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Effects of a fishery closure and prey abundance on seabird diet and breeding success: Implications for strategic fisheries management and seabird conservation

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ABSTRACT

Industrial forage fish fisheries may reduce prey availability affecting diet and breeding success of marine predators. However, evidence for fisheries effects on predator demography remains rare, hindering evaluation of their impact on populations. Using 25 years of data on the commercial lesser sandeel fishery in the north-western North Sea, we evaluated the effectiveness of the closure in safeguarding breeding success of four seabird species - black-legged kittiwake, common guillemot, Atlantic puffin and razorbill. We also tested for effects of a scientific fishery in the closed area on breeding success. We quantified how changes in the diet of chicks for the four seabird species were influenced by the abundance of sandeels and the alternative prey species, European sprat, and the potential prey behavioural disturbance effects of sandeel fishing on the prey. Finally, we examined how changes in chick diet and prey abundance have shaped long-term variation in seabird breeding success. The period of fishery operation was associated with a decline in kittiwake breeding success in colonies with foraging ranges overlapping the closed area, from 52 % of young fledged pre-fishery to 23 % during fishery operation. Breeding success increased by approximately 10 % in the period following fishery closure to 2018. We document wide uncertainty around this increase in breeding success, partly driven by variation in the responses of individual colonies. For guillemot, razorbill and puffin we found no evidence for negative effects of the fishery on breeding success, nor for positive effects arising from its closure. We found no evidence for an impact on breeding success of the scientific fishery. The proportion of sandeel in chick diet was positively associated with breeding success in the four species, albeit with only weak evidence for puffin. Fishing effort was associated with a decreased proportion of sandeel in puffin diet, a lower proportion of the sandeel component of the diet consisting of 0-group in kittiwake, razorbill and puffin, and with decreased kittiwake breeding success. Our findings provide quantitative evidence for how forage fish fisheries may impact seabird demography, highlighting the species-specific nature of responses, and the difficulties in teasing apart drivers amongst ongoing environmental change. Time-area fisheries closures show promise as a tool for positively affecting productivity in some seabird species. However, we identify important caveats around its effectiveness for strategic seabird conservation and aspirations of net gain.

1. Introduction

Sustainable management of marine biodiversity requires an understanding of the ecological consequences of anthropogenic activities such as fishing on both target and non-target species. Marine predators such as seabirds are often used as ocean sentinels (Hazen et al., 2019), because their long lifespan, wide-ranging habitat use and position at the top of the food chain serves as an integrative measure of the health of lower trophic levels in bottom-up controlled systems (Frederiksen et al., 2006). Forage fish landings account for around one third of global

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landings of marine fish (Alder et al., 2008), and evidence indicates that the operation of industrial fisheries targeting forage fish (such as sandeel *Ammodytes* sp. and European sprat *Sprattus sprattus*) may reduce the availability of these important prey for seabirds (Croll and Tershy, 1998; Smith et al., 2011; Pikitch et al., 2014; Sydeman et al., 2017; Gremillet et al., 2018). These reductions may potentially affect seabird breeding success through impacts on foraging efficiency, diet, chick provisioning and parental care (Frederiksen et al., 2008, Bertrand et al., 2012, Pichegru et al., 2012, Sherley et al., 2015, Boyd et al., 2016, Sherley et al., 2018). Yet, quantitative evidence for impacts of fisheries activity on seabird demography is rare (Frederiksen et al., 2008; Sherley et al., 2015, 2018), meaning that the consequences of forage fisheries management on the abundance of seabirds remain poorly understood.

Opportunities to investigate the effect of fisheries activity and management on forage fish populations and seabird population dynamics are limited by the requirement for a large scale, quasi-experimental approach in which affected and unaffected seabird populations experiencing broadly similar environmental conditions may be used to test for effects (Sydeman et al., 2017). In the north-western North Sea, an industrial fishery for lesser sandeel (*Ammodytes marinus*) commenced in 1990 in a region encompassing the complex of sand banks off the Firth of Forth (Wee Bankie, Marr Bank, Scalp Bank and Berwick Bank; Dunn, 1998; Fig. 1). The fishery targeted sandeels aged 1 year and older, which are an important component of the diet in the early part of the breeding season of many seabird species foraging in the North Sea (Furness and Tasker, 2000; Wanless et al., 2018). The activity of this fishery (mainly April to July) coincided with the seabird breeding season, thereby potentially leading to direct competition. Due to

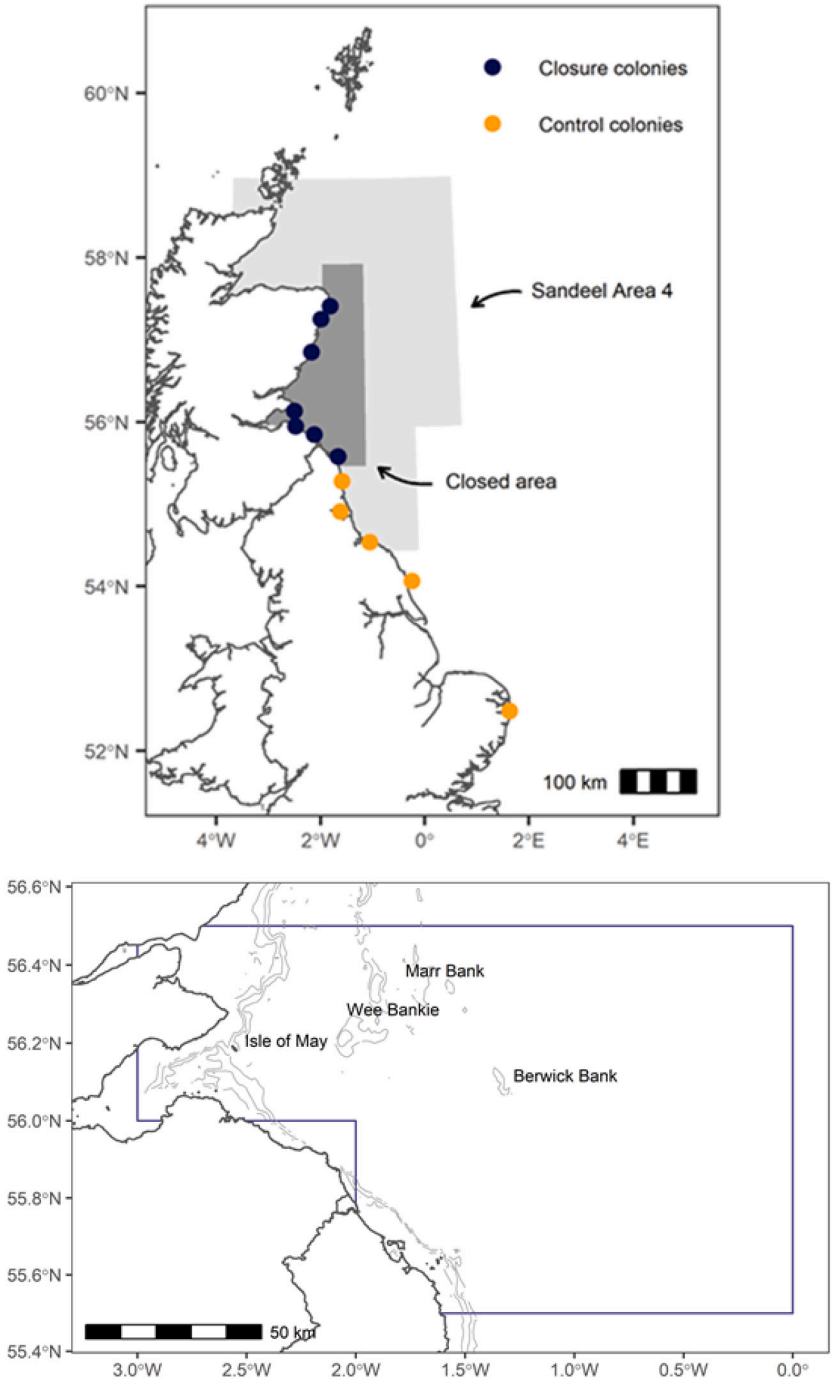

Fig. 1. Top panel: Location of kittiwake breeding colonies used to assess the impact of the sandeel fishery closure on breeding success. Blue dots represent breeding colonies within the 'closed' zone (assumed to be affected by fishery due to overlap with foraging ranges); yellow dots represent breeding colonies within the 'control' zone (assumed to be unaffected by the fishery due to non-overlap with foraging ranges, following Frederiksen et al., 2008). Sandeel closure area and ICES Sandeel Area 4 also shown. Colonies from North to South are: Buchan Ness to Collieston, Sands of Forvie, Fowlsheugh, Isle of May, Dunbar Coast, St Abbs Head, Farne Islands, Coquet Island, Gateshead, Saltburn Cliffs, Flamborough Head and Bempton Cliffs, and Lowestoft. Lower panel: Location of the Isle of May, the sandeel bank areas in the fishery closure zone (Wee Bankie, Scalp Bank, Marr Bank and Berwick Bank) and the five ICES squares (40E8, 40E9, 41E7, 41E8 and 41E9) used to derive fishing effort in the analysis on breeding season diet on the Isle of May (blue outline box). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

concern about negative impacts on top predators including seabirds, an area close to the UK coast was closed to large scale fishing in 2000 (covering approximately 21,000 km^2; EU, 2000; Fig. 1). However, a small annual scientific fishery was continued to obtain information needed for sandeel stock assessments. Initial studies suggested that the closure had been partially effective, with an increase in sandeel abundance and a limited recovery in breeding success of black-legged kittiwakes (*Rissa tridactyla*, hereafter 'kittiwake'), the seabird species that had shown marked reductions in breeding success while the fishery was in operation (Greenstreet et al., 2006; Frederiksen et al., 2008; Daunt et al., 2008). However, subsequent work by Greenstreet et al. (2010) suggested that recoveries in sandeel abundance and kittiwake numbers at sea may have been short-lived. This fishery closure has now been in place for over two decades, yet no comprehensive assessment of the long-term impact of closure on breeding success of kittiwakes and other seabirds breeding in the region has been made since the initial studies, which were based on only six years of data post-closure (Frederiksen et al., 2008; Daunt et al., 2008).

We applied a series of analyses to assess how the fishery closure, measures of prey abundance and fishing effort have influenced the diet and breeding success of kittiwake and three auks: common guillemot *Uria aalge* (hereafter 'guillemot'), Atlantic puffin *Fratercula arctica* (hereafter 'puffin') and razorbill *Alca torda*. Together, these four species comprise a major component of seabird breeding biomass in the North Sea (approximately 40 % based on Seabird 2000 census, Mitchell et al., 2004), with two species (kittiwake and puffin) on the UK's 'red-list' of Birds of Conservation Concern (Stanbury et al., 2021).The response of each species was predicted to vary according to 1) their foraging method, with the pursuit-diving auks expected to be better buffered than the surface-feeding kittiwake. and 2) the importance of sandeel in chick diet, broadly ranked from high to low in kittiwake, puffin, razorbill and guillemot, as derived from intensive studies on the Isle of May National Nature Reserve situated within closure area (Wanless et al., 2018).

We interrogated 20 years of post-closure data for this forage fishery-seabird system to assess the long-term effectiveness of the sandeel fishery closure in safeguarding seabird breeding success. We used both a regional, and single colony-based approach to leverage inference from broader scale comparisons of populations within and outside the closed area, as well as from more detailed, long-term observations of seabird diet and breeding success in populations at a single colony. First, we assessed whether the opening of the fishery and its later closure affected the breeding success of four seabird species breeding on the Isle of May, where a long-term study of seabird populations allows for analyses of potential effects on seabird diet and breeding success. We then quantified if the fishery closure has been effective in halting or reversing the observed decline in regional kittiwake breeding success, using a multi-colony Before-After-Control-Impact (BACI) design, advancing the earlier analysis undertaken by Frederiksen et al. (2008) with a further 16 years of post-fishery closure data. We tested for local effects of the sandeel fishery removals that have continued in the closed area since 2000 through the operation of a scientific fishery on breeding success of the four study species from data from the Isle of May (Wright et al., 2002). We focused on this colony because these birds intensively use the closed area when foraging (Harris et al., 2012; Wakefield et al., 2017), and are therefore likely to be most affected by continued fishing in the closed area. We predicted that kittiwake would be more strongly affected than the three auk species because of its greater dependence on sandeels and inability to dive (Furness and Tasker, 2000; Wanless et al., 2018), in keeping with early studies of the closure that only found an effect of the fishery closure in this species (Frederiksen et al., 2008; Daunt et al., 2008). We then quantified the potential mechanisms driving relationships between fishery management, prey abundance and seabird demography, using detailed data from the Isle of May. We quantified how observed changes in diet, notably, a progressive decline in proportion of sandeel (particularly 1+ sandeels, which are those targeted by the fishery; Rindorf et al., 2000) in chick diet in three of the four seabirds (excluding puffin; Wanless et al., 2018), has been influenced by the abundance of sandeel and the main alternative prey, European sprat (hereafter sprat). We also tested for the potential disturbance effect of sandeel fishery activity in this relationship. Fishing activities may affect seabirds through behavioural disturbance of fish populations as opposed to depletion, because when disturbed, fish may move to different locations or deeper depths (Robertis and Handegard, 2013), potentially becoming less available to seabirds. Finally, we examined how observed changes in chick diet and prey abundance have shaped long-term variation in seabird breeding success. Specifically, we tested (i) the effect of chick diet on local breeding success of the four species on the Isle of May, and (ii) how regional multi-colony (Supplementary Fig. 1) breeding success in the four seabird species was affected by sandeel abundance, sprat abundance and fishing activity. We discuss our results within the wider context of fisheries management as a tool for seabird conservation.

2. Methods

2.1. Fishery data

In this region, sandeel are targeted by a highly seasonal industrial fishery that has progressively shifted towards fewer larger vessels since 2004 (ICES, 2021). Catches consist almost entirely of age 1+ fish (99.2 % of the caught biomass on average in the area), About90% of the fishery activity occurs between April 1st and July 8th (ICES, 2021), which overlaps with the breeding season for all four species of seabirds studies in the region, broadly occurring between April and July (guillemot and razorbill), or April and August (kittiwake and puffin).Sandeels are targeted using small-mesh (<16 mm) demersal trawl gear. The closure zone for sandeel fishing extends from 55$^{\text{o}}$30 N to 58$^{\text{o}}$ N, and from 1$^{\text{o}}$ W to the coast of the United Kingdom (Fig. 1). We collated data on young of the year sandeel ('0-group'; number in millions), one year old sandeel ('1-group'; biomass in tonnes), and one year old sprat ('1-group'; biomass in tonnes). These age classes of sandeel and sprat are common in the diet of chicks in the four species in this study (e.g., Wanless et al., 2018). All sandeel abundance data were obtained from Sandeel Area 4 (SA4; Table 1, Fig. 1). Data on 1-group sprat were derived from the sprat survey area off the northeast coast of Scotland, concentrated around the Firth of Forth. We also included a measure of sandeel fishing effort (Table 1; Figs. S2 & S3). Note that there is currently no specific fishery for sprat in this area of the North Sea. Within the sandeel closure area a limited fishery for stock monitoring purposes occurs in May–June (ICES, 2021). This scientific fishery reported mean annual catches of around 1691 t (SD = 2131 t) during the closure period.

2.2. Seabird diet data

Diet data were collected on the Isle of May, Firth of Forth, southeast Scotland (56° 11′ N, 2° 33′ W). Diet data were collected throughout the chick-rearing period for kittiwake, guillemot, puffin and razorbill from 1993 to 2018 (the temporal period matching available prey data; see Wanless et al., 2018). Briefly, puffin diet was assessed through captures of adults carrying bill loads of fish destined for chicks, visual observations of fish brought back by adults for chicks were used for guillemots and razorbills and kittiwake diet was sampled from regurgitates from chicks or adults with chicks. A full methodology can be found in Wanless et al. (2018). The primary aim of our analysis was to investigate how the importance of sandeels relative to other prey types in the chick diet is influenced by measures of prey abundance and fishing effort. Therefore, the prey in the diet were grouped as 0-group and 1+ group (aged one year and older) sandeels (all those identified to species were almost entirely *Ammodytes marinus*), Clupeidae (mainly sprats *Sprattus* with in some years a small proportion of small herring *Clupea harengus*) and other species (mainly cod-fishes *Gadidae* and rockling *Lotidae*, Wanless et al., 2018). For each seabird species and year, diet was expressed as the

Table 1
Description of data used in analyses of seabird breeding success and diet. All data were from the time period 1993 to 2018.

Data name	Description	Spatial area
Sandeel 0-group	Number of 0-group sandeel (millions) becoming available to seabirds during the breeding season	Sandeel Area 4 (SA4; Fig. 1); Source: (ICES, 2021)
Sandeel 1-group	Biomass of 1-group sandeel (tonnes) becoming available to seabirds during the breeding season	Sandeel Area 4 (SA4; Fig. 1); Source: (ICES, 2021)
Sprat 1-group	Biomass of 1-group sprat (tonnes) from the sprat survey area off the northeast coast of Scotland, concentrated around the Firth of Forth.	Sprat survey area in Firth of Forth, Scotland (Fig. 1); Source: derived from ICES coordinated surveys
Fishing effort	Days fishing (for a standard 200 GT vessel) corrected for differences in vessel size using the approach of ICES (2022a).	Sandeel Area 4 (SA4; Fig. 1); Source: (ICES, 2021) Five ICES squares covering Firth of Forth region (40E8, 40E9, 41E7, 41E8 and 41E9; Supplementary Material Fig. 1)
Scientific fishery mortality	The total fishing mortality in SA4 multiplied by the proportion of SA4 landings that occurred in the closed area.	Portion of Sandeel Area 4 closed to sandeel fishing (see Fig. 1)
Proportion of sandeel in breeding season diet	Proportion by mass of each prey group in the diet after pooling annual samples following Harris & Hislop 1978, Lewis et al., 2003, Howells et al., 2017	Isle of May
Proportion of the sandeel component in the breeding season diet comprising of sandeel 0-group	Derived from proportion by mass of each prey group in the diet after pooling annual samples following Harris & Hislop 1978, Lewis et al., 2003, Howells et al., 2017	Isle of May
Regional seabird breeding success for Analysis 7	Annual colony-level seabird breeding success data, derived primarily from the SMP and augmented by breeding success data for kittiwakes, guillemots, razorbills and puffin for the Isle of May (Newell et al., 2016; updated)	Data on breeding success for colonies within the broad regulatory zones for which relevant prey data were available, Sandeel Area 4 and ICES area IVb (Supplementary Material Fig. 1)
Kittiwake breeding success for Analysis 2 (BACI)	Annual colony-level seabird breeding success data, derived primarily from the SMP and augmented by breeding success data for kittiwakes for the Isle of May (Newell et al., 2016; updated)	All regularly monitored colonies (Seabird Monitoring Programme, SMP) in the closure zone as well as in a control zone extending from 52° N to 55°30, following Frederiksen et al. (2008); Fig. 1
IoM breeding success data for analyses 1, 3, and 6	Annual colony-level breeding success data for kittiwakes, guillemots, razorbills, and puffin for the Isle of May (Newell et al., 2016; updated)	Isle of May
Sea surface temperature (SST)	Marine Scotland Science Scottish Shelf model (Barton et al., 2021)	Gridded SST data were translated into a weighted mean for each colony (following Carroll et al., 2015; Searle et al., 2022)

proportion by mass of each prey group in the diet after pooling annual samples, using species-specific otolith length to fish length and fish length to mass relationships (Harris & Hislop 1978, Lewis et al., 2003, Howells et al., 2017).

2.3. Seabird breeding success data

We used data on kittiwake breeding success from all regularly monitored colonies (Seabird Monitoring Programme, SMP; https://app.bto.org/seabirds/public/index.jsp) in the closure zone as well as in a control zone extending from 52° N to 55°30 N, following Frederiksen et al. (2008) (Fig. 1). The closure and control zones largely correspond to two sandeel aggregations identified in the North Sea (Proctor et al., 1998, Frederiksen et al., 2005; Jensen et al., 2011; Langton et al., 2021). In our regional analysis of drivers of breeding success in kittiwake, guillemot, razorbill and puffin, we selected data on breeding success for colonies within the broad regulatory zones for which relevant prey data were available, Sandeel Area 4 and ICES area IVb (Table 1, Supplementary Material Fig. 1). We excluded seabird colonies with fewer than nine years of breeding success data from 1986 to 2018 (i.e., <25 % coverage of the time period; Table S1). In all analyses, breeding success corresponded to the proportion of chicks fledged per egg laid, assuming a clutch size of one for all species except kittiwake, where we assumed a clutch size of two. Thus, a breeding success of 100 % would mean that every observed breeding pair of guillemots, puffins and razorbills produced one chick, and every kittiwake pair produced two chicks.

2.4. Environmental data

Sea surface temperature data (SST) were derived from the Marine Scotland Science Scottish Shelf model (Barton et al., 2021). Monthly means were averaged over the breeding season for each species to provide a single metric for each colony (puffin and kittiwake: April – August; guillemot and razorbill: April–July). Gridded SST data were translated into a weighted mean for each colony (following Carroll et al., 2015; Searle et al., 2022). We based the weights upon a simple distance-decay rule that allocated more weight to locations close to the colony of the form

$$w \propto exp(-\lambda d)$$

where d represents the distance by sea from the grid cell midpoint to the colony, and λ represents the decay rate. The decay rate λ for each species was the value where 95 % of all weights would, in an area of sea without land, be allocated to locations within the published mean-max foraging range (kittiwake: 60.0 km, guillemot: 84.2 km, puffin: 105.4 km, razorbill: 48.5 km; see Thaxter et al., 2012). Although there is colony specific tracking data for some of the species and colonies used in our analysis, such local data are not available in all years or for all colonies. We therefore chose to use the mean-max foraging ranges from Thaxter et al. (2012) as these represent potential variability across colonies and years within a species. We then set the weights equal to zero for locations beyond the mean-max foraging range and rescaled so that the weights summed to one by dividing each weight by the sum of the weights across all grid cells. This rescaling step was used because the weights were used to solely provide information on the relative importance of each grid cell.

2.5. Statistical models

We ran a series of analyses to test: a) the effectiveness of the sandeel fishery closure in safeguarding the breeding success of kittiwake, guillemot, razorbill and puffin on the Isle of May (Analysis 1), and regional kittiwake breeding success (Analysis 2); b) the impact of the scientific fishery within the fishery closure zone on the breeding success of all species on the Isle of May (Analysis 3); c) the drivers of chick diet in all species on the Isle of May (Analyses 4 & 5); and d) the drivers of breeding success of all species on the Isle of May (Analysis 6), and the wider region (Analysis 7; Table 2; Fig. 1).

2.5.1. Analysis of sandeel fishery closure impact on breeding success

We first quantified how the opening, and subsequent closure, of the sandeel fishery was related to the breeding success of kittiwake, guillemot, razorbill and puffin, using data from the Isle of May in species specific models (Analysis 1, Table 3). Such a single-colony analysis allows us to evaluate species-specific responses more robustly by focusing on populations of each species breeding in the same location, experiencing similar environmental conditions, albeit hindering extrapolation to species level inference. We split annual breeding success data for each species into three periods: (i) before the opening of the fishery (1986–1990; 'before'), (ii) during the fishery (1991–1998; 'during'), and (iii) after the fishery when the closure was imposed (1999–2021; 'after'). As in Frederiksen et al. (2008), we defined the 'during' period as 1991–1998 because sandeel fishery effort and landings in the closed area were very low in 1990 and 1999 and thus more comparable to the scientific fishery from 2000 onwards (Rindorf et al., 2000, Frederiksen et al., 2004, Greenstreet et al., 2006).

Table 2
Summary of the seven main analyses used to examine effects of the sandeel fishery closure and prey metrics on the diet and breeding success of kittiwake, guillemot, razorbill and puffin.

Analysis	Response variable	Species	Colonies	Period
Analysis 1: effect of fishery operation on seabird breeding success	Breeding success	Kittiwake, guillemot, razorbill, puffin	Isle of May	Before, During, After
Analysis 2: BACI analysis of fishery operation on kittiwake breeding success	Breeding success	Kittiwake	Regional	Before, During, After
Analysis 3: impact of scientific fishery on seabird breeding success	Breeding success	Kittiwake, guillemot, razorbill, puffin	Isle of May	1999–2018
Analysis 4: effect of prey abundance on proportion of sandeel in seabird breeding season diet	Proportion of sandeel in diet	Kittiwake, guillemot, razorbill, puffin	Isle of May	1993–2018
Analysis 5: effect of prey abundance on composition of sandeel component of seabird breeding season diet	Proportion of the sandeel component of diet made up of 0-group	Kittiwake, guillemot, razorbill, puffin	Isle of May	1993–2018
Analysis 6: effect of diet on seabird breeding success	Breeding success	Kittiwake, guillemot, razorbill, puffin	Isle of May	1993–2018
Analysis 7: effect of prey abundance and fishing effort on seabird breeding success	Breeding success	Kittiwake, guillemot, razorbill, puffin	Regional	1993–2018

Second, due to availability of data for kittiwakes from multiple colonies, we employed a BACI design to investigate whether the operation of the commercial sandeel fishery between 1991 and 1998 influenced kittiwake breeding success more widely (Analysis 2, Table 3). Following Frederiksen et al. (2008), we grouped kittiwake breeding colonies into 'closure' and 'control' zones, giving seven colonies within the 'closure' zone (which were assumed to be affected by the fishery due to overlap with kittiwake foraging ranges), and five within the 'control' zone (likely to be unaffected by the fishery due to non-overlap with foraging ranges; Fig. 1 and Table S2). Annual breeding success data from 'closure' and 'control' colonies were split into the three fishery periods, as above. In the first model (Model 2a, Table 3), we considered only main effects of the zone a colony belonged to and the period for the year of observation. In the second model (Model 2b, Table 3), we also included the interaction between zone and period to test whether differences in breeding success between the periods differed between zones.

2.5.2. Impact of scientific fishery on breeding success

We examined if the scientific sandeel fishery in the closed area from 1999 to 2018 affected breeding success of the four study species on the Isle of May (Analysis 3, Table 3). We focused on the Isle of May because data are available for all four species, and their foraging ranges fall within the closed area (Harris et al., 2012; Wakefield et al., 2017). To capture the effect of fishery landings in the closed area, we multiplied the total fishing mortality in SA4 by the proportion of SA4 landings that occurred in the closed area. We also included fixed effects for sandeel 0-group abundance, sandeel 1-group abundance, and mean SST in the breeding season foraging range of each species, and random effects for species, year and observation to account for overdispersion, assuming binomial errors (Table 3).

2.5.3. Drivers of diet composition on the Isle of May

We assessed evidence for the influence of both absolute abundance of sandeel and sprat on the proportion of sandeel in chick diet and the relative abundance (ratio) of sandeel to sprat (Analysis 4, Table 3). The use of this ratio (Models 4d and 4e, Table 3) means that ideally the two prey abundance metrics should be measured over similar spatial scales. Whilst the sandeel metrics are derived from a larger spatial area (SA4) compared to the sprat metric (sprat survey area around Firth of Forth), the use of the metric within the model coupled with a slope coefficient allows for scaling of the relative abundances within the model.

We also examined how the total and relative abundances of sandeel 0-group and sandeel 1-group influenced the proportion of the sandeel component (all ages) in chick diet made up of sandeel 0-group (Analysis 5, Table 3). All models included fishing effort in the five ICES squares as a proxy for the disturbance effect of the fishery (e.g., Frederiksen et al., 2008; Table 1).

2.5.4. Drivers of breeding success

We hypothesized that breeding success was related to a range of annual, colony-specific prey abundance, fishery activity and environmental variables, and constructed separate models for each of the four seabird species (Table 3). The first analysis (Analysis 6, Table 3) focused on Isle of May breeding success because this allowed for a more detailed examination of the effect of chick diet. These models included the proportion of sandeel in chick diet as a fixed effect. In the second, regional analysis (Analysis 7, Table 3), we considered breeding success of the four species at 11 colonies (Fig. S1; see Table S1 for data availability per species/colony). We fitted models to assess the influence of sandeel 0-group and 1-group abundance, sprat abundance and fishery activity on breeding success (Table 3). All models included mean SST within

Table 3
Description of statistical models used in analyses of seabird breeding success and diet.

Analysis and model	Response variable	Distribution of response	Fixed and (random) effects	Methods used to implement models
Analysis 1: Effect of fishery operation on seabird breeding success	Breeding success	Binomial	Period	Species-specific GLMs, assuming quasi-binomial errors to account for overdispersion. QAICc to select between alternative models (MuMIn package version 1.46.0; Barton, 2022)
Analysis 2: BACI analysis of fishery operation on kittiwake breeding success	Breeding success	Binomial	Model 2a: Period, Zone, (Zone: Colony), (Period:Year), (Observation) Model 2b: Period, Zone, Period*Zone, (Zone:Colony), (Period:Year), (Observation)	Both models included year nested within period, and site nested within zone as random effects, as well as an observation level effect to account for overdispersion (using 'lme4' package version 1.1–27.1). Pairwise comparisons between different time periods used the 'emmeans' function (emmeans package version 1.7.2; Lenth, 2022).
Analysis 3: impact of scientific fishery on seabird breeding success	Breeding success	Binomial	Amount of total fishery mortality in closure area, SST, sandeel 0-group, sandeel 1-group, (Species), (Year), (Observation)	
Analysis 4: effect of prey abundance on proportion of sandeel in seabird breeding season diet	Proportion of sandeel in diet	Beta	Model 4a: sandeel 0-group + Effort Model 4b: sandeel 1-group + Effort Model 4c: Sprat 1-group + Effort Model 4d: ratio of sandeel 0-group to sprat 1-group + Effort Model 4e: ratio of sandeel 1-group to sprat 1-group + Effort	All models were run using the 'betareg' package (Cribari-Neto and Zeileis, 2010), assuming errors followed a beta distribution with logit link. AICc was used to assess support in the data. We extracted pseudo R^2 from model outputs.
Analysis 5: effect of prey abundance on composition of sandeel component of seabird breeding season diet	Proportion of the sandeel component of diet made up of 0-group	Beta	Model 5a: sandeel 0-group + Effort Model 5b: sandeel 1-group + Effort Model 5c: ratio of sandeel 0-group to sandeel 1-group + Effort	All models were run using the 'betareg' package (Cribari-Neto and Zeileis, 2010), assuming errors followed a beta distribution with logit link. AICc was used to assess support in the data. We extracted pseudo R^2 from model outputs.
Analysis 6: effect of diet on seabird breeding success	Breeding success	Binomial	Expected proportion of sandeel in breeding season diet	GLM assuming quasi-binomial error distribution due to overdispersion. QAICc was used to assess support in the data. The variance explained by each model was calculated using the 'rsq' function (rsq package; Zhang, 2021).
Analysis 7: effect of prey abundance and fishing effort on seabird breeding success	Breeding success	Binomial	Sandeel 0-group, sandeel 1-group, sprat 1-group, fishery effort, SST, (Colony), (Year), (Observation)	GLMMs fitted using 'lme4' package version 1.1–27.1). We included as observation-level random effect to account for overdispersion.

species-specific breeding season foraging areas as a fixed effect to account for ongoing environmental change in the region (Heath et al., 2009), and an observation level random effect to account for overdispersion (Table 3).

2.6. Technical details of statistical modelling and inference

Breeding success (Analyses 1, 2, 3, 6 and 7; Tables 1 & 3) was assumed to have a binomial distribution, with the numerator (i.e., successes) corresponding to the number of fledglings and the denominator (i.e., the number of trials) defined as the number of breeding pairs sampled at each colony multiplied by modal brood size for each species. All species have a clutch size of one, except kittiwake, which was assumed to have a modal clutch size of two (although this species infrequently has clutch sizes of three, we use an upper bound of two in line with previous studies; e.g., Carroll et al., 2017). Regional models of breeding success (Analyses 2, 3 and 7) were fitted as generalized linear mixed models (GLMMs), using 'lme4' package version 1.1–27.1, with "colony" and "year" as random effects to account for the spatial and temporal variation in breeding success unrelated to the explanatory variables, and an observation-level random effect to account for overdispersion. Models of breeding success at the Isle of May alone (Analysis 1, Analysis 6) were fitted as quasi-binomial generalized linear models (GLMs), with the quasi-binomial error distribution used due to overdispersion. Response variables relating to diet (Analyses 4 and 5) were assumed to have a beta distribution, because they are proportions, and were run using beta regression, via the 'betareg' package (Cribari-Neto and Zeileis, 2010). Logit link functions were used for all analyses.

The relative support for models within analyses was assessed using either Akaike's Information Criterion for small sample sizes (AICc) or, for Analyses 1 and 6, a corresponding metric (QAICc) that adjusts for the use of the quasi-likelihood in fitting the models. The variance explained by each model was calculated using the 'rsq' function (rsq package; Zhang, 2021) for Analysis 6, and the 'r.squaredGLMM' function (MuMIn package; Barton, 2022) (other analyses). In Analysis 2 we used the 'emmeans' function (emmeans package version 1.7.2; Lenth, 2022) to make pairwise comparisons between the different time-periods. Note that confidence intervals derived for effects using emmeans do not integrate over random effects.

3. Results

The first part of our analyses assessed the effectiveness of the sandeel fishery closure in safeguarding the breeding success of kittiwake, guillemot, razorbill and puffin on the Isle of May (Analysis 1), and regional kittiwake breeding success (Analysis 2), and the impact of the scientific fishery within the fishery closure zone on the breeding success of kittiwake, guillemot, razorbill and puffin on the IOM (Analysis 3).

3.1. Effectiveness of sandeel fishery closure

On the Isle of May, evidence for effects of the opening and subsequent closure of the sandeel fishery on breeding success differed between species (Analysis 1). In guillemot, razorbill and puffin, we found no evidence for a reduction in breeding success when the sandeel fishery was active relative to the period prior to its opening, whilst for kittiwake we found a significant negative effect of fishery operation and a corresponding 28 % reduction in breeding success (Table 4). For guillemot, razorbill and puffin, there was significantly lower breeding success after fishery closure, indicating that closure of the fishery did not benefit breeding success in these species (Table 4). In contrast, for kittiwake we found a 17 % increase in breeding success in the two decades post-

Table 4

Estimates of changes in breeding success between the pre-fishery period ('before' – reference level), the period when the sandeel fishery was active ('during'), and the period of the closure ('after'). Shown are estimates from single-species analyses for four species breeding on the Isle of May.

Term	Guillemot		Puffin		Razorbill		Kittiwake	
	Est (SE)	P	Est (SE)	P	Est (SE)	P	Est (SE)	P
Intercept	1.38 (0.20)	<0.001	1.57 (0.19)	<0.001	0.85 (0.15)	<0.001	−0.23 (0.28)	0.40
Period (during)	−0.02 (0.28)	0.94	−0.33 (0.27)	0.22	−0.10 (0.19)	0.62	−1.39 (0.42)	0.002
Period (after)	−0.67 (0.22)	0.004	−0.75 (0.22)	0.001	−0.53 (0.16)	0.002	−0.43 (0.33)	0.20

closure (Fig. 2).

In the regional BACI analysis of kittiwake breeding success (Analysis 2), the model featuring an interaction between zone and period was better supported than the model that only included main effects of these terms (reduction in AICc of 10.5), indicating that the 'closure' and 'control' zones differed in how their average breeding success changed between time periods. The most pronounced pattern of temporal change between control and closure zones was from the 'before' fishery to the

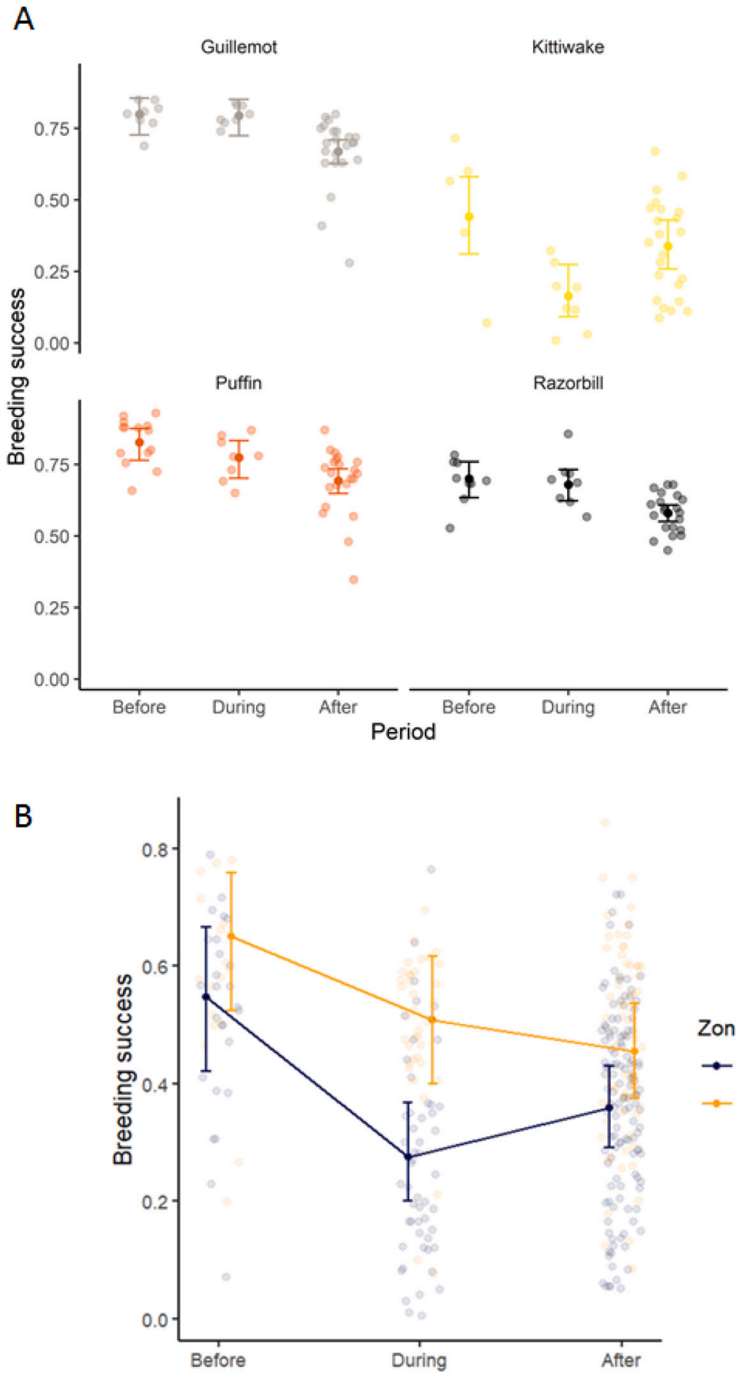

Fig. 2. A. Changes in breeding success (proportion fledged) for four seabird species breeding on the Isle of May, shown for three time periods defined as those years prior to operation of the sandeel fishery (Before), years in which the sandeel fishery operated (During), and years after the closure of the fishery (After). Error bars represent 95 % confidence intervals. Annual breeding success at individual colonies in each period are shown by filled circles in the background. B. Changes in kittiwake breeding success (proportion fledged) in colonies where foraging range overlaps with the sandeel fishery closed area (blue symbols, 'Closure'), and in those colonies whose foraging ranges lie outside of the closed area (yellow symbols, 'Control'). Breeding success is shown in three time periods, Before, During, and After. Error bars represent 95 % confidence intervals. Annual breeding success at individual colonies within Closure (pale blue) and Control (pale yellow) groups are shown by filled circles in the background. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

'during' fishery periods (Fig. 2). For colonies in the 'control' zone, although average breeding success declined, there was no statistically significant difference in breeding success between the 'before' fishery and 'during' fishery periods (pairwise comparison of before – during; est.: 0.51, SE: 0.31, P: 0.23). However, for those colonies in the 'closure' zone, breeding success significantly reduced from 52 % in the 'before' fishery period to 23 % in the 'during' fishery period (pairwise comparison of before – during; est.: 1.27, SE: 0.29, $P < 0.001$; note that a breeding success of 100 % would mean that every observed breeding pair produced two chicks).

In terms of effectiveness of the closure of the sandeel fishery (Analysis 2), a small increase (10 percentage points, 95 % CI: 2–18 percentage points) in kittiwake breeding success for colonies within the closure zone occurred in the 'after' fishery period (Fig. 2), a change that was statistically significant (pairwise comparison during-after; est.: -0.52, SE: 0.21, P: 0.03). In contrast, breeding success in control colonies exhibited a slight, non-significant decline over the same period. Importantly, breeding success at colonies in the 'closure' zone after the fishery was closed was still significantly lower than that recorded prior to the fishery opening (Fig. 2; pairwise comparison before – after; est.: 0.75, SE: 0.26, P: 0.009), despite two decades having elapsed since the onset of the fishery closure. Furthermore, there was considerable variation between colonies in changes in breeding success from the 'during' to the 'after' period (range of −4 % to +25 % in the closure zone; Table S3), with two colonies showing a continued decline in breeding success (Dunbar Coast and Farne Islands; Table S3). Fixed effects in both models (Model 2a: main effects of 'zone' and 'period'; Model 2b: main effects plus interaction for 'zone' and 'period') explained around 20 % of the variation in the data (model with interaction - conditional R^2: 0.99, marginal R^2: 0.23; Table S4).

3.2. *Impact of scientific fishery on seabird breeding success on the Isle of May*

We found little evidence for an effect of the fishing mortality occurring due to the scientific sandeel fishery within the closed area on the breeding success of the four species on the Isle of May (Analysis 3). Although our model indicated that breeding success was reduced when the fishing mortality due to the scientific fishery was greater, this relationship was not statistically significant (est: -0.099, SE: 0.097, z: -1.023, P: 0.307). The model included no strong evidence for an effect of sandeel 0-group or 1-group abundance on breeding success (0-group – est.: 0.160, SE: 0.099, z:1.620, P:0.105, 1-group - est.: 0.158, SE: 0.093, z: 1.698, P: 0.090), nor any effect of SST (est: -0.037, SE: 0.120, z: -0.311, P: 0.756). The fixed effects explained around 7 % of the variation in the data (conditional R^2: 0.99, marginal R^2: 0.07; Table S5).

The second part of our analyses investigated potential underpinning mechanisms for the effects of the fisheries closure on seabird breeding success via the effect of prey abundance and fishing effort on chick diet in kittiwake, guillemot, razorbill and puffin on the IOM (Analyses 4 & 5), the effect of these diets on breeding success of kittiwake, guillemot, razorbill and puffin on the Isle of May (Analysis 6), and the effect of prey abundance, fishing effort and SST on breeding success of all these species over the wider region (Analysis 7).

In general, we found positive effects of sandeel abundance (predominantly 0-group), or the ratio of sandeel to sprat abundance, on the proportion of sandeel in chick diet for the four species on the Isle of May (Table 5). A negative effect of fishing effort on the proportion of sandeel in the diet was only detected for puffin (Table 5). Similarly, we detected largely positive effects of sandeel 0-group abundance, or the ratio of sandeel 0-group to sandeel 1-group, on the proportion of the sandeel component of chick diet consisting of 0-group fish for species on the Isle of May (Table 5). Fishing effort had a negative influence on the proportion of the sandeel component of the diet consisting of 0-group in three species (kittiwake, puffin and razorbill), with no detectable effects of prey abundance or fishing effort in guillemot (Table 5). Regional breeding success was in general positively influenced by the abundance of sandeel 0-group, with evidence for this relationship in kittiwake, guillemot and puffin (Table 5). The effect of fishing effort on regional breeding success was only significant in one species, with a negative association in kittiwake (Table 5).

Table 5
Summary of the significant effects detected for influence of prey abundance and fishing effort on chick diet in kittiwake, guillemot, razorbill and puffin on the Isle of May (Analyses 4 & 5), the effect of these diets on breeding success of kittiwake, guillemot, razorbill and puffin on the Isle of May (Analysis 6), and the effect of prey abundance, fishing effort and SST on seabird breeding success of kittiwake, guillemot, razorbill and puffin over the wider region (Analysis 7). Positive or negative effects of covariates are denoted using '+ve' or '-ve'. The age class of prey is included in parentheses ('0': age 0 year; '1': age 1 year or older). 'Weak' effects are where significance was >0.05 but <0.10.

Species	(A4) Effect of prey abundance and fishing effort on proportion sandeel in diet	(A5) Effect of prey abundance and fishing effort on proportion of sandeel component of diet comprised of 0-group	(A6) Effect of proportion of sandeel in diet on breeding success	(A7) Effect of prey abundance, fishing effort and SST on breeding success
KW	Weak +ve sandeel(0)	+ve sandeel(0): sandeel(1) -ve fishing effort	+ve	+ve sandeel(0) -ve fishing effort
GU	+ve sandeel (1):sprat(1)		+ve	+ve sandeel(0)
PU	+ve sandeel (0):sprat(1) -ve fishing effort	-ve sandeel(1) -ve fishing effort Weak +ve sandeel(0): sandeel(1)		Weak +ve sandeel(0)
RZ	-ve sprat(1)	-ve sandeel(0) -ve fishing effort	+ve	

3.3. *Drivers of chick diet composition on the Isle of May*

3.3.1. *Kittiwake*

Variation in the proportion of sandeel in the chick diet (Analysis 4), was best explained by a model including the abundance of sandeel 0-group and fishing effort (Model 4a, Table 3). This model included a weak positive effect of sandeel 0-group abundance on the proportion of sandeel in chick diet (est: 0.270, SE: 0.0.168, z: 1.611, P: 0.11, pseudo R^2: 12 %; Table S6a and S7). There was no detectable effect of fishing effort on kittiwake chick diet (est: -0.039, SE: 0.149, z: -0.264, P: 0.791; Table S6a). The two models including the ratio of sandeel 0-group or sandeel 1-group to sprat 1-group received similar support in the data to the best supported model (ΔAICc 1.43; Table S6), as did the model including sprat 1-group abundance (ΔAICc 1.61; Table S6) and the model including sandeel 1-group (ΔAICc 1.80; Table S6).

The best supported model for the sandeel component of chick diet comprised of 0-group fish (Analysis 5), included the ratio of sandeel 0-group abundance to sandeel 1-group abundance (Table S6). This model revealed a significant positive effect of the ratio of sandeel 0-group:sandeel 1-group on the proportion of the sandeel component of chick diet made up of sandeel 0-group (est: 0.490, SE: 0.182, z: 2.698, P: 0.007, pseudo R^2: 37 %; Model 5c, Table S6a & S7). There was also evidence for a significant negative effect of fishing effort on the proportion of the sandeel component of chick diet made up of sandeel 0-group (est: -0.715, SE: 0.156, z: -4.589, $P < 0.001$, pseudo R^2: 29 %; Table S6a & S7). The two alternative models received considerably less support in the data when compared to the best model (ΔAICc >3.0; Table S6).

3.3.2. *Guillemot*

Variation in the proportion of sandeel in chick diet (Analysis 4), was best explained by the model including the ratio of sandeel 1-group to sprat 1-group abundance, and an additional effect of fishery effort (Model 4e, Table 3). This model showed evidence for a significant increase in the proportion of sandeel in chick diet as the ratio of sandeel 1-group to sprat 1-group increased (est: 0.678, SE: 0.14, $P < 0.001$, pseudo R^2: 52 %; Table S6b & S7, Fig. 3). This model contained no evidence for an effect of sandeel fishing effort on guillemot chick diet (est: 0.212, SE: 0.158, P: 0.18; Table S6b). Alternative models received considerably less support in the data in this species (ΔAICc >10; Table S6).

The best supported model for the proportion of the sandeel component of chick diet made up of 0-group (Analysis 5), included the abundance of sandeel 0-group and fishing effort (Model 5a), although there was very similar support in the data for the two alternative models, including either the abundance of sandeel 1-group, or the ratio of sandeel 0-group to sandeel 1-group (ΔAICc for all models <0.3; Table S6). In none of the models was there any evidence for significant effects of the absolute or relative abundance of sandeel 0-group or 1-group, nor any effects of fishing effort (Table S6b).

3.3.3. *Puffin*

The best supported model for the proportion of sandeel in chick diet (Analysis 4), included the ratio of sandeel 0-group to sprat 1-group, and an additive effect of fishery effort (Model 4d, Table 3). This model included a significant positive effect of the ratio of sandeel 0-group to sprat 1-group on the proportion of sandeel in puffin chick diet on the Isle of May (est: 0.308, SE: 0.149, P: 0.038, pseudo R^2: 30 %, Table S6c & S7), and a significant negative effect of fishery effort (est: -0.318, SE: 0.130, P: 0.015; Table S6c). The model including sprat 1-group received similar support in the data to the best supported model (ΔAICc 0.78; Table S6), as did the model including the ratio of sandeel 1-group to sprat 1-group (ΔAICc 1.87; Table S6). Models including sandeel 1-group or sandeel 0-group received rather less support in the data compared to the best supported model (ΔAICc >3; Table S6).

The best supported model for the proportion of the sandeel component of chick diet made up of 0-group (Analysis 5), included significant negative effects of 1-group sandeel abundance (est: -0.369, SE: 0.177, z: -2.086, P: 0.037, pseudo R^2: 22 %, Model 5b, Table S6c & S7), and fishing effort (est: -0.604, SE: 0.156, z: -3.881, $P < 0.001$; Table S6c). There was similar support in the data for the model containing an effect of the ratio of sandeel 0-group to 1-group (Model 5c, ΔAICc 1.87; Table S6). In this alternative model, there was some evidence for a positive effect of the ratio of 0-group to 1-group on the proportion of puffin chick diet made up of 0-group sandeel (est: 0.333, SE: 0.190, z: 1.751, P: 0.080, pseudo R^2: 18 %; Table S6c & S7), and a significant negative effect of fishing effort (est: -0.630, SE: 0.164, z: -3.839, $P < 0.001$; Table S6c). The model containing the abundance of sandeel 0-group has considerably less support in the data than the best supported model (ΔAICc 3.72; Table S6), but also contained a significant negative effect of fishery effort on the proportion of the sandeel component of the diet consisting of 0-group (est: -0.579, SE: 0.166, z: -3.498, $P < 0.001$, pseudo R^2: 14 %).

3.3.4. *Razorbill*

The proportion of sandeel in chick diet (Analysis 4), was best explained by a model containing effects of sprat 1-group and fishery effort (Model 4c; Table 3). This model revealed a significant negative effect of sprat 1-group abundance on the proportion of sandeel in chick diet (est: -0.594, SE: 0.215, z: -2.806, P: 0.005, pseudo R^2: 43 %; Table S6d & S7), and no effect of fishery effort (est: 0.034, SE: 0.216, z: 0.159, P: 0.87; Table S6d). The alternative model including the ratio of sandeel 0-group to sprat 1-group received some support in the data compared to the best model (ΔAICc 2.29; Table 3), with the other alternative models receiving considerably less support (ΔAICc >4; Table S6).

The best supported model for the proportion of the sandeel component of chick diet consisting of sandeel 0-group (Analysis 5), included the abundance of 0-group sandeel (Model 5a); however, counterintuitively there was a significant negative effect of the abundance of 0-group (est: -0.442, SE: 0.210, z: -2.106, P: 0.035, pseudo R^2: 18 %; Table S6d & S7). This model also contained a significant negative effect of fishing effort on the proportion of the sandeel component of chick diet consisting of 0-group (est: -0.647, SE: 0.192, z: -3.372, $P < 0.001$; Table S6d). The two alternative models also received some support in the data compared to the best supported model (sandeel 1-group model: ΔAICc 2.73; ratio of 0-group to 1-group model: ΔAICc 1.99; Table S6). Both alternative models revealed significant negative effects of fishing effort on the proportion of the sandeel component of chick diet made up of 0-group, but no significant effects of either sandeel 1-group abundance, or the ratio of sandeel 0-group to 1-group (Table S6d).

3.4. *Drivers of breeding success on the Isle of May*

There was a significant positive effect of the proportion of sandeel in

Fig. 3. Predicted influence of the ratio of 0-group sandeel to sprat abundance on the proportion of sandeel in the diet of breeding seabirds on the Isle of May. Each species was modelled separately, with observed data for each species shown in solid circles. Predicted relationship for the influence of the ratio of 0-group sandeel to sprat abundance on diet derived from a model including the abundance ratio and an additive effect of fishery effort ('Model 4d'), with associated 95 % confidence intervals.

the diet of chicks on breeding success (Analysis 6) in kittiwake (est: 0.456, SE: 0.168, z: 2.717, P: 0.010; Fig. 4), guillemot (est: 0.325, SE: 0.090, z: 3.628, P: <0.001; Fig. 4), and razorbill (est: 0.178, SE: 0.052, z: 2.3.456, P: 0.0014; Fig. 4). For puffin, breeding success increased marginally with the proportion of sandeel in the chick diet, but the effect was small and non-significant (est: 0.044, SE: 0.111, z: 0.395, P: 0.695; Fig. 4). The variance explained differed across the four species, with models explaining around 27 % of the variance in breeding success for guillemot, 25 % of the variance for razorbill, 19 % of the variance for kittiwake and <1 % of the variance for puffin (marginal R^2; Table S7).

3.5. *Drivers of regional breeding success*

3.5.1. *Kittiwake*

Regional breeding success in kittiwake (Analysis 7) was positively associated with the abundance of sandeel 0-group (est: 0.282, SE: 0.095, z: 2.973, P:0.003), and negatively influenced by fishing effort (est: -0.245, SE: 0.115, z: -2.131, P: 0.033; Supplementary Material Table 8a). There was no evidence for an effect of abundance of sandeel 1-group on kittiwake breeding success (est: 0.099, SE: 0.092, z: 1.082, P: 0.279), abundance of sprat 1-group (est: 0.049, SE: 0.079, z: 0.627, P:0.531), nor for SST (est: 0.022, SE: 0.113, z: 0.196, P: 0.845). The fixed effects accounted for 9 % of the variation (marginal R^2; Table S7).

3.5.2. *Guillemot*

The regional analysis of guillemot breeding success (Analysis 7; Table 1, Supplementary Material Fig. 1) revealed evidence for a significant positive effect of sandeel 0-group abundance (est: 0.275, SE: 0.107, z: 2.579, P: 0.010), and non-significant effects of sandeel 1-group abundance (est: 0.066, SE: 0.104, z: 0.637, P: 0.524), sprat 1-group abundance (est: 0.096. SE: 0.114, z: 0.844, P: 0.399), fishing effort (est: -0.044, SE: 0.126, z: -0.348, P: 0.728), and SST (est: -0.172, SE: 0.131, z: -1.306, P: 0.192; Table S8b). The fixed effects accounted for around 15 % of the variation (marginal R^2; Table S7).

3.5.3. *Puffin*

Regional breeding success of puffins (Analysis 7; Table 1, Supplementary Material Fig. 1) showed a weak positive relationship with the abundance of sandeel 0-group (est: 0.214, SE: 0.134, z: 1.597, P: 0.110; Table S8c). The analysis revealed no strong evidence for any effects of sandeel 1-group abundance (est: 0.029, SE: 0.124, z: 0.236, P: 0.814), sprat 1-group abundance (est: 0.013, SE: 0.109, z: 0.116, P: 0.908), fishery effort (est: -0.074, SE: 0.164, z: -0.451, P: 0.652), or SST (est: -0.059, SE: 0.157, z: -0.378, P: 0.706). The fixed effects accounted for approximately 7 % of the variation (marginal R^2; Table S7).

3.5.4. *Razorbill*

We were unable to detect any significant effects for any of our covariates on razorbill breeding success (Analysis 7; Table 1, Supplementary Material Fig. 1), with no influence of prey (sandeel 0-group: est.: 0.007, SE: 0.048, z: 0.138, P: 0.890; sandeel 1-group: est.: 0.047, SE: 0.048, z: 0.987, P: 0.324; sprat 1-group: est.: -0.020, SE: 0.043, z: -0.474, P: 0.635). There was also no evidence for effects of fishing effort on razorbill regional breeding success (est: 0.069, SE: 0.055, z: 1.265, P: 0.206), nor SST (est: -0.008, SE: 0.057, z: -0.148, P: 0.883; Table S8d). The fixed effects accounted for <5 % of the variation (marginal R^2; Table S7).

4. Discussion

Fisheries around the world have been implicated in changes in seabird behaviour, energetics, demography and population dynamics (Frederiksen et al., 2008, Pichegru et al., 2012, Cury et al., 2011, Sherley et al., 2018). In the North Sea, rates of breeding failure in nine seabird species, including the four studied here, have been linked to their sensitivity to fishing pressure (Cook et al., 2014). However, quantifying the effect of fisheries management on seabird demography is inherently difficult, requiring large scale, quasi-experimental field data, ideally from both prey and seabird populations experiencing broadly similar environmental conditions (Frederiksen et al., 2008; Sydeman et al., 2017; Sherley et al., 2018). Due to these constraints, very few such assessments exist. We used two decades of post-closure data from a forage fish fishery-seabird system in the north-western North Sea to quantify changes in seabird diet and breeding success associated with fishery closure and wider changes to prey abundance and availability. We predicted that the closure would be most effective for kittiwake because this species has a greater dependence on sandeels (the target species of the fishery) than the three auk study species (Furness and Tasker, 2000). Unlike the pursuit diving auks, kittiwakes are surface feeders, so are potentially more affected by changes in vertical distribution of prey as

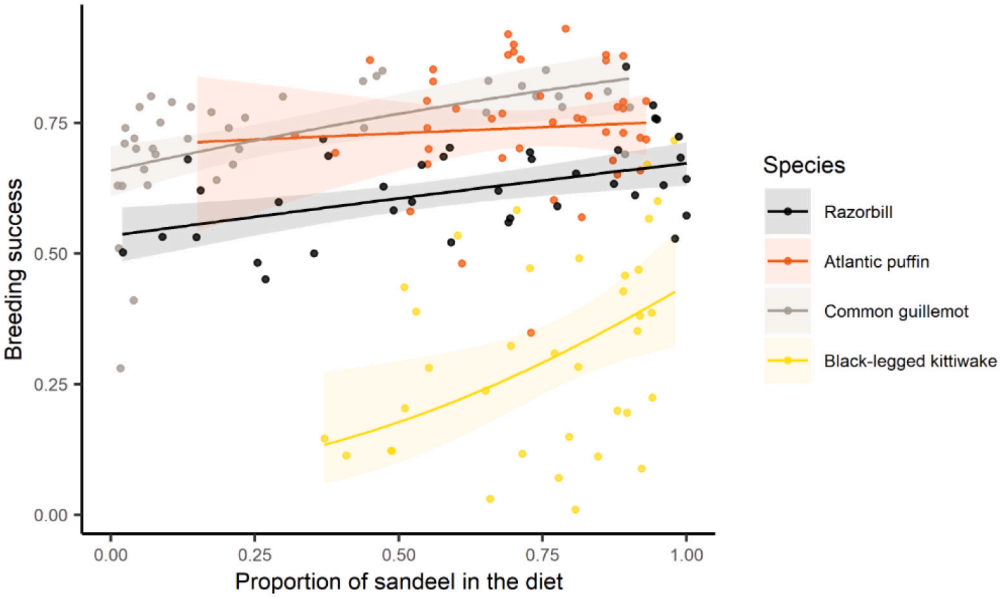

Fig. 4. Predicted variation in seabird breeding success (proportion eggs resulting in fledged chicks) on the Isle of May in relation to the proportion of sandeel in the diet during chick-rearing. Solid circles denote observations for each seabird species.

well as abundance. Our analysis of the breeding success of the four species based on the Isle of May matched our predictions, with only the breeding success of kittiwake appearing to benefit from the closure. In this species, the wider BACI analysis of multiple colonies further demonstrated that the period of operation of the sandeel fishery was correlated with a strong decline in kittiwake breeding success (declining from 52 % of eggs successfully fledging to 23 %) in those colonies whose foraging distributions overlapped with the area of fishery activity. Equivalent declines were not apparent in colonies outside the area where the fishery operated, but still subject to similar broad patterns of environmental change during this period, indicating that the reduction was not simply driven by a more general deterioration of breeding conditions in the region.

Quantifying the effectiveness of the sandeel fishery closure on kittiwake breeding success revealed a marginal increase (defined as the number of chicks fledged per egg laid) of approximately 10 % in those kittiwake colonies thought to be most affected by the fishery operation and subsequent closure. Our results are similar to those obtained in the Western and Eastern Capes of South Africa where the effect of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) fisheries on African penguins (*Spheniscus demersus*) was assessed via a quasi-experimental fisheries closure that utilised a similar BACI approach (Sherley et al., 2018; Sydeman et al., 2021a). Here, breeding success increased during years when fishing was excluded from the foraging areas of breeding penguins (Sherley et al., 2018, 2020). The effect sizes and uncertainty documented in studies of this system were very similar to those identified here, with chick survival increasing by around 10–11 % in both South African populations during fishery closure (Sherley et al., 2018). These studies concluded that permanent fisheries closures could offset ~20 % of the penguin population decline, which has averaged ~5 % per annum (Sherley et al., 2020). The evidence from our study suggests that although the closure may have arrested the decline in kittiwake breeding success in nearby colonies during fishery operation, it has not stimulated a recovery of breeding success to levels observed prior to the start of the fishery, despite twenty years of potential recovery time. Our analysis also revealed wide uncertainty around the marginal increase in breeding success associated with the period post fishery closure (95 % confidence interval 2 % to 18 %). It is, therefore, important to caveat these results, both to recognise this uncertainty as well as the quasi-experimental nature of the analyses. The differential patterns of change in breeding success between colonies in the closure and control zones do indeed correlate with different phases of fishery operation. However, many other ecosystem changes, including anthropogenic disturbance linked to climate change, are known to have occurred during this period (Heath, 2005; Dulvy et al., 2008; Emeis et al., 2015), so it is not possible to pinpoint the causation of the observed changes in breeding success solely on the operation and subsequent closure of the sandeel fishery. Integral to future research to elucidate underpinning mechanisms is to understand the role of competitors for forage fish, including predator species that have increased in recent decades such as gannets (JNCC, 2021), or over recent years such as haddock (ICES, 2022a) and whiting (ICES, 2022b).

Across the seven kittiwake colonies whose foraging ranges overlap with the area targeted by the sandeel fishery, our analysis revealed the fishery closure resulted in widely varying changes in breeding success (from −4 % to +25 %). It is particularly notable that two neighbouring kittiwake colonies, Dunbar Coast and the Isle of May (approximately 40 km apart), showed markedly contrasting changes in breeding success between the period of fishery operation and subsequent closure. Breeding success at Dunbar continued to show a moderate decline, whilst breeding success on the Isle of May increased by around 17 % over the same period. Variation in breeding success at individual colonies must be viewed as an integrative measure of many aspects of the demography (population size, age structure) and environmental conditions (colony disturbance, breeding site quality, local weather, localised variation in prey availability, quality and timing) affecting each population (Bull et al., 2004, Frederiksen et al., 2005). Therefore, whilst our results suggest a beneficial effect of reduced forage fishery activity on kittiwake breeding success, the realisation of any benefit will be heavily mediated by other aspects of the species' ecology and local environment, including climate change and other anthropogenic stressors.

In contrast to the response in the kittiwake, we found no evidence that the fishery closure has been effective in safeguarding the breeding success of guillemot, razorbill or puffin. Rather, the breeding success of these three species declined significantly over four decades of study. We are unable to discount the possibility that the fishery closure may actually have benefitted breeding success of these species (i.e., without it the declines would have been even more marked). However, it is likely that the abundance or availability of sandeels to auks was reduced in the period after the fishery closure. Sandeel populations in this region have shown marked changes in recent decades, with climate affecting sandeel recruitment by altering the timing of key life history events in sandeels and their copepod prey (Régnier et al., 2019). Over the same period, the size of sandeels and proportion of sandeel in the diet of several seabirds breeding on the Isle of May, including kittiwakes, guillemots and razorbills, has declined (Howells et al., 2017; Wanless et al., 2018). Such shifts in sandeel phenology, alongside declines in sandeel abundance and quality may have masked any potential closure-related benefits to breeding success in these three auk species. Indeed, studies from the South African penguin-fishery system have also predicted that the African penguin population decline will continue even with full fishery closures around the colonies due to larger-scale changes in prey availability (Robinson et al., 2015; Sherley et al., 2017).

If the scientific fishery was affecting seabird breeding success, we would expect to see a negative relationship between breeding success and the proportion of total fishery mortality (in Sandeel Area 4) occurring within the closed area. Although our analysis indicated that breeding success of seabirds was reduced when a greater share of the fishing mortality occurred in the closed area, this relationship was not statistically significant. This suggests that the continued operation of some sandeel fishing within the closed area is not significantly affecting the breeding success of these species on the Isle of May, relative to the total fishing mortality occurring across Sandeel Area 4. The absence of an effect may be due to the relatively small size of landings from the scientific fishery (0 to 7158 t from 1999 to 2018 (Supplementary Material Fig. 2) compared to sandeel landings across the closed area during the period of fishery operation (25,496 to 111,783 t) and total sandeel landings over Sandeel Area 4 over the entire study period (0 to 158,690 t; Supplementary Material Fig. 2; see Supplementary Material Fig. 3 for temporal variation in fishing mortality in SA4). However, the relative coarseness of the available data may have hindered our ability to detect such an effect against a background of environmental change, especially if the effect is present, but relatively small.

Reduced prey availability may impact seabird demography through changes in diet. On the Isle of May, evidence from over four decades has revealed a long-term decline in the overall importance of sandeels in the diet of chicks, with a concomitant shift to Clupeidae, predominantly sprat but also some herring *Clupea harengus* in recent years (Wanless et al., 2018). This shift was particularly pronounced in guillemot, but was also apparent to a lesser extent in kittiwake and razorbill. Furthermore, there has been a shift from older 1+ group to 0-group sandeels in all four study species. However, Wanless et al. (2018) found no evidence that the sandeel fishery closure reversed the decline in the importance of sandeels in the diet of any of the species considered here. Our analysis does suggest potential consequences for breeding success linked to these shifts in diet with a positive link between the proportion of sandeel in the diet of chicks and subsequent breeding success in all four seabird species, albeit with weaker evidence for puffin. 0-group sandeel become available to seabirds during late incubation and are the most important prey in the diet during chick-rearing for all of our study species except guillemot, which predominantly feed chicks on 1-group fish (Lewis et al., 2001; Daunt et al., 2008; Howells et al., 2017). Chick-rearing is the period of peak energy demand during the breeding season, which may explain the strong link between 0-group sandeel abundance and breeding success. The proportion of sandeel in chick diet is inevitably associated with the proportion of sprat, because together they comprise 92–99 % of chick diet across the four study species. These results suggest that the observed declines in the proportion of sandeel in the diet of chicks may be linked with lower breeding success, though the precise mechanisms for this remain unclear.

Given these links between diet of chicks and subsequent breeding success, we further examined how diet was influenced by the absolute and relative abundances of the two most important prey species, sandeel (0-group and 1-group) and sprat (1-group). For kittiwake on the Isle of May, there was some evidence that as the abundance of 0-group sandeel increased there was a corresponding increase in the proportion of sandeel in the diet during chick rearing. The proportion of the sandeel component of kittiwake diet comprised of 0-group increased as the ratio of the abundances of 0-group to 1-group sandeel increased. These findings point to the importance of 0-group sandeel abundance in influencing chick diet in this species. For both guillemot and puffin, the relative abundance of sandeel to sprat most influenced the proportion of sandeel in the diet, with this proportion increasing with a higher ratio of 1-group sandeel to 1-group sprat in guillemot, and with a higher ratio of 0-group sandeel to 1-group sprat in puffin. These findings suggest that the relative abundances of sandeel and sprat shape chick diet in these two species, with both guillemot and puffin tending to increase the proportion of sandeel in the diet in line with increasing abundance of either 1-group (guillemot) or 0-group (puffin) sandeels. Guillemots are single prey loaders, bringing only a single prey item to the young, which may explain the strong support for the importance of 1-group sandeel (in relation to 1-group sprat abundance) rather than 0-group sandeel in the diet of chicks in this species. However, the guillemot's overall relationship with the prey may be more nuanced because the diet of adult guillemots differs markedly from that of chicks, with 0-group sandeels forming an important component of their diet (Wilson et al., 2004). In puffin, the proportion of sandeel consisting of 0-group decreased as the abundance of 1-group sandeel increased, suggesting that the relative availability of sandeel age classes affects the composition of the sandeel component of chick diet in this species. In razorbill, the proportion of sandeel in chick diet was negatively influenced by the abundance of 1-group sprat, indicating that as abundance of sprat increased the sandeel proportion in chick diet decreased. Whilst our measures of prey abundance may not have perfectly captured corresponding prey availability for the four seabird species, our results do indicate important links between the absolute and relative abundances of sandeels and sprat on chick diet, with likely important consequences for subsequent breeding success.

Only puffin showed an effect of fishery effort on the proportion of sandeel in the diet, with a decline in this proportion in years when fishery effort was high. However, in puffin, kittiwake and razorbill, we found evidence for a negative effect of fishery effort on the proportion of the sandeel component of the diet comprising of 0-group. This is somewhat counterintuitive, suggesting that when fishing effort is high, the relative proportion of 1-group sandeel (the target of the fishery) to 0-group sandeel in the diet of these species is also greater. Moreover, this result runs counter to those of Hillborn et al. (2017) in an analysis of other predator-forage fish fishery systems where a lack of overlap in the age of fish taken by predators and fisheries was associated with an absence of strong relationships between prey abundance and predator population change. Beyond direct removals of prey, fishery activity may lead to behavioural disturbance effects on fish (e.g., Frederiksen et al., 2008; Diaz Pauli and Sih, 2017). However, it is likely that quantifying such changes and any subsequent effect on diet is inherently difficult using broad scale measures of fishing effort across large spatial areas. Indeed, there is currently a lack of empirical evidence for fishing induced behavioural change in this species of sandeel, so potential behavioural mechanisms for how fishing activity alters prey availability to seabirds remain unknown. Sandeel fishing targeting 1+ group may disturb other fish populations, including 0-group sandeels and sprat in complex ways, resulting in nuanced effects on the relative proportions of 0-group versus 1+ group availability and subsequent predator diet. Our results highlight that even with comprehensive long-term dietary data, identifying the influence of fishing activity on prey availability, and hence on seabird diet is challenging, in part because the scale of the prey data is much coarser than the scale at which the birds forage.

We also considered prey-related drivers of breeding success across the wider region. In kittiwake, guillemot and puffin, regional breeding success was higher in years with greater sandeel 0-group abundance. No species appeared to show an effect of sandeel 1-group or sprat 1-group abundance on breeding success, and indeed, we were unable to detect effects of any metrics for prey abundance on breeding success in razorbills. These results align with the dietary shift from 1+ group to 0-group sandeel that has occurred over the course of the study period (Wanless et al., 2018). In terms of fishery activity, we detected no links between effort and breeding success in the three auk species. However, a strong negative effect of fishery effort on breeding success in kittiwake was in line with results from the BACI on effects of the fishery closure in this species. Previous research has documented that kittiwake breeding success at two of the study colonies in our analysis (the Isle of May and St Abbs Head) was positively related to abundance of sandeels (Daunt et al., 2008). However, that study found no association between breeding success and sandeel abundance in either guillemot, puffin or razorbill, although it was based on a shorter data set (Daunt et al., 2008). Seabird breeding success is not only influenced by overall prey abundance, but also the timing of high prey availability in relation to peak energetic demands of breeding birds. Trophic mismatches have the potential to modify the transfer of energy from prey to predators, and previous work has demonstrated that breeding success in kittiwake and guillemot on the Isle of May is lower when the timing of peak sandeel availability occurs early, or when sandeel availability is low in June (Rindorf et al., 2000). More recent work also suggests that 1+ group sandeels are now burying earlier in the year than historically, potentially making them less available to foraging seabirds during chick-rearing (Harris et al., 2022). Whilst fisheries management is unlikely to directly influence the timing of peak sandeel availability to seabirds, fishery activity could potentially act additively to reduce availability of 1+ group fish for seabirds (Rindorf et al., 2000).

In none of the analyses were we able to detect an additional effect of SST on breeding success, over and above any effect of prey abundance. This supports the assertion that the primary mechanism by which climate warming has affected seabird breeding success is via changes to prey availability, particularly that of their dominant prey, sandeels (Carroll et al., 2017). Evidence for a negative effect of warming SST on seabird breeding success is variable, with some previous studies supporting this link in kittiwake (Frederiksen et al., 2004, Wanless et al., 2018), but not others (Carroll et al., 2017; Eerkes-Medrano et al., 2017). An analysis of climate impacts on breeding success in ten seabird species along the eastern seaboard of the UK also revealed variable evidence for links between SST and breeding success, documenting a negative relationship between SST and breeding success in puffin and guillemot, but not in kittiwake or razorbill (Searle et al., 2022). Similarly, Sydeman et al. (2021b) found variable responses of seabird breeding success to temperature globally, in part explained by variation in the trophic level at which they fed. The influence of climate warming on ocean temperatures driving cascading effects up the food chain to seabird predators is complex, requiring further research on oceanographic influences on marine food webs to understand the implications of rising temperatures on all trophic levels (Carroll et al., 2017; Searle et al., 2022). All our models for breeding success assumed linear effects of predictors. Non-linear effects of variables such as prey abundance or SST on seabird breeding success have been documented (e.g., Cury et al., 2011, Sydeman et al., 2021b). We were limited by data availability in terms of the complexity of the models we were able to fit, and the existence of non-linear interactions is an important area for future research, particularly due to their relevance to potential threshold effects in seabird-prey relationships. It has been suggested that for many forage fish species, recruitment, and therefore abundance of age-0 fish, is more strongly influenced by environmental variables such as SST than fishing activity, particularly when the fishery targets older age classes of fish (Hilborn et al., 2017). It is possible that this is also the case for the Firth of Forth region, although no link has been established between temperature and recruitment across nine sub-areas for sandeel assessment in the North Sea, covering most of the sandeel habitat in this region (Henriksen et al., 2021). Our failure to detect any relationship between seabird breeding success and SST in our regional analysis may be because our models of breeding success included a direct measure of sandeel 0-group abundance, hence any mediated effect of SST on breeding success via recruitment in sandeels was masked by the more direct link between sandeel 0-group abundance and breeding success. The effect of fishing in this region may therefore be acting through removal of fish from the spawning population, potentially leading to lower abundance in the subsequent year class, though the link between the biomass of spawning fish and the subsequent abundance of 0-group sandeel is very weak in the area (ICES, 2021).

In summary, our results demonstrate important, but nuanced links between fishery activity, prey abundance, and seabird diet and breeding success. We found significant negative associations between the operation of a forage fish fishery on kittiwake breeding success, with generally beneficial effects after its subsequent closure. However, impacts of the fishery operation and closure on breeding success in the three auk species were much less clear, with no detectable positive effects on breeding success after closure in these species. Whilst sandeels form an important component of chick diet in all four seabird species, albeit to a lesser extent in guillemot (Wanless et al., 2018; Harris et al., 2022), kittiwake differ from the other species in the form of their foraging behaviour, being surface feeders rather than divers. It appears that some aspect of the fishery operation reduced the availability of sandeel for the surface feeding kittiwake more strongly than for the diving auks. Higher fishing effort was linked directly to lower regional breeding success in kittiwake, but only linked to breeding success indirectly via changes in diet in the auk species. For both puffin and razorbill there was an association between fishing effort and a reduced proportion of the sandeel component of the diet consisting of 0-group sandeel, and in puffin, a reduced proportion of sandeel in the overall diet. Although the precise mechanisms underpinning the relationships between fishery activity and seabird breeding success are difficult to determine with currently available data, our results are strongly suggestive of the potential for negative effects of forage fish fisheries on seabird demography, both directly on seabird breeding success in one species, kittiwake, and indirectly through effects on diet in two species, puffin and razorbill. However, our results also indicate the importance of environmental conditions on the effectiveness of the fishery closure. The limited recovery of kittiwake breeding success was potentially due to shifts in the timing of sandeel phenology, and to low abundance and quality of sandeels after closure, which may also have had a negative impact on the breeding success of the three auk species. Our results also posit the potential for species interactions to play a role in shaping seabird diet and subsequent breeding success. In two species, guillemot and puffin, the proportion of sandeel in the diet was positively associated with the ratio of sandeel to sprat abundance, and in puffin this diet proportion was lower when the abundance of sprat was higher. This suggests that direct or indirect interactions between these two prey species has the potential to influence seabird diet, and subsequent breeding success. Differential responses of each prey species to environmental drivers may also play a role, particularly in a region undergoing considerable ecosystem change. Further research is needed to determine if these associations operate through direct or indirect mechanisms, and if there are potentially lagged relationships between adult prey biomass and younger age classes.

4.1. *Implications for fisheries management as a strategic tool for seabird conservation*

Governments are seeking to implement policies of nature restoration and improvement, including ambitions for marine net gain (e.g., UK Marine Plans, Marine Management Organisation, 2020). With widespread anthropogenic change occurring in many seabird habitats, including both climate change and a rapid expansion of offshore renewable energy in shelf seas such as the North Sea, the desire for net gain is thought to be best delivered through a systems-based approach (Hooper et al., 2021), including the designation of no-take zones. The potential success of such strategies in delivering net gain for seabirds will be determined by the ecological processes we have considered in this study. Our findings and those of others (Sherley et al., 2015, 2018), documenting increased breeding success in some species associated with a fisheries closure, suggest its potential for offsetting negative impacts from anthropogenic impacts is warranted, facilitating aspirations to deliver marine net gain. However, many studies, including our own, point to some important caveats around this goal. Analyses of this type, even when able to apply relatively robust methods such as BACI, are still inherently correlative. Intensive research using the BACI approach in two fishery-seabird systems has revealed effects that are subtle and inconsistent, highlighting the extremely challenging nature of quantifying forage fishery impacts (Frederiksen et al., 2008; Sherley et al., 2015, 2018). The relatively low levels of variance explained by our models (ranging from around 4 % to 50 %) should engender caution when interpreting the size of any effects quantitatively. Low explanatory power is not unusual with ecological data. Seabird demography is also shaped by inter-annual environmental fluctuations, including lag effects, which are difficult to capture precisely with relatively coarse scale environmental data. Moreover, available data on seabird prey species are limited, and tend to be collected with the intent of informing fisheries management, which may mean the estimates of fish abundance are not closely related to the availability of fish to seabirds. These limitations should promote caution when interpreting our results quantitatively in terms of any potential impacts of fisheries management on seabird breeding success.

Of particular importance, when setting expectations for impacts of fisheries closures on seabird demography, and specifying subsequent monitoring design to determine effectiveness, is a recognition of the required periods of study, potentially needing decades. Such time scales may well conflict with a desire for rapid management action (Sherley et al., 2018), such as any monitoring of outcomes that may trigger the need for adaptive management, which is an integral component of the application of the mitigation hierarchy (Hooper et al., 2021). More readily accessible behavioural data, such as foraging effort and provisioning rates, are more easily captured, but present difficulties in robustly linking to demography (Sherley et al., 2018). Additionally, our results, and those from similar systems (Sherley et al., 2015, 2018), demonstrate the importance of long-term prey data to account for extreme years or temporal trends, which are common with prey species such as sandeels (Alder et al., 2008). Other sources of environmental change in the North Sea ecosystem are known to be affecting prey populations (Heath et al., 2012; Clausen et al., 2018; Régnier et al., 2019), so the relative contribution of any fishery activity on prey abundance and availability is inherently difficult to tease apart from other long-term changes occurring within the system. Yet, this understanding is crucial to predicting whether changes in forage fish fishery activity will lead to more available prey for predators during key seasonal periods such as chick-rearing.

In conclusion, our results demonstrate important links between a fishery closure, prey abundance and availability, and seabird diet and breeding success. These findings substantiate previous evidence from marine systems around the world for the potential for forage fisheries to impact upon seabird demography (Pichegru et al., 2012; Cury et al., 2011; Sydeman et al., 2021a). However, they also serve to highlight the difficulties and complexities in teasing apart the contributions of different drivers against a backdrop of environmental change, hindering their practical application to strategic seabird conservation via fisheries management.

CRediT authorship contribution statement

The paper was conceived by KS, FD and MP. KS led the writing with inputs from all co-authors. KS, CR, AB, FD and AR conceived and conducted the statistical analyses. AR processed all fish data used within analyses, and CR, AB and KS processed all seabird and environmental data.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are freely available, as described in our cover letter

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Appendix A. Supplementary data

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