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Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts

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ABSTRACT: Ocean warming and anthropogenic activities such as fishing, shipping and marine renewable developments are affecting marine top predators. Research has focussed on the impacts of single stressors on single species, yet understanding cumulative effects of multiple stressors on communities is vital for effective conservation management. We studied a marine bird community (45 species; 11 families) that used the Forth and Tay region of the North Sea for breeding, overwintering or migration between 1980 and 2011. Local sea surface temperature (SST) increased significantly over this period, with concomitant changes in lower trophic levels. Simultaneously, the region has been subject to fishing pressure and shipping disturbance and is a priority area for renewable energy developments. We used colony-based and at-sea data to quantitatively assess relationships between SST and counts, productivity and survival of 25 species for which sufficient data were available for analysis. For the remaining species, we applied a qualitative approach using published population trends, published climate relationships and foraging sensitivity. In total, 53 % of species showed negative relationships with SST. Trends in counts and demography were combined with climate vulnerability to give an index of population concern to future climate warming, and 44 % of species were classified as high or very high concern, notably cormorants, grebes, skuas, shearwaters, terns and auks, as well as species breeding in the region. Qualitative assessments of vulnerability to fisheries, pollutants, disturbance (including introduced predators), marine renewables and climate found that 93 % of species were vulnerable to ≥2 threats, and 58 % to ≥4. Our results indicate that the majority of birds in this region of the North Sea face an uncertain future, potentially threatening the resilience of this important marine bird community.

KEY WORDS: Global warming · Marine renewables · European Birds Directive · Seabird · Fisheries · SST · Resilience · Demography

INTRODUCTION

Global climate change is altering the physiology, phenology, abundance and distribution of species, resulting in dramatic changes in ecosystem structure (McCarty 2001, Walther et al. 2002, Thackeray et al. 2010). Warming of the oceans is evident throughout the globe (Levitus et al. 2000, Gille 2002), with a higher pace of climate change in the ocean than on land (Burrows et al. 2011, Poloczanska et al. 2013). Increased sea temperatures have already had significant impacts on marine ecosystems (Harley et al. 2006, Parry et al. 2007, Alheit 2009), modifying water stratification and nutrient availability (Sathyendranath et al. 2001, Hays et al. 2005), with associated effects on the distribution, abundance and popula-

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tion dynamics of phytoplankton, zooplankton and mid-trophic level fish (Beaugrand et al. 2002, Edwards et al. 2002, Hays et al. 2005, Perry et al. 2005, Behrenfeld et al. 2006, Brander 2007, van Deurs et al. 2009, Ottersen et al. 2013). Marine top predators are vulnerable to bottom-up effects of climate change on lower trophic levels (Frederiksen et al. 2006, Stige et al. 2010, Schwarz et al. 2013, Springer & van Vliet 2014). Globally, there is extensive evidence that marine bird species are experiencing predominantly negative impacts of climate change operating indirectly on prey species (Votier et al. 2005, Lee et al. 2007, Monticelli et al. 2007, Grémillet & Boulinier 2009, Sydeman & Bograd 2009, Lehikoinen et al. 2013, Paiva et al. 2013). Furthermore, climate projections indicate that sea temperatures will continue to increase globally throughout the 21st century (Parry et al. 2007).

Marine systems are also subject to a wide variety of other anthropogenic pressures acting simultaneously with climate warming, most notably fisheries, introduced predators and pollution (Halpern et al. 2007). Such anthropogenic pressures may intensify in the future, due to increased exploitation associated with human population growth (Sanderson et al. 2002). Furthermore, a large expansion of marine renewable developments is underway, potentially placing additional pressure on marine ecosystems, particularly in coastal areas. The cumulative effects of multiple stressors, and in particular how they interact, are generally poorly understood (Sala et al. 2000, Møller 2013). A recent review of experimental manipulations of multiple stressors in marine environments concluded that overall interactions tended to be synergistic, suggesting this may be common in the wild (Crain et al. 2008). For marine top predators, there is some evidence that interactions between climate and other threats may be additive (Frederiksen et al. 2004, Votier et al. 2005, Ainley & Blight 2009). However, most studies have tended to consider the impacts of single stressors on single species at certain times of the year, and hence may be unrepresentative of the suite of pressures that top predator communities are experiencing over the annual cycle. Since many marine bird populations are of conservation concern (Croxall et al. 2012), community-wide approaches that consider responses to multiple threats, including climate change, are critical in order to provide a comprehensive evaluation of vulnerability and to provide a baseline from which to assess future changes and inform management practices such as marine spatial planning (Grandgeorge et al. 2008).

Here, we evaluated the vulnerability of a marine bird community in the Forth and Tay coastal region of the western North Sea, UK, to climate and other anthropogenic threats, using data on counts and demographic rates (productivity and adult survival) from 1980 to 2011. This internationally important bird community comprises breeding, wintering and migrating birds from the following families: Anatidae, Gaviidae, Procellariidae, Hydrobatidae, Sulidae, Phalacrocoracidae, Podicepedidae, Scolopacidae, Stercorariidae, Laridae, Sternidae and Alcidae. Sea temperatures in the North Sea have increased significantly since the 1970s (Edwards et al. 2002), particularly following a major regime shift in the late 1980s (Beaugrand 2004). Associated with this warming there have been profound and sustained changes in distribution and abundance of plankton and fish (Edwards et al. 2002, Perry et al. 2005, Lindley et al. 2010, Frederiksen et al. 2013). Several long-term datasets on marine bird abundance and demography have been collected over this period, and previous studies have shown that some species are sensitive to indirect effects of climate change (Frederiksen et al. 2007, 2008, Burthe et al. 2012, Luczak et al. 2012). The North Sea is currently under intense pressure from multiple anthropogenic threats. It is one of the most heavily fished areas of the world, traditionally supporting a range of fish and shellfish fisheries (Worm et al. 2009). Furthermore, a large expansion of marine renewable developments is proposed for the region (Marine Scotland 2011). Therefore, there is an urgent need to quantify the vulnerability of this marine bird community to these multiple anthropogenic threats. Two studies have undertaken qualitative assessments of vulnerability of a subset of this bird community to specific threats. Furness & Tasker (2000) used species' foraging strategies to classify those that were potentially vulnerable to climate-induced changes in sandeel prey availability. More recently, Furness et al. (2013) evaluated the vulnerability of species to collision and displacement associated with the development of marine renewables in the region. Here, we considered a wider community of species and larger suite of anthropogenic threats, and undertook quantitative assessments of climate impacts. This study is the first, to our knowledge, to assess the vulnerability of a marine bird community to indirect effects of climate change and other anthropogenic pressures including fisheries, disturbance, development of offshore wind farms and pollution. We aimed to determine which species and families are most vulnerable to climate change and multiple threats in this region, and provide an overall assessment of the vulnerability of the marine bird community to future climate warming.

METHODS

Study species and data coverage

We focused on the Forth and Tay region, east Scotland (Fig. 1). This region is important for a wide range of marine bird species throughout the year, supporting nationally and internationally important populations of summer visitors, migrants, breeding and overwintering species (Söhle et al. 2007, JNCC 2013). We extracted data for the 45 marine bird species from 11 families protected by the European Birds Directive 79/409/EEC because they are listed in Annex 1 or because they are regularly occurring migratory species, and for which data were available for the western North Sea (Lack 1986, Mitchell et al. 2004, Forrester et al. 2007, Worm et al. 2009) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m507p277_supp.pdf for details). Data were obtained from 4 sources: the European Seabirds at Sea database (ESAS); the Seabird Monitoring Programme (SMP); the Wetlands Bird Survey (WeBS); and the Isle of May Long-term Study (IMLOTS). We focused analyses on the period between 1980 and 2011, as prior to this period, many data sets were too sparse.

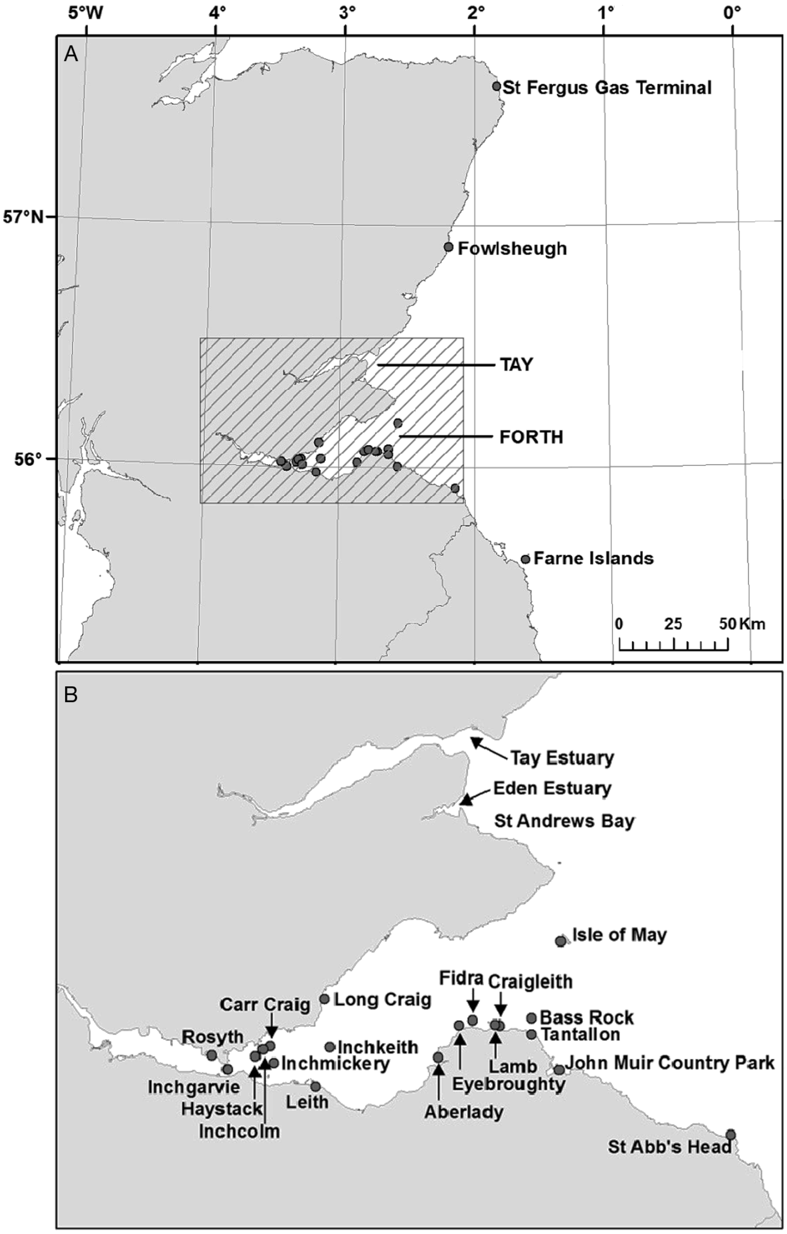

Fig. 1. (a) Study area in eastern Scotland, indicating the locations of the Forth and Tay estuaries (shaded box) and Seabird Monitoring Programme (SMP) sites outside the main Forth/Tay region that were included in analysis. The area of the North Sea for which European Seabirds at Sea (ESAS) and sea surface temperature (SST) data were analysed was between 55 and 58° N and between 4° W and 0° E. (b) Larger-scale map of the shaded box in (a), indicating SMP breeding colonies and Wetlands Bird Survey (WeBS) estuary sites

ESAS data

The ESAS database is a collaborative scheme managed by the Joint Nature Conservation Committee (JNCC; http://jncc.defra.gov.uk/page-4469) and contains data on the distribution and abundance of seabirds in European waters recorded during ship and aerial surveys. Data were extracted for an area of the western North Sea between 55° and 58° N and between 4° W and 0° E (Fig. 1), in order to provide a balance between areas that lie within the foraging range of birds at major breeding sites in the Forth and Tay region and sampling resolution, since data were very sparse for many species. The total area surveyed was 24 159 km^2 (range per season per year: 0–1791 km^2). Data were collected throughout the year, so we considered 2 seasons in our analysis: summer (April to September) and winter (October to March). The winter season for a particular year consisted of the last 3 mo of the preceding year and first 3 mo of the year in question (e.g. winter 1997 included October to December 1996). We analysed counts of birds from aerial and boat-based transects, and we included snapshot counts for flying birds, but excluded incidental sightings, presence/absence data and records not identified to species (see Tasker et al. 1984 for detailed methods). For each species, analysis was undertaken on the summed counts in each season in each year, offset by the total area surveyed. ESAS data have limited power for detecting trends in abundance (Maclean et al. 2013). Therefore, we took the following steps to ensure robust analyses. Data per season per species were only analysed if 10 or more years of non-0 counts were available. Counts for some species were low and/or contained large single peaks which could have strong leverage in analyses. We therefore excluded data if average counts for a species in a season were <20 birds per 100 km^2 or if the time series showed single peaks 5 times greater in size than the average count of the remaining data points. Time series for further analysis were available for 7 species: razorbill *Alca torda* in summer; herring gull *Larus argentatus* and great black-backed gull *L. marinus* in winter; and northern fulmar *Fulmarus glacialis*, northern gannet *Morus bassanus*, black-legged kittiwake *Rissa tridactyla* and guillemot *Uria aalge* in both seasons.

SMP data

The SMP is a joint scheme managed by JNCC (http://jncc.defra.gov.uk/page-4460). The online database contains complete breeding colony censuses or counts of subsets of colonies (plots). Annual estimates of productivity were also available for some colonies (average number of young fledged per apparently occupied nest; see Walsh 1995 for full method details). We included data for all major breeding colonies in the Forth and Tay where data were available for 10 or more years, to ensure that sufficient data were available for analyses (Fig. 1). In addition, data for the St Fergus gas terminal (120 km north of the northern boundary of our core study area) were included because this was one of the best time series of Arctic tern *Sterna paradisaea* and common tern *S. hirundo* productivity. We also included 2 major breeding colonies with good quality data (Farne Islands and Fowlsheugh; Fig. 1) that were in close proximity to the study area (ca. 40 and 50 km to the south and north, respectively) and whose birds were likely to be subject to the same local climatic conditions. In the analysis, productivity data were treated as binomial counts, relative to the number of possible chicks per nest based on maximum brood size (Cramp 1977, 1983).

WeBS data

The WeBS is a joint scheme coordinated by the British Trust for Ornithology, the Wildfowl and Wetlands Trust, the Royal Society for the Protection of Birds and JNCC (www.bto.org/volunteer-surveys/webs/data). Volunteers undertake monthly land-based counts of birds. Counts are classed as being 'good' or 'poor' quality, depending on whether the count is regarded as a reliable estimate of the numbers of birds present at a site. We analysed data from 4 sites (the Forth Estuary, Eden Estuary, Tay Estuary and St Andrews Bay; Fig. 1). Data for each species for all sites were examined to establish when the peak count occurred. If there was a clear tendency for peaks to occur in a particular month, then years were excluded if data for that month were missing from the dataset or confidence in the count was poor. We analysed the maximum monthly count per site occurring in winter and/or summer. We included sites where data were available for 10 or more years, to ensure that sufficient data were available for analyses. We excluded sites where counts were of poor quality, where more than 1 month out of 6 was missing, or time series where average counts were <10 birds. Data were available for further analysis from 13 species: 5 in summer, 7 in winter and 1 in both seasons.

IMLOTS data

IMLOTS is the long-term study of seabird populations breeding on the Isle of May, south-east Scotland, carried out by the Centre for Ecology & Hydrology (CEH) (www.ceh.ac.uk/sci_programmes/isleofmaylong-termstudy.html). Annual adult survival estimates were calculated for 5 species between 1986 and 2009 (see Frederiksen et al. 2004, 2008, Harris et al. 2005 for details): black-legged kittiwake, razorbill, guillemot, Atlantic puffin *Fratercula artica* and European shag *Phalacrocorax aristotelis*. M-arrays of recaptures for each cohort of ringed birds were used to calculate Jolly-Seber survival estimates per year and species between 1986 and 2009 (see Lebreton et al. 1992 for details).

Environmental data

Monthly average SST data were obtained from NOAA Pathfinder version 5.0 (Kilpatrick et al. 2001) for the same area as the ESAS data (55–58° N, 4° W–0° E). We analysed annual mean values across this area for the following seasons: winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November). SST values were generally not highly correlated between seasons except for winter vs. spring and summer vs. autumn (correlation coefficients: winter vs. spring = 0.80; spring vs. summer = 0.51; spring vs. autumn = 0.50; summer vs. autumn = 0.80; summer vs. winter = 0.39; autumn vs. winter = 0.60). Previous research has found correlations between SST lagged by 1 yr and seabird productivity indicative of indirect effects of climate (Frederiksen et al. 2007, Burthe et al. 2012). We therefore considered SST lagged by up to 2 yr in our analysis.

Statistical analysis

Relationships with climate

We examined whether each data series was correlated with climate by regressing each time series against current and lagged SST. Fifteen measures of SST were considered: spring, summer, autumn, winter and annual (January to December) mean SST values for the current year and for each of the previous 2 years. The same model structures were used as for the temporal trends (generalized linear mixed models [GLMMs] fitted in glmmPQL incorporating an AR[1] correlation structure). As time series were generally limited in length, we only fitted one climate term at a time to avoid overparameterisation of models. Tables of model results for relationships with climate and trends are provided in the Supplement (Tables S2–S7).

Temporal trends

We analysed trends in SST and in count and demography (productivity and survival) data separately for each data source and, where appropriate, season for each species. For each combination, the relationship with year was analysed using a GLMM. Count data were modeled with a Poisson distribution and productivity and survival data with a binomial distribution. GLMMs were run using the glmmPQL function in the MASS package in program R (Venables & Ripley 2002) because this automatically adjusts for overdispersion, if present, and because it enabled us to include an AR(1) correlation structure in all models in order to account for temporal autocorrelation. Site was included as a random effect when analysing WeBS count data for species with data from multiple estuaries/bays, and colony was included as a random effect when analysing SMP count and productivity data for species with data from multiple colonies. Hence, models provide an estimate of overall trends rather than site-specific estimates. For other data, a redundant random effect with a single category was included. This redundant random effect had a variance of 0, but including it in the model allowed us to fit the models as GLMMs rather than GLMs, and so allowed us to include AR(1) correlation structure. For the ESAS data, the logarithm of total area surveyed was included as an offset in all models. Visual examination of bird time series suggested that some may have exhibited non-linear trends. For these, we confirmed that a model fitted with year as a quadratic term was not better than a model fitted with year as a linear term. Detrending of the data was not undertaken in this analysis because we were primarily interested in constructing an index that represents the risk to a species within a changed climate, and the index of risk includes both the relationship with climate and trend in time as separate components. Constructing a meaningful index using a detrending approach would be difficult because robust projections for how detrended climate variables will change in the future are not readily available.

Assessing vulnerability to climate and other impacts

Quantitative assessment of vulnerability

An index of vulnerability to climate was constructed based on the statistical analysis of relationships with climate and trends in counts and/or demographic rates. In total, 25 species had sufficient data for quantitative analysis.

For each species, we synthesised the relationships with climate to assign climate vulnerability in 2 steps. First, for each particular combination of data source and season, we assessed whether relationships with climate were consistently in 1 direction (positive, no relationships or negative). Our criteria for consistency where models were significant (positively or negatively related to climate) were that at least 2 models were significant and that 75% of significant models had relationships in the same direction. Relationships that could not be classed as either consistently positive or consistently negative (<2 models were significant) were considered to show no relationship with climate. This approach used all 15 climate variables in determining whether there was evidence for a relationship with climate, rather than attempting to interpret each of the 15 relationships individually, so no explicit adjustment for multiple testing was required.

In a second step, we synthesised these data source/season level results into an overall index of climate vulnerability for the species, as follows:

(1) Positive response to climate change: counts or demographic rates showing positive relationships with climate (counts or demographic rates increase with warmer SST)

(2) No response to climate change: counts or demographic rates showing no relationships with climate

(3) Negative response to climate change: counts or demographic rates showing negative relationships with climate (counts or demographic rates decrease with warmer SST)

For 9 species, there was only 1 data source/season combination available and hence for these species climate vulnerability was based on this single assessment. Multiple data source/season combinations were available for the other 16 species. For 2 of these, there was no evidence of relationships with climate. In the remaining 14, some data sources showed significant relationships with climate, so we assigned vulnerability to climate based on the direction of these relationships, because we cannot exclude the possibility that climate may be accounting for variation in the data for non-relationships. Crucially, however, this approach was balanced with both positive and negative relationships favoured over no response. For 9 species, 1 data source showed negative relationships with climate, and for 3 species, 1 data source showed positive relationships with climate that overrode data sources for the species showing no relationships with climate. For 2 species (common guillemot and razorbill), different data sources showed opposing relationships with climate, and these species were therefore qualitatively assessed for climate vulnerability (see next section). Thus, quantitative assessment was undertaken on a total of 23 species.

We calculated an index of population concern to future climate warming incorporating 2 sources of information: the vulnerability to climate index described above (positive, no or negative response) and count/demographic trends (increasing, stable or decreasing). In synthesising trends, we took a similar approach to climate vulnerability; thus, if multiple data were available and showed evidence of significant trends in some data sources and no trends in others, trends were assigned based on the direction of significant trends. The index of population concern ranged from a score of 0 (very low concern: counts or demographic rates increasing and positive response to climate) to 4 (very high concern: counts or demographic rates decreasing and negative response to climate; Table 1).

Qualitative assessment of vulnerability

A qualitative assessment of vulnerability to climate was undertaken for the remaining 22 species. This assessment was carried out by first reviewing published relationships with climate in the literature. These were only available for Manx shearwater *Puffinus puffinus*, great skua *Stercorarius skua*, common guillemot and razorbill. Vulnerability for the 18 remaining species was based on the foraging ecology sensitivity index of Furness & Tasker (2000). This index is based on sum of scores (0–4 per category for 6 categories, with 4 being the highest in terms of vulnerability to climate-induced changes in sandeel prey availability; hence minimum score 0 and maximum of 24) for body size, costs of foraging, foraging range, ability to dive, amount of spare time and ability to switch diet (see Furness & Tasker 2000 and the Supplement for full details).

Vulnerability to climate was assigned as follows:

(1) Positive response or low foraging sensitivity to climate change: counts or demographic rates showing positive relationships with climate variables or low foraging sensitivity score (<10).

Table 1. Index of population concern to future climate warming, calculated according to vulnerability to climate and whether populations or demography showed evidence of increasing, no trend or decreasing. The shading indicates the level of the index of population concern, ranging from white (very low concern) to dark grey (very high concern)

Relationship with climate	Population and/or demographic rates Increasing	Stable	Decreasing
Positive	Very Low (0)	Low (1)	Moderate (2)
None	Moderate (2)	Moderate (2)	Moderate (2)
Negative	Moderate (2)	High (3)	Very High (4)

(2) No response or moderate foraging sensitivity to climate change: counts or demographic rates showing no relationships with climate variables or medium foraging sensitivity score (10–14).

(3) Negative response or high foraging sensitivity to climate change: counts or demographic rates showing negative relationships to climate variables or high foraging sensitivity score (>14).

Published population trends (increasing, stable, decreasing, unknown) were combined with the climate vulnerability index to assign an index of population concern to future climate based on the same criteria as for the quantitative assessment (Table 1). In order to be as relevant as possible to the study area, published trend information for Scotland (Perkins et al. 2005, Newson et al. 2008, Dillon et al. 2009, Daunt & Mitchell 2013, JNCC 2013) was used where available (9 species: red-throated diver *Gavia stellata*, Slavonian grebe *Podiceps auritus*, Leach's storm-petrel *Oceanodroma leucorhoa*, Arctic skua *Stercorarius parasiticus*, great skua, common gull *Larus canus*, roseate tern *Sterna dougallii*, common guillemot and razorbill). Data at this scale were not available for Mediterranean gull *Ichthyaetus melanocephalus*, so population trend data for the UK were used for this species (JNCC 2013). Published population trends were not available for the remaining 12 species. For 11 of these species, we used conservation status (Eaton et al. 2009) with 'green' conservation status assumed to be equivalent to increasing populations, 'amber' to populations showing no trend, and 'red' to declining populations. No information was available for surf scoter *Melanitta perspicillata*, and this species' index of population concern was scored according to vulnerability to climate.

Non-climate threats

We also assessed the vulnerability of species to anthropogenic threats other than climate during the time of year they are present in the Forth and Tay region. Threats from wind farm developments were based on scores presented by Furness et al. (2013). Collision risk was assessed from flight height and agility, % of time flying and tendency for night flight. Disturbance and displacement were scored based on reaction distances and flexibility of habitat use. We modified the scores of Furness et al. (2013) to make them comparable to our scoring system for climate vulnerability. Species with collision scores <150 were assigned a collision risk score of 1 (low vulnerability), 150–299 as 2 (moderate vulnerability) and >299 as 3 (high vulnerability). Displacement or disturbance scores of 0–6 were coded as 1, 7–12 as 2 and >12 as 3. For 7 species not included by Furness et al. (2013), we assigned scores based on those for related species (see Table S9 in the Supplement).

We also assessed vulnerability to reduction in fisheries discards, fisheries bycatch, competition with fisheries, oil pollution, contaminants other than oil, plastics, introduced predators (brown rats *Rattus norvegicus*, American mink *Neovison vison*, domestic cats *Felis catus* and white-tailed eagles *Haliaeetus albicilla* for this study area) and disturbance associated with boats and/or human presence in breeding colonies. Assessment of vulnerability was based on the scoring system of Frederiksen (2010), where vulnerability was scored from 0 (no threat) to 3 (severe threat). Scores were adjusted to have the same scale as our other vulnerability assessments: a score of 0 was coded 1 (low vulnerability), 1 as 2 (moderate vulnerability) and ≥2 as 3 (high vulnerability). In addition, scores for 17 species were modified to take account of local conditions in the Forth and Tay region. Data from Forrester et al. (2007) and our own experience of the species and study area were used to assign vulnerability scores for 20 species not included in Frederiksen (2010). See the Supplement (Table S10) for full details of these scores.

Overall vulnerability to multiple threats

To obtain an overall vulnerability index to multiple threats, we first consolidated the single non-climate threats into 4 main threats: fisheries (bycatch, discards or competition), pollutants (oil pollution, contaminants and plastics), disturbance (introduced predators, human disturbance in breeding colonies) and wind farms (collision risk, displacement and boat disturbance). For each species, we adopted the highest vulnerability score per individual threat as the score for the representative main threat. We calculated 2 indices of vulnerability to multiple threats. The first indicated the severity of combined threats by summing the scores of vulnerability indices from each main threat (climate and 4 non-climate threats). The second index summed the number of main threats a species was vulnerable to: species were considered vulnerable to climate if scored as 3 and vulnerable to other threats if scored as moderate or above (≥2). This was justified because the middle category of vulnerability to climate represents no relationships between bird data and climate in the quantitative analysis, whereas for other threats the middle category infers some negative impact or risk.

We calculated an overall index of population concern to multiple threats based on vulnerability to multiple threats (not vulnerable: vulnerable to <2 threats; vulnerable to ≥2 main threats) and the status of population trends using the following index:

0: Very low concern: population or demographic rates increasing and not vulnerable to multiple threats

1: Low concern: population or demographic rates showing no trend and not vulnerable to multiple threats

2: Moderate concern: population or demographic rates decreasing but not vulnerable to multiple threats; population or demographic rates increasing but vulnerable to multiple threats

3: High concern: population or demographic rates showing no trend and vulnerable to multiple threats

4: Very high concern: population or demographic rates decreasing and vulnerable to multiple threats

For 11 species where population trends were not available, we based our assessments on the current conservation status (Eaton et al. 2009). Thus we assumed that species with 'green' status were the equivalent of increasing populations and 'amber' the equivalent of no trends in the designations above. One species (surf scoter) with no population trends or conservation status was assumed to show no trend.

RESULTS

Climate trends

Between 1980 and 2011, SST in the Forth and Tay region increased significantly (mean rate 0.05°C yr^{-1}) with the effect apparent in each season of the year (Table 2). This equates to a predicted increase in annual SST in absolute terms of 1.57°C between 1980 and 2010 (1980: 9.04 ± 0.13°C SE; 2010: 10.61 ± 0.12°C).

Vulnerability to climate and other impacts

Quantitative assessment of vulnerability

In total, 25 species had sufficient data to assess relationships with climate and trends in counts and/or demography (productivity or survival). Of these, common guillemot and razorbill showed inconsistent relationships with climate and were therefore assessed qualitatively.

Table 2. Trends in sea surface temperature (SST): annual (January to December); during winter (December, January, February); spring (March, April, May); summer (June, July, August) and autumn (September, October, November) in the Forth and Tay region of Scotland between 1980 and 2011 based on linear regressions of SST against year, with temporal autocorrelation accounted for

Season SST	Estimate (°C yr^{-1})	SE (°C yr^{-1})	t	p
Annual	0.051	0.010	5.029	0.000
Winter	0.050	0.010	4.858	0.000
Spring	0.056	0.015	3.779	0.001
Summer	0.048	0.013	3.629	0.001
Autumn	0.055	0.012	4.752	0.000

Overall, of the 23 remaining species, 13 (57%) showed negative relationships between SST and count or demography data, 5 species (22%) showed positive relationships, and 5 species (22%) showed no relationships.

Of the species with count data, 10 showed negative relationships with climate, 7 had no relationships, 5 had positive relationships, and 1 had inconsistent relationships with climate (European shag; Table 3 and see Table S2 in the Supplement). None of the demographic data showed positive relationships with climate. Of the 10 species with productivity data, 5 showed negative and 5 no relationships with climate (Tables 3 & S3). Of the 5 species with survival data, 3 showed negative relationships with climate and 2 showed no relationship with climate (Tables 3 & S4).

Seven of the 23 species showed significant declines in counts, 12 showed no trend and 4 showed significant increases in counts (Tables 3 & S5). Two out of 10 species showed significant decreases in productivity and 8 showed no trend (Tables 3 & S6). Two out of 5 species showed significant declines in survival and 3 showed no trend (Tables 3 & S7). Five species were of very high population concern to future climate change because they showed a negative response to climate and declining population counts or demography: great crested grebe *Podiceps cristatus*, northern fulmar, European shag, greater scaup *Aythya marila* and black-legged kittiwake. A further 7 species were considered to have high population concern because they showed a negative response to climate but no trends in population counts or demography: black scoter *Melanitta americana*, red-breasted merganser *Mergus serrator*, herring gull, common tern, Arctic tern, little tern *Sternula albifrons* and Atlantic puffin. Six species were considered of moderate population concern, 3 of low concern and 2 of very low concern (Table 3).

Table 3. Quantitative assessment of vulnerability of seabirds to climate based on relationships with climate and trends in counts and/or demographic rates. We present significant trends in counts and demographic rates and whether relationships with climate are consistent. We also provide an overall index of vulnerability to climate ranging from 1 (positive) to 3 (negative) and an index of population concern to future climate based on vulnerability to climate and population trends ranging from 0 (very low) to 4 (very high; see Table S8 in the Supplement info for a more extensive version of this table). ESAS: European Seabirds at Sea; SMP: Seabird Monitoring Programme; WeBS: Wetlands Bird Survey

Species	No. of datasets analysed	Direction of significant trends	Climate regressions consistently in one direction? (no. of models)	Climate vulnerability	Index of population concern
Great crested grebe *Podiceps cristatus*	1	Decline	Yes (13 negative)	3	4
Northern fulmar *Fulmarus glacialis*	4	Decline (productivity), no trend (counts)	Yes (productivity 9 negative; ESAS winter 6 negative); No (SMP counts)	3	4
Northern gannet *Morus bassanus*	2	Increase (ESAS summer)	Yes (ESAS summer 8 positive)	1	0
Great cormorant *Phalacrocorax carbo*	2	Decline (SMP & WeBS)	Yes (SMP 1 negative; WeBS 12 positive)	1	2
European shag *Phalacrocorax aristotelis*	3	Decline (counts), no trend (productivity or survival)	Yes (survival 4 negative); No (counts 5 negative & 5 positive)	3	4
Greater scaup *Aythya marila*	1	Decline	Yes (12 negative)	3	4
Common eider *Somateria mollissima*	2	No trend	Yes (SMP 2 positive)	1	1
Long-tailed duck *Clangula hyemalis*	1	No trend	Yes (3 positive)	1	1
Black scoter *Melanitta nigra*	1	No trend	Yes (7 negative)	3	3
Velvet scoter *Melanitta fusca*	1	No trend	No significant relationships	2	2
Common goldeneye *Bucephala clangula*	1	No trend	No significant relationships	2	2
Red-breasted merganser *Mergus serrator*	2	No trend	Yes (winter 2 negative)	3	3
Goosander *Mergus merganser*	1	No trend	No significant relationships	2	2
Black-headed gull *Chroicocephalus ridibundus*	1	Increasing (SMP)	Yes (3 positive)	1	0
Lesser black-backed gull *Larus fuscus*	2	Increase (counts), no trend (productivity)	No significant relationships	2	2
Herring gull *Larus argentatus*	3	No trend (counts or productivity)	Yes (ESAS winter 6 negative)	3	3
Great black-backed gull *Larus marinus*	3	Increase (SMP), no trend (WeBS; ESAS)	Yes (ESAS 8 negative)	3	2
Black-legged kittiwake *Rissa tridactyla*	5	Decline (SMP counts, survival & productivity)	Yes (productivity 7 negative; survival 7 negative; ESAS counts 75% negative); No (SMP)	3	4
Sandwich tern *Sterna sandvicensis*	2	Decline (SMP), no trend (WeBS)	No significant relationships	2	2
Common tern *Sterna hirundo*	3	No trend (counts or productivity)	Yes (productivity 3 negative)	3	3
Arctic tern *Sterna paradisaea*	3	No trend (counts or productivity)	Yes (SMP 2 negative; productivity 5 negative)	3	3
Little tern *Sternula albifrons*	1	No trend	Yes (3 negative)	3	3
Atlantic puffin *Fratercula arctica*	4	No trend (SMP, productivity or survival)	Yes (productivity 5 negative); no relationship (counts; survival)	3	3

Qualitative assessment of vulnerability

In the qualitative assessment, 11 species had a climate vulnerability index of 3 (4 species with negative responses to climate and 7 with high foraging sensitivity to climate), 10 species had an index of 2 (all with moderate foraging sensitivity to climate), and 1 had an index of 1 (low foraging sensitivity to climate; Table 4).

Population trend data were available for 10 species, of which 7 declined and 3 increased (Table 4). Based on trends or conservation status combined with climate vulnerability, 5 species were of very high population concern to future climate change (Slavonian grebe, Arctic skua, roseate tern, common guillemot and razorbill), 3 of high concern (Manx shearwater; black-necked grebe *Podiceps nigricollis* and little gull *Hydrocoloeus minutus*), 13 of moderate

Table 4. Qualitative assessment of vulnerability to climate for species where robust data were not available for quantitative assessment or for species that showed inconsistent quantitative trends. Climate vulnerability was based on published relationships with climate or foraging sensitivity and ranges from 1 (positive response or low foraging sensitivity to climate change) to 3 (negative response or high foraging sensitivity to climate). Climate vulnerability was combined with population trends for Scotland or, where unavailable, conservation status (see Eaton et al. 2009) to provide an index of population concern to future climate ranging from 0 (very low) to 4 (very high). 'Green' conservation status was assumed to be equivalent to increasing populations, 'amber' to populations showing no trend

Species	Population trend (or conservation status)	Relationships with climate	Foraging sensitivity index	Climate vulnerability	Index of population concern
Red-throated diver *Gavia stellata*	Increasing (Dillon et al. 2009)	Unknown	12	2	2
Black-throated diver *Gavia arctica*	Unknown (amber)	Unknown	12	2	2
Surf scoter *Melanitta perspicillata*	Unknown	Unknown	13	2	2
Great northern diver *Gavia immer*	Unknown (amber)	Unknown	11	2	2
Red-necked grebe *Podiceps grisegena*	Unknown (amber)	Unknown	14	2	2
Slavonian grebe *Podiceps auritus*	Declining (Perkins et al. 2005)	Unknown	15	3	4
Black-necked grebe *Podiceps nigricollis*	Unknown (amber)	Unknown	15	3	3
Sooty shearwater *Puffinus griseus*	Unknown (amber)	Unknown	4	1	1
Manx shearwater *Puffinus puffinus*	Unknown (amber)	Negative (Riou et al. 2011, Bicknell et al. 2013)	7	3	3
European storm-petrel *Hydrobates pelagicus*	Unknown (amber)	Unknown	10	2	2
Leach's storm-petrel *Oceanodroma leucorhoa*	Declining (Newson et al. (2008)	Unknown	10	2	2
Pomarine skua *Stercorarius pomarinus*	Unknown (green)	Unknown	15	3	2
Arctic skua *Stercorarius parasiticus*	Declining	Unknown	15	3	4
Long-tailed skua *Stercorarius longicaudus*	Unknown (green)	Unknown	15	3	2
Great skua *Stercorarius skua*	Increasing	Negative (Oswald et al. 2008)	13	3	2
Mediterranean gull *Ichthyaetus melanocephalus*	Increasing[a]	Unknown	14	2	2
Little gull *Hydrocoloeus minutes*	Unknown (amber)	Unknown	16	3	3
Common gull *Larus canus*	Declining	Unknown	14	2	2
Roseate tern *Sterna dougallii*	Declining	Unknown	22	3	4
Little auk *Alle alle*	Unknown (green)	Unknown	13	2	2
Common guillemot *Uria aalge*	Declining	Negative (Votier et al. 2005, Lahoz-Monfort et al. 2011)	9	3	4
Razorbill *Alca torda*	Declining	Negative (Lahoz-Monfort et al. 2011)	12	3	4

[a] Trend is for the entire UK population

concern, 1 of low concern and none of very low concern (Table 4).

Non-climate threats

Species were considered to have moderate to high vulnerability to the following non-climate threats: changes to discard policy (15 species), bycatch (18), fisheries competition (17), oil pollution (33), contaminants (8), plastics (5), introduced predators (17), disturbance (18), collision risk from wind farms (27) and displacement from wind farms (21; Table 5).

Of the 4 main threats that were defined by integrating the above single threats (see 'Methods'), 35 species (78%) were considered to have moderate to high vulnerability to fisheries, 34 (76%) to pollutants, 25 (56%) to disturbance and 39 (87%) to wind farms (Table 6).

Overall vulnerability to climate and multiple threats

In total, 24 species (53%) were considered to have a negative relationship with or high foraging sensitivity to climate (Table 6). Furthermore, 42 species (93%) were considered vulnerable to >1 main anthropogenic threat, with 8 species considered vulnerable to 5 threats, 18 species to 4 threats, 11 to 3 threats, 5 to 2 threats, 2 to 1 threat and 1 to 0 threats (Table 6). Thirteen species (29%) were considered of very high population concern to multiple threats, exhibiting declines in counts or demographic rates in conjunction with vulnerability to multiple threats. A further 21 species (47%) were of high population concern.

All of the 24 species in the highest climate vulnerability category were considered to have moderate to high vulnerability to at least 2 other anthropogenic threats. Twelve of these species breed in the Forth and Tay region (8 of which also overwinter

Table 5. Vulnerability of species to non-climate threats. Vulnerability to each threat is ranked as 1 (low), 2 (moderate) or 3 (high). Only threats applicable when a species is present in the study area are considered. See Table S1 in the Supplement for full species names

Species	Discards	Bycatch	Competition with fisheries	Oil pollution	Contaminants	Plastics	Introduced predators	Disturbance (non-wind farm related)	Collision impacts with wind farms	Displacement and disturbance from wind farms
Red-throated diver	1	2	1	3	1	1	1	2	2	3
Black-throated diver	1	1	1	3	1	1	1	2	2	3
Great northern diver	1	1	1	3	1	1	1	2	2	3
Great crested grebe	1	2	1	3	1	1	1	1	2	2
Red-necked grebe	1	2	1	3	1	1	1	1	2	2
Slavonian grebe	1	2	1	3	1	1	1	1	2	2
Black-necked grebe	1	2	1	3	1	1	1	1	2	2
Northern fulmar	3	2	1	2	2	3	3	2	2	1
Sooty shearwater	2	2	1	2	1	3	1	1	1	1
Manx shearwater	2	2	1	2	1	3	1	1	1	1
European storm-petrel	1	1	1	2	1	2	1	1	1	1
Leach's storm-petrel	1	1	1	2	1	2	1	1	1	1
Northern gannet	3	2	2	2	2	1	1	1	3	1
Great cormorant	1	2	3	2	1	1	3	2	1	2
European shag	1	2	1	2	1	1	3	2	1	2
Greater scaup	1	1	2	3	1	1	1	1	2	3
Common eider	1	2	3	2	1	1	3	2	1	2
Long-tailed duck	1	1	2	3	1	1	1	2	1	2
Black scoter	1	1	2	3	1	1	1	2	1	3
Surf scoter	1	1	2	3	1	1	1	2	1	3
Velvet scoter	1	1	2	3	1	1	1	2	1	3
Common goldeneye	1	1	1	3	1	1	1	2	1	3
Red-breasted merganser	1	1	2	2	1	1	1	1	1	3
Goosander	1	1	3	1	1	1	1	1	1	3
Pomarine skua	3	1	2	1	1	1	1	1	3	1
Arctic skua	1	1	2	1	1	1	2	1	3	1
Long-tailed skua	1	1	2	1	1	1	1	1	3	1
Great skua	3	2	2	1	2	1	1	1	2	1
Mediterranean gull	1	1	1	2	1	1	1	1	3	1
Little gull	1	1	1	2	1	1	1	1	2	1
Black-headed gull	1	1	1	2	2	1	1	1	3	1
Common gull	1	1	1	2	2	1	1	1	3	1
Lesser black-backed gull	3	2	1	2	2	1	2	1	3	1
Herring gull	3	2	1	2	2	1	2	1	3	1
Great black-backed gull	3	2	1	2	2	1	2	1	3	1
Black-legged kittiwake	2	1	3	2	1	1	2	1	3	1
Sandwich tern	2	1	1	1	1	1	3	2	2	1
Roseate tern	2	1	1	1	1	1	3	3	2	1
Common tern	2	1	1	1	1	1	3	3	2	1
Arctic tern	2	1	1	1	1	1	3	3	2	1
Little tern	2	1	1	1	1	1	3	3	2	2
Common guillemot	1	2	2	2	1	1	3	1	1	2
Razorbill	1	2	1	2	1	1	3	1	1	2
Little auk	1	1	1	1	1	1	1	1	1	1
Atlantic puffin	1	1	2	1	1	1	3	2	1	1

Table 6. Overall summary of vulnerability to multiple anthropogenic threats. The main use of the study area is denoted as B (breeding), OW (over-wintering), SV (summer visitor) or PM (passage migrant). We present the highest vulnerability score per main threat (fisheries, pollutants, disturbance, windfarms and climate). Summed vulnerability is the summed score for the 5 categories (including climate). We indicate the total number of threats the species is vulnerable to (climate scored as 3 or other threats scored as ≥2; table ordered by this column). The index of population concern (IPC) to climate and multiple threats incorporated climate vulnerability or number of threats a species is vulnerable to and population status, respectively. 'Green' conservation status (see Eaton et al. 2009) assumed to be equivalent to increasing populations, 'amber' to populations showing no trend. See Table S1 in the Supplement for full species names

Species	Main use of study area	Fisheries	Pollutants	Disturbance	Windfarms	Climate	Summed vulnerability score	No. of threats vulnerable to	Pop. trend or status	IPC to climate	IPC to multiple threats
Northern fulmar	B,OW	3	3	3	2	3	14	5	Decline	4	4
European shag	B,OW	2	2	3	2	3	12	5	Decline	4	4
Black scoter	OW	2	3	2	3	3	13	5	No trend	3	3
Herring gull	B,OW	3	2	2	3	3	13	5	No trend	3	3
Great black-backed gull	B,OW	3	2	2	3	3	13	5	Increase	2	2
Black-legged kittiwake	B,OW	3	2	2	3	3	13	5	Decline	4	4
Common guillemot	B,OW	2	2	3	2	3	12	5	Decline	4	4
Razorbill	B,OW	2	2	3	2	3	12	5	Decline	4	4
Red-throated diver	OW	2	3	2	3	2	12	4	Increase	2	2
Great crested grebe	OW	2	3	1	2	3	11	4	Decline	4	4
Slavonian grebe	OW	2	3	1	2	3	11	4	Decline	4	4
Black-necked grebe	PM	2	3	1	2	3	11	4	Amber	3	3
Great cormorant	B,OW	3	2	3	2	1	11	4	Decline	2	4
Greater scaup	OW	2	3	1	3	3	12	4	Decline	4	4
Common eider	B,OW	3	2	3	2	1	11	4	No trend	1	3
Long-tailed duck	OW	2	3	2	2	1	10	4	No trend	1	3
Surf scoter	OW	2	3	2	3	2	12	4	No trend	2	3
Velvet scoter	OW	2	3	2	3	2	12	4	No trend	2	3
Red-breasted merganser	OW	2	2	1	3	3	11	4	No trend	3	3
Arctic skua	PM	2	1	2	3	3	11	4	Decline	4	4
Great skua	PM	3	2	1	2	3	11	4	Increase	2	2
Lesser black-backed gull	B,OW	3	2	2	3	2	12	4	No trend	2	3
Roseate tern	B	2	1	3	2	3	11	4	Decline	4	4
Common tern	B	2	1	3	2	3	11	4	No trend	3	3
Arctic tern	B	2	1	3	2	3	11	4	No trend	3	3
Little tern	B	2	1	3	2	3	11	4	No trend	3	3
Black-throated diver	OW	1	3	2	3	2	11	3	Amber	2	3
Great northern diver	OW	1	3	2	3	2	11	3	Amber	2	3
Red-necked grebe	OW	2	3	1	2	2	10	3	No trend	2	3
Manx shearwater	SV	2	3	1	1	3	10	3	No trend	3	3
Northern gannet	B,OW	3	2	1	3	1	10	3	Increase	0	2
Common goldeneye	OW	1	3	2	3	2	11	3	No trend	2	3
Pomarine skua	PM	3	1	1	3	3	11	3	Green	2	2
Long-tailed skua	PM	2	1	1	3	3	10	3	Green	2	2
Little gull	PM	1	2	1	2	3	9	3	Amber	3	3
Sandwich tern	B	2	1	3	2	2	10	3	Decline	2	4
Atlantic puffin	B,OW	2	1	3	1	3	10	3	No trend	3	3
Sooty shearwater	PM	2	3	1	1	1	8	2	Amber	1	3
Goosander	OW	3	1	1	3	2	9	2	No trend	2	3
Mediterranean gull	SV	1	2	1	3	2	9	2	Increase	2	2
Black-headed gull	B,OW	1	2	1	3	1	8	2	Increase	0	2
Common gull	OW	1	2	1	3	2	9	2	Decline	2	4
European storm-petrel	SV	1	2	1	1	2	7	1	Amber	2	1
Leach's storm-petrel	SV	1	2	1	1	2	7	1	Decline	2	2
Little auk	OW	1	1	1	1	2	6	0	Green	2	0

there), with a further 5 species overwintering and 7 species being migratory or summer visitors to the area (Table 6). Threats were applicable to species present in the region in both the summer and winter (breeding species: 94 % vulnerable to fisheries, 67 % to pollutants, 89 % to disturbance, 94 % to wind farms, 67 % to climate; overwintering species: 79 % to fisheries, 90 % to pollutants, 66 % to disturbance, 93 % to wind farms, 45 % to climate).

A breakdown of vulnerability to climate and multiple threats by family and main use of the region is provided in Table 7. Cormorants, grebes, skuas, terns and auks had markedly high percentages of species vulnerable to climate and high or very high population concern to future climate warming (≥50 % of species for both; Table 7). All families had high vulnerability to multiple threats with ducks, cormorants, grebes, terns and auks of particularly high population concern to multiple threats (≥75 % of species; Table 7). Birds breeding in the region were especially vulnerable to climate, with 67 % (18 species) in the highest vulnerability category. Overall vulnerability and population concern to multiple threats was high across all main use groups, with 100 % of breeding species and 97 % of overwintering species considered vulnerable to multiple threats.

Table 7. Vulnerability of birds grouped by family and main use the Forth and Tay area to climate and multiple threats. The 5 right hand columns indicate the % of species in each family/main use that are in the highest climate vulnerability category; have high or very high population concern to future climate warming; are vulnerable to multiple threats; have high or very high population multiple threats; or are vulnerable to climate and other threats

Grouping category	Family/ main use	No. of species	% species with high vulnerability to climate	% species with high/very high population concern to future climate	% species vulnerable to ≥2 threats	% species with high/very high population concern to multiple threats	% species vulnerable to climate and at least 1 other threat
Family	Anatidae	9	33	33	100	100	33
	Gaviidae	3	0	0	100	67	0
	Procellaridae	3	67	67	100	100	67
	Hydrobatidae	2	0	0	0	0	0
	Sulidae	1	0	0	100	0	0
	Phalacrocoracidae	2	50	50	100	100	50
	Podicepedidae	4	75	75	100	100	75
	Stercorariidae	4	100	50	100	25	100
	Laridae	8	50	38	100	63	50
	Sternidae	5	80	80	100	100	80
	Alcidae	4	75	75	75	75	75
Use of study area	Breeding	5	80	80	100	100	80
	Breeding & Overwintering	13	62	54	100	77	62
	Overwintering	16	31	31	94	88	31
	Migrant or summer visitor	11	64	36	73	45	63

DISCUSSION

The Forth and Tay region of the North Sea supports a large and diverse community of marine birds throughout the year that are of national and international importance (Söhle et al. 2007, JNCC 2013). SST has increased rapidly in the region since 1980, comparable to rates observed in the North Atlantic and Pacific (Parry et al. 2007). Our quantitative assessment demonstrated negative correlations between SST and abundance, adult survival and/or productivity of 57 % of the investigated marine bird species. Combining quantitative and qualitative assessments of climate vulnerability with population and demographic trends, we found that 44 % of the 45 study species were of high or very high population concern to rising sea temperatures in the future. Breeding, overwintering and migrating species were all affected, with the largest proportion of high or very high population concern found in the former. Crucially, all species with negative responses to climate change were also vulnerable to at least 2 other anthropogenic threats operating in the region, with 76 % of the 45 species of high or very high population concern to multiple threats, potentially impacting the resilience of this marine bird community.

Vulnerability to climate

Globally, seabirds have declined faster than terrestrial bird groups with comparable numbers of species (Croxall et al. 2012), with the majority of trends consistent with climate change (Poloczanska et al. 2013). In accordance with this global picture, we found that only 13 % of the marine bird community in the Forth and Tay region was of low or very low population concern to future warming. The effects of climate on lower trophic levels results in complex spatial and temporal variation in prey availability, making it challenging to establish links between top predator abundance or demography and environmental drivers (Le Bohec et al. 2008, Bond et al. 2011, Lahoz-Monfort et al. 2013). It is therefore of considerable concern that negative associations between climate and abundance and demographic rates were so widespread across the community. Synchronous responses to bottom-up processes occur where species are dependent on a common prey base or exhibit similar life-history strategies, and have been demonstrated in seabird species in this region (Lahoz-Monfort et al. 2011, 2013). We found that cormorants, grebes, skuas, shearwaters, terns, auks and some individual species in other families (e.g. greater scaup and black-legged kittiwake) were particularly vulnerable to increased SST. Many of these species are heavily reliant on lesser sandeels *Ammodytes marinus*, which are sensitive to changes in SST (Arnott & Ruxton 2002, van Deurs et al. 2009) and have restricted capacity to shift distribution (Wright et al. 2000, Heath et al. 2012). In contrast, divers, sea ducks, gannets, gulls and storm petrels were less vulnerable. This may have arisen because of insufficient resolution in the data or lack of data on demographic rates that are more sensitive to changes in climate. However, several of these groups, in particular sea ducks, gannets and gulls, have more generalist diets which may buffer them from indirect climate impacts. Gulls and gannets exploit fisheries discards, which have provided an alternative source of food to naturally available prey, although this will alter in the coming years with changes in EU policy on discards (Bicknell et al. 2013). Increased abundances of swimming crabs (subfamily Polybiinae) have been associated with climate change and fisheries management (Lindley & Kirby 2010). Crabs are an important dietary component of sea ducks (Ouellet et al. 2013) and have been linked with population increases of lesser black-backed gull (Luczak et al. 2012, Schwemmer et al. 2013).

We found that productivity was more sensitive to climate change than count data, in line with other studies (Frederiksen et al. 2007, Cook et al. 2014). This is of particular concern given the international conservation importance of breeding colonies in the region, with many designated as Special Protection Areas. We also found that adult survival rate was sensitive to climate change in 3 (European shag, black-legged kittiwake and Atlantic puffin) of the 5 breeding species for which data were available. This is despite the fact that the latter 2 species have broad overwintering ranges across the North Sea and North Atlantic and hence will be encountering non-local climate at the time when most mortality takes place (Harris et al. 2010, Bogdanova et al. 2011). Factors that impact adult survival rates are of particular significance since the latter are the key determinant of population size in *K*-selected species such as marine birds (Gaillard et al. 1989). However, our study highlights that survival data are generally lacking. Collection of mark–recapture data is difficult and time-consuming, requiring specialised skills for catching and ringing birds at accessible breeding sites, and such data are therefore only available for a limited subset of species. Furthermore, survival analysis from dead recoveries of ringed birds is challenging in marine birds because of poor recovery rates (Robinson 2010). However, there is a need to fill this knowledge gap, especially for the 16 species wintering in the region and hence likely to be experiencing the main period of mortality.

In addition to the indirect effects of climate operating via food webs, marine bird species may also be sensitive to direct impacts of climate. Direct climate effects may be particularly important for species wintering in the region, when increased mortality can occur during prolonged periods of poor weather (Frederiksen et al. 2008, Harris & Elkins 2013). Temperature extremes, heavy rainfall or high winds may also affect productivity during the breeding season (Mallory et al. 2009, Oswald & Arnold 2012). These effects may become increasingly important since most climate models predict that future warming will be associated with increasing climate variability and hence frequency of extreme weather events (Solomon et al. 2007, Rahmstorf & Coumou 2011). Furthermore, predicted sea-level rise may lead to loss of suitable foraging habitat for tidally feeding species or breeding habitat for ground-nesting species such as common eider and terns (van de Pol et al. 2010). Complementary approaches to our study have used climate envelope models based on air temperature data from a baseline period to assess the climatic suitability of terrestrial grid squares in the UK in 2070–99 (Huntley et al. 2007). Based on these models, which integrate direct and indirect effects of climate, it is predicted that by the end of the century the Forth and Tay region will become climatically unsuitable, or at the southern edge of the breeding range, for 10 of the 18 breeding species we considered (Huntley et al. 2007). These include 8 (northern fulmar, European shag, black-legged kittiwake, Atlantic puffin, common tern, Arctic tern, common guillemot and razorbill) of the 11 breeding species identified in our analyses as being of high or very high population concern to future warming. It is therefore possible that direct climate impacts may adversely affect species not currently considered vulnerable to climate as well as exacerbate impacts on species already under threat.

Vulnerability to multiple impacts

Climate change comprises part of a suite of anthropogenic threats to this bird community, with 93% of species vulnerable to multiple anthropogenic threats and 73% considered of high or very high population concern to multiple threats in the future. The threats pertinent to the North Sea are also threatening seabird populations globally, in particular invasive species, pollution, commercial fisheries and human disturbance (Croxall et al. 2012). In contrast to marine birds in many other areas, mammalian predation has not been widely recorded in the Forth and Tay region. However, reintroduction of white-tailed sea-eagles has recently occurred in the region, potentially having a negative impact via predation on breeding seabirds, as observed in Norway (Hipfner et al. 2012). Furthermore, introduced plants can have significant impacts on breeding habitat available for seabirds. Expansion of tree mallow *Lavatera arborea* has substantially reduced suitable nesting habitat for Atlantic puffins at several colonies in the region. Moreover, this expansion was in part due to increases in germination opportunity due to higher temperatures (van der Wal et al. 2008), and climate warming may therefore favour further increases. In recent decades, levels of plastic pollution have increased in marine environments, and such pollution impairs digestive function and causes reproductive failure (Azzarello & Van Vleet 1987, Avery-Gomm et al. 2012). Furthermore, contaminants such as brominated flame retardants and perfluorinated compounds have increased in tissues of predators (Dietz et al. 2008, 2013), with negative consequences for survival rates and productivity (Votier et al. 2005, 2011, Letcher et al. 2010, Miljeteig et al. 2012). Large-scale marine renewable developments are proposed for this region as part of a broader strategy to meet green energy targets, with the potential for negative impacts from collision and displacement (Furness et al. 2013). Although future policy on fisheries for prey of marine birds such as lesser sandeel is hard to predict, upcoming changes in EU policy are expected to reduce fishery discards, which may have a negative impact on scavenging species such as gulls and northern gannet (Bicknell et al. 2013). In contrast, policy changes on seabird bycatch are predicted to reduce mortality. The relative importance of these drivers is therefore predicted to change in the future, but the overall threat is likely to remain high.

The high vulnerability of the Forth and Tay region marine bird community to multiple threats means that there is an urgent need to evaluate their cumulative impacts in conjunction with climate change. While qualitative approaches such as those undertaken here are undoubtedly useful, they cannot identify whether multiple threats are additive, synergistic or antagonistic. This requires robust, quantitative analyses of the interaction between multiple impacts on marine bird communities. However, this is a huge challenge because potential drivers are difficult to quantify at the appropriate scale and will often covary. The few studies that have undertaken quantitative analyses of multiple impacts in wild populations have focused on effects on single species. These studies have shown that interactions between climate and other factors such as fisheries or pollution may be additive or synergistic (Frederiksen et al. 2004, Votier et al. 2005, Ainley & Blight 2009, McKinney et al. 2013). Fisheries may directly compete with marine birds or be beneficial by removing competitors, depending on what species they are harvesting (review by Lewison et al. 2012), but interactions with climate are likely to be complex and hard to predict. Impacts of marine renewable developments on bird breeding colonies may change if species adjust foraging ranges due to climate warming, potentially altering overlap.

Despite the lack of a strong predictive framework, there are opportunities for quantitative investigation of multiple impacts on marine bird communities. Controlled experiments are an appealing option for establishing causality, but are logistically challenging in marine environments; however, opportunities such as new marine renewable developments or changes in discard policy would enable marine bird responses to be partitioned unequivocally among drivers, especially in species groups where demographic sensitivity to climate has been demonstrated and which are particularly amenable to study, such as European shag, black-legged kittiwake and auks. Mechanistic studies of diet and foraging energetics would greatly enhance understanding of the impacts of multiple drivers mediated via changes at lower trophic levels (Thaxter et al. 2013), since such studies have proved powerful in elucidating responses of top predators to changing abundance in prey associated with climate change and other drivers such as pollution (Provencher et al. 2012, McKinney et al. 2013, Anderson et al. 2014). Comparisons of multi-species colonies across broad spatial scales, across a gradient of severity of anthropogenic threats, would be another fruitful avenue of research.

CONCLUSIONS

To our knowledge, this study is the first comprehensive assessment of vulnerability to climate change and a suite of anthropogenic threats in a community of marine birds and builds substantially on previous evaluations of species in this assemblage to single stressors such as climate (Sandvik et al. 2005, Frederiksen et al. 2007), fisheries (Furness & Tasker 2000) and marine renewables (Furness et al. 2013). A previous assessment of changes in the size of breeding populations of the UK marine bird community between 1969 and 2002 found that most populations had increased; however, terns and black-legged kittiwakes were notable exceptions, and extensive breeding failures were apparent in several species at the very end of the study period (Grandgeorge et al. 2008). Our study extended this time series by almost a decade in the Forth and Tay region, and found that, in addition to terns and black-legged kittiwakes, many other species are now declining and showing evidence of negative associations with climate. These results therefore support the concerns raised by Grandgeorge et al. (2008) and indicate that climate change is now having a substantial impact on this marine bird community.

Our study highlights the value of long-term demographic studies of marine birds in elucidating anthropogenic threats to species communities and emphasizes the need for continuation and expansion of such studies. However, even in the Forth and Tay region, where spatially and temporally comprehensive data on abundance and demography are available, almost half of the species present had insufficient data to enable associations with climate to be assessed quantitatively.

Development of forecasting models to predict the interaction between climate and other drivers on marine bird communities is an important research priority. Progress using this approach is currently hampered by the lack of predicted regional SST data between now and 2070. However, based on our retrospective assessment of impacts of climate and other factors, we suggest that the majority of marine birds in the Forth and Tay region of the North Sea face an uncertain future because of simultaneous and likely increasing threats from climate warming and a suite of other anthropogenic stressors. In particular, reductions in discard policy and expansion of marine renewables may impact this bird community further over the coming decades. In conjunction with climate change, such factors may threaten community resilience in the near future.

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