern diver	3950	3′
		Gavia stellata	Red-throated diver	1625	3′
Podicipediformes	Podicipedidae	*Podiceps auritus*	Slavonian grebe	412	3′
		Podiceps cristatus	Great Crested grebe	975	3′
		Podiceps grisegena	Red-necked grebe	800	3′
Anseriformes	Anatidae	*Somateria mollissima*	Common eider	1600	1, 3′

Mitchell et al. 2004). The quality of the data also improved with time through the development of improved methods (e.g. Seabird 2000 was the first survey to use tape-playback methods and consequently achieved much more accurate estimates of shearwaters and petrels).

Since we were primarily interested in global trends, we used total numbers for each species (sum of all individuals at all breeding sites) and we calculated species-specific population growth rates between the different censuses. For each census period, we also calculated the average body mass of all seabirds within the community (BM_{ac}; g):

$$BM_{ac} = \sum \frac{BM_i \times Numbers_i}{Numbers_{community}} \quad (1)$$

where BM_i is the body mass of each species i in grams (Cramp 1992, Wilson et al. 2004), $Numbers_i$ is the number of individuals for each species i and $Numbers_{community}$ is the total size of the community.

Seabird predation around Britain and Ireland. We used the bioenergetics approach detailed in Tasker & Furness (1996), and Grémillet et al. (2003) to estimate the yearly food requirements of 40 seabird species for time periods 1969 to 1970, 1985 to 1988 and 1998 to 2002. These species are listed in Table 1 (Category 3).

Population size was calculated by adding total numbers of breeding birds, extracted from Mitchell et al. (2004) and estimates of numbers of juveniles and of adult non-breeders. The proportion of juveniles was calculated after Cairns et al. (1991), and the proportion of adult non-breeders after Barrett et al. (2006). Species-specific energy requirements of adults and chicks were taken from the literature when available, or estimated using allometric equations detailed in Ellis & Gabrielsen (2002). Field metabolic rates (FMR) were used to estimate energy requirements (ER; kJ d^{-1}) of seabirds during the breeding season (those of adults ER_{adult}, plus those of the chick) and during the non-breeding season (ER_{adult} only) (see Tables 2 & 3). The average number of chicks per nest was taken from the database of the British Trust for Ornithology (available at www.bto.org). Body masses (BM; g) were extracted from Cramp (1992) and Wilson et al. (2004). A fixed energy density of prey of 5.5 kJ g^{-1} wet mass was assumed (see Barrett et al. 2006). The assimilation efficiency (%) was set to 75% for adults (ICES 2000) and to 80% for chicks (Ellis & Gabrielsen 2002), except when specific information was available for the species considered (Ellis & Gabrielsen 2002).

Seabird predation in the North Sea. We followed the same bioenergetics approach as above, but instead of calculating the predation using total population numbers, we investigated the spatial distribution of seabird predation in the North Sea. Energy requirements were calculated as previously (see 'Seabird predation around Britain and Ireland'). We used data from the ESAS database (from 1979 to 2002), covering 3 235 434 km^2 of the North Sea and including 310 000 seabird sightings. In the 3 235 434 km^2 sampled, 37 different species were observed (Table 1). These observations were compiled using a spatial resolution of 15′ latitude × 30′ longitude for 2 time periods: 1979 to 1985 and 1990 to 1995, which were split into 2 phases: (1) the breeding season (April to June) and (2) the non-breeding season (October to February); 36 species were considered (Table 1). Species with <100 individuals for each time period and season were excluded from the analysis. Since sampling effort was not uniform in space and time we used bootstrapping methods to resample all data and reduce this bias. Bootstrapping is often used as an alternative to inference based on parametric assumptions when those assumptions are in doubt, or where parametric inference is impossible or requires very complicated formulas for the calculation of standard errors (Efron & Tibshirani 1993). Seabird predation was then calculated per square kilometer of the entire study area for each time period and season by multiplying the estimated abundance of each seabird species by its food requirements and adding these total requirements for all species present (ICES 2000). Firstly, we estimated daily food intake (DFI):

$$DFI_i = \frac{ER_i}{FED_{prey}} \times \frac{1}{0.75} \quad (2)$$

where DFI_i is the daily food intake for each species i (kg of food), ER_i is the energy requirements for each species i (in kJ d^{-1}), FED_{prey} is the fixed energy density of prey of 5.5 kJ g^{-1} wet mass and 0.75 (75% is the mean assimilation efficiency for each species i).

Total food consumption per square kilometer was then estimated as:

$$PP_{km^2} = \sum (FI_{i\,season} \times AD_i) \quad (3)$$

where PP_{km2} is the predation per square kilometer (kg of food), $FI_{i\ season}$ is the food intake for each species i according to the target season (kg of food), and AD_i is the adjusted density of each species i (density per km^2 sampled; seabird density at sea is adjusted by using various correction factors to account for, e.g., detectability of different species at various distances from the survey platform; details in Stone et al. 1995). Predation per square kilometer was calculated separately for each season (the breeding season lasts for 91 d and the non-breeding season for 151 d) and each time period. Data were projected into a standard background map of the North Sea provided by ICES (www.ices.dk, accessed 31 July 2007) with the planar projection GSC WGS 1984 using ArcView 8.2.

Statistical analyses. We considered 3 factors according to their ecological importance (e.g. Nagy et al. 1999): taxonomic status (i.e. family), ecological niche (i.e. diet; Cramp 1992) and average body mass of each species. To standardise these 3 factors in qualitative data, we used body mass classes for all species. According to Sturges' rule (Sturges 1926), we divided the community into 5 classes of very small (0 to 603 g), small (604 to 1206 g), intermediate (1207 to 1809 g), large (1810 to 2412 g) and very large species (2313 to 3015 g). We used Dixon's test to detect outlier species on a whole-species basis (Gibbons 1994). Two-factor ANOVA or general linear models (i.e. GLM) were used to test for these factors (i.e. family, diet and body mass class) and periods (i.e. 1875 to 1900 and 1968 to 1972) on occupied county numbers of breeding seabirds and proportional species composition (i.e. seabird numbers of each species divided by total seabird numbers). Student's *t*-tests were used to examine change in seabird numbers between the different censuses according to the same 3 ecological factors. Kruskal-Wallis tests allowed us to perfect these analyses, and Wilcoxon *U*-tests, to compare the average body mass of community members at the different periods. We also employed a standardised principal component analysis (PCA) and a cluster analysis to detect spatial and temporal trends in the seabird community using data from Mitchell et al. (2004). The standardised PCA was applied on a table of 108 observations (36 counties × 3 time periods) and 14 variables (14 species). Prior to the analysis, abundance data for each county and species (x_i) were normalised so that the sum of the square of the time periods was equal to 1. The transformation y_i was done as follows:

$$y_i = \frac{x_i}{\sqrt{\sum_{i=1}^{n} x_i^2}} \quad (4)$$

y_i is the transformed abundance data for time period i, x_i the original abundance data for time period i, and n the number of time periods (n = 3). This normalisation procedure was used to give the same weight to each species and county (Beaugrand & Ibañez 2004). Such transformation is commonly applied in 3-mode PCA (Beaugrand et al. 2000).

Eigenvectors were normalised as follows:

$$\mathbf{U_n} = \mathbf{U}\Lambda^{\frac{1}{2}} \quad (5)$$

$\mathbf{U_n}$ being the matrix of normalised eigenvectors, $\mathbf{U}$ being the matrix of eigenvectors and Λ being the diagonal matrix of eigenvalues. Thus, the variables in the space of eigenvectors represented the linear correlation with the first and the second principal component (Legendre & Legendre 1998). This allowed us to add a circle of correlation of 1. When variables are close to this circle, they contribute significantly to the space. The circle of equilibrium descriptor contribution C (Legendre & Legendre 1998) was also represented to see which variables contribute most strongly to the reduced space. C was calculated as follows:

$$C = \sqrt{\frac{d}{p}} \quad (6)$$

d is the number of dimensions, and p is the number of variables used in the analysis. d was equal to 2 in the PCA, p = 14 species and therefore C = 0.38. All variables inside the circle are not correctly represented in this space.

A cluster analysis based upon Ward's procedure (i.e. minimization of intra-class variance) was employed to further investigate spatial structure. Regions showing homogeneous variation over time were identified and combined to represent county clusters based on species composition. This cluster analysis was applied for each time period over the period 1969 to 1970 and 1985 to 1988, we did not take inland zones into account because they were not, or only partially, surveyed (Mitchell et al. 2004).

Analyses were conducted using Minitab and Matlab, with an accepted p-level at 0.05.

RESULTS

Seabird populations of Britain and Ireland between 1875 and 1972

Between 1875 and 1972 no seabird species was lost and there was an overall expansion in breeding range of the seabird population of Britain and Ireland, with the number of counties occupied increasing from 31 to 47 ($F_{1,48}$ = 5.43, p = 0.024). This geographical expansion likely stems from population growth. For instance, northern gannets *Morus bassanus* markedly extended both their breeding range (10 counties occupied in 1900 and 19 in 1969 to 1970) and total population size (49 000 breeding pairs in 1900 and 187 908 from 1984 to 1988) during this period. Changes in species range expansion were also significantly influenced by taxonomy ($F_{8,41}$ = 6.06, p < 0.001), but not by body mass ($F_{5,45}$ = 1.61, p = 0.189). Out of 9 studied families, only the Sternidae and Laridae occupied significantly more counties in 1972 than in 1875 (t_5 = 6.80, p = 0.002 and t_6 = 7.48, p = 0.001, respectively; Fig. 1). Piscivorous species occupied more counties in later periods (t_{13} = 3.60, p = 0.004), as well as the smallest species (class of body mass 0 to 603 g; t_{14} = 3.68, p = 0.002), and the largest species (classes of body mass 1207 to 3015 g; t_6 = 2.98, p = 0.031; Table 1).

Seabird populations of Britain and Ireland between 1969 and 2002

Between 1969 and 2002 there was no species loss and proportional species composition remained unchanged ($F_{2,56}$ < 0.001, p = 1.000; e.g. European shag featured 1.2% of the overall populations in 1969 to 1970, 3.3% in 1985 to 1988 and 1.7% in 1998 to 2002). Our analysis revealed a significant effect of seabird body mass classes on community composition (H_4 = 23.32, p < 0.001). The body mass class 604 to 1206 g was the most numerous in recent times; for example, it corresponded to approximately 60% of total numbers between 1998 and 2002. Piscivorous species were also numerous (65.75% in 1969 to 1970, 74.3% in 1985 to 1988 and 75% in 1998 to 2002).

Seabird breeding populations increased by 34% (4 780 000 to 6 396 000 ind.) between 1969 and 2002, representing an augmentation of approximately 1% yr^{-1}. The initial growth rate was 25% between 1969 and 1988, subsequently decreasing to 7% between 1985 and 2002. This rate was not influenced by body mass classes ($F_{4,52}$ = 0.54, p = 0.704), with the exception of species weighing between 1207 and 3015 g. The 9 species contained in this class declined by 12.7% between 1969 to 1970 and 1985 to 1988 (t_5 = 7.18, p = 0.002). Taxonomic status had a significant impact on population trends ($F_{6,43}$ = 3.88, p = 0.003). The Sternidae declined significantly (t_5 = –7.43, p = 0.002). In 1969, tern numbers corresponded to 3.6% of total community numbers, against 2.2% in 2002. Laridae numbers also decreased between 1969 and 1988 (t_5 = –4.40, p = 0.012), but stabilized between 1988 and 2002, with a similar growth rate to the whole community (t_5 = 1.09, p = 0.336). Piscivorous species had a higher population growth rate than other species between 1969 and 1988 (t_{11} = –3.98, p = 0.003), but not between 1988 and 2002 (t_{11} = –1.68, p = 0.124).

The average body mass of community members showed no significant change during the study period (U_{22} = 115.0, p = 0.721). Nevertheless, it increased slightly from 804 g in 1969 to 860 g in 2002.

Spatial analyses of seabird population trends between 1969 and 2002

Long-term spatial changes were examined for 14 species using a standardised PCA. Values of the first principal component increased with time for nearly all counties taken into consideration in the analysis (Fig. 2). Species that were positively correlated with the first component exhibited an increase in abundance between 1969 to 1970 and 1985 to 1988, the time of the North Sea regime shift. Timing of the regime shift in the North Sea is between 1982 and 1988 according to species (Beaugrand 2004). Herring gull

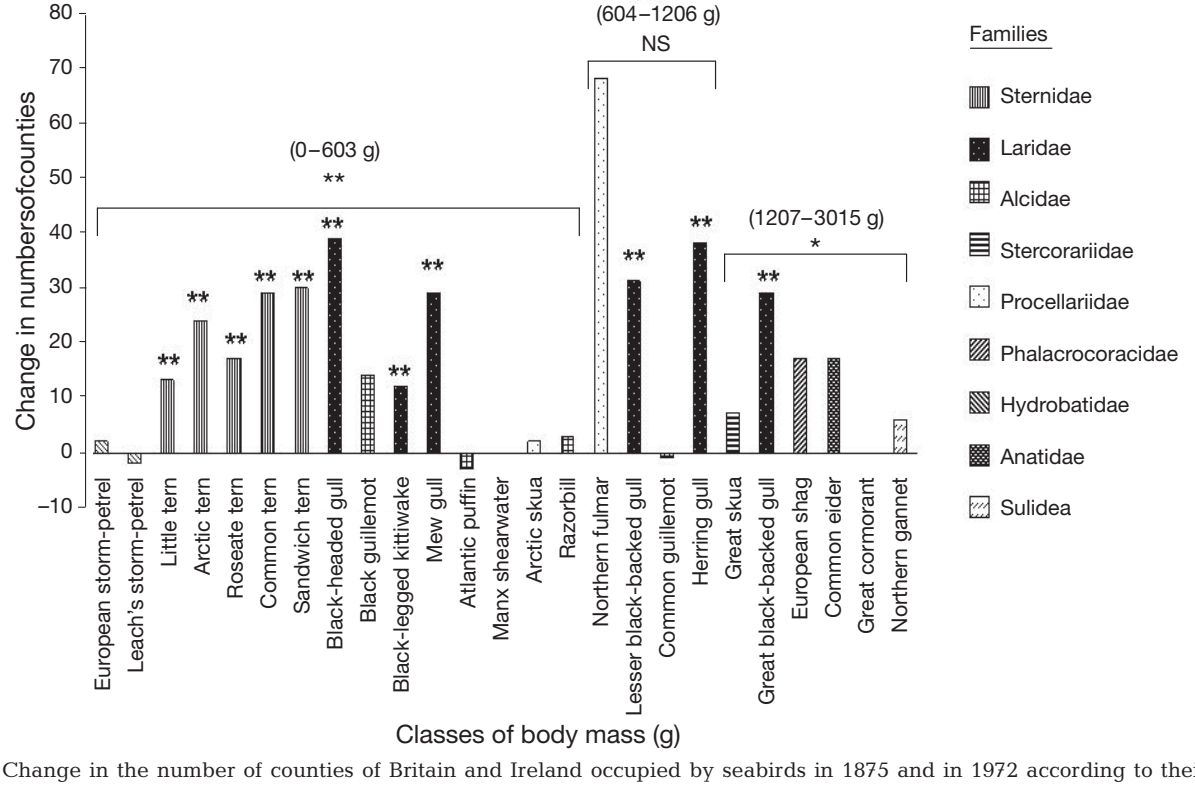


Fig. 1. Change in the number of counties of Britain and Ireland occupied by seabirds in 1875 and in 1972 according to their taxonomic status and their body mass (g). NS: non-significant difference between the 2 time periods; *p < 0.05; **p < 0.025

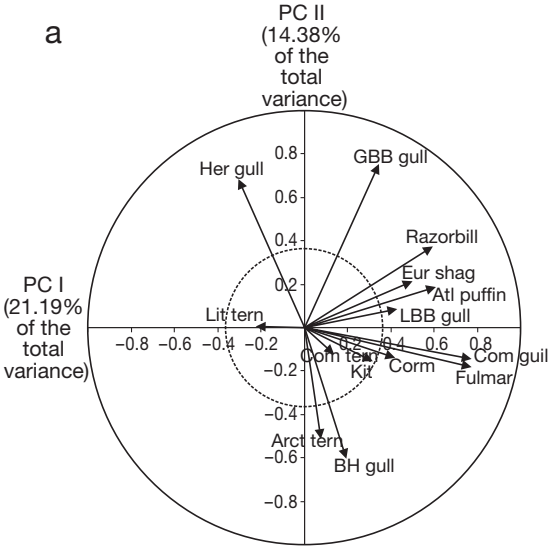
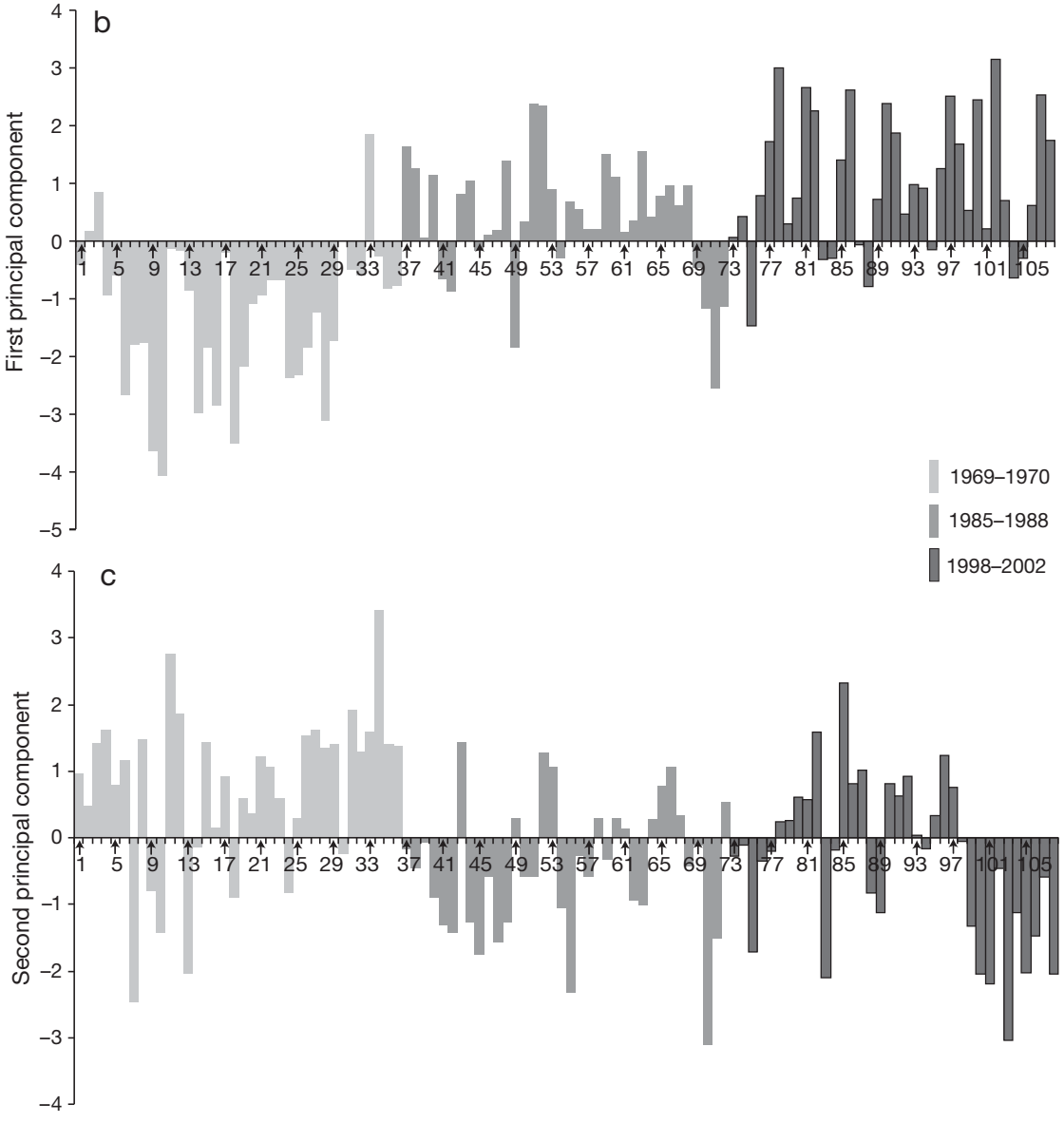


Fig. 2. Standardised PCA for 108 observations (counties and periods) × 14 species. (a) Normalised Eigenvectors 1 and 2 (35.57% of the total variance); both circle of correlation (outer circle) and circle of equilibrium (inner circle) descriptor contribution (C = 0.38) are displayed. The latter circle allows an examination of the contribution of each descriptor in the reduced space. A variable inside this circle has a non-significant contribution. (b) Long-term changes in the first principal component. (c) Long-term changes in the second principal component. Numbers are counties and the 3 levels of grey indicate the 3 time periods considered in the analysis. Counties were coded as follows: (1, 37, 73 for time periods 1, 2 and 3, respectively) Shetland; (2, 38, 74) Orkney; (3, 39, 75) Caithness; (4, 40, 76) Sutherland; (5, 41, 77) Ross & Cromarty; (6, 42, 78) Banff & Buchan; (7, 43, 79) Gordon; (8, 44, 80) Kincardine & Deeside; (9, 45, 81) Northeast Fife; (10, 46, 82) East Lothian; (11, 47, 83) Stewartry; (12, 48, 84) Wigtown; (13, 49, 85) Kyle & Carrick; (14, 50, 86) Argyll & Bute; (15, 51, 87) Lochaber; (16, 52, 88) Skye & Lochalsh; (17, 53, 89) Western Isles Comhairle nan eilean; (18, 54, 90) Northumberland; (19, 55, 91) Dorset; (20, 56, 92) Channel Islands; (21, 57, 93) Cornwall; (22, 58, 94) Isles of Scilly; (23, 59, 95) Devon; (24, 60, 96) Cumbria; (25, 61, 97) Isle of Man; (26, 62, 98) Dyfed; (27, 63, 99) Gwynedd; (28, 64, 100) Co. Antrim; (29, 65, 101) Co. Down; (30, 66, 102) Co. Dublin; (31, 67, 103) Co. Wexford; (32, 68, 104) Co. Cork; (33, 69, 105) Co. Kerry; (34, 70, 106) Co. Galway; (35, 71, 107) Co. Mayo; (36, 72, 108) Co. Donegal



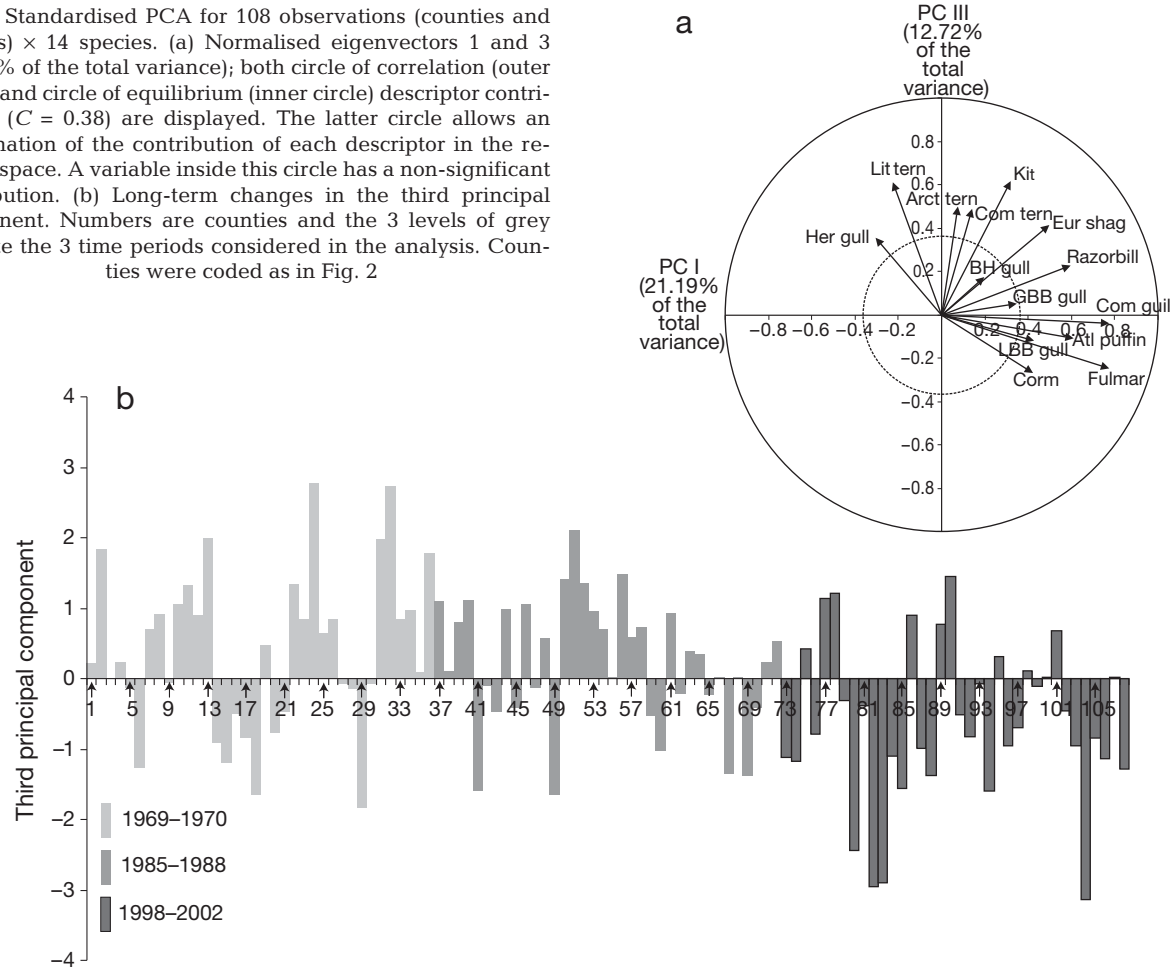


Fig. 3. Standardised PCA for 108 observations (counties and periods) × 14 species. (a) Normalised eigenvectors 1 and 3 (33.91% of the total variance); both circle of correlation (outer circle) and circle of equilibrium (inner circle) descriptor contribution (C = 0.38) are displayed. The latter circle allows an examination of the contribution of each descriptor in the reduced space. A variable inside this circle has a non-significant contribution. (b) Long-term changes in the third principal component. Numbers are counties and the 3 levels of grey indicate the 3 time periods considered in the analysis. Counties were coded as in Fig. 2

Larus argentatus and great black-backed gull *Larus marinus* showed a decrease in abundance between 1969 to 1970 and 1985 to 1988, which reversed in some counties between 1998 and 2002 (Fig. 2). All terns, and black-legged kittiwakes *Rissa tridactyla*, showed a decrease in abundance after the period from 1985 to 1988 in the majority of the counties (Fig. 3).

For the remaining seabird species within the community, the PCA did not reveal significant changes for the 1962 to 2002 time period, except in Shetland. In this region there was a decrease in the size of colonies for all species except black-headed gull after the period from 1985 to 1988 (Figs. 2 & 3). Long-term changes in the Shetland colonies are distinct but not opposite from other regions as demonstrated by the first 3 principal components. Similar changes, but not as pronounced as in Shetland, were also observed in a few locations across Britain (Sutherland, Kincardine & Deeside, Wigtown, Lochaber, Gwynedd).

Finally, our cluster analysis revealed spatial structuring of the community with 4 independent zones, but with very little variability across the study period. A northern cluster gathering Shetland, Orkney and the Western Isles-Comhairle nan eilean (Fig. 4, purple), was clearly isolated from the rest. A second cluster (Fig. 4, green), representing primarily Sternidae, the black-headed gull and the lesser black-backed gull, expanded northwards during 1985 to 1988, but subsequently retreated. The third cluster (Fig. 4, yellow) mainly contained northern gannets and black-legged kittiwakes, and tended to decrease its distributional range during the study period. Finally, a last area corresponding to inland populations could only be displayed for the 1998 to 2002 period, and showed no specific core area (Fig. 4, blue).

Seabird predation around Britain and Ireland

The seabird community of Britain and Ireland weighed a total of 40 380 t in 1969 to 1970, 58 910 t in 1985 to 1988 and 71 200 t in 1998 to 2000. We estimated that it consumed 378 500 t of food yr^{-1} in 1969 to 1970, 577 200 t yr^{-1} in 1985 to 1988 and 813 200 t yr^{-1} in 1999 to 2002. Seabird predation around Britain and Ireland has therefore increased by 115% since the 1970s.

Seabird predation in the North Sea

Our calculations indicate that northern gannets have the highest daily food requirements of all North Sea seabirds (1360 g d^{-1} in summer and 1179 g d^{-1} in winter), followed by great cormorants (1337 g d^{-1} in summer and 801 g d^{-1} in winter). These values accord well with previous estimates provided by Grémillet et al. (2000) and Enstipp et al. (2006). Conversely, Sandwich terns and Leach's storm-petrels are predicted to have the lowest food requirements (32 and 35 g d^{-1} in summer and 16 and 29 g d^{-1} in winter, respectively). Note that summer food requirements are higher because of the additional energy demand of the brood (Tables 2 & 3).

During the summers of 1979 to 1985, predation was highest in the western North Sea, more specifically, along the east coast of Scotland, around Orkney, Shetland, and in the northern North Sea. Summer predation increased markedly during the 1990 to 1995 time period, with a north-eastward shift in predation pressure (Fig. 5a). During the winter period from 1979 to 1985, predation was most intense in the central western North Sea, off the east coast of England and Scotland, and south of Shetland. The pattern generally remained during the 1990 to 1995 period, although there was also a shift in predatory pressure towards the eastern North Sea (Fig. 5b). These eastward shifts during the winter and summer periods 1990 to 1995 compared to 1979 to 1985 might be partly due to more extensive seabird monitoring in the eastern North Sea and the Baltic Sea.

DISCUSSION

Our results indicate that the seabird community of Britain and Ireland has prospered in the 20th century. This contrasts with the fate of the global avifauna (Owens 2000, Pimm et al. 2006), land bird communities from tropical and sub-tropical areas (Sekercioglu et al. 2002, Sodhi et al. 2004), the European land bird community (Julliard et al. 2004) and the worldwide seabird community, within which the petrels have been massively affected by incidental catches on fishing lines (BirdLife International 2001).

Some caution is nevertheless required in interpreting our findings. The databases used are outstanding sources of information but remain incomplete. For instance, population data (Mitchell et al. 2004) were not recorded for some zones and species during Operation Seafarer and the SCR census. In addition, although we included a spatial dimension to our analysis, the lack of real time series might have blurred any potential impact of the 1980s regime shift on the seabird community (Beaugrand 2004). Furthermore, sampling of seabird abundance and distribution in the North Sea was not standardised, i.e. some zones and/or time periods were more intensively monitored than others. We did, however, use a bootstrapping resampling technique to reduce this spatiotemporal bias. Data randomisation tempered the fact that: (1) estimates of population numbers obtained at sea were not temporally and spatially uniform (Camphuysen et

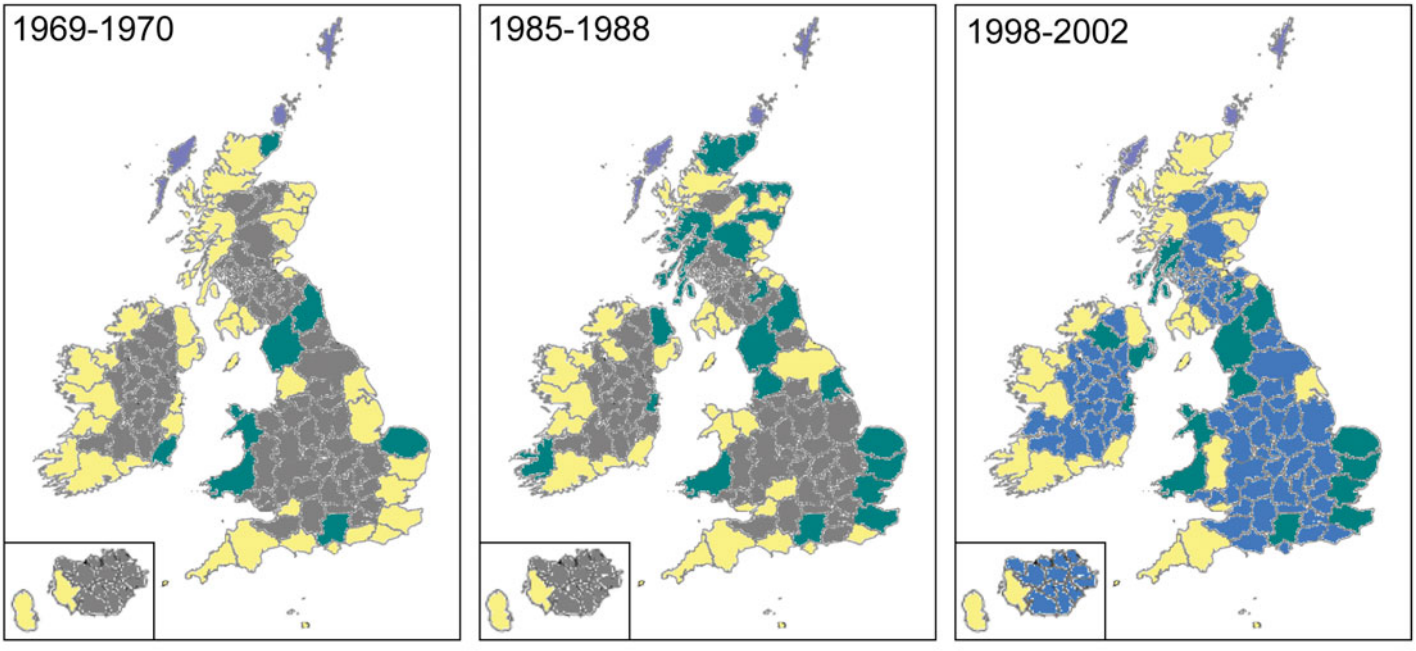


Fig. 4. Cluster analyses of seabird breeding distribution in Britain and Ireland in 1969 to 1970, 1985 to 1988 and 1998 to 2002 allowed the distinction of 4 different zones (marked in purple, green, yellow and blue; see 'Results' for details). Grey zones show areas for which no data were recorded. Inset: Glasgow detail

Table 2. Daily food intake (DFI) of the breeding seabird species considered in our study, according to their field metabolic rates (FMR) or allometric equation for species or species groups (Ellis & Gabrielsen 2002). *m*: body mass in grams (allometric equation)

Breeding species	FMR (kJ h^{-1} g^{-1}) or allometric equation (kJ d^{-1})	DFI (g d^{-1}) Summer	Winter
Arctic skua	$11.49m^{0.718}$	269.26	229.15
Arctic tern	0.127	83.45	75.37
Atlantic puffin	0.0768	192.25	178.30
Black guillemot	0.0942	242.48	211.01
Black-backed gull	$11.49m^{0.718}$	599.67	457.50
Black-headed gull	$11.49m^{0.718}$	186.80	153.03
Common / Arctic tern	$11.49m^{0.718}$	96.61	83.25
Common / Herring gull	$11.49m^{0.718}$	383.81	307.07
Common guillemot / Razorbill	$11.49m^{0.718}$	334.30	325.00
Mew gull	$11.49m^{0.718}$	262.64	209.35
Common tern	0.1125	96.78	81.82
Great cormorant	$3.90m^{0.871}$	1093.15	719.19
European shag	$3.90m^{0.871}$	893.50	595.80
European storm-petrel	$22.06m^{0.594}$	40.82	36.19
Great black-backed gull	$11.49m^{0.718}$	746.51	561.97
Great cormorant	$3.90m^{0.871}$	1337.39	801.13
Great skua	$11.49m^{0.718}$	590.52	472.66
Guillemot	0.0893	426.11	417.65
Herring / Lesser black-backed gull	$11.49m^{0.718}$	393.87	368.46
Herring gull	$11.49m^{0.718}$	480.93	371.39
Black-legged kittiwake	0.0848	237.30	191.35
Leach's storm-petrel	0.114	35.18	29.18
Lesser black-backed gull	$11.49m^{0.718}$	437.45	342.55
Little gull	$11.49m^{0.718}$	99.29	86.65
Manx shearwater	$22.06m^{0.594}$	230.17	193.10
Northern fulmar	0.0826	373.43	329.17
Northern gannet	0.0672	1359.87	1178.81
Razorbill	$11.49m^{0.718}$	298.39	288.55
Sandwich tern	$11.49m^{0.718}$	166.59	144.73
Small gull[a]	$11.49m^{0.718}$	48.29	16.21
Tern	$11.49m^{0.718}$	120.96	105.90
Unidentified gull	$11.49m^{0.718}$	417.08	337.09
Unidentified large gull	$11.49m^{0.718}$	559.15	428.96
Unidentified storm-petrel	$11.49m^{0.718}$	50.36	43.82

[a]Small gulls are unidentified gulls that are the same size or smaller than mew gulls (i.e. 410 g)

al. 1995) and (2) estimates were inaccurate because when data on at-sea seabird distribution and abundance were collected, specific areas were surveyed and these were not chosen randomly (Van der Meer & Camphuysen 1996). Finally, although both the structure and the input values of our bioenergetics models were as realistic as possible, we must stress that all calculations presented here are theoretical.

Further investigations are therefore required, and, in particular, continued, accurate long-term monitoring of seabird numbers, investigations of seabird at-sea distribution and abundance, and refined knowledge of seabird foraging behaviour and energetics, especially for species <1000 g, which dominate the community, but have been far less studied than larger species.

Despite such limitations, important conclusions emerge from our analyses. Unlike in many perturbed ecosystems, no species has disappeared from the seabird community of Britain and Ireland during the 20th century, and, generally speaking, abundance has been increasing. Moreover, the phylogenic and geographic structure of the community has remained fairly stable during the study period (no species loss, no major change in geographic structure), despite a slight increase in average body mass potentially suggesting an impoverishment of trophic width typical of strongly perturbed marine food webs (Pauly et al. 1998).

Despite a marked disturbance, the seabird community of Britain and Ireland on the whole has prospered during the 20th century. We propose 3 potential, mutually non-exclusive explanations for this community growth.

Firstly, it is highly likely to have featured a recovery period after centuries of persecution: seabirds were extensively hunted, but protection measures since the end of the 19th century (1869 'Protection of Birds at Sea' Act) have meant that their exploitation has now largely diminished. Initially, legislation proved most beneficial for the Laridae and Sternidae. This could be explained by the fact that these 2 groups usually breed at sites which are accessible and are consequently more open to persecution than other seabird species (Lloyd et al. 1991). As seabirds are long-lived animals with a low reproductive rate, the majority of their populations only started to show signs of recovery after several decades, with growth being most apparent during the second half of the 20th century. Over the last 15 yr population growth rates have declined, suggesting that some species, such as northern gannets and black-legged kittiwakes, are now being regulated via density-dependent effects (Frederiksen et al. 2005, Wanless et al. 2005).

Secondly, the impact of human fisheries appears to have been mostly beneficial to the seabird community of Britain and Ireland, mainly by removing potential seabird competitors from the system (large predatory fish) and/or by producing vast amounts of additional seabird food via fishery refuses (see 'Introduction'). For instance, seabird species weighing >1200 g declined between 1969 and 1988, but became constant afterwards. This stabilization and consequent range expan-

sion (Lloyd et al. 1991) may have been due to increased levels of fishery discard, food which is predominantly gathered by large species such as great skua, great black-backed gull and northern gannet (Garthe & Hüppop 1994, Votier et al. 2004).

Finally, climate change and the accompanying ecosystem shift, which affected the entire North Atlantic during the 1980s, significantly raised ocean temperatures in the North Sea (Beaugrand 2004), and may have created more favourable environmental conditions for some seabird species (Thompson 2006).

Overall, our study shows that the seabird community of Britain and Ireland has been remarkably resilient to environmental change in the 20th century. However, the relative importance of protection measures at breeding sites, positive and negative impacts of industrial fisheries and climate change remain unclear and deserve further analysis.

The apparent growth of the seabird community of Britain and Ireland in the 20th century contrasts strongly with some regional and species-specific patterns during this period. For example, seabird breeding numbers in Shetland, in particular for terns and black-legged kittiwakes, showed dramatic declines from the late 1980s, and remain in comparatively low numbers (Suddaby & Ratcliffe 1997, Heubeck et al. 1999, Frederiksen et al. 2005, Harris et al. 2006). Reasons for these trends remain unclear, although they might be linked to a fishery-induced and/or climate-driven regional population crash of the lesser sandeel *Ammodytes marinus*, an essential prey item for the local marine avifauna (Arnott & Ruxton 2002).

Since 2004, spectacular breeding failures of formerly abundant species, such as the black-legged kittiwake, have not only been recorded in Shetland, but also all along the east coast of Britain (Mavor et al. 2005, 2006, Wanless et al. 2005). The current hypothesis states that these declines are linked to low availability and low energy content of lesser sandeels. This may have resulted from a trophic cascade driven by warmer water temperatures in the eastern Atlantic (Beaugrand et al. 2000, Wanless et al. 2007).

Table 3. Daily food intake (DFI) of non-breeding seabird species considered in our study, according to their field metabolic rate (FMR), estimated by an allometric equation (Ellis & Gabrielsen 2002). *m*: body mass in grams

Non breeding species in the zone	Allometric equation (kJ d^{-1})	DFI (g d^{-1}) Summer	Winter
Black-throated diver	$16.69m^{0.651}$	742.40	742.40
Common eider	$16.69m^{0.651}$	493.08	493.08
Cory's shearwater	$22.06m^{0.594}$	272.88	272.88
Glaucous gull	$11.49m^{0.718}$	486.28	486.28
Great Crested grebe	$16.69m^{0.651}$	357.17	357.17
Great Northern diver	$16.69m^{0.651}$	888.01	888.01
Great shearwater	$22.06m^{0.594}$	293.94	293.94
Great / Cory's shearwater	$22.06m^{0.594}$	283.54	283.54
Little auk	$11.49m^{0.718}$	104.12	104.12
Long-tailed skua	$11.49m^{0.718}$	186.87	186.87
Pomarine skua	$11.49m^{0.718}$	315.22	315.22
Red-necked grebe	$16.69m^{0.651}$	314.01	314.01
Red-throated diver	$16.69m^{0.651}$	498.08	498.08
Slavonian grebe	$16.69m^{0.651}$	204.02	204.02
Sooty shearwater	$22.06m^{0.594}$	287.52	287.52
Unidentified auk	$11.49m^{0.718}$	239.33	239.33
Unidentified diver	$16.69m^{0.651}$	719.50	719.50

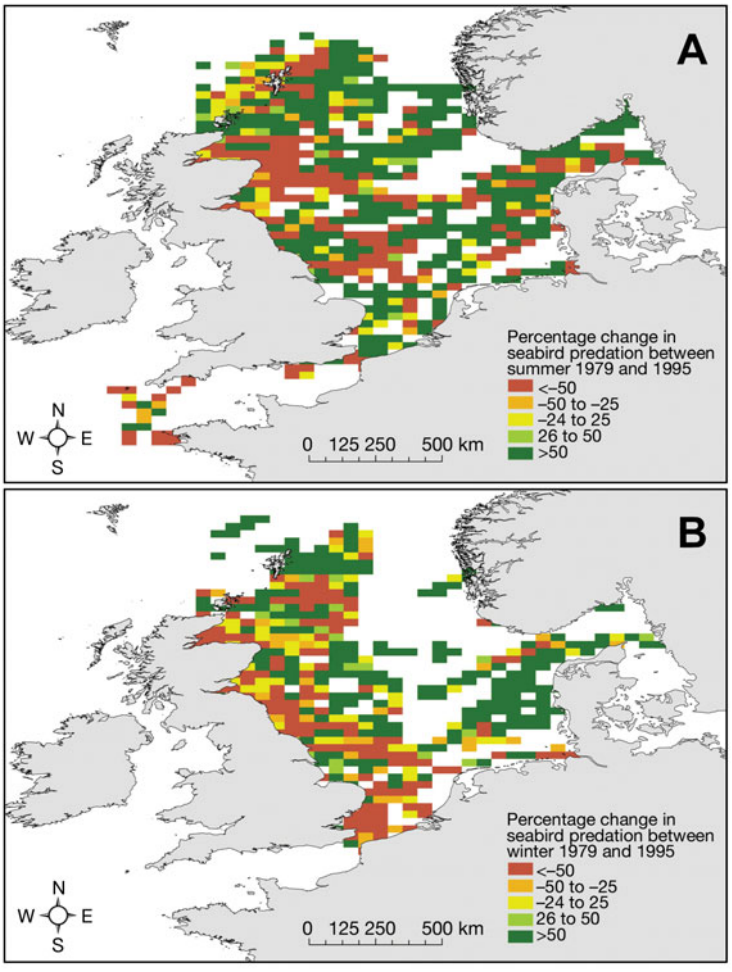


Fig. 5. Percentage change in: (a) summer and (b) winter seabird predation between the 1979 to 1985 and 1990 to 1995 time periods

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