Effects of sea temperature and stratification changes on seabird breeding success

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ABSTRACT: As apex predators in marine ecosystems, seabirds may primarily experience climate change impacts indirectly, via changes to their food webs. Observed seabird population declines have been linked to climate-driven oceanographic and food web changes. However, relationships have often been derived from relatively few colonies and consider only sea surface temperature (SST), so important drivers, and spatial variation in drivers, could remain undetected. Further, explicit climate change projections have rarely been made, so longer-term risks remain unclear. Here, we use tracking data to estimate foraging areas for 11 black-legged kittiwake *Rissa tridactyla* colonies in the UK and Ireland, thus reducing reliance on single colonies and allowing calculation of colony-specific oceanographic conditions. We use mixed models to consider how SST, the potential energy anomaly (indicating density stratification strength) and the timing of seasonal stratification influence kittiwake productivity. Across all colonies, higher breeding success was associated with weaker stratification before breeding and lower SSTs during the breeding season. Eight colonies with sufficient data were modelled individually: higher productivity was associated with later stratification at 3 colonies, weaker stratification at 2, and lower SSTs at one, whilst 2 colonies showed no significant relationships. Hence, key drivers of productivity varied among colonies. Climate change projections, made using fitted models, indicated that breeding success could decline by 21 to 43% between 1961–90 and 2070–99. Climate change therefore poses a longer-term threat to kittiwakes, but as this will be mediated via availability of key prey species, other marine apex predators could also face similar threats.

KEY WORDS: Black-legged kittiwake · Oceanography · Potential energy anomaly · Productivity · *Rissa tridactyla* · SST · Tracking data

1. INTRODUCTION

Ecological impacts of climate change are increasingly well-understood, with changes in species' ranges and phenology predicted and observed in both terrestrial and marine environments (Parmesan 2006, Doney et al. 2012). Some species may be primarily affected via changed biotic interactions (e.g.

Pearce-Higgins et al. 2010), but such impacts can be harder to predict and observe (Tylianakis et al. 2008, Gilman et al. 2010). These 'indirect' impacts are likely to be widespread and bring with them substantial extinction risks (Cahill et al. 2013, Ockendon et al. 2014), but they also pose considerable conservation challenges. Species at higher trophic levels attract most attention (Sergio et al. 2008), but their populations may depend more on species at lower trophic levels and their abiotic drivers.

Seabirds are the world's most threatened group of birds (Croxall et al. 2012). As apex predators, they are likely to experience indirect climate change impacts through their supporting food webs (Sydeman et al. 2012). Their populations are responsive to changes in breeding success (Sandvik et al. 2012), which is influenced by prey availability during the breeding period (Hamer et al. 1993, Regehr & Montevecchi 1997, Wanless et al. 2004). Under poorer feeding conditions, body condition is lower, nest attendance falls, and chicks can starve (Wanless & Harris 1992, Frederiksen et al. 2004b, Vincenzi & Mangel 2013). Hence, climatic and oceanographic changes affecting food webs could impact seabird productivity. Whilst identifying underlying mechanisms is challenging, it is informative to examine relationships between physical ocean conditions and demographic parameters (e.g. Frederiksen et al. 2004b, Wanless et al. 2007), as these can indicate the ultimate drivers of population declines.

In the UK and Ireland, abundances of several seabird species have fallen substantially since the mid-1980s (JNCC 2014). Some declines have been linked to rising sea surface temperatures (SSTs) (e.g. Frederiksen et al. 2004b, 2007). A possible mechanism behind this is reduced prey availability and nutritional value due to changing zooplankton communities (Arnott & Ruxton 2002, Wanless et al. 2004, van Deurs et al. 2009). Although strong relationships with SST have been derived for individual colonies (Frederiksen et al. 2004b), its importance varies spatially, with colonies in some regions showing only weak SST relationships (Frederiksen et al. 2007, Lauria et al. 2012). Further, other oceanographic drivers, notably density stratification, may also be important (Scott et al. 2006). Stratification occurs when temperature or salinity differences cause pronounced density differences between deep and shallow waters. Associated changes in nutrient availability and light regimes influence plankton growth, and in turn fish activity and growth (Scott et al. 2006, Sharples et al. 2006). Under earlier stratification, key fish species may be available too early or be less nutritious

(Wright & Bailey 1996, Wanless et al. 2004, Scott et al. 2006), whilst abundance of key zooplankton and fish species may fall under stronger stratification (Beare et al. 2002, Jensen et al. 2003). To improve understanding of the physical drivers of seabird productivity and identify underlying biological mechanisms, it is therefore necessary to consider multiple colonies across multiple regions (Lauria et al. 2012, Sydeman et al. 2012), and multiple oceanographic variables.

With improved understanding of physical drivers of productivity, longer-term climate change impacts can be considered. Longer-term impacts have been implied from observed changes, but few studies have made explicit projections (but see Frederiksen et al. 2013, Sandvik et al. 2014). A clearer understanding of future impacts is essential when considering possible conservation strategies in a changing climate, especially in light of legislative frameworks that consider seabird productivity under prevailing climatic conditions (HM Government 2012). Therefore, both observed relationships and explicit climate change projections are necessary to provide a more complete understanding of the impacts of oceanographic change and stochasticity on seabird populations.

Here, we examine drivers of productivity for multiple seabird colonies, considering SST and stratification. We consider the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'), as it is a sensitive indicator of environmental conditions (Wanless et al. 2007, Cook et al. 2014). We focus on the UK and Ireland, which support around 14% of the biogeographic kittiwake population and for which population data are routinely collected (JNCC 2014). Specifically, we consider the following hypotheses:

(1) Higher SSTs are associated with reduced kittiwake breeding success

(2) Strong, early stratification is associated with reduced kittiwake breeding success

(3) Modelled kittiwake productivity will be reduced in future scenarios due to the impacts of climate change

2. MATERIALS AND METHODS

2.1. Study species

Despite being one of the most abundant seabirds in the UK and Ireland, kittiwakes have declined substantially since 1986 (JNCC 2014). They nest on cliffs in colonies of up to tens of thousands of pairs (Coulson 2011). Egg-laying occurs from April to June, and incubation and fledging each take approximately

1 mo (Coulson 2011). During breeding, kittiwakes feed primarily on fish, with sandeels (Ammodytidae; particularly the lesser sandeel *Ammodytes marinus*) a key prey resource (Furness & Tasker 2000, Wanless et al. 2007). However, clupeids (e.g. herring, sprat), gadids (e.g. cod, pollock) and planktonic crustacea can also be important (e.g. Lewis et al. 2001, Chivers et al. 2012). Colonies with diverse diets may be buffered from fluctuating prey availability (Coulson 2011), while those dependent upon a single species are more likely to be sensitive to climatic variability.

2.2. Kittiwake foraging areas

Previous analyses have extracted oceanographic predictor variable values from arbitrary areas near colonies (e.g. Frederiksen et al. 2004b, Burthe et al. 2012, Sandvik et al. 2014). However, seabird tracking has indicated variability among colonies in the size and shape of areas used (e.g. Wakefield et al. 2013), so the area of sea influencing breeding success is also likely to vary. Hence, here, tracking data were used to define colony-specific areas.

Data were acquired for 11 colonies where kittiwakes were tracked during the 2010–12 breeding seasons, and for which productivity data were available (Table 1, Fig. 1). Tracked birds had high-resolution GPS tags (modified IgotU GT 120, Mobile Action) attached with adhesive tape to back feathers whilst at the colony. Tags recorded a location fix
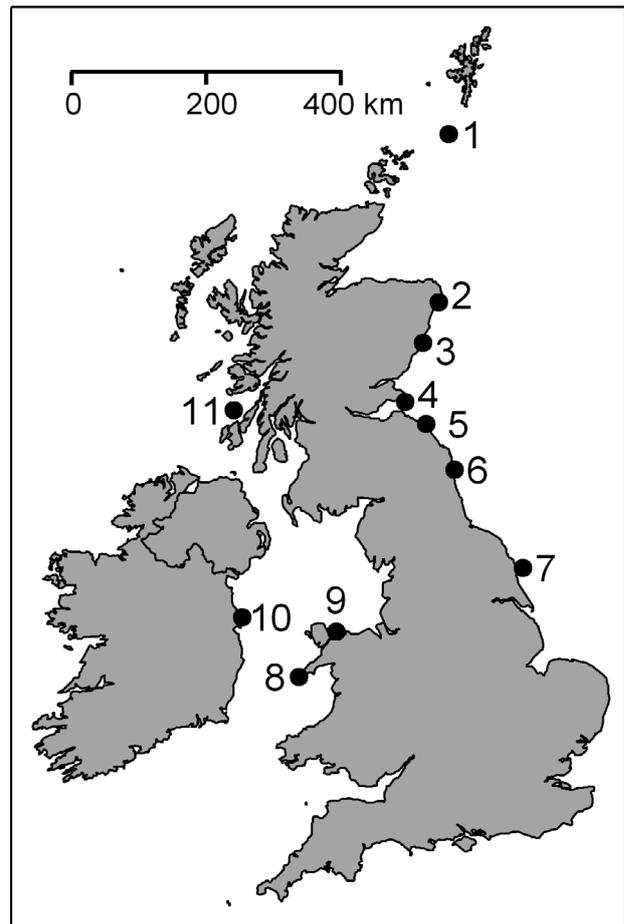

Fig. 1. Locations of kittiwake colonies included in the analyses. Numbers refer to colony descriptions in Table 1

Table 1. Sites included in analyses of effects of sea temperature and stratification changes on kittiwake breeding success. 'Site' refers to the name in the SMP database, and 'map site number' to the location shown in Fig. 1. Regions listed are based on Frederiksen et al. (2005). Oceanographic data were available up to 2004, whilst breeding success data were available from 1986, meaning that the maximum possible overlap was 19 yr. NNR: National Nature Reserve

Site	Map site number	Region	Coordinates	Years of breeding success data overlapping oceanography	Years of tracking data	Total birds tracked
Fair Isle	1	Shetland	1.65° W, 59.52° N	19	3	11
Boddam to Collieston	2	East Scotland	1.85° W, 57.42° N	15	1	25
Fowlsheugh	3	East Scotland	2.20° W, 56.92° N	17	1	15
Isle of May NNR	4	East Scotland	2.57° W, 56.18° N	18	1	17
St. Abb's Head NNR	5	East Scotland	2.13° W, 55.91° N	18	1	15
Coquet Island	6	East England	1.52° W, 55.34° N	12	2	36
Flamborough Head and Bempton Cliffs	7	East England	0.08° W, 54.12° N	18	3	51
Bardsey Island NNR	8	Irish Sea	4.83° W, 52.76° N	17	1	8
Puffin Island	9	Irish Sea	4.03° W, 53.32° N	1	3	70
Lambay	10	Irish Sea	6.03° W, 53.50° N	1	2	14
Isle of Colonsay	11	West Scotland	6.21° W, 56.08° N	6	3	59

accurate to 20 m approximately every 100 s, and remained attached for 2 to 5 d. Tracking occurred from May to July, but mostly in June, covering late incubation and chick rearing periods.

It was assumed that oceanographic conditions primarily affect kittiwake productivity via food webs, so the most relevant areas from which to extract oceanographic data were those associated with foraging. Therefore, GPS records were filtered to identify relevant locations. Records within 1 km of the colony centre were removed to exclude fixes associated with behaviours around the nest, which are rarely associated with foraging (Suryan et al. 2002). Travel speeds between points were calculated; these formed a bimodal distribution, with lower speeds likely to be associated with foraging (e.g. Kotzerka et al. 2010). Based on preliminary analysis of a subset of data, records with speeds over 14 km h^{-1} were removed (see Supplement 1 at www.int-res.com/articles/suppl/c066p075_supp.pdf). Filtering left 192 638 records. Although filtering did not exclude behaviours such as resting on the sea, the range of kittiwake foraging behaviours (Coulson 2011) makes a more inclusive approach preferable. A sensitivity analysis indicated that threshold selection made little difference to extracted oceanographic variable values (Supplement 1), so analyses presented here should be robust to threshold specification within the ranges considered.

Kernel density estimates (KDEs) were calculated to convert GPS records into estimated foraging areas. For each colony, data were pooled across all birds and years to estimate the 'core' foraging area; whilst interannual variation was found, most colonies used similar areas each year (Supplement 2), so pooling was considered appropriate. Although kernel density estimation is sensitive to the number of birds included, all colonies had at least the number required to describe >50% of the 'true' foraging area (Soanes et al. 2013). Kernel densities were evaluated on a regular 30 arc-second by 30 arc-second rectangular grid with limits 1.25° away from the most extreme observations.

KDEs were based on a bivariate Gaussian kernel, and were evaluated using the 'ks' R package (Duong 2013). A bivariate plug-in estimator (Duong & Hazelton 2003) and a rule-of-thumb approach (Silverman 1986) were considered for choosing the degree of smoothing. The rule-of-thumb approach took bandwidth to be $1.06 \cdot \sigma_x \cdot n^{(-0.2)}$ and $1.06 \cdot \sigma_y \cdot n^{(-0.2)}$, where n denotes sample size and σ_x and σ_y denote standard deviations of longitudes and latitudes; this is derived in a univariate setting under an assumption of normality, so should be interpreted cautiously here.

However, the plug-in was highly computationally intensive for datasets of this size, so the approaches were compared using a subset of sites: extracted oceanographic data were highly correlated (r ≥ 0.99), so the rule-of-thumb approach was used for all sites. Foraging areas were defined by the 90% density contour, which has been recommended for home range estimates (Börger et al. 2006). Kernels are presented in Supplement 2.

2.3. Kittiwake breeding success data

Breeding success data were acquired from the seabird monitoring programme (SMP; http://jncc.defra. gov.uk/smp; Walsh et al. 1995). The SMP is an annual sample survey of seabird breeding population size and productivity, which started in 1986 and is coordinated by the Joint Nature Conservation Committee (JNCC). Data from the Isle of May National Nature Reserve were acquired from the Centre for Ecology & Hydrology (https://eip.ceh.ac.uk/, accessed 12 Apr 2013). Productivity data were not available for all years for all colonies, leaving 142 site-by-year combinations (Table 1).

SMP breeding success is often analysed as mean fledged chicks per nest (e.g. Frederiksen et al. 2007). However, it was preferable to avoid this here, as Gaussian responses could become negative in projections, and varying numbers of nests contributed to observations (range 21 to 1446). Therefore, numbers of fledged and failed chicks were modelled as a binomial response, with fledged chicks taken from the data, and failed chicks estimated as [(2 × nests) − fledged], based on the mean and modal UK kittiwake clutch size of 2 (range 1 to 3; Coulson & Porter 1985, Coulson 2011), thus preventing negative predictions and allowing prior weights to account for varying nest numbers. Hence, breeding success was modelled as chicks fledged per egg (Cook et al. 2014). To ensure results were robust to these assumptions, fledged chicks were also modelled as a Poisson response with an offset of log(nests); results were very similar to the binomial analysis (Supplement 3).

2.4. Oceanographic data

Two oceanographic datasets were acquired: one covered recent years (hereafter, 'hindcast'), whilst the other covered 30 yr periods for the mid 20th and late 21st centuries (hereafter, 'projections'). Both were produced from the Proudman Oceanographic

Laboratory Coastal Ocean Modelling System (POL-COMS), which simulates ocean hydrodynamics as driven by atmospheric inputs (Holt & James 2001). Data acquired were monthly mean temperature and salinity on a $^1/_6°$ longitude × $^1/_9°$ latitude grid (~12 × 12 km) over multiple vertical layers.

Hindcast data were acquired from the MyOcean project (http://marine.copernicus.eu/, product NORTHWESTSHELF_REANALYSIS_PHYS_004_005, accessed 23 Apr 2013), and represented an estimate of conditions experienced between 1967 and 2004, so could be used to establish relationships with kittiwake productivity. Further information on this dataset is provided by Holt et al. (2012). Projection data were acquired from the British Atmospheric Data Centre (http://badc.nerc.ac.uk/data/link, accessed 01 Mar 2013; access provided by the UK Met Office), and represented baseline (1961−90) and future (2070−99, SRES Scenario A1B) periods. Projections did not correspond to conditions in specific years, so could only be used to predict breeding success under average conditions in each period. Further information on this dataset is provided by Lowe et al. (2009).

2.5. Explanatory variables

Three oceanographic variables that could influence kittiwake productivity were calculated: SST (e.g. Frederiksen et al. 2004b), stratification strength, and the timing of seasonal stratification onset (e.g. Scott et al. 2006, 2010). SST was calculated by extracting the top layer of temperature data.

Stratification strength was expressed using the potential energy anomaly (PEA), as defined by Holt et al. (2010). PEA indicates the energy per unit depth required to mix the water column. Hence, higher values indicate stronger stratification. PEA was calculated as

$$-\frac{g}{h} \int_{z=-h}^{0} z\{\rho[T(z), S(z)] - \rho[\overline{T}, \overline{S}]\} \, dz \qquad (1)$$

Here, g = gravitational acceleration, h = water depth (or 400 m if h exceeds this), z = the vertical coordinate (0 indicating the surface, negative values indicating deeper water), ρ = density (calculated using a polynomial function [Jackett et al. 2006]), T = temperature, S = salinity; the overbar indicates that the quantity is averaged from h to the surface. As data were available for discrete depths, the integral was evaluated numerically using Simpson's rule.

Seasonal stratification onset was calculated similarly to previous analyses of POLCOMS data (Lowe et al. 2009, Holt et al. 2010), but as daily outputs were unavailable, additional assumptions were made. Stratification onset was defined as the first day of the year with mixed layer depth (MLD) < 50 m (Holt et al. 2010). MLD was defined as the depth at which density differed from surface density by an amount equivalent to a 0.5°C temperature reduction. Only monthly outputs were available, so daily MLD values were interpolated by fitting a cubic spline through monthly values; whilst this retains the seasonal pattern of MLD, it may underestimate true variability. Hence, whilst the stratification onset metric is relatively coarse, variability among years and sites should be adequately described.

For SST and PEA, winter and spring means were calculated. Winter (December, January, February) corresponded to the period important for sandeel spawning and egg hatching (Arnott & Ruxton 2002). Spring (March, April, May, June) corresponded to the period when kittiwakes commence breeding, sandeel larvae grow and sandeel abundance peaks (Wright & Bailey 1996, Coulson 2011). For stratification onset, only annual means could be defined.

As well as oceanographic influences, breeding success could be influenced by density-dependence, with reduced productivity at higher population sizes (Furness & Birkhead 1984). Therefore, for the subset of sites and years with SMP data on kittiwake breeding population size available (9 colonies; 78 site-by-year combinations), log(population) was considered as a further predictor variable (Supplement 4). Across all sites and at 3 of 4 individual colonies, there was no significant relationship between population size and breeding success; at the remaining colony, a positive relationship was found. Relationships between breeding success and oceanographic variables were not influenced by inclusion of population size. Consequently, in the present study there is little evidence of density-dependent effects on breeding success (Supplement 4); due to the much-restricted dataset involved in this analysis, further discussion relates to models excluding population size.

2.6. Statistical analysis

Analyses were conducted in R version 3.1.0 (R Core Team 2014). Mean oceanographic variable values within foraging areas were calculated using the 'raster' R package (Hijmans 2013). Variables were explored for collinearity and temporal trends (Supplement 5). PEA values displayed skewed distributions, so logged and untransformed values were compared

in preliminary productivity models (Supplement 5): logged PEA performed better, so further models used log(PEA). Previous analyses have shown that variables with and without a 1 yr lag may influence productivity (Frederiksen et al. 2004b), so both were trialled: relationships were similar, but lagged variables produced higher AICs (Supplement 5), so further analyses considered unlagged variables.

Breeding success was modelled using generalised linear mixed models (GLMMs) with binomial error and logit link. Models were fitted using the 'lme4' R package (Bates et al. 2014), with time as a predictor to identify temporal trends, and then with oceanographic predictors to explore drivers of productivity. Models were first fitted for individual sites, considering single predictors only. Then, equivalent single-predictor models were fitted using data from all sites. Finally, multiple-site models were fitted with multiple predictors, to allow a more complete examination of oceanographic drivers.

For single-site models, only colonies with ≥10 yr of productivity and oceanography data were used. Data were deemed insufficient to include multiple explanatory variables (minimum 12 data points, maximum 19), so only single predictors were considered. An observation-level factor was included as a random effect to model overdispersion in the response (e.g. Browne et al. 2005). Variable influence was assessed by comparing sample-size-corrected Akaike information criterion (AICc) to that from a null model with intercept and random effects only: ΔAICc ≤ 0 was considered to indicate some support, and ΔAICc ≤ −2 to indicate substantial support.

To account for spatial and temporal structuring of data, models including data from all sites were fitted with 'site', 'region', 'year', 'site × year' and 'region × year' random effects. 'Site × year' was an observation-level factor to model overdispersion. 'Region' was included to account for spatial clustering of colonies, and was based on regions previously identified from kittiwake productivity trends (Frederiksen et al. 2005); if a region was not stated for a specific site, the nearest region was used. These models were assessed by comparing uncorrected AIC (due to the larger sample size) to that from a null model. Next, models were fitted with multiple predictors. Interaction terms were not considered, as this would lead to overfitting and reduce interpretability. Model comparison was conducted using the 'MuMIn' R package (Barton 2014); performance was assessed by comparing AIC values to that from the model with lowest AIC, with ΔAIC ≤ 2 considered to indicate similar support.

2.7. Climate change projections

Climate change impacts were estimated using the multiple-predictor models. To account for model and parameter uncertainty, a randomisation procedure with 1 000 000 runs was used: on each run, one model was picked with probability equal to its Akaike weight, and new parameter estimates were simulated. Fixed effect estimates were simulated from a multivariate normal distribution, with mean and covariance matrix taken from the chosen model, using the 'mvtnorm' R package (Genz et al. 2014). 'Site' and 'region' effects were extracted from the model, whilst 'year', 'site × year' and 'region × year' were simulated from normal distributions with mean = 0 and standard deviations taken from the model.

Simulated parameters were applied to oceanographic projections to produce breeding success estimates for 'baseline' and 'future' periods. As these periods represented average conditions, the mean across all years in each period was calculated. Proportional change in breeding success was calculated as [(future − baseline)/baseline]; probability of decline was examined by calculating the proportion of randomisation runs that did not show a decline between baseline and future periods. Differences between periods were tested using Wilcoxon rank sum tests.

3. RESULTS

3.1. Temporal trends and cross correlations

Across all sites, breeding success showed no significant temporal trend (p = 0.141; Supplement 5). Spring SST increased significantly (p = 0.026), and winter SST showed a non-significant increase (p = 0.054). Winter PEA showed a weakly significant increase (p = 0.046), but spring PEA (p = 0.173) and stratification onset (p = 0.096) showed no significant change.

Breeding success decreased significantly at Flamborough Head, Fowlsheugh and St. Abb's Head, but increased at Bardsey Island (0.003 ≤ p ≤ 0.047). Winter SST increased significantly at Bardsey Island, Coquet Island, Flamborough Head and Lambay (0.029 ≤ p ≤ 0.043), whilst spring SST increased significantly at Bardsey Island, Flamborough Head and Puffin Island (p < 0.01). Winter PEA increased significantly at Isle of May (p = 0.016) and St. Abb's Head (p = 0.048), but spring PEA showed no trends. Stratification onset became significantly earlier at Boddam

to Collieston, Fowlsheugh and Isle of May (0.014 ≤ p ≤ 0.020).

Correlations between variables were moderate or weak (Supplement 5), with the highest between winter and spring PEA (ρ = 0.669), winter and spring SST (ρ = 0.672), and stratification onset and PEA (spring ρ = −0.559; winter ρ = −0.485), so it was considered acceptable to include multiple predictors in the same model. Strong or moderate correlations were found between lagged and unlagged forms of all variables (0.647 ≤ ρ ≤ 0.950).

3.2. Single predictor variable models

The strongest predictor of breeding success differed among sites (Table 2; Supplement 6). Stratification onset provided the best model at Isle of May and St. Abb′s Head, with higher productivity associated with later stratification. Spring PEA provided the best model at Flamborough Head, whilst winter PEA provided the best model at Bardsey Island, with both showing higher productivity to be associated with lower PEA; winter PEA attained significance at Coquet Island but was not supported over the null model. Spring SST provided the best model at Fair

Isle, showing higher breeding success was associated with lower SSTs. Winter SST did not perform better than the null model at any site. At Boddam to Collieston and Fowlsheugh, no variable performed better than the null model.

The best all-sites single-predictor model showed higher breeding success with lower winter PEA (Table 2; Fig. 2). A similar relationship was found with spring PEA, but the model received less support. There was also evidence of a negative relationship with spring SST and a positive relationship with stratification onset (Table 2). Therefore, breeding success was higher under lower SSTs, later stratification and when the water column was better mixed early in the year.

3.3. Multiple predictor variable models

The best multiple-predictor model (Table 3; Supplement 6) contained significant, negative coefficients for winter PEA and spring SST, showing that higher breeding success was associated with weaker stratification before breeding and lower SSTs during breeding. Three other models showed similar empirical support: all contained significant, negative coef-

Table 2. Results from models relating breeding success of kittiwakes to single oceanographic predictor variables. See text for model fitting details. Parameter estimates (±SE) are given, followed by ΔAIC (for all-sites models) or ΔAICc (for individual site models) relative to a null model fitted with intercept and random effects only. **Bold**: significantly different from 0 at p < 0.05, as indicated by Wald *Z* tests; *italics*: close to significance with 0.05 ≤ p < 0.1. Full model details are given in Supplement 6. PEA: potential energy anomaly; SST: sea surface temperature

|	Null model	Spring PEA	Spring SST	Strat. onset	Winter PEA	Winter SST
Bardsey Island	AICc = 187.621	−1.719 ± 2.266 ΔAICc = 2.420	1.311 ± 0.877 ΔAICc = 0.807	**0.041 ± 0.019** **ΔAICc = −1.356**	**−1.645 ± 0.693** **ΔAICc = −2.090**	0.928 ± 0.579 ΔAICc = 0.516
Boddam to Collieston	AICc = 178.476	−0.123 ± 1.414 ΔAICc = 3.174	0.057 ± 0.593 ΔAICc = 3.172	0.024 ± 0.018 ΔAICc = 1.561	−0.141 ± 0.488 ΔAICc = 3.099	0.175 ± 0.498 ΔAICc = 3.059
Coquet Island	AICc = 103.824	1.228 ± 0.968 ΔAICc = 2.140	−0.061 ± 0.351 ΔAICc = 3.636	0.018 ± 0.014 ΔAICc = 1.992	**−0.697 ± 0.346** **ΔAICc = 0.109**	−0.075 ± 0.315 ΔAICc = 3.610
Fair Isle	AICc = 278.788	**−13.414 ± 5.33** **ΔAICc = −3.316**	**−4.280 ± 1.189** **ΔAICc = −8.679**	0.042 ± 0.058 ΔAICc = 2.348	−0.942 ± 1.295 ΔAICc = 2.336	**−3.661 ± 1.474** **ΔAICc = −2.561**
Flamborough Head and Bempton Cliffs	AICc = 225.489	**−2.502 ± 0.909** **ΔAICc = −3.417**	**−0.663 ± 0.300** **ΔAICc = −1.416**	−0.023 ± 0.029 ΔAICc = 2.321	0.253 ± 0.509− ΔAICc = 2.668	0.434 ± 0.393 ΔAICc = 1.733
Fowlsheugh	AICc = 214.311	−1.176 ± 1.244 ΔAICc = 2.117	−0.239 ± 0.407 ΔAICc = 2.264	0.013 ± 0.020 ΔAICc = 2.561	−0.388 ± 0.451 ΔAICc = 2.263	−0.270 ± 0.366 ΔAICc = 2.453
Isle of May	AICc = 254.784	0.689 ± 2.371 ΔAICc = 2.830	−0.488 ± 0.601 ΔAICc = 2.264	**0.092 ± 0.030** **ΔAICc = −4.855**	−1.478 ± 1.192 ΔAICc = 2.738	−0.283 ± 0.535 ΔAICc = 2.636
St. Abb′s Head	AICc = 230.539	−1.177 ± 1.241 ΔAICc = 2.034	−0.024 ± 0.361 ΔAICc = 2.910	**0.034 ± 0.013** **ΔAICc = −2.665**	*−1.085 ± 0.613* *ΔAICc = 0.029*	−0.122 ± 0.328 ΔAICc = 2.777
All sites	AIC = 1803.730	**−0.602 ± 0.285** **ΔAIC = −2.669**	**−0.700 ± 0.264** **ΔAIC = −5.242**	*0.014 ± 0.007* *ΔAIC = −3.383*	**−0.641 ± 0.201** **ΔAIC = −11.502**	−0.240 ± 0.231 ΔAIC = 0.994
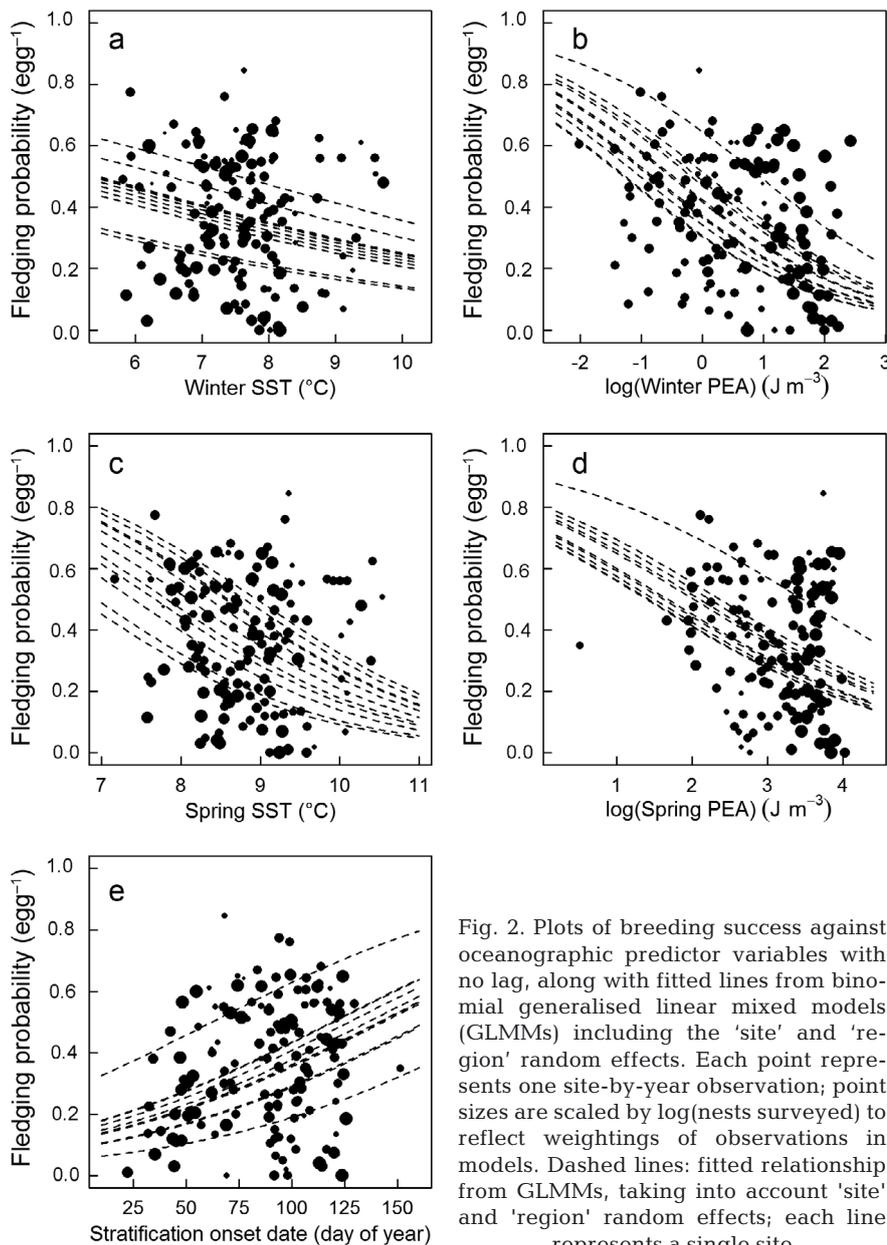
Fig. 2. Plots of breeding success against oceanographic predictor variables with no lag, along with fitted lines from binomial generalised linear mixed models (GLMMs) including the 'site' and 'region' random effects. Each point represents one site-by-year observation; point sizes are scaled by log(nests surveyed) to reflect weightings of observations in models. Dashed lines: fitted relationship from GLMMs, taking into account 'site' and 'region' random effects; each line represents a single site

3.4. Climate change projections

Projections indicated that climate change could drive substantial productivity declines (Table 4; Fig. 3). For the baseline period, mean projected breeding success across all sites was 0.560 (~1.12 chicks per pair); by 2070–99, this had declined by 32.6% to 0.377 (~0.754 chicks per pair). Only 3.0% of simulations did not predict a decline.

All sites showed projected declines (Table 4). The largest proportional decline was for Fair Isle (43.2%), whilst the smallest was at Coquet Island (21.4%). The largest absolute decline was at Flamborough Head (−0.214), and the smallest was at Boddam to Collieston (−0.161). At Bardsey Island and Fair Isle, only 1.8 and 1.1% of simulations respectively did not predict a decline, whilst for Boddam to Collieston, Coquet Island, Fowlsheugh, Isle of May and St. Abb's Head, between 7.9 and 16.9% of simulations did not predict declines. Therefore, the magnitude and probability of declines varied among sites.

Neither stratification onset nor winter PEA changed significantly between periods (Fig. 3). Spring PEA increased significantly (Fig. 3), but the absolute change was small (1961–90 mean 10.02 J m^{-3} [log scale 2.034]; 2070–99 mean 12.13 J m^{-3} [log scale 2.215]) and spring PEA coefficients in high-ranking models were small. Hence, these 3 variables changed too little or had too little an effect on productivity to drive the projected productivity declines. SST increased significantly in spring (1961–90 mean 7.95°C; 2070–99 mean 10.46°C; Fig. 3) and winter (1961–90 mean 7.08°C; 2070–99 mean 9.58°C; Fig. 3); spring SST model coefficients were large and negative, whilst winter SST coefficients were small and positive or large and negative. Hence, rising SSTs appeared to be the major driver of projected declines.

ficients for winter PEA and spring SST, and one non-significant variable. The second-ranked model (ΔAIC = 1.649) contained a non-significant positive effect of winter SST, contrasting with single predictor models; this possibly reflects collinearity between winter and spring SST. The third-ranked model (ΔAIC = 1.861) contained a non-significant positive coefficient for stratification onset, whilst the fourth-ranked model (ΔAIC = 1.926) showed a non-significant negative effect of spring PEA. Therefore, results highlighted the importance of lower winter PEAs and spring SSTs for kittiwake productivity.

Table 3. Top-ranked models from the all-sites analysis relating breeding success of kittiwakes to oceanographic variables. Those shown have ΔAIC ≤ 2 relative to the best model; the null model, fitted with intercept and random effects only, is shown at base of table for comparison. See text for details of model fitting. Parameter estimates (±SE) are given, followed by p values from Wald Z tests. **Bold**: $p < 0.05$; *italics*: $0.05 \leq p < 0.1$. AIC values are shown, and corresponding ΔAIC values relative to the best model. Weight: Akaike weight of each model in the full set, with higher values indicating higher relative support for that model. Full details are in Supplement 6

Intercept	Spring PEA	Spring SST	Stratification onset date	Winter PEA	Winter SST	AIC	ΔAIC	Weight
4.429 ± 2.181 **p = 0.042**	–	**−0.539 ± 0.244** **p = 0.027**	–	**−0.602 ± 0.190** **p = 0.002**	–	1789.734	0	0.263
4.308 ± 2.185 **p = 0.049**	–	**−0.674 ± 0.336** **p = 0.045**	–	**−0.609 ± 0.192** **p = 0.001**	0.173 ± 0.295 p = 0.556	1791.383	1.649	0.115
4.206 ± 2.269 *p = 0.064*	–	**−0.544 ± 0.245** **p = 0.027**	0.003 ± 0.008 p = 0.712	**−0.566 ± 0.214** **p = 0.008**	–	1791.595	1.861	0.104
4.706 ± 2.408 *p = 0.051*	−0.090 ± 0.333 p = 0.786	**−0.541 ± 0.244** **p = 0.027**	–	**−0.574 ± 0.217** **p = 0.008**	–	1791.659	1.926	0.100
−0.677 ± 0.268 **p = 0.012**	–	–	–	–	–	1803.730	15.336	0.000

Table 4. Projected breeding success for the UKCP09 climatic baseline period of 1961–90 and for 2070–99 under the SRES A1B scenario. Reported breeding success values are the mean of 100 000 randomisation runs, where each run produces a mean breeding success across all years in the time period; breeding success is here defined as the proportion of successfully fledged chicks. The standard deviation of 1 000 000 projections is also given. Percentage change is calculated as [(future − baseline)/baseline]×100, based on the mean for each period. To indicate the probability of decline, the difference between the baseline and future projections was calculated for each run, and the proportion of these differences >0 (i.e. those not showing a decline) was calculated. See 'Materials and methods' for randomisation procedure details

Site	Breeding success (±SD) 1961–1990	2070–2099	Absolute change	Percentage change	Proportion not showing decline
Bardsey Island	0.426 ± 0.090	0.246 ± 0.121	−0.181	−42.4	0.018
Boddam to Collieston	0.578 ± 0.109	0.418 ± 0.107	−0.161	−27.8	0.169
Coquet Island	0.776 ± 0.077	0.610 ± 0.123	−0.166	−21.4	0.125
Fair Isle	0.431 ± 0.091	0.245 ± 0.068	−0.186	−43.2	0.011
Flamborough Head and Bempton Cliffs	0.591 ± 0.108	0.378 ± 0.112	−0.214	−36.1	0.028
Fowlsheugh	0.606 ± 0.106	0.442 ± 0.109	−0.164	−27.0	0.168
Isle of Colonsay	0.535 ± 0.101	0.350 ± 0.104	−0.185	−34.6	0.035
Isle of May	0.492 ± 0.097	0.308 ± 0.084	−0.183	−37.3	0.098
Lambay	0.500 ± 0.077	0.318 ± 0.139	−0.182	−36.4	0.087
Puffin Island	0.633 ± 0.106	0.437 ± 0.158	−0.197	−31.0	0.026
St. Abb's Head	0.592 ± 0.088	0.401 ± 0.097	−0.191	−32.2	0.079
Across all sites	0.560 ± 0.074	0.377 ± 0.095	−0.183	−32.6	0.030

4. DISCUSSION

Weaker, later stratification and lower SSTs were associated with higher kittiwake productivity. Individual colonies also showed such relationships, but the most important driver varied among colonies. Projections indicated that climate change could drive longer-term productivity declines. The analytical approach reduced reliance on intensively-studied colonies, accounted for colony-specific habitat use, allowed examination of spatial heterogeneity, and considered short- and longer-term effects; thus providing a more complete examination of drivers of kittiwake productivity. The study therefore provides an example of how changing physical conditions, presumably acting via supporting food webs, can influence apex predators, leading to indirect climate change impacts.
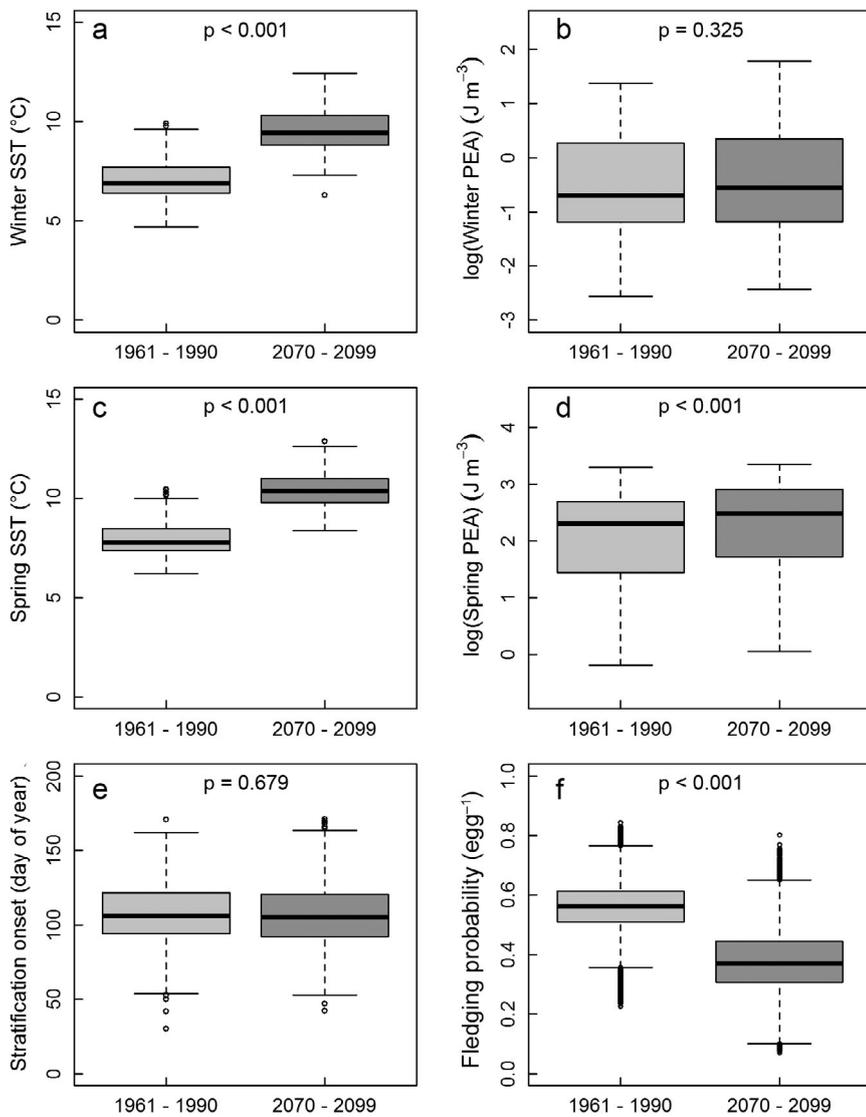
Fig. 3. Boxplots comparing oceanographic variables and projected breeding success between 1961–90 and 2070–99. For plots of oceanographic variables, input values were 30 yr of projection data for each foraging area used in all-sites analyses; for breeding success, input values were 1 000 000 annual breeding success projections (see Section 2.7 for details). Boxes indicate interquartile range (IQR) and median; whiskers indicate 1.5 × IQR; outliers indicate points outside 1.5 × IQR. Results of Wilcoxon rank sum tests are shown at top of each diagram, indicating whether there is a significant difference between periods

tently, but foraging locations may vary (e.g. Ainley et al. 2003, Robertson et al. 2014). However, kittiwakes can display high foraging site fidelity (Irons 1998) and kernels were often similar among years (Supplement 2), indicating that 'core' foraging areas may retain importance. Further, kernel density estimation is sensitive to the number of birds, trips and years included (Soanes et al. 2013, Bogdanova et al. 2014), so areas estimated here may not adequately represent 'whole colony' foraging areas. However, all colonies passed the threshold required to estimate >50% of the core foraging area, and many passed that required for estimating 95% (Soanes et al. 2013). Collection of further tracking data could resolve such issues, providing increased understanding of spatiotemporal variability in foraging areas and more robust kernel estimates. Finally, if prey species are transported or migrate into foraging areas, physical conditions elsewhere could be more important in determining prey availability. However, after settlement, adult sandeels do not move to other areas, and larval sandeel transport towards the UK is limited (Christensen et al. 2008), so local conditions are likely to remain important in areas where sandeels dominate seabird diets. Improved understanding of seabird diet, and the population dynamics of key prey species, could help to clarify such uncertainties.

4.1. Use of colony-specific areas

Previous analyses have extracted oceanographic data from arbitrary areas or broad regions (e.g. Frederiksen et al. 2004a, Lauria et al. 2012), but here, colony-specific areas were produced. This allowed the analysis to reflect observed habitat use, but several caveats apply when interpreting results. It was assumed that colonies use foraging areas consis-

4.2. Drivers of kittiwake productivity

As in previous analyses (e.g. Frederiksen et al. 2004b) a negative relationship between breeding success and SST was found. However, the strongest relationship showed a negative relationship with winter PEA. This suggests that examining multiple variables is necessary to improve our understanding of physical drivers of kittiwake productivity,

and the biological mechanisms through which they act.

Stratification timing and strength are likely to interact to influence feeding conditions. Seasonal stratification influences plankton growth, which can in turn cause fish to move towards the surface to feed (e.g. Greenstreet et al. 2006, Buren et al. 2014). Hence, early stratification can cause a mismatch between peak fish availability or size and the seabird breeding period (Scott et al. 2006, Burthe et al. 2012). Although seabirds can adjust the timing of breeding, such changes may not be sufficient to track prey availability, leading to phenological mismatch (Burthe et al. 2012). Relationships with winter PEA may themselves reflect timing effects, with high PEA values simply indicating areas likely to stratify early. However, kittiwakes avoid foraging in very strongly stratified areas (Scott et al. 2010), suggesting that stratification strength could directly affect breeding success. Strong stratification could reduce sandeel availability, as larvae are more abundant in weakly-stratified surface waters (Jensen et al. 2003), and oxygen deficits under stronger stratification reduce habitat suitability (Behrens et al. 2009). Stronger stratification is also associated with lower abundance of *Calanus finmarchicus* (Beare et al. 2002), a key prey species for North Sea forage fish (e.g. van Deurs et al. 2009). As stratification is likely to become stronger and earlier under climate change (Lowe et al. 2009), investigating mechanisms linking stratification, fish and seabirds is a priority.

It has been suggested that SST relationships could reflect stratification conditions (Scott et al. 2006), but the best models here included both PEA and SST, indicating that temperature has an independent effect. For sandeels, increased metabolic costs at higher temperatures may inhibit growth or cause them to remain buried in the sediment (Greenstreet et al. 2006), and can reduce recruitment (Arnott & Ruxton 2002). Higher temperatures also influence plankton communities, with smaller, less nutritious species replacing larger, cold-adapted species (Beaugrand et al. 2002, Morán et al. 2010); such changes could reduce fish survival or growth. It should also be noted that if climate change affects the distribution of temperature through the water column, stratification could itself be affected by temperature increases (Lowe et al. 2009). It therefore appears beneficial to consider both temperature and stratification effects on food webs when considering drivers of seabird productivity.

Single-site models highlighted spatial variation in oceanographic drivers of productivity, but where foraging areas overlapped, similar patterns were observed. At Isle of May and St. Abb's Head, which overlapped somewhat (Supplement 2), stratification onset provided the best model, whilst at Boddam to Collieston and Fowlsheugh, which overlapped substantially, no relationships were significant. This supports the idea that clustering of kittiwake population trends is driven by local foraging conditions (Frederiksen et al. 2005). Further, only Isle of May and St. Abb's Head showed a lagged variable to perform better than the unlagged equivalent (Supplement 5). Similar results have previously been taken to show that 1-group sandeels influence productivity more than 0-group (Frederiksen et al. 2004b); weak lagged effects elsewhere imply that other colonies may rely more on 0-group sandeels or other species. More seabird diet data are required to improve understanding of such spatial patterns.

4.3. Climate change impacts

Projections indicated that kittiwake productivity could decline by 21 to 43% between the mid 20th and late 21st centuries. The largest absolute decline was projected for Flamborough Head, likely reflecting the strong warming forecast there (Lowe et al. 2009). Smaller declines, with lower probabilities of occurrence, were projected for colonies further up the east coast, but the largest proportional decline occurred at Fair Isle, indicating that larger impacts may not be limited to southerly colonies. Indeed, as dramatic declines have already occurred in northern Scotland (JNCC 2014), these colonies are likely to face the greatest climate change threats.

Between 1986 and 2008, UK kittiwake productivity declined by 31% (Cook & Robinson 2010), comparable to declines projected here over longer timescales. This does not, however, indicate that declines have reached their maximum: realised magnitudes of longer-term declines will be determined by factors including anthropogenic influences (e.g. Furness & Tasker 2000) and adult condition (Frederiksen et al. 2004a). Notably, although no density-dependence was found in the present study or several previous studies of kittiwakes (Frederiksen et al. 2005, Sandvik et al. 2014), density-dependence could exacerbate or ameliorate productivity declines, through processes such as reduced local competition for food in smaller populations (Furness & Birkhead 1984), or reduced threats from predators in larger populations (Massaro et al. 2001). Therefore, further information about how kittiwake be-

haviour and breeding success interact with population size could be important in understanding population-scale impacts of climate change. Further, various methodological processes and assumptions influence the magnitude of projected declines. Projections describe 30 yr means for 11 colonies, whereas observed decline estimates are based on individual years of data for over 50 colonies (Cook & Robinson 2010). Data were extracted from recent foraging areas, but birds might shift their foraging areas under climate change to track prey. However, if kittiwakes remain reliant upon sandeels, it is unlikely that important new areas will emerge due to patchy distribution of sandeels, the sparse distribution of sandeel habitat and limited transport among sandbanks (Christensen et al. 2008); shifts to new dominant prey species cannot be predicted using currently-available data. Finally, climate projections represented only one possible future scenario, so cannot account for the full range of conditions that may be experienced, and whilst the projections present a plausible future scenario, they are subject to uncertainty (Holt et al. 2012) so realised future conditions may differ from projections. Overall, however, results indicate that climate change is expected to reduce kittiwake productivity in the longer term.

Although projections suggest that climate change will drive declines in breeding success, the conservation status of kittiwake populations will be influenced by more than just productivity. Adult and juvenile survival declines under higher SSTs (Frederiksen et al. 2004b, Sandvik et al. 2014), and population size is sensitive to declining survival (Sandvik et al. 2012). Hence, if rising temperatures drive declines in both productivity and survival, abundances could fall very rapidly. If, by contrast, warmer temperatures cause higher adult survival, as has been found in some cases (Sandvik et al. 2014), population trends may be somewhat buffered from declining productivity. There may also be impacts on individual-level responses such as stress hormone levels (Brewer et al. 2008) and chick development rates (Vincenzi & Mangel 2013); such responses could combine to produce substantial population-level effects. Collection of data on these other demographic parameters, and examination of how they interact with SST and stratification, could prove highly informative in understanding population-level climate change impacts.

Global SSTs are projected to increase by 1 to 3°C by the end of the 21st century (Collins et al. 2013), so further impacts on seabirds may be unavoidable.

However, appropriate marine management could ameliorate some negative effects. Sandeel fisheries can reduce seabird productivity (Frederiksen et al. 2004b, Daunt et al. 2008), so any action that reduces prey abundance in key foraging areas is also likely to affect seabirds. With improved knowledge of foraging locations, it may be possible to grant important areas enhanced environmental protection, minimising negative anthropogenic influences on fish populations, and thus providing a more resilient food web; this is in line with previous recommendations for marine climate change adaptation (Mawdsley et al. 2009). Establishing marine management strategies to promote healthy forage fish populations may provide the best approach for conserving kittiwakes and other apex predators under uncertain future conditions.

5. CONCLUSIONS

This study suggests that weaker, later stratification and lower SSTs are beneficial for kittiwake productivity, and that climate change is a longer-term threat. Kittiwakes are surface-feeding apex predators, so some findings may be primarily relevant to similar species: if oceanographic changes reduce prey availability near the surface, this may explain why surface feeders such as kittiwakes and Arctic terns *Sterna paradisaea* appear most sensitive to changing conditions (Enstipp et al. 2006). If, however, overall prey abundance or quality is reduced, more species could be affected. Indeed, declines have been observed in North Sea harbour seal *Phoca vitulina* populations (Lonergan et al. 2007), increased harbour porpoise *Phocoena phocoena* starvation might be linked to reduced sandeel availability (MacLeod et al. 2007b; but see MacLeod et al. 2007a, Thompson et al. 2007), and productivity of guillemots *Uria aalge* and razorbills *Alca torda* has declined (JNCC 2014). These findings suggest that impacts of changing oceanographic conditions on marine food webs affect more than just surface-feeding birds. Climate change could therefore have substantial ecosystem-wide impacts.

This study provides an example of possible indirect climate change impacts, with effects mediated via supporting food webs. Such impacts are possible whenever predators depend upon prey species that are sensitive to climate change, and may be more important than previously understood (Cahill et al. 2013, Ockendon et al. 2014). Given the complexity associated with identifying and understanding these

impacts, there is an urgent need to investigate biotic mechanisms linking physical drivers to higher consumers. By identifying the specific physical conditions, prey species and community changes that drive population-level responses in apex predators, we may be better-able to target conservation actions. If appropriate management allows apex predators to maintain high productivity in some years, it may still be possible to ameliorate population-level impacts of climate change.

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