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1   **Predicting the impacts of climate change-driven changes in sea temperature and**

2   **stratification on seabird breeding success**

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4   Running head: Seabird breeding success and oceanographic change

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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 eleven 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 three colonies, weaker stratification at two, and lower SSTs at one, whilst two 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 – 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.

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.

4

83 In the UK and Ireland, abundances of several seabird species have fallen substantially since

84 the mid-1980s (JNCC 2014). Some declines have been linked to rising sea surface

85 temperatures (SSTs) (e.g., Frederiksen et al. 2004b, Frederiksen et al. 2007). A possible

86 mechanism behind this is reduced prey availability and nutritional value due to changing

87 zooplankton communities (Arnott & Ruxton 2002, Wanless et al. 2004, van Deurs et al.

88 2009). Although strong relationships with SST have been derived for individual colonies

89 (Frederiksen et al. 2004b), its importance varies spatially, with colonies in some regions

90 showing only weak SST relationships (Frederiksen et al. 2007, Lauria et al. 2012). Further,

91 other oceanographic drivers, notably density stratification, may also be important (Scott et al.

92 2006). Stratification occurs when temperature or salinity differences cause pronounced

93 density differences between deep and shallow waters. Associated changes in nutrient

94 availability and light regimes influence plankton growth, and in turn fish activity and growth

95 (Scott et al. 2006, Sharples et al. 2006). Under earlier stratification, key fish species may be

96 available too early or be less nutritious (Wright & Bailey 1996, Wanless et al. 2004, Scott et

97 al. 2006), whilst abundance of key zooplankton and fish species may fall under stronger

98 stratification (Beare et al. 2002, Jensen et al. 2003). To improve understanding of the physical

99 drivers of seabird productivity and identify underlying biological mechanisms, it is therefore

100 necessary to consider multiple colonies across multiple regions (Lauria et al. 2012, Sydeman

101 et al. 2012), and multiple oceanographic variables.

102

103 With improved understanding of physical drivers of productivity, longer-term climate change

104 impacts can be considered. Longer-term impacts have been implied from observed changes,

105 but few studies have made explicit projections (but see Frederiksen et al. 2013, Sandvik et al.

106 2014). A clearer understanding of future impacts is essential when considering possible

107 conservation strategies in a changing climate, especially in light of legislative frameworks that

108 consider seabird productivity under prevailing climatic conditions (HM Government 2012).

109 Therefore, both observed relationships and explicit climate change projections are necessary

110 to provide a more complete understanding of the impacts of oceanographic change and

111 stochasticity on seabird populations.

112

113 Here, we examine drivers of productivity for multiple seabird colonies, considering SST and

114 stratification. We consider the black-legged kittiwake (*Rissa tridactyla*, hereafter

115 "kittiwake"), as it is a sensitive indicator of environmental conditions (Wanless et al. 2007,

116 Cook et al. 2014). We focus on the UK and Ireland, which support around 14% of the

117 biogeographic kittiwake population and for which population data are routinely collected

118 (JNCC 2014). Specifically, we consider the following hypotheses:

119   1) higher SSTs are associated with reduced kittiwake breeding success;

120   2) strong, early stratification is associated with reduced kittiwake breeding success;

121   3) modelled kittiwake productivity will be reduced in future scenarios due to the impacts

122   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 one month (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), with those dependent

upon a single species 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, Taiwan)

attached with adhesive tape to back feathers whilst at the colony. Tags recorded a location fix

accurate to 20 m approximately every 100 seconds, and remained attached for two to five

148   days. Tracking occurred from May to July, but mostly in June, covering late incubation and

149   chick rearing periods.

150

151   It was assumed that oceanographic conditions primarily affect kittiwake productivity via food

152   webs, so the most relevant areas from which to extract oceanographic data were those

153   associated with foraging. Therefore, GPS records were filtered to identify relevant locations.

154   Records within 1 km of the colony centre were removed to exclude fixes associated with

155   behaviours around the nest, which are rarely associated with foraging (Suryan et al. 2002).

156   Travel speeds between points were calculated; these formed a bimodal distribution, with

157   lower speeds likely to be associated with foraging (e.g., Kotzerka et al. 2010). Based on

158   preliminary analysis of a subset of data, records with speeds over 14 km h^{-1} were removed

159   (Appendix S1). Filtering left 192,638 records. Although filtering did not exclude behaviours

160   such as resting on the sea, the range of kittiwake foraging behaviours (Coulson 2011) makes a

161   more inclusive approach preferable. A sensitivity analysis indicated that threshold selection

162   made little difference to extracted oceanographic variable values (Appendix S1), so analyses

163   presented here should be robust to threshold specification within the ranges considered.

164

165   Kernel density estimates (KDEs) were calculated to convert GPS records into estimated

166   foraging areas. For each colony, data were pooled across all birds and years to estimate the

167   'core' foraging area; whilst interannual variation was found, most colonies used similar areas

168   each year (Appendix S2), so pooling was considered appropriate. Although kernel density

169   estimation is sensitive to the number of birds included, all colonies had at least the number

170   required to describe >50% of the 'true' foraging area (Soanes et al. 2013). Kernel densities

171   were evaluated on a regular 30 arc-second by 30 arc-second rectangular grid with limits 1.25

172   degrees away from the most extreme observations.

173

174   KDEs were based on a bivariate Gaussian kernel, and were evaluated using the 'ks' R package

175   (Duong 2013). A bivariate plug-in estimator (Duong & Hazelton 2003) and a rule-of-thumb

176   approach (Silverman 1986) were considered for choosing the degree of smoothing. The rule-

177   of-thumb approach took bandwidth to be $1.06 \cdot \sigma_x \cdot n^{(-1/5)}$ and $1.06 \cdot \sigma_y \cdot n^{(-1/5)}$, where n denotes

178   sample size and σ_x and σ_y denote standard deviations of longitudes and latitudes; this is

179   derived in a univariate setting under an assumption of normality, so should be interpreted

180   cautiously here. However, the plug-in was highly computationally intensive for datasets of

181   this size, so the approaches were compared using a subset of sites: extracted oceanographic

182   data were highly correlated ($r \geq 0.99$), so the rule-of-thumb approach was used for all sites.

183   Foraging areas were defined by the 90% density contour, which has been recommended for

184   home range estimates (Börger et al. 2006). Kernels are presented in Appendix S2.

185

186   **2.3. Kittiwake breeding success data**

187   Breeding success data were acquired from the seabird monitoring programme (SMP;

188   http://www.jncc.defra.gov.uk/smp; Walsh et al. (1995)). The SMP is an annual sample survey

189   of seabird breeding population size and productivity, which started in 1986 and is coordinated

190   by the Joint Nature Conservation Committee (JNCC). Data from the Isle of May National

191   Nature Reserve were acquired from the Centre for Ecology & Hydrology

192   (http://gateway.ceh.ac.uk; accessed 12/04/2013). Productivity data were not available for all

193   years for all colonies, leaving 142 site-by-year combinations (Table 1).

194

195   SMP breeding success is often analysed as mean fledged chicks per nest (e.g., Frederiksen et

196   al. 2007). However, it was preferable to avoid this here, as Gaussian responses could become

197   negative in projections, and varying numbers of nests contributed to observations (range 21 –

198   1446). Therefore, numbers of fledged and failed chicks were modelled as a binomial

199   response, with fledged chicks taken from the data, and failed chicks estimated as ((2 × nests) -

200   fledged), based on the mean and modal UK kittiwake clutch size of 2 (range 1 - 3; Coulson &

201   Porter 1985, Coulson 2011), thus preventing negative predictions and allowing prior weights

202   to account for varying nest numbers. Hence, breeding success was modelled as chicks fledged

203   *per egg* (Cook et al. 2014). To ensure results were robust to these assumptions, fledged chicks

204   were also modelled as a Poisson response with an offset of log(nests); results were very

205   similar to the binomial analysis (Appendix S3).

206

207   **2.4. Oceanographic data**

208   Two oceanographic datasets were acquired: one covered recent years (hereafter, 'hindcast'),

209   whilst one covered 30-year periods for the mid 20th and late 21st Centuries (hereafter,

210   'projections'). Both were produced from the Proudman Oceanographic Laboratory Coastal

211   Ocean Modelling System (POLCOMS), which simulates ocean hydrodynamics as driven by

212   atmospheric inputs (Holt & James 2001). Data acquired were monthly mean temperature and

213   salinity on a $^1/_6$° long × $^1/_9$° lat grid (~12 km × 12 km) over multiple vertical layers.

214

215   Hindcast data were acquired from the MyOcean project (http://www.myocean.eu; product

216   NORTHWESTSHELF_REANALYSIS_PHYS_004_005; accessed 23/04/2013), and

217   represented an estimate of conditions experienced between 1967 and 2004, so could be used

218   to establish relationships with kittiwake productivity. Further information on this dataset is

219   provided by Holt et al. (2012). Projection data were acquired from the British Atmospheric

220   Data Centre (http://badc.nerc.ac.uk/data/link; accessed 01/03/2013; access provided by the

221   UK Met Office), and represented baseline (1961-90) and future (2070-99, A1B SRES

222   scenario) periods. Projections did not correspond to conditions in specific years, so could only

223   be used to predict breeding success under average conditions in each period. Further

224   information on this dataset is provided by Lowe *et al*. (2009).

225

226   **2.5. Explanatory variables**

227   Three oceanographic variables that could influence kittiwake productivity were calculated:

228   SST (e.g., Frederiksen et al. 2004b), stratification strength, and the timing of seasonal

229   stratification onset (e.g., Scott et al. 2006, Scott et al. 2010). SST was calculated by extracting

230   the top layer of temperature data.

231

232   Stratification strength was expressed using the potential energy anomaly (PEA; Equation 1),

233   as defined by Holt et al. (2010). PEA indicates the energy per unit depth required to mix the

234   water column. Hence, higher values indicate stronger stratification. PEA was calculated as

235

236 $$-\frac{g}{h}\int_{z=-h}^{0} z\left(\rho\big(T(z), S(z)\big) - \rho(\bar{T}, \bar{S})\right) dz \qquad (1).$$

237

238   Here, g = gravitational acceleration, h = water depth (or 400 m if h exceeds this), z = the

239   vertical coordinate (0 indicating the surface, negative values indicating deeper water), ρ =

240   density (calculated using a polynomial function (Jackett et al. 2006)), T = temperature,

241   S = salinity; the overbar indicates that the quantity is averaged from h to the surface. As data

242   were available for discrete depths, the integral was evaluated numerically using Simpson's

243   rule.

244

245   Seasonal stratification onset was calculated similarly to previous analyses of POLCOMS data

246   (Lowe et al. 2009, Holt et al. 2010), but as daily outputs were unavailable, additional

247   assumptions were made. Stratification onset was defined as the first day of the year with

248 mixed layer depth (MLD) <50 m (Holt et al. 2010). MLD was defined as the depth at which

249 density differed from surface density by an amount equivalent to a 0.5°C temperature

250 reduction. Only monthly outputs were available, so daily MLD values were interpolated by

251 fitting a cubic spline through monthly values; whilst this retains the seasonal pattern of MLD,

252 it may underestimate true variability. Hence, whilst the stratification onset metric is relatively

253 coarse, variability among years and sites should be adequately described.

254

255 For SST and PEA, winter and spring means were calculated. Winter (December, January,

256 February) corresponded to the period important for sandeel spawning and egg hatching

257 (Arnott & Ruxton 2002). Spring (March, April, May, June) corresponded to the period when

258 kittiwakes commence breeding, sandeel larvae grow and sandeel abundance peaks (Wright &

259 Bailey 1996, Coulson 2011). For stratification onset, only annual means could be defined.

260

261 As well as oceanographic influences, breeding success could be influenced by density-

262 dependence, with reduced productivity at higher population sizes (Furness & Birkhead 1984).

263 Therefore, for the subset of sites and years with SMP data on kittiwake breeding population

264 size available (9 colonies; 78 site-by-year combinations), log(population) was considered as a

265 further predictor variable (Appendix S4). Across all sites and at three of four individual

266 colonies, there was no significant relationship between population size and breeding success;

267 at the remaining colony, a positive relationship was found. Relationships between breeding

268 success and oceanographic variables were not influenced by inclusion of population size.

269 Consequently, in the present study there is little evidence of density-dependent effects on

270 breeding success (Appendix S4); due to the much-restricted dataset involved in this analysis,

271 further discussion relates to models excluding population size.

272

2.5. Statistical analysis

Analyses were conducted in R v.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 (Appendix S5). PEA values

displayed skewed distributions, so logged and untransformed values were compared in

preliminary productivity models (Appendix S5): logged PEA performed better, so further

models used log(PEA). Previous analyses have shown that variables with and without a 1-

year lag may influence productivity (Frederiksen et al. 2004b), so both were trialled:

relationships were similar, but lagged variables produced higher AICs (Appendix S5), 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 years 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

298   and random effects only: ΔAICc ≤ 0 was considered to indicate some support, and ΔAICc ≤

299   -2 to indicate substantial support.

300

301   To account for spatial and temporal structuring of data, models including data from all sites

302   were fitted with 'site', 'region', 'year', 'site*year' and 'region*year' random effects.

303   'Site*year' was an observation-level factor to model overdispersion. 'Region' was included to

304   account for spatial clustering of colonies, and was based on regions previously identified from

305   kittiwake productivity trends (Frederiksen et al. 2005); if a region was not stated for a specific

306   site, the nearest region was used. These models were assessed by comparing uncorrected AIC

307   (due to the larger sample size) to that from a null model. Next, models were fitted with

308   multiple predictors. Interaction terms were not considered, as this would lead to overfitting

309   and reduce interpretability. Model comparison was conducted using the 'MuMIn' R package

310   (Barton 2014); performance was assessed by comparing AIC values to that from the model

311   with lowest AIC, with ΔAIC ≤ 2 considered to indicate similar support.

312

313   **2.6. Climate change projections**

314   Climate change impacts were estimated using the multiple-predictor models. To account for

315   model and parameter uncertainty, a randomisation procedure with 1,000,000 runs was used:

316   each run, one model was picked with probability equal to its Akaike weight, and new

317   parameter estimates were simulated. Fixed effect estimates were simulated from a

318   multivariate normal distribution, with mean and covariance matrix taken from the chosen

319   model, using the 'mvtnorm' R package (Genz et al. 2014). 'Site' and 'region' effects were

320   extracted from the model, whilst 'year', 'site*year' and 'region*year' were simulated from

321   normal distributions with mean = 0 and standard deviations taken from the model.

322

14

323   Simulated parameters were applied to oceanographic projections to produce breeding success

324   estimates for 'baseline' and 'future' periods. As these periods represented average conditions,

325   the mean across all years in each period was calculated. Proportional change in breeding

326   success was calculated as ((future - baseline)/baseline); probability of decline was examined

327   by calculating the proportion of randomisation runs that did not show a decline between

328   baseline and future periods. Differences between periods were tested using Wilcoxon rank

329   sum tests.

3. RESULTS

3.1. Temporal trends and cross correlations

Across all sites, breeding success showed no significant temporal trend ($P = 0.141$; Appendix S5). 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 ($0.003 \leq P \leq 0.047$). Winter SST increased significantly at Bardsey Island, Coquet Island, Flamborough Head and Lambay ($0.029 \leq P \leq 0.043$), 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 ($0.014 \leq P \leq 0.020$).

Correlations between variables were moderate or weak (Appendix S5), with the highest between winter and spring PEA ($\rho = 0.669$), winter and spring SST ($\rho = 0.672$), and stratification onset and PEA (spring $\rho = -0.559$; winter $\rho = -0.485$), 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 ($0.647 \leq \rho \leq 0.950$).

3.2. Single predictor variable models

The strongest predictor of breeding success differed among sites (Table 2; Appendix S6). 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

355   Flamborough Head, whilst winter PEA provided the best model at Bardsey Island, with both

356   showing higher productivity to be associated with lower PEA; winter PEA attained

357   significance at Coquet Island but was not supported over the null model. Spring SST provided

358   the best model at Fair Isle, showing higher breeding success was associated with lower SSTs.

359   Winter SST did not perform better than the null model at any site. At Boddam to Collieston

360   and Fowlsheugh, no variable performed better than the null model.

361

362   The best all-sites single-predictor model showed higher breeding success with lower winter

363   PEA (Table 2; Fig. 2). A similar relationship was found with spring PEA, but the model

364   received less support. There was also evidence of a negative relationship with spring SST and

365   a positive relationship with stratification onset (Table 2). Therefore, breeding success was

366   higher under lower SSTs, later stratification and when the water column was better mixed

367   early in the year.

368

369   **3.3. Multiple predictor variable models**

370   The best multiple-predictor model (Table 3; Appendix S6) contained significant, negative

371   coefficients for winter PEA and spring SST, showing higher breeding success was associated

372   with weaker stratification before breeding and lower SSTs during breeding. Three other

373   models showed similar empirical support: all contained significant, negative coefficients for

374   winter PEA and spring SST, and one non-significant variable. The second-ranked model

375   (ΔAIC = 1.649) contained a non-significant positive effect of winter SST, contrasting with

376   single predictor models; this possibly reflects collinearity between winter and spring SST.

377   The third-ranked model (ΔAIC = 1.861) contained a non-significant positive coefficient for

378   stratification onset, whilst the fourth-ranked model (ΔAIC = 1.926) showed a non-significant

379 negative effect of spring PEA. Therefore, results highlighted the importance of lower winter

380 PEAs and spring SSTs for kittiwake productivity.

381

382 **3.4. Climate change projections**

383 Projections indicated that climate change could drive substantial productivity declines (Table

384 4; Fig. 3). For the baseline period, mean projected breeding success across all sites was 0.560

385 (~1.12 chicks per pair); by 2070-99, this had declined by 32.6% to 0.377 (~0.754 chicks per

386 pair). Only 3.0% of simulations did not predict a decline.

387

388 All sites showed projected declines (Table 4). The largest proportional decline was for Fair

389 Isle (43.2%), whilst the smallest was at Coquet Island (21.4%). The largest absolute decline

390 was at Flamborough Head (-0.214), and the smallest was at Boddam to Collieston (-0.161). At

391 Bardsey Island and Fair Isle, only 1.8% and 1.1% of simulations respectively did not predict a

392 decline, whilst for Boddam to Collieston, Coquet Island, Fowlsheugh, Isle of May and St.

393 Abb's Head, 7.9 − 16.9% of simulations did not predict declines. Therefore, the magnitude

394 and probability of declines varied among sites.

395

396 Neither stratification onset nor winter PEA changed significantly between periods (Fig. 3).

397 Spring PEA increased significantly (Fig. 3), but the absolute change was small (1961-90

398 mean 10.02 Jm^{-3} (log scale 2.034); 2070-99 mean 12.13 Jm^{-3} (log scale 2.215)) and spring

399 PEA coefficients in high-ranking models were small. Hence, these three variables changed

400 too little or had too little an effect on productivity to drive the projected productivity declines.

401 SST increased significantly in spring (1961-90 mean 7.95°C; 2070-99 mean 10.46°C; Fig. 3)

402 and winter (1961-90 mean 7.08°C; 2070-99 mean 9.58°C; Fig. 3); spring SST model

403 coefficients were large and negative, whilst winter SST coefficients were small and positive

404   or large and negative. Hence, rising SSTs appeared to be the major driver of projected

405   declines.

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.

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 consistently, 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 (Appendix S2), 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

431   estimates. Finally, if prey species are transported or migrate into foraging areas, physical

432   conditions elsewhere could be more important in determining prey availability. However,

433   after settlement, adult sandeels do not move to other areas, and larval sandeel transport

434   towards the UK is limited (Christensen et al. 2008), so local conditions are likely to remain

435   important in areas where sandeels dominate seabird diets. Improved understanding of seabird

436   diet, and the population dynamics of key prey species, could help to clarify such uncertainties.

437

438   **4.2. Drivers of kittiwake productivity**

439   As in previous analyses (e.g., Frederiksen et al. 2004b) a negative relationship between

440   breeding success and SST was found. However, the strongest relationship showed a negative

441   relationship with winter PEA. This suggests that examining multiple variables is necessary to

442   improve our understanding of physical drivers of kittiwake productivity, and the biological

443   mechanisms through which they act.

444

445   Stratification timing and strength are likely to interact to influence feeding conditions.

446   Seasonal stratification influences plankton growth, which can in turn cause fish to move

447   towards the surface to feed (e.g., Greenstreet et al. 2006, Buren et al. 2014). Hence, early

448   stratification can cause a mismatch between peak fish availability or size and the seabird

449   breeding period (Scott et al. 2006, Burthe et al. 2012). Although seabirds can adjust the

450   timing of breeding, such changes may not be sufficient to track prey availability, leading to

451   phenological mismatch (Burthe et al. 2012). Relationships with winter PEA may themselves

452   reflect timing effects, with high PEA values simply indicating areas likely to stratify early.

453   However, kittiwakes avoid foraging in very strongly stratified areas (Scott et al. 2010),

454   suggesting that stratification strength could directly affect breeding success. Strong

455   stratification could reduce sandeel availability, as larvae are more abundant in weakly-

456 stratified surface waters (Jensen et al. 2003), and oxygen deficits under stronger stratification

457 reduce habitat suitability (Behrens et al. 2009). Stronger stratification is also associated with

458 lower abundance of *Calanus finmarchicus* (Beare et al. 2002), a key prey species for North

459 Sea forage fish (e.g., van Deurs et al. 2009). As stratification is likely to become stronger and

460 earlier under climate change (Lowe et al. 2009) investigating mechanisms linking

461 stratification, fish and seabirds is a priority.

462

463 It has been suggested that SST relationships could reflect stratification conditions (Scott et al.

464 2006), but the best models here included both PEA and SST, indicating that temperature has

465 an independent effect. For sandeels, increased metabolic costs at higher temperatures may

466 inhibit growth or cause them to remain buried in the sediment (Greenstreet et al. 2006), and

467 can reduce recruitment (Arnott & Ruxton 2002). Higher temperatures also influence plankton

468 communities, with smaller, less nutritious species replacing larger, cold-adapted species

469 (Beaugrand et al. 2002, Morán et al. 2010); such changes could reduce fish survival or

470 growth. It should also be noted that if climate change affects the distribution of temperature

471 through the water column, stratification could itself be affected by temperature increases

472 (Lowe et al. 2009). It therefore appears beneficial to consider both temperature and

473 stratification effects on food webs when considering drivers of seabird productivity.

474

475 Single-site models highlighted spatial variation in oceanographic drivers of productivity, but

476 where foraging areas overlapped, similar patterns were observed. At Isle of May and St.

477 Abb's Head, which overlapped somewhat (Appendix S2), stratification onset provided the

478 best model, whilst at Boddam to Collieston and Fowlsheugh, which overlapped substantially,

479 no relationships were significant. This supports the idea that clustering of kittiwake

480 population trends is driven by local foraging conditions (Frederiksen et al. 2005). Further,

481 only Isle of May and St. Abb's Head showed a lagged variable to perform better than the

482 unlagged equivalent (Appendix S5). Similar results have previously been taken to show that

483 1-group sandeels influence productivity more than 0-group (Frederiksen et al. 2004b); weak

484 lagged effects elsewhere imply that other colonies may rely more on 0-group sandeels or

485 other species. More seabird diet data are required to improve understanding of such spatial

486 patterns.

487

488 **4.3. Climate change impacts**

489 Projections indicated that kittiwake productivity could decline by 21 – 43% between the mid

490 20th and late 21st Centuries. The largest absolute decline was projected for Flamborough

491 Head, likely reflecting the strong warming forecast there (Lowe et al. 2009). Smaller declines,

492 with lower probabilities of occurrence, were projected for colonies further up the east coast,

493 but the largest proportional decline occurred at Fair Isle, indicating that larger impacts may

494 not be limited to southerly colonies. Indeed, as dramatic declines have already occurred in

495 northern Scotland (JNCC 2014), these colonies are likely to face the greatest climate change

496 threats.

497

498 Between 1986 and 2008, UK kittiwake productivity declined by 31% (Cook & Robinson

499 2010), comparable to declines projected here over longer timescales. This does not, however,

500 indicate that declines have reached their maximum: realised magnitudes of longer-term

501 declines will be determined by factors including anthropogenic influences (e.g., Furness &

502 Tasker 2000) and adult condition (Frederiksen et al. 2004a). Notably, although no density-

503 dependence was found in the present study or some previous studies of kittiwakes

504 (Frederiksen et al. 2005, Sandvik et al. 2014), density-dependence could exacerbate or

505 ameliorate productivity declines, through processes such as reduced local competition for

506   food in smaller populations (Furness & Birkhead 1984), or reduced threats from predators in

507   larger populations (Massaro et al. 2001). Therefore, further information about how kittiwake

508   behaviour and breeding success interact with population size could be important in

509   understanding population-scale impacts of climate change. Further, various methodological

510   processes and assumptions influence the magnitude of projected declines. Projections describe

511   30-year means for 11 colonies, whereas observed decline estimates are based on individual

512   years of data for over 50 colonies (Cook & Robinson 2010). Data were extracted from recent

513   foraging areas, but birds might shift their foraging areas under climate change to track prey.

514   However, if kittiwakes remain reliant upon sandeels, it is unlikely that important new areas

515   will emerge due to patchy distribution of sandeels, the sparse distribution of sandeel habitat

516   and limited transport among sandbanks (Christensen et al. 2008); shifts to new dominant prey

517   species cannot be predicted using currently-available data. Finally, climate projections

518   represented only one possible future scenario, so cannot account for the full range of

519   conditions that may be experienced, and whilst the projections present a plausible future

520   scenario, they are subject to uncertainty (Holt et al. 2012) so realised future conditions may

521   differ from projections. Overall, however, results indicate that climate change is expected to

522   reduce kittiwake productivity in the longer term.

523

524   Although projections suggest that climate change will drive declines in breeding success, the

525   conservation status of kittiwake populations will be influenced by more than just productivity.

526   Adult and juvenile survival declines under higher SSTs (Frederiksen et al. 2004b, Sandvik et

527   al. 2014), and population size is sensitive to declining survival (Sandvik et al. 2012). Hence, if

528   rising temperatures drive declines in both productivity and survival, abundances could fall

529   very rapidly. If, by contrast, warmer temperatures cause higher adult survival, as has been

530   found in some cases (Sandvik et al. 2014), population trends may be somewhat buffered from

24

531   declining productivity. There may also be impacts on individual-level responses such as stress

532   hormone levels (Brewer et al. 2008) and chick development rates (Vincenzi & Mangel 2013);

533   such responses could combine to produce substantial population-level effects. Collection of

534   data on these other demographic parameters, and examination of how they interact with SST

535   and stratification, could prove highly informative in understanding population-level climate

536   change impacts.

537

538   Global SSTs are projected to increase by $1 - 3°C$ by the end of the 21st Century (Collins et al.

539   2013), so further impacts on seabirds may be unavoidable. However, appropriate marine

540   management could ameliorate some negative effects. Sandeel fisheries can reduce seabird

541   productivity (Frederiksen et al. 2004b, Daunt et al. 2008), so any action that reduces prey

542   abundance in key foraging areas is also likely to affect seabirds. With improved knowledge of

543   foraging locations, it may be possible to grant important areas enhanced environmental

544   protection, minimising negative anthropogenic influences on fish populations, and thus

545   providing a more resilient food web; this is in line with previous recommendations for marine

546   climate change adaptation (Mawdsley et al. 2009). Establishing marine management

547   strategies to promote healthy forage fish populations may provide the best approach for

548   conserving kittiwakes and other apex predators under uncertain future conditions.

549

550   **4.4. Conclusions**

551   This study suggests that weaker, later stratification and lower SSTs are beneficial for

552   kittiwake productivity, and that climate change is a longer-term threat. Kittiwakes are surface-

553   feeding apex predators, so some findings may be primarily relevant to similar species: if

554   oceanographic changes reduce prey availability near the surface, this may explain why surface

555   feeders such as kittiwakes and Arctic terns (*Sterna paradisaea*) appear most sensitive to

556   changing conditions (Enstipp et al. 2006). If, however, overall prey abundance or quality is

557   reduced, more species could be affected. Indeed, declines have been observed in North Sea

558   harbour seal (*Phoca vitulina*) populations (Lonergan et al. 2007), increased harbour porpoise

559   (*Phocoena phocoena*) starvation might be linked to reduced sandeel availability (MacLeod et

560   al. 2007b; but see MacLeod et al. 2007a, Thompson et al. 2007), and productivity of

561   guillemots (*Uria aalge*) and razorbills (*Alca torda*) has declined (JNCC 2014), suggesting that

562   impacts of changing oceanographic conditions on marine food webs affect more than just

563   surface-feeding birds. Climate change could therefore have substantial ecosystem-wide

564   impacts.

565

566   This study provides an example of possible indirect climate change impacts, with effects

567   mediated via supporting food webs. Such impacts are possible whenever predators depend

568   upon prey species that are sensitive to climate change, and may be more important than

569   previously understood (Cahill et al. 2013, Ockendon et al. 2014). Given the complexity

570   associated with identifying and understanding these impacts, there is an urgent need to

571   investigate biotic mechanisms linking physical drivers to higher consumers. By identifying

572   the specific physical conditions, prey species and community changes that drive population-

573   level responses in apex predators we may be better-able to target conservation actions. If

574   appropriate management allows apex predators to maintain high productivity in some years, it

575   may still be possible to ameliorate population-level impacts of climate change.

27

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859

860

Table 1. Descriptions of sites included in analyses. Site refers to the name in the SMP

database. Map site number refers to location on Fig. 1. Oceanographic data were available up

to 2004, whilst productivity data were available from 1986, meaning that the maximum

possible overlap was 19 years. Regions listed were based on those specified by Frederiksen et

al. (2005).

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

881

882

883 Table 2. Results from models relating breeding success to single oceanographic predictor

884 variables. See text for model fitting details. Parameter estimates (± SE) are given, along with

885 ΔAIC (for all-sites models) or ΔAICc (for individual site models) relative to a null model

886 fitted with intercept and random effects only. Parameter estimates significantly different from

887 0 at *P* < 0.05, as indicated by Wald Z tests, are bold; results approaching but not attaining

888 significance with 0.05 ≤ *P* < 0.1 are italic. Full model details are given in Appendix S6.

	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 (± 5.332), 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 = 2.647	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

889

890 Table 3. Top-ranked models from the all-sites analysis relating breeding success to

891 oceanographic variables; those shown have ΔAIC ≤ 2 relative to the best model; the null

892 model, fitted with intercept and random effects only, is shown for comparison. See text for

893 details of model fitting. Parameter estimates (± SE) are given, along with the ΔAIC value

894 relative to the best model and *P* values from Wald Z tests: *P* < 0.05 are highlighted in bold,

895 0.05 ≤ *P* < 0.1 are highlighted in italic. Full details are in Appendix S6.

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

896

897   Table 4. Projected breeding success for the UKCP09 climatic baseline period of 1961-90 and

898   for 2070-99 under the SRES A1B scenario. Reported breeding success values are the mean of

899   100,000 randomisation runs, where each run produces a mean breeding success across all

900   years in the time period; breeding success is here defined as the proportion of successfully

901   fledged chicks. The standard deviation of the 1,000,000 projections is also given. Pertentage

902   change is calculated as ((future - baseline)/baseline)*100, based on the mean for each period.

903   To indicate the probability of decline, the difference between the baseline and future

904   projections was calculated for each run, and the proportion of these differences > 0 (i.e. those

905   not showing a decline) was calculated. See Methods for randomisation procedure details.

Site	Mean predicted 1961 – 1990 breeding success (± SD)	Mean predicted 2070 – 2099 breeding success (± SD)	Absolute change	Percentage change	Proportion of projections 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

906

907 **Figure legends**

908 Figure 1. Map indicating locations of kittiwake colonies included in analyses. Numbers refer

909 to colony descriptions in Table 1.

910

911 Figure 2. Plots of breeding success against oceanographic predictor variables with no lag,

912 along with fitted lines from binomial GLMMs including the 'site' and 'region' random

913 effects. Each point represents one site-by-year observation; point sizes are scaled by log(nests

914 surveyed) to reflect weightings of observations in models.

915

916 Figure 3. Boxplots comparing oceanographic variables and projected breeding success

917 between 1961-90 and 2070-99. For oceanographic variables plots, input values were 30 years

918 of projection data for each foraging area used in all-sites analyses; for breeding success, input

919 values were 1,000,000 annual breeding success projections (see text for details). Boxes

920 indicate interquartile range and median; whiskers indicate 1.5×IQR; outliers indicate points

921 outside 1.5×IQR. Results of Wilcoxon rank sum tests shown, indicating whether there is a

922 significant difference between periods.

923

924   Figure 1

925