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RESEARCH ARTICLE

Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality

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Abstract

1. In the North Sea, sandeels provide a vital food source for breeding seabirds, but are also the target of an industrial fishery. GPS tracking suggests that the most productive fishing grounds overlap with foraging areas of black-legged kittiwakes from eastern England, raising the prospect that the fishery could affect the birds. Rising sea temperatures also threaten sandeels, so kittiwake food supplies could be affected by local and larger-scale processes.
2. Drivers of kittiwake breeding success at Flamborough Head and Bempton Cliffs Special Protection Area, the UK's largest colony, and one of the closest to the sandeel fishing grounds, were examined. Relationships between sandeel stocks, sea surface temperature and kittiwake breeding success were analysed with generalized linear mixed models and generalized linear models, with model performance assessed using the Akaike Information Criterion and R^2.
3. Higher kittiwake breeding success was associated with higher sandeel spawning stock biomass (SSB; biomass of sexually mature fish) the preceding winter ($R^2 = 21.5\%$) and lower sandeel fishing mortality two years previously ($R^2 = 22.3\%$). After temporal trends were removed, only the fishing mortality effect remained. Models with multiple predictors supported the importance of fishing mortality. Higher sandeel SSB was associated with lower temperatures ($R^2 = 15.2–38.6\%$) and lower sandeel fishing mortality ($R^2 = 24.2–26.1\%$).
4. Hence, lower temperatures and fishing mortality were positively associated with sandeel biomass, and higher sandeel biomass and lower fishing mortality were positively associated with kittiwake productivity. In light of worsening environmental conditions and declining sandeel and kittiwake populations, careful consideration should be given to the requirements of sandeel-dependent predators when making fishery management decisions.

KEYWORDS
birds, climate change, fish, fishing, ocean, sustainability, tracking

1 | INTRODUCTION

Forage fish are small, pelagic, planktivorous species that provide an important food resource for predatory fish, seabirds and marine mammals, thus playing a vital role in marine ecosystems (Alder, Campbell, Karpouzi, Kaschner, & Pauly, 2008; Essington et al., 2015; Rice, 1995). In the North Sea, western Europe, forage fish species include sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and Norway pout (*Trisopterus esmarkii*) (Dickey-Collas et al., 2014; Engelhard et al., 2014). However, sandeels, especially the lesser sandeel (*Ammodytes marinus*), are particularly important, constituting a large proportion of the diet of several seabird species during the breeding season (Anderson, Evans, Potts, Harris, & Wanless, 2014; Furness & Tasker, 2000; Hamer et al., 2007; Lewis et al., 2001) . In some parts of the North Sea, seabird productivity and survival have been linked to sandeel availability (Frederiksen, Edwards, Richardson, Halliday, & Wanless, 2006; Frederiksen, Wanless, Harris, Rothery, & Wilson, 2004; Frederiksen et al., 2005; Wanless, Harris, Redman, & Speakman, 2005), so the fate of internationally-important seabird populations appears to be linked to that of sandeels.

Sandeels are the focus of an industrial fishery that, in recent years, has been the biggest single-species fishery in the North Sea (Furness, 2002; Reilly, Fraser, Fryer, Clarke, & Greenstreet, 2014). The fishery started in the 1950s, reaching peak landings of around 1 million tonnes in the late 1990s, before declining to 100 000–400 000 tonnes per year since 2003 (Furness, 2002; ICES, 2015). Since the early 2000s the fishing fleet has declined in size, but in spite of this, sandeel stock biomass has declined and is often below stock reference points (ICES, 2015). The most productive fishery area is the Dogger Bank, a shallow area in the southern North Sea that supports an important sandeel sub-population (Christensen, Jensen, Mosegaard, St. John, & Schrum, 2008; ICES, 2015). Consequently, the western edge of the Dogger Bank and the smaller sandbanks to the south and west are important fishing grounds (Engelhard et al., 2008; ICES, 2007; Jensen, Rindorf, Wright, & Mosegaard, 2011; South et al., 2009).

The importance of sandeels in the North Sea can lead to conflicts over the stock (Raakjær Nielsen & Mathiesen, 2006). When a sandeel fishery operated off eastern Scotland in the 1990s, sandeel abundance declined and black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') in the region showed reduced breeding success and survival (Daunt et al., 2008; Frederiksen et al., 2004; Rindorf, Wanless, & Harris, 2000). A closed area encompassing much of Scotland's east coast was established in 2000 to protect the sandeel stock: sandeel biomass initially rebounded, but has since continued to decline, likely due to worsening environmental conditions (Greenstreet, Fraser, Armstrong, & Gibb, 2010). The closure, which is still in place, appeared to provide some benefit to kittiwakes, although other seabird species showed less response to the fishery and its closure, possibly because diving or prey-switching ability may have reduced their sensitivity (Daunt et al., 2008; Frederiksen et al., 2004).

The main focus of the industrial sandeel fishery is the Dogger Bank in the southern North Sea. To date, there has been little evidence that seabirds in the region are affected by the fishery, with the relatively large distance to colonies a possible mitigating factor (Engelhard et al., 2008). However, the major fishing grounds are approximately 100 km from the UK coast and smaller grounds to the south and west are even closer (ICES, 2007; Jensen et al., 2011; South et al., 2009). Although the maximum foraging distance for kittiwakes is considered to be 120 km (Thaxter et al., 2012), GPS tracking has shown that kittiwakes from eastern England forage throughout this area (Figure 1b). Sandeels constitute up to 60% of kittiwake diet in this region (Furness & Tasker, 2000), and the fishery could exceed sustainable levels for kittiwakes (Cook, Dadam, Mitchell, Ross-Smith, & Robinson, 2014), so kittiwake populations may still be affected by the fishery. One such colony is at Flamborough Head and Bempton Cliffs Special Protection Area (SPA) in east Yorkshire (Figure 1a). This is the largest kittiwake colony in the UK, but productivity has declined since the 1980s (JNCC, 2015), so it is important to establish whether the sandeel fishery has any impact.

Sandeels are also affected by large-scale environmental changes. Rising sea temperatures have caused community shifts in sandeels' zooplankton prey (Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002; van Deurs, van Hal, Tomczak, Jónasdóttir, & Dolmer, 2009), in turn affecting sandeel growth, survival and distribution (Greenstreet et al., 2006; van Deurs, Hartvig, & Steffensen, 2011). Similar relationships have been observed in seabirds: changing sea temperatures and thermohaline stratification have been linked to kittiwake declines, likely reflecting changing prey populations (Carroll et al., 2015; Frederiksen, Edwards, Mavor, & Wanless, 2007; Frederiksen et al., 2004; Scott et al., 2006). Hence, both large-scale and local pressures could affect seabird food supplies.

Here, statistical relationships between data on sandeel stocks, sea surface temperatures, and kittiwake breeding success are examined. Specifically, regressions are carried out to establish whether sandeel biomass and recruitment, fishing mortality, and sea surface temperatures affect kittiwake breeding success at Flamborough Head and Bempton Cliffs SPA. Further, effects of fishing mortality and sea temperatures on sandeel recruitment and stock biomass are tested. Examining these links should indicate drivers of sandeel populations and dependent seabirds in the region, and hence aid efforts to conserve declining seabirds.

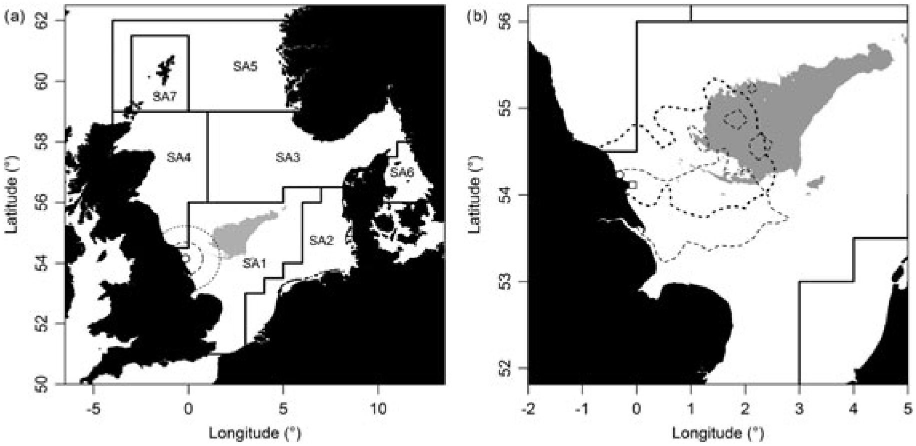

FIGURE 1 Map of North Sea study area. (a) wider study area: Flamborough Head and Bempton Cliffs SPA colony indicated as circle at 54° N on east coast of UK; 120 km maximum foraging range (Thaxter et al., 2012) indicated by dotted line; Dogger Bank indicated by grey shading (derived from GEBCO gridded bathymetric data, www.Gebco.Net); ICES Sandeel assessment areas in North Sea delimited by solid lines. (b) 95% kernel density estimates of foraging locations for kittiwakes tracked in the focal region (Filey: Thick, dotted line; circle to indicate colony. Flamborough: Thin, dashed line; square to indicate colony), in the 2010 to 2015 breeding seasons (updated from Carroll et al. (2015); for description of methods see Appendix S1)

2 | METHODS

2.1 | Study species

2.1.1 | Sandeels

Five species of sandeel (family Ammodytidae) occur in the North Sea, with *Ammodytes marinus* the most abundant and important for seabirds and the fishery (Heath et al., 2012; ICES, 2015; Nielsen, 1994). Hereafter, 'sandeels' refers to *A. marinus*. Sandeels spawn in December and January; eggs are laid on the sea bed, hatching into the water column from February to April; after metamorphosis around May to June, juveniles bury into the sediment alongside adults (Winslade, 1974; Wright & Bailey, 1996). After settling, individuals undertake daily migrations into the water column to feed on zooplankton, notably calanoid copepods (Reay, 1970; van der Kooij, Scott, & Mackinson, 2008; van Deurs et al., 2009; Winslade, 1974). Once critical size and condition thresholds are reached, sandeels bury into the sediment to overwinter, with mature individuals emerging in midwinter to spawn (van Deurs et al., 2011). From April to July they recommence feeding, during which period the fishery is active (Winslade, 1974). Maturation mostly occurs at age 2, but can occur at age 1 (Boulcott, Wright, Gibb, Jensen, & Gibb, 2007). Age 1–3 individuals constitute the majority of stock biomass (Reay, 1970). Sandeels require sediments containing a high proportion of coarse sand and gravel, thus populations are patchily distributed (Holland, Greenstreet, Gibb, Fraser, & Robertson, 2005; Wright, Jensen, & Tuck, 2000). There is mixing among subpopulations as larvae, but after settling there is limited mixing, leading to the risk of local stock depletion (Christensen et al., 2008; Jensen et al., 2011).

2.1.2 | Kittiwakes

Black-legged kittiwakes are gulls in the family Laridae. Egg laying occurs around April and May; chicks hatch after one month and fledge after a further month (Coulson, 2011). Birds overwinter away from breeding colonies (Frederiksen et al., 2012). North Sea kittiwakes eat a high proportion of 1-group (last year's recruits) and older sandeels early in the breeding season, but switch to 0-group (current year's recruits) in late May to early June (Bull et al., 2004; Lewis et al., 2001). In the UK, abundance and breeding success have declined since the 1980s, with declines probably linked to reduced sandeel size and availability (JNCC, 2015; Wanless, Frederiksen, Daunt, Scott, & Harris, 2007). Consequently, kittiwakes are red-listed in the UK (Eaton et al., 2015).

2.2 | Data acquisition

2.2.1 | Sandeel data

Sandeel data were acquired from International Council for the Exploration of the Sea (ICES) stock assessments (ICES, 2015). North Sea sandeel stocks are assessed in areas corresponding to sub-populations with independent dynamics (Christensen et al., 2008). Data were extracted for Sandeel Assessment Area 1 (hereafter, 'SA1'; Figure 1a), which, since the late 1990s, has supported the largest fishery (ICES, 2015).

Data on sandeel recruitment, spawning stock biomass (SSB), total stock biomass (TSB) and fishing mortality (F) were acquired from ICES sandeel stock assessments (ICES, 2015). Recruitment refers to the number of age 0 fish produced, estimated for summer. Here, fish ages are determined from 1 January: fish are age 0 from hatching, becoming age 1 on 1 January the next year, and age 2 on 1 January the following year. SSB refers to the biomass of sexually mature fish, estimated for 1 January. TSB refers to the entire stock's biomass on 1 January. Fishing mortality is defined as in ICES (2012), and higher values indicate higher mortality imposed by the fishery. The fishery primarily targets age 1 and 2 individuals (ICES, 2015), and as these age classes contribute to population dynamics and kittiwake diet differently (recruitment is influenced positively by SSB and negatively by age 1 abundance (van Deurs et al., 2009); kittiwakes switch between older and younger sandeels during the breeding season (Lewis et al., 2001)), separate mortality estimates for age 1 and 2 were used (F1 and F2 respectively). Fishing mortality is estimated annually, but mainly occurs in spring and summer (ICES, 2015; Winslade, 1974). Variables were estimated from population models informed by fishery data and dredge surveys; estimates are considered to be of good quality, but misreporting of catches in 2014 increases uncertainty that year (ICES, 2015). Sandeel stocks could also be influenced by recovering piscivorous fish populations (Furness, 2002; Reilly et al., 2014), but the complexity of multispecies interactions (ICES, 2013) meant that considering predatory fish was not possible within this analysis.

2.2.2 | Kittiwake data

Kittiwake data were acquired from the Seabird Monitoring Programme (SMP) database (Walsh et al., 1995; http://jncc.defra.gov.uk/smp, accessed 1 October 2015). The SMP is an annual sample survey that records seabird breeding abundances and productivity at representative colonies throughout the UK, coordinated by the Joint Nature Conservation Committee. Data were extracted for Flamborough Head and Bempton Cliffs SPA (54.14° N, 0.16° W; Figure 1a), for 1986 to 2014 (no data were available for 2000). This colony was selected because of its proximity to sandeel fishing grounds, availability of tracking data for local colonies (Figure 1b, Appendix S1 in Supporting material) and availability of monitoring data. Data described the number of nests sampled each year (referring to the number of completed nests in the survey plot) and the number of chicks fledged. Population estimates were available only for 3 years, so density-dependent influences could not be considered, but an examination of UK kittiwake colonies previously found little evidence of density dependence from the 1980s onwards (Frederiksen et al., 2005).

2.2.3 | Sea surface temperature data

Sea surface temperature (SST) data were acquired from the UK Met Office HadISST dataset (Rayner et al., 2003; www.metoffice.gov.uk/hadobs, accessed 28 September 2015). Data described interpolated monthly mean SSTs on a 1° × 1° grid. Mean SST within SA1 was calculated for 'winter' (January, February and March) and 'spring' (April, May and June): 'winter' corresponds to the period of sandeel egg hatching and larval development, while 'spring' corresponds to the period of sandeel larval metamorphosis, fishery activity and kittiwake breeding (Arnott & Ruxton, 2002; Coulson, 2011).

2.3 | Data preparation

Owing to large values and positively-skewed distributions, TSB, SSB and recruitment were log$_e$-transformed. Previous studies have shown relationships between kittiwake breeding success and lagged SST (Frederiksen et al., 2004; Wanless et al., 2007) or lagged larval sandeel biomass (Frederiksen et al., 2006; Wanless et al., 2007). Furthermore, sandeel biomass may show a lagged relationship with copepods (Lynam et al., 2017). Such lags could occur because the birds sometimes feed on older fish (Lewis et al., 2001), because there is a 2 year lag between sandeel spawning and maturity (Boulcott et al., 2007), or because of indirect effects such as density-dependent interactions between sandeel age classes (van Deurs et al., 2009). Hence, 1 and 2 year lags (representing data from 1985 to 2013 and 1984–2012 respectively), corresponding to the time difference between sandeel spawning and maturation, were calculated for all predictor variables (i.e. SSB, TSB, recruitment, F, SST). Long time series were available for all predictors, so even lagged models contained the same number of observations, allowing comparison via the Akaike Information Criterion (AIC; see below). In text, lagged variables are referred to with subscripts (e.g. recruitment$_{-2}$, SSB$_{-1}$).

2.4 | Statistical analysis

2.4.1 | Preliminary analyses

Analyses were conducted in R v.3.2.1 (R Core Team, 2015). Variables were tested for cross-correlation (Appendix S2), with degrees of freedom corrected following the modified Chelton method (Pyper & Peterman, 1998). Correlations >0.7 were found between F1 and F2, SSB and TSB$_{-1}$, TSB and recruitment$_{-1}$, and winter and spring SST. For models with single predictors, all variables were examined, but for models with multiple predictors, several variables were excluded to avoid these strong correlations (see below). Nevertheless, given moderate correlations between some variables with lagged forms (e.g. F1 vs. F1$_{-1}$ = 0.574), models including multiple predictors should be interpreted with some caution.

Variables were tested for temporal trends (Figure 2). Regressions describing each variable as a function of year showed that several changed significantly over time (see Results). Such a situation can lead to spurious correlations if two variables change simultaneously but independently; detrending variables by taking residuals from regressions against time can account for this (Votier, Bearhop, Attrill, & Oro, 2008). Detrending may obscure longer-term signals (Pyper &

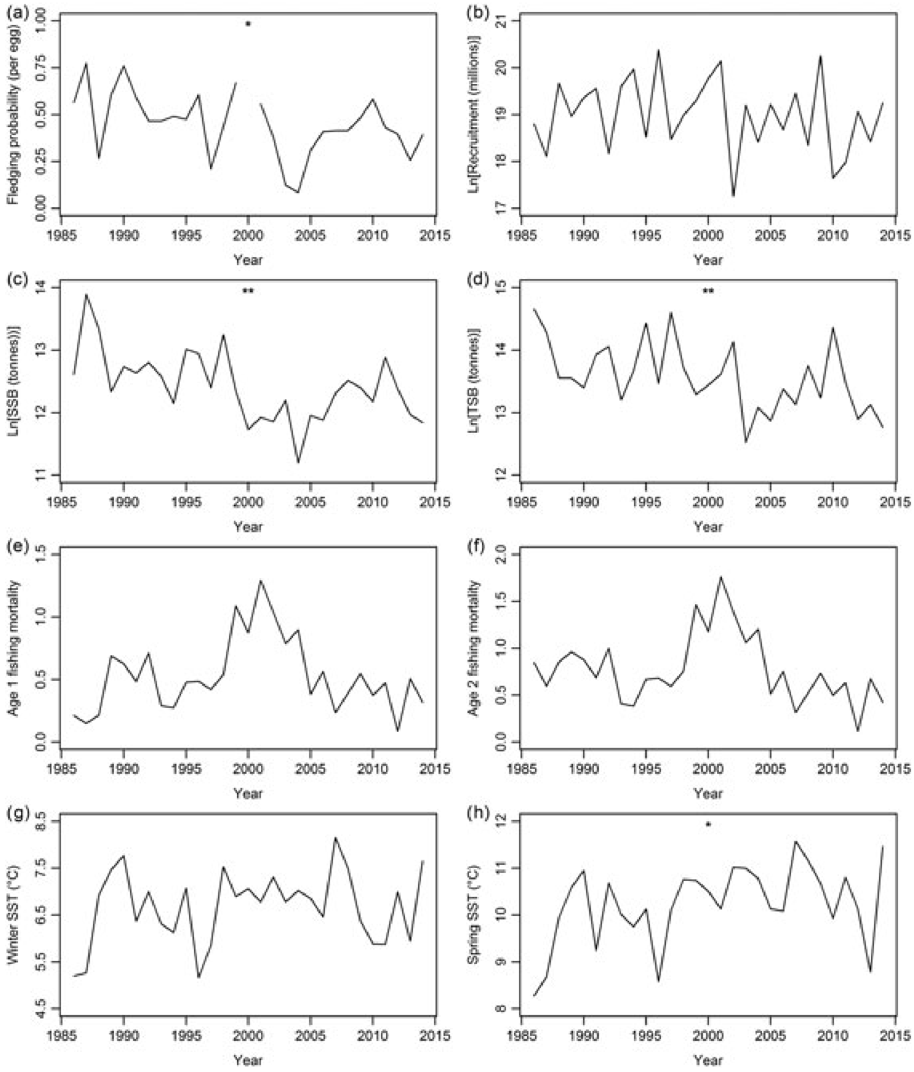

FIGURE 2 Time series of predictor and response variables. Asterisks indicate *P*-value from models testing significance of temporal trends; *** indicates $P \leq 0.001$, ** indicates $P \leq 0.01$, * indicates $P \leq 0.05$

Peterman, 1998; Wynn, Josey, Martin, Johns, & Yésou, 2008), but despite this conservative nature, models were repeated using detrended variables to examine whether relationships were robust to removal of temporal trends (for full results see Appendix S3).

2.4.2 | Modelling breeding success

To examine relationships with breeding success, generalized linear mixed models (GLMMs) were fitted, with binomial error and logit link function. The response variable was the number of fledged chicks (taken directly from the data) and failed chicks (estimated based on the assumption of two eggs per nest) each year, thus accounting for varying numbers of nests surveyed, and representing breeding success as 'fledging probability per egg' (Carroll et al., 2015; Cook et al., 2014). To aid model convergence, fixed effects were scaled by subtracting the mean and dividing by the standard deviation. An observation-level random effect (here, 'year') was included to account for overdispersion in the response (Browne, Subramanian, Jones, & Goldstein, 2005; Carroll et al., 2015). Models were fitted in the 'lme4' R package (Bates, Maechler, Bolker, & Walker, 2015). Model performance was assessed using AIC and a measure of R^2, calculated as the squared Pearson correlation between observed and fitted values. For well-performing models, Wald test P-values of individual parameters were considered.

Owing to the limited dataset (28 observations), models were first fitted with single predictors to avoid overfitting. All possible predictor variables were trialled at this stage. AICs were compared with that from a null model, fitted with intercept and random effect only: the model with lowest AIC was deemed to be the best-performing; those within 2 AIC units of the best were considered to show equivalent support (Burnham & Anderson, 2002).

It was also desirable to consider multiple effects in the same model, to examine the relative contribution of different variables. To avoid collinearity problems, a restricted model set was considered: TSB, F2 and spring SST were excluded owing to strong correlations with other variables that performed better in single predictor models. To avoid overfitting, only models including up to four variables were considered: this would allow seven observations per variable, thus tending toward overfitting, but still allowing all four variables (SSB, Recruitment, F1, winter SST) to enter a single model simultaneously. All combinations of these variables, including their lagged forms, were considered. Model performance was again assessed using AIC.

To ensure results were robust to the assumptions of the binomial framework, modelling was repeated using mean chicks per nest as the response in linear models, including the number of nests as a weight. Results were highly similar to the binomial framework, so are shown in Appendix S4.

2.4.3 | Modelling drivers of sandeel populations

For sandeel population variables, a similar modelling approach was used, but with TSB, SSB or recruitment as the response. These were assumed to follow a Gaussian distribution, so were fitted using linear models. Only SST and fishing mortality were considered as predictors, as population variables were derived from the same model. For recruitment (estimated for the end of June) lagged and unlagged variables were considered, but for TSB and SSB (estimated for 1 January), unlagged predictors were not considered, because they could not be influenced by conditions the following spring/summer. Only single predictor models were considered for sandeel variables, thus performance was indicated by comparing AICs to that from a null model.

3 | RESULTS

3.1 | Temporal trends

Breeding success declined significantly (Figure 2a; Table 1): from 1986 to 1990, it averaged ~1.2 chicks per pair, while in 2010–2014 it averaged ~0.8; success was particularly low in 1997, 2003 and 2004. SSB declined from an average > 500 000 tonnes from 1986 to 1990, to ~225 000 tonnes from 2010 to 2014 (Figure 2c), while TSB declined from an average of >1 million tonnes from 1986 to 1990, to <750 000 tonnes from 2010 to 2014 (Figure 2d). Spring SST increased from an average of ~9.7°C from 1986 to 1990, to 10.2°C from 2010 to 2014 (Figure 2h); winter SST showed no significant trend (Figure 2g). Recruitment, F1, and F2 showed no significant trends (Figure 2b, 2e, 2f), but fishing mortality peaked from the late 1990s to early 2000s.

3.2 | Breeding success: Single predictor models

Four variables performed better than the null model (Figure 3; Table 2). The best was $F1_{-2}$ (AIC = 347.60, R^2 = 22.3%, P = 0.002), showing that higher breeding success was associated with lower fishing mortality two years previously (Figure 3a). SSB performed similarly (AIC = 348.10, R^2 = 21.5%, P = 0.002), showing a positive association with breeding success (Figure 3b). SSB_{-2} (AIC = 351.58, R^2 = 15.4%, P = 0.026) and TSB (AIC = 352.13, R^2 = 12.4%, P = 0.037) also showed positive relationships with breeding success (Figure 3c, 3d) but AICs were larger. Of these, only the negative relationship with fishing mortality (AIC = −27.16, R^2 = 0.197, P = 0.018) continued to perform better than the null model after detrending (AIC = −23.00; Appendix S3). SSB continued to show a positive relationship that explained more variation (R^2 = 0.100) than all predictors except fishing mortality, but it no longer performed significantly better than the null model (AIC = −23.94). Hence, higher breeding success was associated with lower fishing mortality of age 1 fish and larger sandeel spawning stocks, although this latter relationship did not persist after detrending.

TABLE 1 Results from models testing for temporal trends in variables, showing slope estimate ± standard error, P-value and model R^2; year was entered into models after being centred and scaled

	Coefficient ± standard error	P-value	R^2
Breeding success	−0.314 ± 0.137	0.022	0.187
Recruitment	−0.130 ± 0.149	0.392	0.027
SSB	-0.030 ± 0.091	0.003	0.285
TSB	-0.277 ± 0.092	0.006	0.249
F1	0.011 ± 0.057	0.854	0.001
F2	-0.079 ± 0.689	0.263	0.046
Winter SST	0.147 ± 0.148	0.330	0.035
Spring SST	0.341 ± 0.150	0.031	0.161

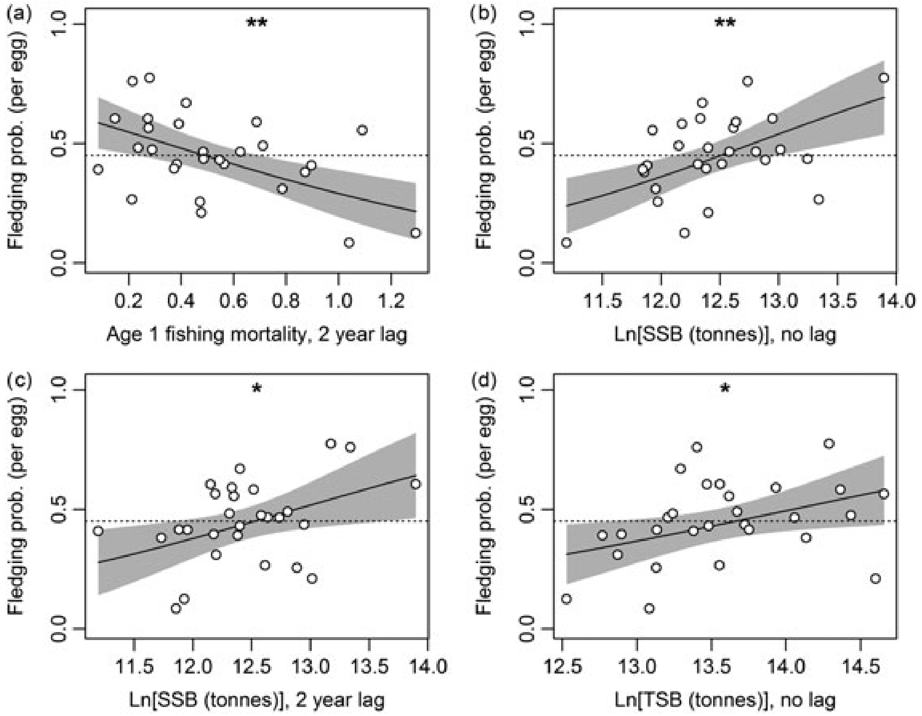

FIGURE 3 Relationships from models describing kittiwake breeding success as a function of (a) $F1_{-2}$, (b) SSB, (c) SSB_{-2} and (d) TSB, which all performed better than the null model. Open circles indicate data points; solid lines indicate fitted relationships; shading indicates 95% confidence intervals; dotted lines indicate mean response. Asterisks indicate *P*-values: *** indicates $P \le 0.001$, ** indicates $P \le 0.01$, * indicates $P \le 0.05$

TABLE 2 Results from GLMMs describing kittiwake breeding success as a function of sandeel population variables and SST. Table shows parameter estimate (± standard error), AIC value, allowing comparison among models, and R^2 value, indicating amount of variation explained by the model. Models with $\Delta AIC < -2$ relative to the null model are in bold. Models performing better than the null model after detrending are indicated with asterisks; full results from detrended analyses are presented in Appendix S3

	No lag	1 year lag	2 year lag
Recruitment	0.114 ± 0.150 AIC = 355.59 R^2 = 0.023	0.173 ± 0.146 AIC = 354.78 R^2 = 0.050	0.253 ± 0.142 AIC = 353.13 R^2 = 0.088
SSB	**0.407 ± 0.133 AIC = 348.10 R^2 = 0.215**	0.188 ± 0.145 AIC = 354.52 R^2 = 0.060	**0.318 ± 0.143 AIC = 351.58 R^2 = 0.154**
TSB	**0.289 ± 0.139 AIC = 352.13 R^2 = 0.124**	0.266 ± 0.142 AIC = 352.84 R^2 = 0.100	−0.013 ± 0.149 AIC = 356.15 R^2 = 0.001
F1	-0.065 ± 0.153 AIC = 355.98 R^2 = 0.001	−0.208 ± 0.156 AIC = 354.42 R^2 = 0.045	**−0.406 ± 0.129 AIC = 347.60* R^2 = 0.223**
F2	-0.014 ± 0.153 AIC = 356.15 R^2 = 0.001	−0.070 ± 0.159 AIC = 355.97 R^2 = 0.002	−0.238 ± 0.143 AIC = 353.51 R^2 = 0.059
Winter SST	−0.119 ± 0.148 AIC = 355.52 R^2 = 0.028	0.066 ± 0.149 AIC = 355.97 R^2 = 0.013	−0.117 ± 0.152 AIC = 355.57 R^2 = 0.017
Spring SST	−0.211 ± 0.144 AIC = 354.09 R^2 = 0.075	−0.089 ± 0.150 AIC = 355.81 R^2 = 0.006	−0.174 ± 0.147 AIC = 354.80 R^2 = 0.044

AIC of null model fitted with intercept only = 354.16

3.3 | Breeding success: multiple predictor models

Two multiple predictor models performed similarly (Table 3). In both, $F1_{-2}$ showed a negative effect, $recruitment_{-1}$ showed a positive effect and, against expectations, winter SST_{-1} showed a positive effect. In the top-ranked model, SSB showed a positive effect, while in the second-ranked model, $recruitment_{-2}$ showed a positive effect. After detrending, five models performed similarly (Appendix S3); all contained a negative effect of $F1_{-2}$ and a positive effect of winter SST_{-1}. Remaining variables were weakly significant or non-significant: two models contained a positive effect of $recruitment_{-2}$, two contained a positive effect of $recruitment_{-1}$, two contained a negative

TABLE 3 Results from top-ranked ($\Delta AIC \le 2$) models of kittiwake breeding success including multiple predictors. Table indicates parameter estimate ± standard error, *P* value from Wald test, R^2 and AIC. Null model AIC shown for comparison. Expanded model set shown in Appendix S3

$Recruitment_{-2}$	$F1_{-2}$	Winter SST_{-1}	$Recruitment_{-1}$	SSB	R^2	AIC	ΔAIC
	-0.293 ± 0.116 *P* = 0.012	0.340 ± 0.109 *P* = 0.002	0.263 ± 0.102 *P* = 0.010	0.438 ± 0.126 *P* < 0.001	0.532	338.69	0.00
0.353 ± 0.106 *P* = 0.001	−0.468 ± 0.106 *P* < 0.001	0.265 ± 0.106 *P* = 0.012	0.292 ± 0.106 *P* = 0.006		0.516	339.45	0.76
					–	354.16	15.47

effect of SSB$_{-1}$, one contained a positive effect of SSB, and one contained a negative effect of winter SST$_{-1}$.

Hence, models with multiple predictors showed negative effects of F1$_{-2}$ and, against expectations, a positive effect of winter SST$_{-1}$. Beyond this, there was evidence of positive effects of recruitment at both one and two year lags, and of a positive effect of unlagged SSB, but these relationships appeared sensitive to detrending.

3.4 | Drivers of sandeel stocks

For recruitment, the smallest AIC value was produced by a positive relationship with winter SST$_{-1}$, but this was not significantly better than the null model (AIC = 70.88, R^2 = 0.076, P = 0.147; Table 4). The best SSB model showed a negative relationship with spring SST$_{-2}$: higher SSBs occurred two years after cooler springs (AIC = 39.24, R^2 = 0.386, P < 0.001; Figure 4a). Negative relationships were also found with spring SST$_{-1}$, winter SST$_{-2}$, winter SST$_{-1}$, F1$_{-2}$ and F1$_{-1}$ (Figure 4b–4f; Table 4). After detrending, only the relationships with F1$_{-2}$, F1$_{-1}$, winter SST$_{-2}$ and spring SST$_{-2}$ remained; the lowest AIC was produced by F1$_{-1}$ (Appendix S3). TSB showed negative relationships with spring SST-$_{1}$ and winter SST$_{-1}$ (spring, Figure 5a, AIC = 46.35, R^2 = 0.207, P = 0.013; winter, Figure 5b, AIC = 48.44, R^2 = 0.148, P = 0.039), but after detrending, neither performed better than the null model (Appendix S3).

4 | DISCUSSION

Breeding success at the UK's largest kittiwake colony was higher in years with higher sandeel spawning stock biomass, and lower two years after high fishing mortality in the adjacent part of the North Sea. The SSB effect was sensitive to detrending and inclusion of other predictors, but the fishing mortality effect was robust to detrending and was present in all top-ranked multiple predictor models. SSB decreased at higher sea temperatures and following higher fishing mortality. Taken together, the relationships identified (summarized graphically in Figure 6) indicate that global and local pressures could influence North Sea sandeels and their dependent predators.

4.1 | Fisheries, sandeels and kittiwakes

Sandeel fisheries can negatively affect sandeel-dependent seabirds. On the Isle of May, kittiwake productivity declined when an industrial sandeel fishery was active locally (Frederiksen et al., 2004). More widely, North Sea seabird productivity is sensitive to the proportion of sandeels taken by fisheries (Cook et al., 2014). The negative correlation found in the present study provides first evidence of a link between the Dogger Bank fishery and seabirds in the southern North Sea. This may provide an early warning that kittiwake populations of eastern England are not isolated from effects of the fishery operating tens of kilometres from the coast.

High fishing mortality was associated with reduced SSB in each of the next two years, and lower kittiwake breeding success two years later. Higher SSBs were associated with higher kittiwake productivity, supporting previously-published relationships (Frederiksen et al., 2006; Furness, 2007). Hence, fishery impacts could occur via SSB depletion. However, the SSB effect deteriorated after detrending. Detrending reduces the risk of spurious correlations (Votier et al., 2008), so the SSB effect must be interpreted cautiously. However, detrending emphasizes interannual variation over longer-term trends (Byrd, Sydeman, Renner, & Minobe, 2008), and in complex ecological systems, such tight correlations may be unlikely (Wynn et al., 2008). Given established sandeel–kittiwake relationships and the conservative analytical approach, reduced breeding success may still be linked to reduced SSB. Indeed, even after detrending, SSB performed better than most other variables.

The fishing mortality relationship did not deteriorate after detrending, and was present in all top-ranked multiple predictor models, indicating a robust effect. The relationship showed a 2 year lag, suggesting a more complex link than direct, within-year competition. The lag may be due to the fishery focusing on age 1 and 2 sandeels: even under high fishing mortality kittiwakes could feed on the 0-group, and on the same cohort at age 1 the following year, thus buffering impacts. However, fishing mortality reduced SSB for at least two years, so impacts may only arise after this 'buffered' period. Alternatively, as North Sea sandeels show a positive recruitment–SSB relationship (van Deurs et al., 2009), the lag may occur owing to reduced

TABLE 4 Results from models describing sandeel recruitment, SSB and TSB as functions of SST and fishing mortality. Table shows parameter estimate (± standard error) AIC value and R^2. Models with ΔAIC < −2 relative to the null model are in bold. Models performing better than the null model after detrending indicated with asterisks; full detrended analyses presented in Appendix S3

Predictor		Response		
		Recruitment	SSB	TSB
F1	Unlagged	0.026 ± 0.520 AIC = 73.19 R^2 = 0.000	–	–
	1 year lag	0.078 ± 0.510 AIC = 73.16 R^2 = 0.001	**−0.963 ± 0.312 AIC = 44.62* R^2 = 0.261**	−0.460 ± 0.350 AIC = 52.51 R^2 = 0.019
	2 year lag	−0.261 ± 0.501 AIC = 72.90 R^2 = 0.010	**−0.915 ± 0.312 AIC = 45.38* R^2 = 0.242**	−0.395 ± 0.348 AIC = 51.72 R^2 = 0.046
F2	Unlagged	0.024 ± 0.412 AIC = 73.19 R^2 = 0.000	–	–
	1 year lag	−0.030 ± 0.413 AIC = 73.18 R^2 = 0.000	−0.488 ± 0.278 AIC = 50.27* R^2 = 0.102	−0.067 ± 0.292 AIC = 53.02 R^2 = 0.002
	2 year lag	−0.268 ± 0.515 AIC = 72.72 R^2 = 0.016	−0.306 ± 0.285 AIC = 52.19*R^2 = 0.041	−0.023 ± 0.289 AIC = 53.07 R^2 = 0.000
Winter SST	Unlagged	0.039 ± 0.193 AIC = 73.14 R^2 = 0.002	–	–
	1 year lag	0.278 ± 0.186 AIC = 70.88 R^2 = 0.076	**−0.278 ± 0.127 AIC = 48.62 R^2 = 0.152**	**−0.273 ± 0.126 AIC = 48.44 R^2 = 0.148**
	2 year lag	0.025 ± 0.193 AIC = 73.17 R^2 = 0.001	**−0.364 ± 0.118 AIC = 44.68* R^2 = 0.260**	−0.007 ± 0.137 AIC = 53.07 R^2 = 0.000
Spring SST	Unlagged	−0.080 ± 0.177 AIC = 72.97 R^2 = 0.008	–	–
	1 year lag	0.194 ± 0.174 AIC = 71.88 R^2 = 0.044	**−0.296 ± 0.113 AIC = 46.80 R^2 = 0.203**	**−0.297 ± 0.112 AIC = 46.35 R^2 = 0.207**
	2 year lag	−0.066 ± 0.178 AIC = 73.04 R^2 = 0.005	**−0.409 ± 0.099 AIC = 39.24* R^2 = 0.386**	−0.122 ± 0.124 AIC = 52.06 R^2 = 0.034
Null model		AIC = 71.19	AIC = 51.40	AIC = 51.07

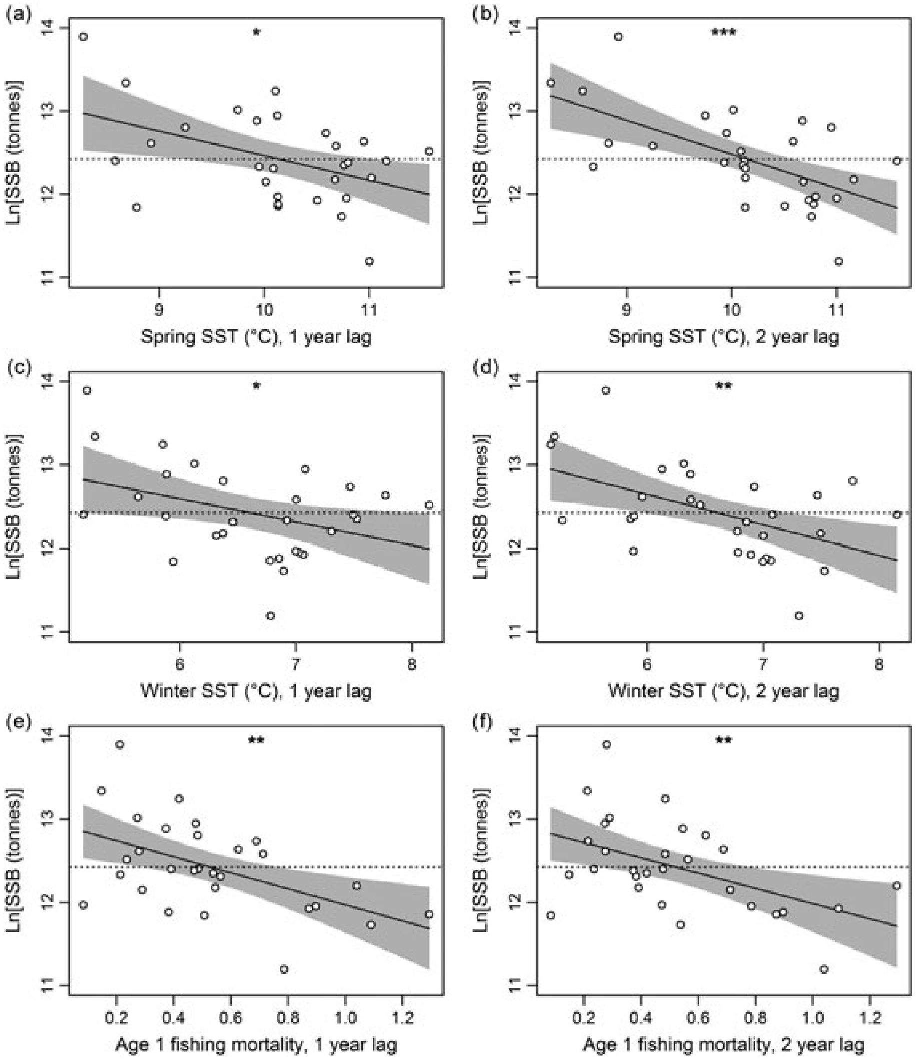

FIGURE 4 Relationships from models describing sandeel SSB as a function of (a) spring SST$_{-1}$, (b) spring SST$_{-2}$, (c) winter SST$_{-1}$, (d) winter SST$_{-2}$, (e) F1$_{-1}$, and (f) F1$_{-2}$, which all performed better than the null model. Open circles indicate data points; solid lines indicate fitted relationships; shading indicates 95% confidence intervals; dotted lines indicate mean response. Asterisks indicate *P*-values: *** indicates $P \le 0.001$, ** indicates $P \le 0.01$, * indicates $P \le 0.05$

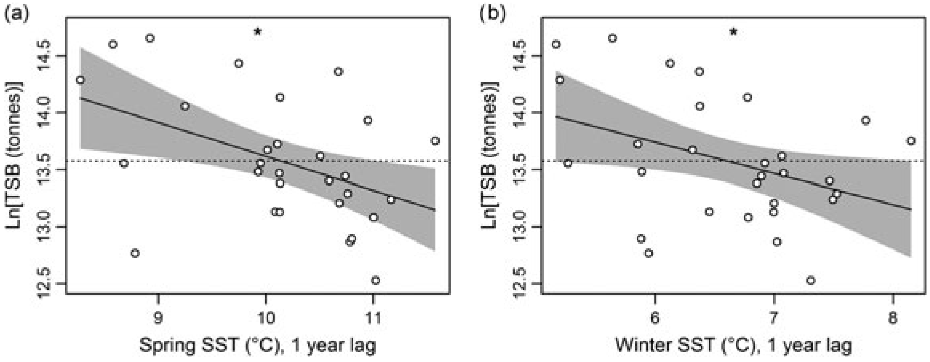

FIGURE 5 Relationships from models describing sandeel TSB as a function of (a) spring SST$_{-1}$ and (b) winter SST$_{-1}$, both of which performed better than the null model. Open circles indicate data points, solid lines indicate fitted relationships; shading indicates 95% confidence intervals; dotted lines indicate mean response. Asterisks indicate *P*-values: *** indicates $P \le 0.001$, ** indicates $P \le 0.01$, * indicates $P \le 0.05$

supply of young fish in subsequent years; this may be supported by the occurrence of a positive recruitment$_{-1}$ effect in top-ranked multiple predictor models.

Another possible explanation for the lagged response relates to spatial sandeel population dynamics. While the main Dogger Bank aggregations are within kittiwake foraging ranges, smaller aggregations

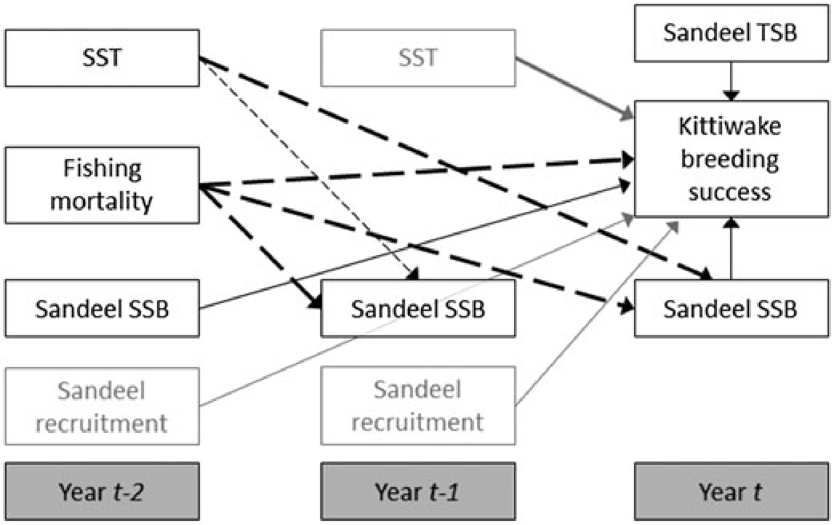

FIGURE 6 Graphical depiction of identified relationships. Black boxes and arrows indicate relationships shown in single-predictor models; grey boxes and arrows indicate relationships only found in multiple-predictor models. Arrow points from the predictor to the response. Solid arrows indicate positive relationships; dashed arrows indicate negative relationships. Thick arrows indicate relationships that remained significant after detrending; thin arrows indicate relationships that lost significance after detrending

close to shore could provide important foraging grounds because of reduced travel distances. However, these smaller aggregations may depend on the main Dogger Bank population. As populations decline, sandeel distributions contract into 'core' habitats, allowing fisheries to maintain catch rates even as peripheral populations decline strongly (Wright et al., 2000). Further, when biomass in core areas is high, larvae, and potentially even adults, could spill over, increasing abundance in (or repopulating) adjacent areas (Christensen, Mosegaard, & Jensen, 2009; Jensen et al., 2011; Wright, 1996). Hence, if Dogger Bank biomass is fished down, smaller aggregations nearer to the coast could become depleted over time, leading to reduced food availability and lagged impacts on seabirds.

Available data are insufficient to discriminate between possible mechanisms. Acquiring data on sandeel age structure, fine-scale sandeel population structure, and local seabird diet should therefore be a focus of future research. Even without clear mechanisms, the result adds to the weight of evidence (Cook et al., 2014; Frederiksen et al., 2004; Lewis et al., 2001; Rindorf et al., 2000) that sandeel fisheries can affect kittiwake food availability and, therefore, productivity.

4.2 | Environmental effects

Previous analyses have shown lower sandeel recruitment at higher temperatures, likely linked to changes to sandeels' copepod prey (Arnott & Ruxton, 2002; van Deurs et al., 2009). Here, higher SSTs did not affect recruitment, but were associated with lower SSB and TSB. Sandeels face greater metabolic costs at higher temperatures and under these conditions their prey may be less abundant (van Deurs, Koski, & Rindorf, 2014; van Deurs et al., 2011), leading to slower growth, reduced maturation, reduced reproductive investment, increased overwintering weight loss, and reduced survival (Heath et al., 2012; van Deurs, Jørgensen, & Fiksen, 2015; van Deurs et al., 2009; Wright, Orpwood, & Scott, 2017). However, whilst expected impacts of high temperatures on sandeels were observed, impacts on kittiwakes appeared more complex.

Impacts of high SSTs on kittiwake breeding success have been reported previously (Cook et al., 2014; Frederiksen et al., 2004; Wanless et al., 2007). Here, SST showed no relationship with breeding success in single predictor models. One explanation is that other oceanographic conditions, such as thermohaline stratification, may influence the focal colony more (Carroll et al., 2015). Indeed, a kittiwake colony in eastern Scotland has also shown limited SST effects (Eerkes-Medrano, Fryer, Cook, & Wright, 2017), indicating that SST may not always influence kittiwakes.

In multiple predictor models, however, winter SST_{-1} showed a positive effect. The effect was only significant when variables associated with increased sandeel availability were also included, so it may imply improved food availability, contrasting with previous findings. Mechanisms behind such a relationship are unclear, but the weak positive relationship observed between winter SST_{-1} and recruitment could provide some explanation. Indeed, under very low fishing pressure, there may be positive effects of warming for seabirds (Lynam et al., 2017). Alternatively, the effect may be spurious: multiple predictor models with a dataset of this size risk overfitting, so the effect may be describing minor fluctuations.

SST effects in this system appear more complex than anticipated. There is a clear negative impact of SST on sandeel biomass; given the likely importance of SSB to kittiwake breeding success, longer-term SST increases will probably harm sandeel-dependent predators. However, no negative SST effect was seen for kittiwake breeding success. Given that kittiwakes may not show a simple negative relationship with SST in all areas (Carroll et al., 2015; Eerkes-Medrano et al., 2017), further research on oceanographic influences on kittiwake food webs is required to understand the implications of rising temperatures under climate change.

4.3 | Conservation implications

Sandeel biomass has declined throughout the North Sea since the 1980s, and total catch has been much-reduced since 2003 (ICES, 2015). Large-scale ecosystem changes are partly responsible: rising temperatures may reduce recruitment and biomass (see above), and recovering predatory fish populations consume large numbers of forage fish such as sandeels (Furness, 2002; ICES, 2013; Reilly et al., 2014). However, rising temperatures cannot be easily controlled and fish stock recovery is a desirable change. Therefore, to conserve North

Sea sandeels and their dependent predators, closer consideration should be given to potential impacts of the targeted sandeel fishery.

Here, relationships between kittiwake productivity and fishing mortality were found, but results are essentially correlative. The first priority should therefore be to investigate possible mechanisms, which may, in turn, provide opportunities to alleviate any detrimental fishery impacts. Meanwhile, a more precautionary approach to management should be considered. There is a precedent for altering sandeel fishery management to mitigate predator impacts: the fishery off the east coast of Scotland was closed in 2000 in response to its impact on kittiwakes (Daunt et al., 2008; Greenstreet et al., 2010). For the Dogger Bank fishery, where possible impacts on kittiwakes are less well understood, it may be more appropriate to consider other management options.

Advice is currently provided to avoid fishing beyond sustainable levels, but the SA1 sandeel population remains below precautionary limits (ICES, 2015). Further, the stock may have been regularly fished beyond the 'one third [of unfished biomass] for the birds' rule (Cook et al., 2014; Cury et al., 2011). Hence, while management measures for the North Sea sandeel fishery have been strengthened in recent years (e.g. smaller management units, in-year stock assessment), further measures may be required. One option is to institute a spatial management plan, such as that used in the Norwegian exclusive economic zone (within SA3), whereby subareas within actively fished grounds are closed to prevent stock depletion (ICES, 2017). Another option would be to limit fishing mortality: relationships here suggest that when age-1 fishing mortality was below 0.5, kittiwake breeding success (Figure 2a) and SSB (Figure 3).were above their long-term averages. ICES (2015) have independently suggested fishing mortality limits of 0.4–0.6 for SA1, SA2 and SA3. While fishing mortality has declined from the high levels of 1999–2004, it has been >0.5 several years since then (ICES, 2015). To aid SSB recovery and account for the needs of predators, it may therefore be appropriate to limit fishing mortality to a maximum of 0.5.

Reducing fishing mortality in SA1 is unlikely to reverse widespread kittiwake declines. Key colonies in north and west Scotland have declined 50–90% since 2000 (JNCC, 2015), but there is limited sandeel fishing in these areas, and natural recruitment variability explains some sandeel declines (Poloczanska, Cook, Ruxton, & Wright, 2004). The negative impacts of SST on sandeel populations suggest that these colonies may continue to face food shortages as the climate warms. However, this makes conserving the Flamborough Head and Bempton Cliffs population more important still: it is the largest UK colony, and east coast populations are declining slower than northern colonies (JNCC, 2015), meaning that it represents a large, and increasing, proportion of the UK's kittiwakes. Given the proximity of fishing grounds to the coast (South et al., 2009), other kittiwake colonies in eastern England might also benefit from reduced sandeel fishing mortality, such as the small but growing colony in Lowestoft. Further, benefits may not be restricted to seabirds, as the fishery could affect commercially-important predatory fish populations (Engelhard et al., 2008, 2013). Hence, more precautionary management of the sandeel fishery may be necessary to conserve dependent predators and give the sandeel stock the best chance of recovering in the light of increasingly challenging environmental conditions.

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CONFLICT OF INTEREST

The authors declare no financial conflict of interest. However, we note that Professor Furness was an invited external expert on the ICES Benchmark Working Group on Sandeels; this was an unpaid position and represented a review group. We also note that the RSPB is an environmental NGO and a registered UK charity with a long-standing interest and engagement in promoting sustainable fisheries.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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