FEATURE ARTICLE

Effect of timing and abundance of lesser sandeel on the breeding success of a North Sea seabird community

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ABSTRACT: Understanding the responses of seabirds to climate-induced variations in phenology and abundance of their prey is key to developing ecosystem-based fisheries management measures that benefit higher trophic levels. The match/mismatch hypothesis (MMH) emphasizes the need to consider synchrony in the seasonal cycles of predators and prey, while the match/mismatch/abundance hypothesis (MMAH) proposes that prey abundance may reinforce/compensate mismatch effects. This study considers the effects of both variations in seasonal availability and abundance of lesser sandeel *Ammodytes marinus* on hatching, fledging and breeding success of 5 seabird species: black-legged kittiwake *Rissa tridactyla*, Atlantic puffin *Fratercula arctica*, razorbill *Alca torda*, common guillemot *Uria aalge* and European shag *Gulosus aristotelis*. Consistent with MMH, temporal asynchrony between sandeel availability and seabird breeding schedules affected productivity in 4 species. The effects of trophic asynchrony were either reinforced or compensated by sandeel abundance for some species, supporting MMAH. Breeding success in the late-breeding kittiwake was high when conditions favoured both high sandeel abundance and temporal synchrony while the cost of asynchrony could be compensated by high sandeel abundance in the earlier-breeding puffin. Differential effects of sandeel abundance and trophic synchrony at different stages of the seabird breeding season suggest that distinct mechanisms are involved. The effects were most evident in the most sandeel-reliant seabirds. As further disruption of sandeel phenology and abundance is anticipated under the current climate crisis, the present study is an important step towards understanding bottom-up effects of environmental change on higher trophic levels.

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Atlantic puffin *Fratercula arctica* with a bill load of sandeel *Ammodytes marinus* during the chick-rearing period.
Photo: Ken Ritchie

KEY WORDS: *Ammodytes marinus* · *Rissa tridactyla* · *Fratercula arctica* · *Alca torda* · *Uria aalge* · *Gulosus aristotelis* · Match/mismatch hypothesis · Match/mismatch/abundance hypothesis

1. INTRODUCTION

Seasonal cycles in the life history and behaviour of a species are expected to have evolved to be synchro-

nised with the environmental conditions that maximise its fitness (Futuyma 1998). However, the rate of response to climate-driven changes in seasonality can differ among trophic levels, which in turn may disrupt the relative timing of predator and prey cycles (Stenseth & Mysterud 2002, Visser & Both 2005, Thackeray et al. 2010, Poloczanska et al. 2013, Keogan et al. 2018). These dynamics are central to the match/mismatch hypothesis (MMH), in which predator fitness is predicted to depend on temporal synchrony with the peak availability of prey (Cushing 1969, 1990, Stenseth & Mysterud 2002, Samplonius et al. 2021). While the focus of MMH is on the overlap in timing of key predator and prey events, variations in the abundance of prey may also be expected to reinforce or compensate the asynchronous responses in predators; for example, high levels of food availability may partially compensate fitness from asynchrony with prey (the match/mismatch/abundance hypothesis, MMAH; Durant et al. 2005, 2007) while low prey abundance may negate the benefits of a good match. However, few studies have tested these coupled hypotheses due to lack of sufficient data on the fitness consequences of both the timing of predator/prey schedules and prey abundance (but see Hipfner 2008, Watanuki et al. 2009).

Phenological overlap is most relevant when prey display a clear seasonal pattern in activity that affects their availability to predators. The degree of predator specialisation is also important, as generalist predators may compensate for a lack of trophic synchrony by switching their foraging effort to alternative prey. Temperate marine food webs, where a single forage fish species often dominates the intermediate trophic link between top predators and zooplankton, provide a unique system for exploring the importance of mismatch, as variability in the phenology of multiple predators is likely to result in variable degrees of synchrony with a dominant forage fish species. Climate impacts on predator and prey phenology can potentially have major repercussions on the food web, given the strong bottom-up and top-down control of this intermediate trophic link (Cury et al. 2000) and cascading effects across trophic levels (Pinnegar et al. 2000, Frederiksen et al. 2006, Österblom et al. 2008, Casini et al. 2009, Macdonald et al. 2015).

In the northeast Atlantic, the sandeel *Ammodytes marinus* is the main prey of many predators, and sandeel abundance has been linked to annual variation in the breeding success of a wide range of seabird species (Frederiksen et al. 2006, Olin et al. 2020, Searle et al. 2023, Wanless et al. 2023). Seabird breeding success is the product of hatching success (i.e. the proportion of eggs that hatch) and fledging success (i.e.

the proportion of these chicks that fledge). Both processes may respond directly or indirectly to prey abundance and phenology (Regehr & Montevecchi 1997). Hatching success is related to feeding conditions in the pre-breeding season that affect maternal investment in the egg (Houston et al. 1983, Shultz et al. 2009) and feeding conditions experienced during incubation which determine the extent to which eggs are continuously attended and, therefore, protected from predators (Regehr & Montevecchi 1997). Similarly, fledging success may be related to prey availability resulting from prey abundance and overlap in predator–prey phenologies that affect parental ability to provision and protect the brood (Regehr & Montevecchi 1997, Regular et al. 2014). In addition, in species where prey are carried back to the brood in the parent's bill, parental and chick diets may differ, with the latter potentially receiving higher-quality prey (Wilson et al. 2004). Parental provisioning strategy, where individual or multiple prey items are delivered to the chicks per foraging trip, may amplify this difference. Therefore, fledging success may depend on the degree of synchrony and abundance of prey fed to chicks or prey eaten by the parents.

Sandeel abundance is largely driven by inter-annual variation in the numbers of young of the year (age 0), which reflects the synchrony between larval hatch time and the production of their plankton prey (Wright & Bailey 1996, Eliasen et al. 2011, Régnier et al. 2017, 2019), itself linked to temperature (Régnier et al. 2019). During the autumn and winter months, sandeels bury into sandy sediments from which they emerge in March or early April (Wright et al. 2000, Henriksen et al. 2021). Consequently, 1 yr old (age 1) and older sandeels (age >1) are usually available to seabirds by the time they return to their colonies in March or April. In contrast, age-0 sandeels become available slightly later once they metamorphose from larvae and form pelagic feeding schools (Wright 1996, Wright & Bailey 1996, Gibb et al. 2017). Both age-0 and older sandeels show a condition-dependent decrease in activity in summer, with larger and older sandeels disappearing earlier from the water column (Bergstad et al. 2002, Haynes et al. 2007, Rindorf et al. 2016). Variability in the availability of the different age classes of sandeel is conditioned by changes in the date on which age-0 sandeels settle (based on observed sandeel size in seabird diet and otolith macrostructure, Lewis et al. 2001, Gibb et al. 2017) and older sandeels emerge from the sand early in the season, and by the timing of a condition-dependent decrease in activity towards the end (Wright 1996, Rindorf et al. 2016). Variations in both the seasonality

of sandeel availability and seabird breeding phenology may then result in changes in the synchrony of predator and prey (Lewis et al. 2001).

This study investigates the impacts of variation in both sandeel phenology and abundance on hatching, fledging and overall breeding success of members of a North Sea seabird community where sandeels are an important prey (Wanless et al. 2018). Variation in the phenology of older sandeels is difficult to assess and requires dedicated repeated surveys to assess the timing of both their appearance (i.e. emergence from the sand) and disappearance (i.e. condition-dependent decrease in activity) from the water column. However, the timing of age-0 sandeel availability can be derived from the appearance of newly hatched larvae in repeated plankton surveys (Wright & Bailey 1996, Régnier et al. 2017, 2019). As older sandeels, of which the most abundant age class is age 1, are available to pre-breeding and breeding seabirds, and due to the lack of phenology data, this age class was considered just in terms of abundance (based on standardised surveys). However, as age-0 biomass proportion and body size increase significantly in the diet of chicks or parents during the chick-rearing period (Lewis et al. 2001, Wilson et al. 2004, Howells et al. 2017) and phenology could be estimated for this age class, we were able to consider both their abundance and timing of availability.

We first developed a sandeel growth model to estimate key elements of age-0 phenology in order to assess the combined effects of trophic asynchrony and sandeel abundance on measures of seabird hatching and fledging success. In order to gain a deeper understanding of the relative contribution of prey phenology and abundance during incubation and chick rearing, 5 species were considered: black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake), Atlantic puffin *Fratercula arctica* (hereafter puffin), razorbill *Alca torda*, common guillemot *Uria aalge* (hereafter guillemot) and European shag *Gulosus aristotelis* (hereafter shag). The response of hatching success to sandeel age-0 abundance and synchrony was expected to be the strongest in kittiwakes, razorbills and guillemots, due to their relatively late incubation periods (Burthe et al. 2012), resulting in overlap between the incubation period and age-0 sandeel availability, and the presence of 0 group in the diet during incubation (Lewis et al. 2001, Wilson et al. 2004, Daunt et al. 2008). Of the 3 species, the strongest response was expected in kittiwakes due to their poor ability to dive and to switch prey, making them generally more sensitive to variation in prey availability (Furness & Tasker 2000). Smaller effects were expected on the hatching success

of shags and puffins, as their timing of laying is earlier than that of the other 3 species (Burthe et al. 2012), resulting in little overlap between incubation and age-0 sandeel availability, and limited importance of this age class of sandeel in diet during incubation in shags (Howells et al. 2017; little is known about the diet of puffins during incubation). All seabird species are considered to rely on age-1 sandeel during incubation (Lewis et al. 2001, Wilson et al. 2004, Daunt et al. 2008, Howells et al. 2017, Wanless et al. 2018, Harris et al. 2022; again, note the limited information on adult puffin diet at this time), and so a positive effect of age-1 abundance was predicted. The relationship between hatching success and age-1 sandeel abundance was expected to be strongest in kittiwakes, again due to their sensitivity to variation in prey abundance, and the importance of this age class in their diet during incubation (Lewis et al. 2001). Puffins and shags were predicted to be more sensitive than razorbills and guillemots due to the timing of incubation relative to 1-group availability. Age-0 sandeels are a very important prey resource during chick-rearing in all species except guillemot and shag (Wanless et al. 2018). However, while age-0 sandeels are generally not fed to guillemot chicks, because the adults are single-prey loaders, it is important in the diet of adults in this population (Wilson et al. 2004). Furthermore, 0-group sandeels are an important component of shag diet in some years (Howells et al. 2017). All species are therefore expected to respond to both age-0 sandeel abundance and synchrony during chick-rearing. However, we predicted the response of fledging success to both age-0 abundance and synchrony to be strongest in kittiwakes (Furness & Tasker 2000), followed by puffin and razorbill. As age-0 sandeels are not as important a component in the diet of shags (Howells et al. 2017), and, for guillemots, are only important in the diet of adults, we expected that fledging success would show a weaker response to age-0 sandeel abundance and synchrony than the other 3 species. Age-1 sandeels are an important prey item for both parents and chicks in all species, are likely to be present for much of the day in or close to the sea floor and are characterised by an earlier seasonal decrease in activity than age-0 sandeels (Bergstad et al. 2002, Haynes et al. 2007, Rindorf et al. 2016). The response of fledging success to this variable is expected to depend on the importance in chick-rearing diet (highest in shag and guillemot; Howells et al. 2017, Wanless et al. 2018) and species-specific abilities to dive and switch prey (Furness & Tasker 2000, Thaxter et al. 2010, Dunn et al. 2019). Thus, we predicted the strongest response to age-1 sandeel abundance to be, in order, shags, guillemots,

kittiwakes, puffins and razorbills. We also predicted that the extent to which the effects of synchrony would be reinforced or compensated by sandeel abundance would depend on species-specific abilities to dive and switch prey, with kittiwakes more likely to involve reinforcement and diving species to involve compensation.

Our specific objectives in this study were to quantify (1) the temporal variation in sandeel phenology and abundance, (2) the overlap between sandeel phenology and the incubation and chick-rearing periods of the 5 seabird species and (3) whether seabird hatching and fledging success were dependent on the temporal overlap with age-0 sandeels and/or abundance of age-0 and age-1 sandeels. The overall aim was to test whether variation in productivity of members of this seabird community was better explained by the MMH or the MMAH. The potential consequences of these relationships given the forecasted changes in environmental conditions in this region were then considered.

2. MATERIALS AND METHODS

2.1. Data sources

The data used in this study were collected between 2000 and 2016 on the Scottish East coast, between the Firth of Forth to the south and Stonehaven to the north for sandeel data and on the Isle of May National Nature Reserve (within the Firth of Forth) for seabirds (Fig. 1). The sandeel study area covers the majority of the foraging range of breeding seabirds on the Isle of May (Wakefield et al. 2017) and a well-mixed component of the SA4 stock (Wright et al. 2019). Sandeel data consisted of observations from various surveys and gears (see Text S1 & Table S1 in the Supplement at www.int-res.com/articles/suppl/m727p001_supp. pdf) composed of (1) length-at-date data used to fit the age-0 sandeel growth model and estimate key life-history traits (growth rate, phenology) and (2) abundance data to use as a covariate in models of seabird breeding success. Sandeel age-0 and age-1 abundances are presented in Fig. 2.

Data on a range of breeding parameters for the 5 species of seabird were compiled from standardised monitoring studies carried out annually on the Isle of May between 2000 and 2016 (Fig. 2; Table S2). These breeding parameters included phenology with laying, hatching and fledging dates (Text S2) and measures of hatching, fledging and breeding success. The same study plots were used to monitor year-specific hatching success (proportion of nests where an egg was laid where hatching occurred) and fledging success (proportion of nests with hatched chicks where fledging occurred). In order to keep breeding success on the same scale for all species (single and multiple egg layers), this measure was calculated as the product of hatching and fledging success (clutch size was not
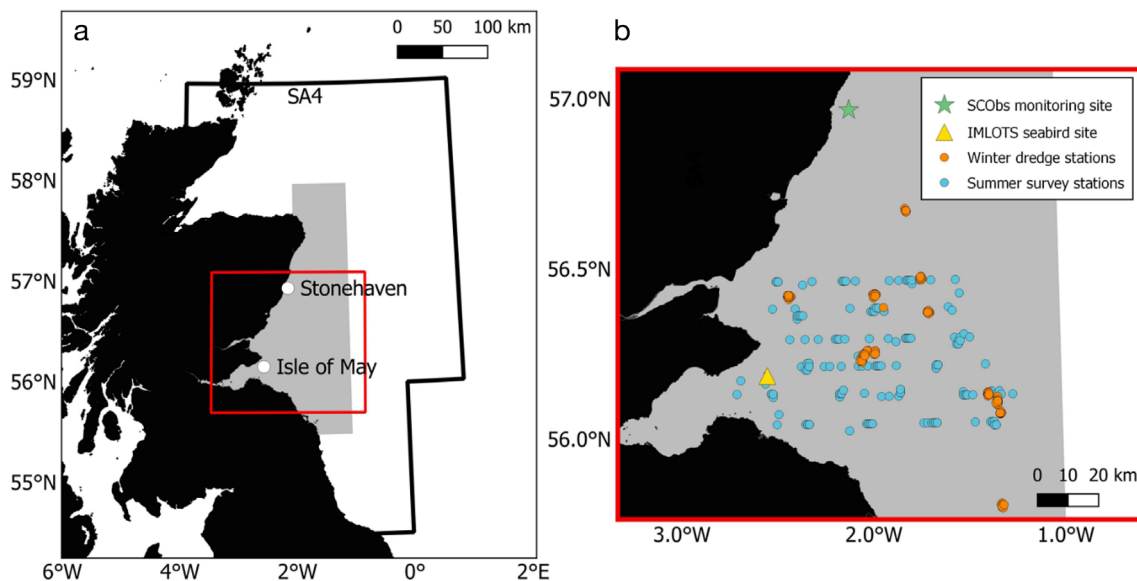

Fig. 1. (a) Overview of the northeast UK coast, showing ICES sandeel management area SA4 (delimited by a solid black line), sandeel closed area (shaded grey) and long-term monitoring sites at Stonehaven and the Isle of May (white circles). (b) Close-up of the study area (red frame in panel a) indicating positions of the Scottish Coastal Observatory (SCObs) monitoring site at Stonehaven, Isle of May Long-Term Study (IMLOTS) site and winter dredge and summer sandeel surveys in the Firth of Forth
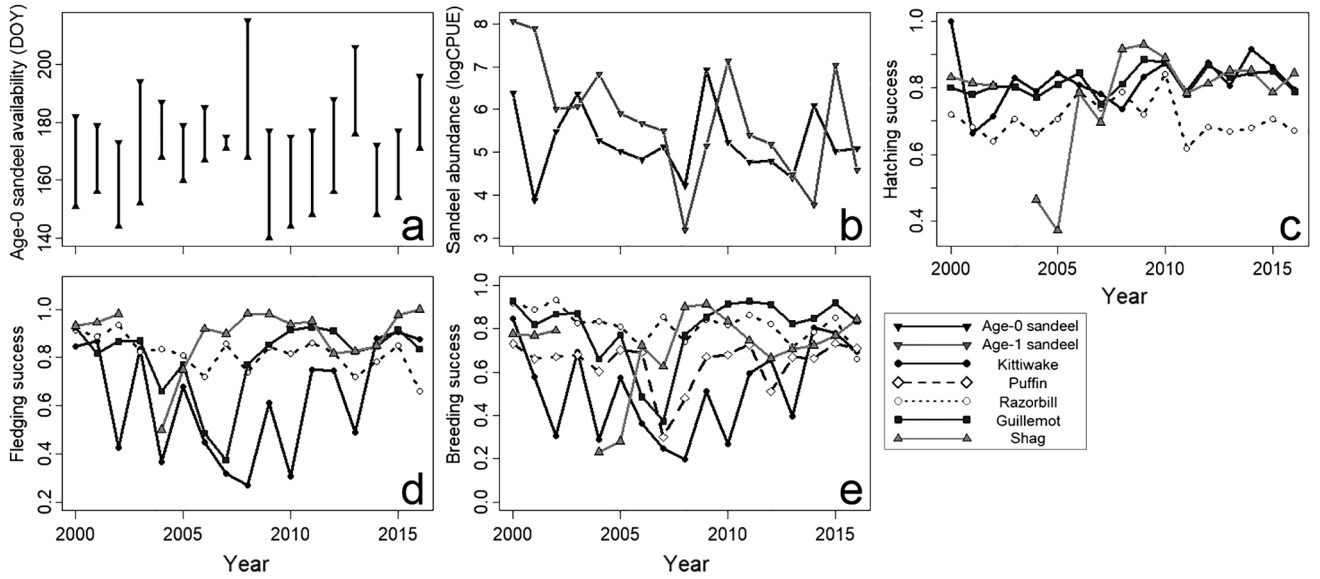
Fig. 2. (a) Estimated period (day of year; black lines) of age-0 sandeel *Ammodytes marinus* availability. The bottom triangles correspond to the start peak in availability (average date at which age-0 sandeel reach a size of 50 mm) while the top triangles represent the peak end (average date at which age-0 sandeel have reached 95% of age-0 asymptotic size, *L*inf). (b) Sandeel abundance from winter surveys in the Firth of Forth for age 0 (black solid line) and age 1 (grey solid line) in catch per hour (CPUE: catch per unit effort). Also shown are annual variation in seabird (c) hatching, (d) fledging and (e) breeding success

used in the product). Annual mean number (and range) of pairs sampled for each species for phenology and breeding data during the study were: kittiwake 156 (88−225), puffin 176 (132−196), razorbill 173 (121−209), guillemot 867 (761−990) and shag 79 (43−134), summarised in Table S2. Puffins carrying fish destined for chicks were caught in mist-nets at approximately weekly intervals throughout the chick-rearing period, and sandeels were measured (snout to tip of tail to the nearest mm) and aged by otolith macrostructure.

Sea temperature data, used to assess the relevance of the sandeel growth model parameters, were collected at a depth of 45 m at the Marine Directorate (MD) coastal ecosystem monitoring site in Stonehaven (Scottish Coastal Observatory: https://data.marine.gov.scot/dataset/scottish-coastal-observatory-stonehaven-site) in parallel with the biological sampling (Fig. 1).

2.2. Sandeel growth model

Sandeel age-0 growth was modelled using a Bayesian hierarchical framework (Fig. S1) relying on observed length (total length: TL)-at-date data obtained from various sources (surveys, bird diet) which together provided 33 598 data points (Table S1). Observation error was modelled as:

$$obsTL_{it} \sim Normal\left(TL_{it}, \sigma^2_{sampler}\right) \quad (1)$$

where $obsTL_{it}$ (in mm) is the observed total length of individual i measured at time t (day of the year) and $\sigma^2_{sampler}$ is a source-specific variance term accounting for both potential measurement error and deviation from a 'true' total length modelled with a Gompertz growth function as:

$$TL_{it} = L0 + Linf_i \times \exp\left(-\exp\left(-K_i \times (t_i - Ti_i)\right)\right) \quad (2)$$

where $L0$ is an offset value corresponding to size at hatching, $Linf_i$ is the asymptotic size, K_i is a growth rate coefficient, and Ti is the date (day of the year) of the inflection point used as a proxy for settlement. The parameters Ti_i, $Linf_i$ and K_i were estimated at the individual level while initial size, $L0$, was assumed to be constant. The program JAGS (Plummer 2003) was used to run the model through an R interface (R 4.1.2; R Core Team 2021) using the 'rjags' package (a detailed description of the model can be found in Text S3).

2.3. Sandeel phenology

The dependence of age-0 sandeel growth rate (K) on food availability and water temperature was tested using a generalized linear model (GLM) with quasibinomial error and logit link with growth rate (K) as the dependent variable and the measure of asynchrony be-

tween sandeel hatching and egg production of their copepod prey (from Régnier et al. 2019), average temperature in the 60 d following sandeel hatching and their interaction fitted as independent variables. The relevance of the Ti parameter as a proxy for settlement date was measured against the date of settlement, values back-calculated from age-0 sandeel otoliths (Régnier et al. 2017) using a linear model. Age-0 sandeels appear in seabird diets after settlement; therefore, the date at which sandeels reached a size of 50 mm was used as a proxy for the start of the seasonal peak in age-0 sandeel availability (hereafter $sandeelSTART_y$). While smaller sandeels are observed in puffin diet, their corresponding energetic content is very low (Wanless et al. 2005), and 75% of age-0 sandeels in puffin diet in 1999–2016 were above this threshold size. This measure therefore incorporates elements of phenology and prey quality and is indicative of the availability of profitable prey. The end of the seasonal peak in age-0 sandeel abundance (hereafter $sandeelEND_y$) was assumed to occur when sandeels reached their maximum length during the first year and their growth ceased. The asymptotic nature of the growth model results in important variation in the date at which the asymptotic size is reached (Linf); therefore as a conservative measure, the end of the seasonal peak in age-0 sandeel abundance was estimated using the date at which 95% of the asymptotic size was reached. The relevance of this measure as an indication of the end of the seasonal peak in age-0 sandeel availability was assessed visually by comparing these dates to the seasonal decline of large age-0 sandeels in puffin chick diet. The period between $sandeelSTART_y$ and $sandeelEND_y$ corresponds to the period of time during which age-0 sandeels of a profitable size are available.

2.4. Sandeel abundance

The relationships between sandeel recruitment and sandeel growth and phenology were assessed using linear models with log-transformed age-0 sandeel abundance as a measure of recruitment, and parameters of the growth model (growth rate, date at settlement and asymptotic size) and the derived phenology measures ($sandeelSTART_y$ and $sandeelEND_y$) used as independent variables.

2.5. Predator–prey overlap

For each seabird species, 2 indices were calculated to represent the overlap between the incubation period and the period of age-0 sandeel availability ('overlap.inc'), and the overlap between the chick-rearing period and the period of age-0 sandeel availability ('overlap.cr') with:

$$overlap.inc_{s,y} = \frac{\min(sandeelEND_y, Hatch_{s,y}) - \max(sandeelSTART_y, Lay_{s,y})}{(Hatch_{s,y} - Lay_{s,y})} \quad (3)$$

$$overlap.cr_{s,y} = \frac{\min(sandeelEND_y, Fledge_{s,y}) - \max(sandeelSTART_y, Hatch_{s,y})}{(Fledge_{s,y} - Hatch_{s,y})} \quad (4)$$

where $sandeelSTART_y$ and $sandeelEND_y$ are the dates at which sandeel reach 50 mm and 95% of the modelled asymptotic size (Linf, see Eq. 2) in a given year (y). Parameters $Lay_{s,y}$, $Hatch_{s,y}$ and $Fledge_{s,y}$ are the laying, hatching and fledging dates, respectively, for seabird species s in year y. With these formulations, the overlap indices were sensitive to asynchronies at both the start and the end of the period of age-0 sandeel availability. An index close to 1 indicates good synchrony between the incubation or chick-rearing period and age-0 sandeel availability, while an index close to 0 indicates an asynchrony. The use of calculated or back-calculated laying, hatching or fledging dates for some seabird species relies on the assumption that incubation or fledging periods do not vary among years. Observed annual variation in the incubation period was only 5 d in razorbills and 2 d in guillemots between 2000 and 2016, suggesting that this assumption would have limited consequences on the overlap measures.

2.6. Effects of sandeel phenology and abundance on seabird hatching and fledging success

For all seabird species, except puffins, breeding success could be partitioned between hatching success and fledging success. The effects of age-0 and age-1 abundances and trophic asynchrony (overlap.inc, Eq. 3; and overlap.cr, Eq. 4, respectively) on seabird hatching and fledging success were tested in kittiwake, razorbill, guillemot and shag using logistic regressions. For puffins, the effects of age-0 and age-1 abundances and trophic asynchrony (overlap.cr) were tested on breeding success using logistic regression. In order to test whether trophic asynchrony reduces the benefit of high age-0 sandeel abundance or compensates for the negative effects of low age-0 sandeel abundance (i.e. MMAH), the initial models included an interaction between age-0 sandeel abundance and trophic synchrony measures (overlap.inc and overlap.cr). The presence of either positive main

effects of age-0 sandeel abundance and synchrony or a significant interaction between these terms is considered as evidence in support of the MMAH, while only a main effect of a trophic synchrony measure (i.e. no significant interaction with sandeel abundance) is assumed to support the MMH.

Stepwise backward model selection was used to select the best model based on the decrease in deviance and Bayesian information criterion (BIC), as it gives a greater penalty to complex models. All analyses were done in R 4.1.2 (R Core Team 2021).

3. RESULTS

3.1. Sandeel growth model

The model provided a good fit to the data overall (Fig. S2). Sampling processes unaccounted for in the model led to occasional lacks of fit (e.g. year 2010, Figs. S2 & S3) but had minor effects on the predictive power of the model. Model parameters showed variability at the individual level, and similarly, annual parameters were variable (Fig. 3). However, there was no consistent trend in settlement time, size or growth rate,

as indicated by an increase or decrease of the key annual parameters (settlement date Ti, asymptotic size Linf and growth rate K) observed throughout the 17 yr period considered. Initial size at hatching ($L0$) was estimated at 5.33 mm (95% CI: 5.17−5.49 mm), annual hyper parameters Ti (settlement date) varied from Day 119 (late April) to 143 (mid-May, Fig. S4), the growth rate parameter (K) varied from 0.028 to 0.048, and was related to sea temperature and the degree of mismatch between sandeel hatching and egg production in their copepod prey (from Régnier et al. 2019, our Fig. S5). Asymptotic size (Linf) varied from 50.0 to 74.5 mm (Fig. 3). The derived estimates of age-0 sandeel phenology (start and end of the period of age-0 availability) were related to the estimated growth rate and date of settlement, such that fast growth and early settlement both led to an early start and end of the period of age-0 sandeel availability (Fig. S6).

3.2. Sandeel abundance

Indices of sandeel abundance were characterised by marked variation between 2000 and 2016 (Fig. 2b). Abundance of age-0 sandeel (i.e. recruitment) varied
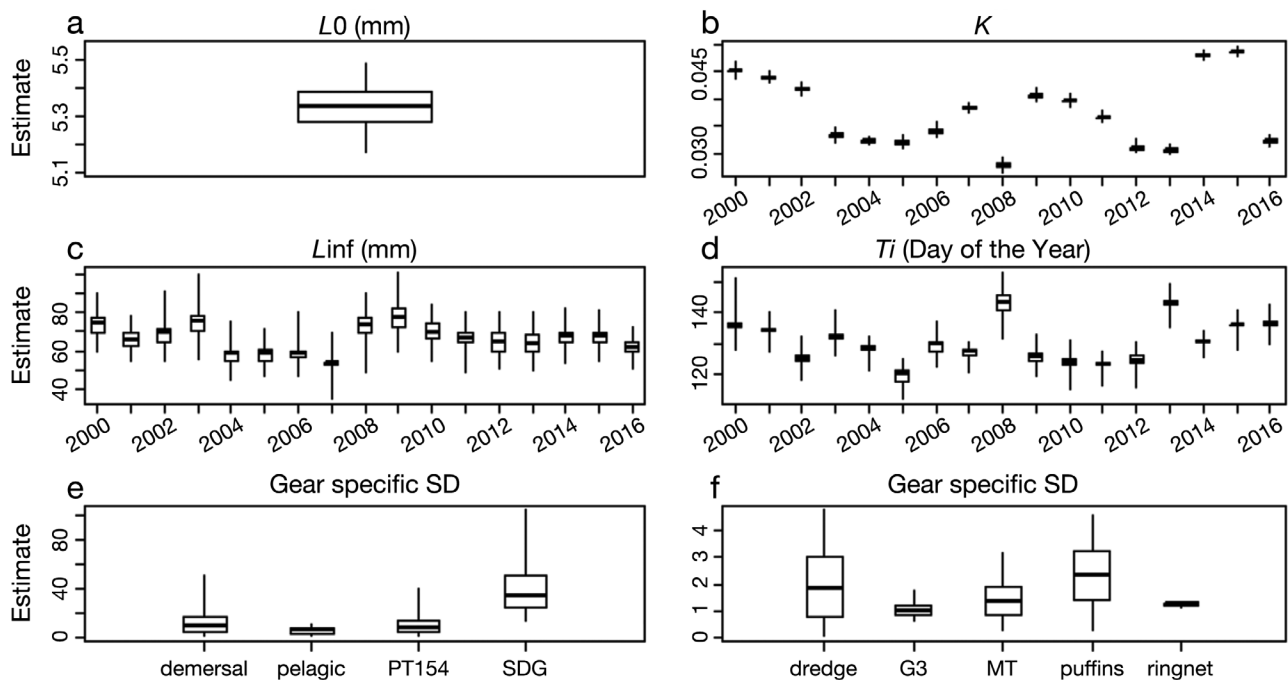

Fig. 3. Sandeel *Ammodytes marinus* growth model outputs showing (a) initial size at hatching ($L0$); trends in key annual parameters: (b) growth rate, K, (c) asymptotic size, Linf, (d) settlement date, Ti; and (e,f) gear-specific standard deviations where 'demersal' = a demersal net, 'pelagic' = a pelagic net ,'PT154' = the International Young Gadoid Pelagic Trawl, 'SDG' = summer dredge survey, 'dredge' = the winter sandeel dredge survey, 'G3' = the Gulf III plankton sampler, 'MT' = the Methot net, 'puffins' = sandeel collected from chick-feeding puffins and 'ringnet' = an ichthyoplankton net, details provided in Text S1. Thick horizontal line: median; box bottom and top: 25% and 75% quantiles, respectively; whiskers: 95% interval of the posterior distributions of estimated parameters

from only 48 individuals caught per hour (in the MD sandeel dredge survey) in 2001, to 1023 ind. h^{-1} in 2009. Similarly, abundance of age-1 sandeel varied from only 24 ind. h^{-1} (in the MD sandeel dredge survey) in 2008 to 3170 ind. h^{-1} in 2000.

3.3. Seabird/sandeel phenology and overlap

No directional trends were detected in the timing of the start of age-0 sandeel availability or kittiwake, puffin, razorbill or guillemot hatching dates over the period considered in this study. However, a monotonic decrease in shag hatching date (towards earlier hatching) was found over the course of the study. The timing of the start of age-0 sandeel availability (Fig. 4) and the start of seabird breeding seasons (Fig. 4) were variable across the study period, although none of the measures showed any consistent trend over time. Seabird incubation periods showed a moderate overlap with the estimated period of age-0 sandeel availability in kittiwake (mean overlap.inc [range] = 0.5 [0–0.96]), virtually no overlap in puffin (0.01 [0–0.1]), little overlap in razorbill (0.2 [0–0.54]) and guillemot (0.17 [0–0.59]) and almost no overlap in shag (0.06 [0–0.6]).

In contrast, there was limited overlap between the chick–rearing period and age 0 sandeel availability in kittiwake (mean overlap.cr [range] = 0.30 [0–0.86]), a good overlap was found in puffin (0.64 [0.1–0.95]), razorbill (0.79 [0.21–1]) and guillemot (0.75 [0.19–1]), and moderate overlap was found in shag (0.44 [0.02–0.77]) (Fig. 4). The measure of overlap between age-0 sandeel availability and the seabird chick-rearing period was related to both the date of the start and end of the period of age-0 sandeel availability (Fig. S7) with the overlap maximised when sandeels settled early and remained active late in the season. However, in kittiwakes, variation in the overlap measure was mostly driven by the end date of the period of age 0 sandeel availability (Fig. S7).

3.4. Seabird productivity (hatching success) and sandeel phenology and abundance

A negative effect of age-1 sandeel abundance and a positive interaction between sandeel age-0 and age-1 abundances were found on kittiwake hatching success. The effect size of the interaction was 4 times superior to the negative effects of age-1 abundance, resulting in hatching success being maximised when both age-0 and age-1 were high (Fig. 5, Table 1). In razorbills, no effects of age-0 or age-1 abundances

or the overlap between age-0 sandeel availability and razorbill incubation period were found (Fig. 5, Table 1). With guillemot hatching success, negative effects of both age-0 abundance and the overlap between age-0 sandeel availability and guillemot incubation period and a positive effect of their interaction were found. However, most of the effect was driven by the interaction between these 2 variables (Fig. 5, Table 1), as the confidence interval of the effect size of age-0 abundance included 0 and the effect size of the interaction term was twice the effect size of the overlap measure. Hatching success was therefore maximised at higher overlap and higher age-0 sandeel abundances (Fig. 5). Age-1 sandeel abundance had no detectable effect on guillemot hatching success (Table 1). As shag incubation period overlapped with the period of age-0 sandeel availability in only 3 out of 16 years, only age-1 abundance was used as an independent variable; however, no significant effect was found (Table 1).

3.5. Seabird productivity (fledging and breeding success) and sandeel phenology and abundance

In kittiwakes, fledging success reflected significant effects of all covariates and their 2-way interactions (Table 2). While the main effects of both age-0 and age-1 abundances were both positive, the effect of the overlap was negative; however, the effect size was small and its confidence interval included 0 (Table 2). Nevertheless, the overlap had a pronounced effect on kittiwake fledging success through its positive interaction with age-0 sandeel abundance (Table 2). The positive effect of age-0 abundance on fledging success was reinforced by a strong overlap (Fig. 6). While the significant interaction between age-0 and age-1 sandeel abundance had a clear negative effect size (Table 2), the positive effects of these variables as main effects resulted in fledging success being poor when both age-0 and age-1 abundances were low. However, the benefits to fledging success of an increase in age-1 sandeel abundance decreased with increasing age-0 abundances (and vice versa, Fig. 6).

In puffins, breeding success could not be partitioned between hatching and fledging success but overall breeding success was found to vary with all covariates and their 2-way interactions (Table 2). In particular, high age-0 sandeel abundance seemed to compensate for a low overlap between age-0 sandeel availability and the chick-rearing period, and conversely, a good overlap compensated for a low abundance of age-0 sandeel (Fig. 6, Table 2). Accordingly,
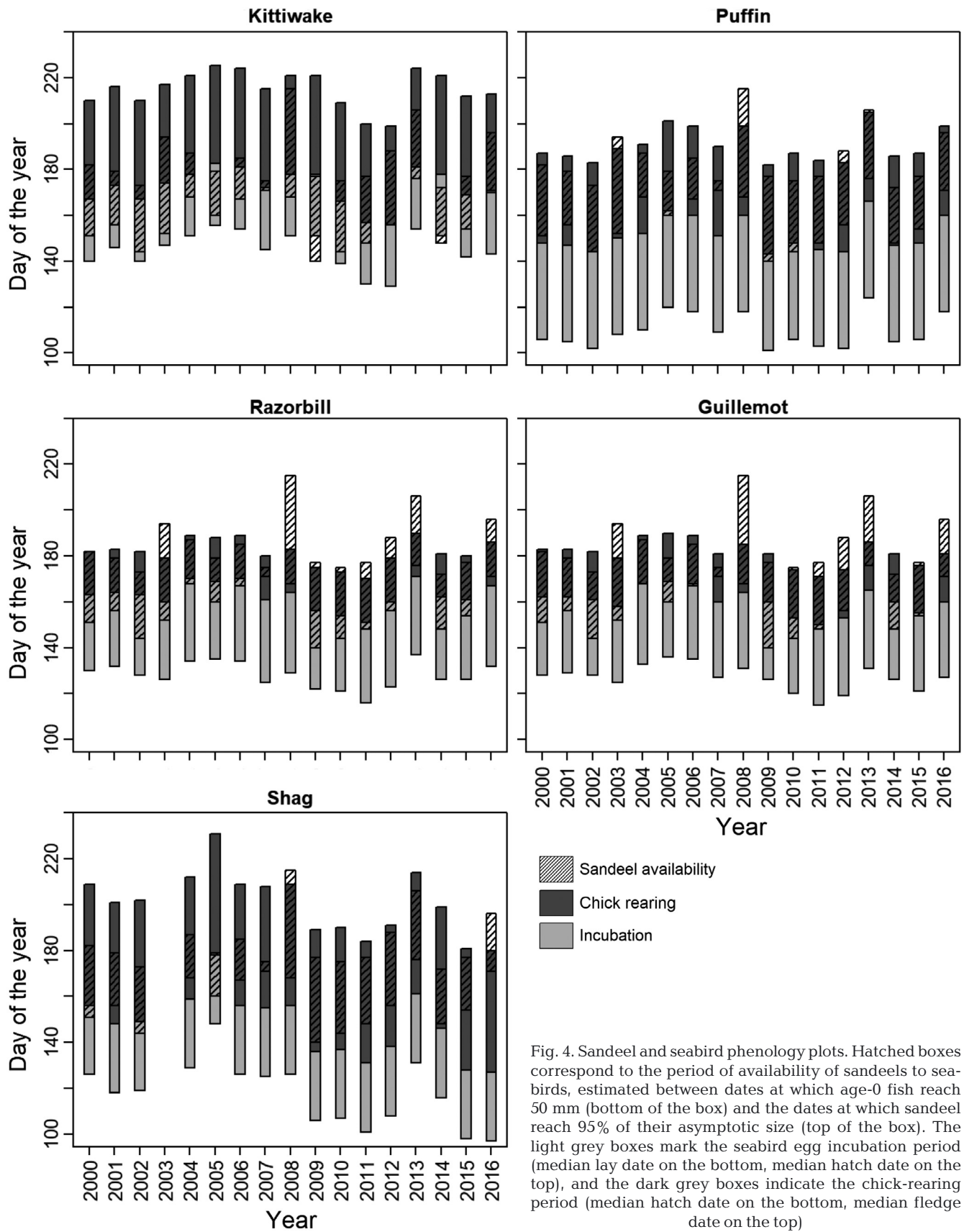
Fig. 4. Sandeel and seabird phenology plots. Hatched boxes correspond to the period of availability of sandeels to seabirds, estimated between dates at which age-0 fish reach 50 mm (bottom of the box) and the dates at which sandeel reach 95% of their asymptotic size (top of the box). The light grey boxes mark the seabird egg incubation period (median lay date on the bottom, median hatch date on the top), and the dark grey boxes indicate the chick-rearing period (median hatch date on the bottom, median fledge date on the top)
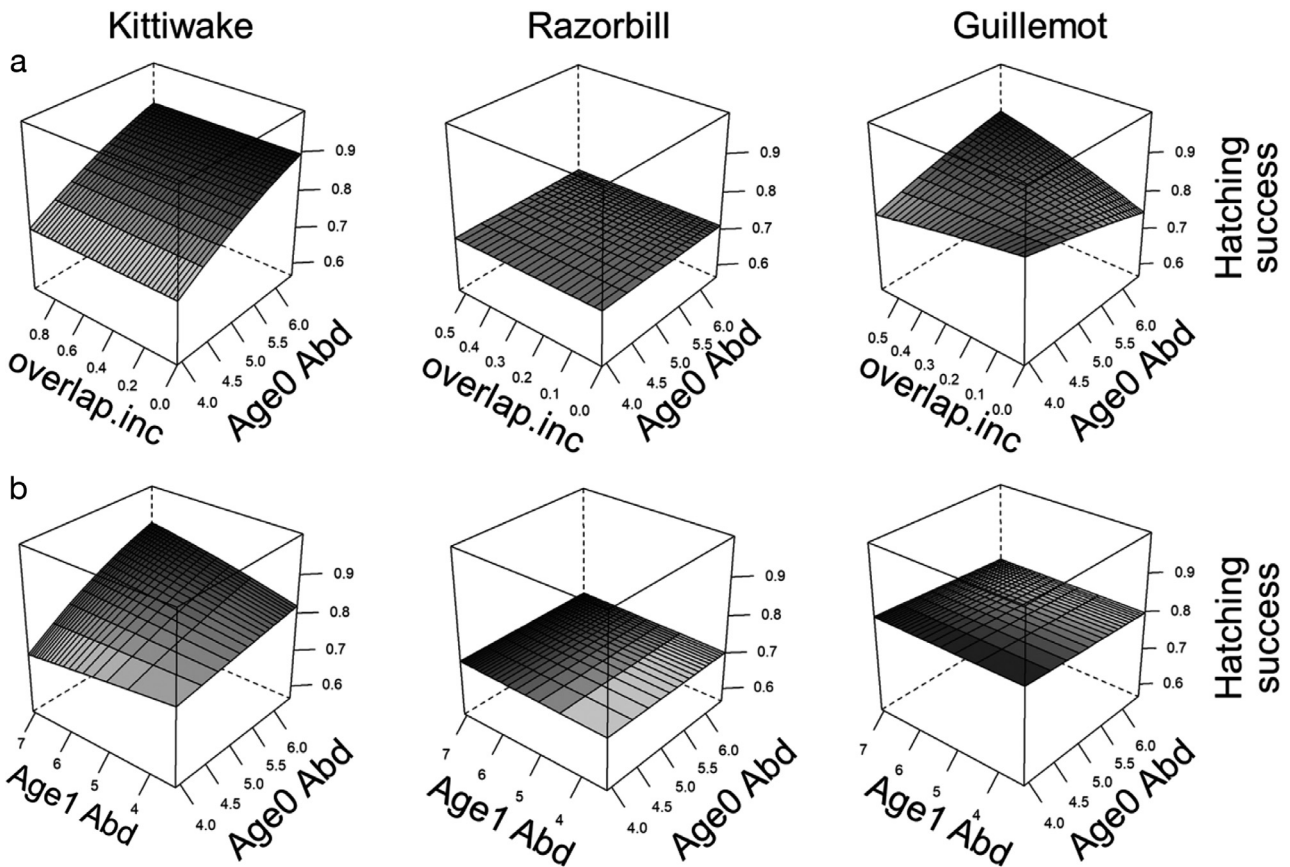
Fig. 5. Relationship between hatching success in black-legged kittiwake, razorbill and common guillemot and the model covariates with (a) the measure of overlap between the incubation period ('overlap.inc') and the period of age-0 sandeel availability and age-0 sandeel abundance (age-1 sandeel abundance fixed at the average value) and (b) age-0 sandeel abundance and age-1 sandeel abundance (the measure of overlap between the incubation period and the period of age-0 sandeel availability fixed at the average value). To obtain these figures, stepwise backward selection was applied to the respective generalized linear models until either the best model was selected or the model included only the single effects described above

Table 1. Outputs of the generalized linear model (logistic regression) used to assess the effect of seasonal sandeel availability on seabird hatching success. Overlap.inc: overlap between the incubation period and the period of age-0 sandeel availability. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.0001$

Species	Predictors	Estimate (SE)	Effect size (95% CI)	p	Pseudo-R^2
Kittiwake	Intercept	2.45 (1.35)	1.36 (1.15, 1.57)	0.07	0.3
	log(age-0 sandeel abundance)	−0.25 (0.28)	0.05 (−0.29, 0.41)	0.36	
	log(age-1 sandeel abundance)	−0.5 (0.23)	−0.39 (−0.7, −0.07)	0.03*	
	log(age-0 sandeel abundance) × log(age-1 sandeel abundance)	0.11 (0.048)	1.54 (0.87, 2.28)	0.02*	
Razorbill	Intercept	0.81 (0.18)	0.85 (0.74, 0.96)	<0.0001***	0.004
	log(age-1 sandeel abundance)	0.013 (0.03)	0.08 (−0.1, 0.26)	0.67	
Guillemot	Intercept	2.24 (0.26)	1.51 (1.43, 1.59)	<0.0001***	0.26
	log(age-0 sandeel abundance)	−0.16 (0.053)	−0.18 (−0.34, −0.02)	0.0024**	
	Overlap.inc	−4.1 (0.99)	−0.07 (−0.16, 0.02)	<0.0001***	
	log(age-0 sandeel abundance) × overlap.inc	0.81 (0.18)	0.33 (0.18, 0.48)	<0.0001***	
Shag	Intercept	1.95 (0.31)	1.27 (1.08, 1.46)	<0.0001***	0.04
	log(age-1 sandeel abundance)	−0.11 (0.05)	−0.03 (−0.32, 0.26)	0.02*	

Table 2. Outputs of the generalized linear model (logistic regression) used to assess the effect of sandeel availability on seabird fledging success (or breeding success in puffins). *p < 0.05, **p < 0.01, ***p < 0.0001

Species	Predictors	Estimate (SE)	Effect size (95% CI)	p	Pseudo-R^2
Kittiwake	Intercept	−16.45 (1.95)	−0.58 (−0.84, −0.34)	<0.0001***	0.39
	log(age-0 sandeel abundance)	3.22 (0.34)	2.65 (2.06, 3.28)	<0.0001***	
	overlap.cr	−10.99 (2.13)	−0.15 (−0.31, 0.02)	<0.0001***	
	log(age-1 sandeel abundance)	2.84 (0.3)	1.12 (0.72, 1.52)	<0.0001***	
	log(age-0 sandeel abundance) × overlap.cr	2.68 (0.43)	1.65 (1.17, 2.18)	<0.0001***	
	log(age-0 sandeel abundance) × log(age-1 sandeel abundance)	−0.56 (0.06)	−2.12 (−2.73, −1.51)	<0.0001***	
Puffin	Intercept	−9.43 (2.571)	0.30 (0.09, 0.50)	0.0002***	0.46
	log(age-0 sandeel abundance)	1.58 (0.472)	0.38 (−0.03, 0.79)	0.0008***	
	overlap.cr	8.13 (2.759)	0.35 (0.17, 0.53)	0.002**	
	log(age-1 sandeel abundance)	0.695 (0.172)	0.50 (0.22, 0.78)	<0.0001***	
	log(age-0 sandeel abundance) × overlap.cr	−1.28 (0.517)	−0.28 (−0.64, 0.06)	0.01*	
	log(age-0 sandeel abundance) × log(age-1 sandeel abundance)	−0.1 (0.032)	−0.28 (−0.65, 0.09)	0.0018**	
Razorbill	Intercept	0.22 (0.24)	1.19 (1.04, 1.34)	0.36	0.44
	log(age-1 sandeel abundance)	0.22 (0.04)	0.69 (0.41, 0.98)	<0.0001***	
Guillemot	Intercept	−0.64 (0.19)	1.21 (1.12, 1.30)	0.0007***	0.29
	log(age-0 sandeel abundance)	0.19 (0.03)	0.42 (0.30, 0.54)	<0.0001***	
	overlap.cr	1.91 (0.1)	0.40 (0.35, 0.45)	<0.0001***	
	log(age-1 sandeel abundance)	−0.06 (0.02)	0.05 (−0.07, 0.18)	0.002**	
Shag	Intercept	8.92 (3.76)	2.35 (1.98, 2.74)	0.01*	0.08
	log(age-0 sandeel abundance)	−1.45 (0.75)	−0.20 (−0.87, 0.49)	0.05	
	overlap.cr	−12.7 (7.02)	−0.17 (−0.62, 0.24)	0.07	
	log(age-0 sandeel abundance) × overlap.cr	2.8 (1.41)	1.10 (0.10, 2.38)	0.04*	

breeding success was maximised when both age-0 and age-1 sandeel abundances were high (Fig. 6, Table 2). However, only the overlap between age-0 sandeel availability and chick-rearing period or age-1 sandeel abundance had effect sizes departing from 0 (Table 2), resulting in an increased fledging success. In contrast, fledging success of razorbills was only influenced by a positive effect of age-1 sandeel abundance (Fig. 6, Table 2). In guillemots, while a marginal negative effect of age-1 abundance was found (noting that the confidence interval of effect size included 0), fledging success was mostly positively influenced by both age-0 sandeel abundance and the overlap between age-0 sandeel availability and guillemot chick-rearing period (Fig. 6, Table 2). Most of the variation was driven by the latter effect, with fledging success maximised by a strong overlap (Fig. 6).

In shags, the main effects of the overlap between age-0 sandeel availability and chick-rearing period, age-0 and age-1 abundance were not significant but a weak but significant interaction between age-0 sandeel abundance and the overlap between age-0 sandeel availability and the chick-rearing period was found on fledging success, which was marginally higher when age-0 sandeel were abundant and their availability overlapped with the chick-feeding period (Fig. 6, Table 2). However, as the model explained a negligible amount of the variation in fledging success, this interaction must be regarded with caution (Table 2).

4. DISCUSSION

This study demonstrates that some aspects of seabird productivity can be better explained by the MMAH than the MMH, in that high prey abundance was found to compensate or reinforce the MMH response in some circumstances. Durant et al. (2005) first demonstrated the concept of the MMAH by showing that herring abundance was the most important factor explaining puffin chick survival in the Norwegian Sea and models improved when a time component was added. However, very little empirical support for the MMAH has been reported since (but see Regular et al. 2014), with
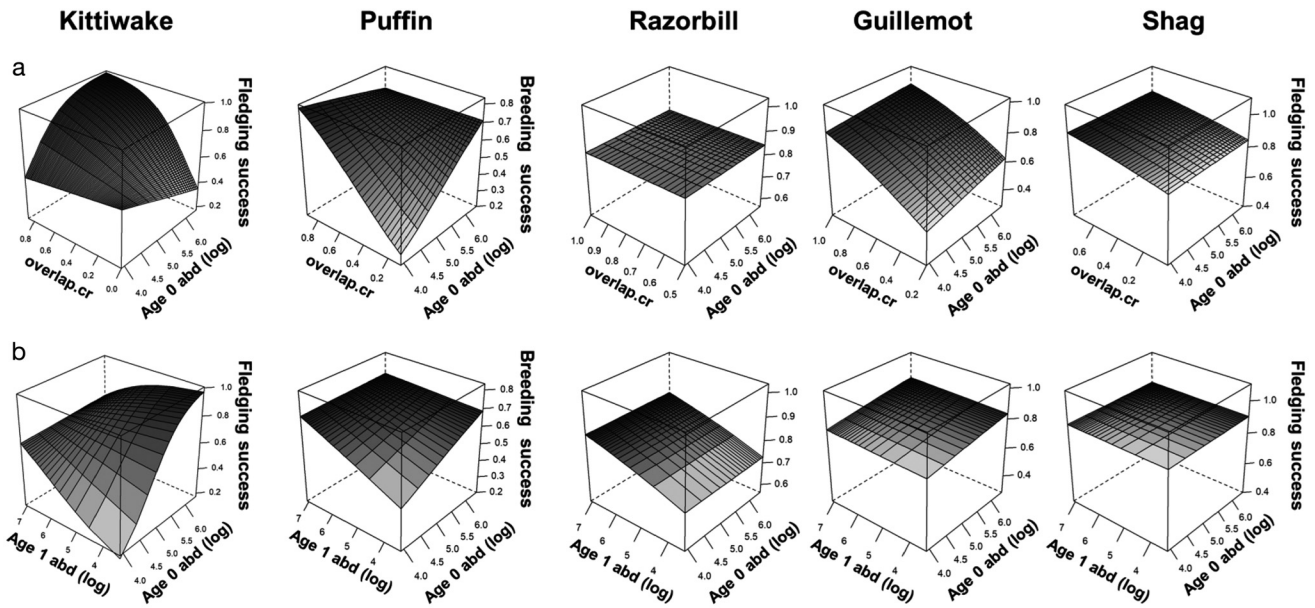
Fig. 6. Relationship between fledging success (or breeding success for puffins) in the respective seabird species and the model covariates with (a) the measure of overlap between the chick-rearing period ('overlap.cr') and the period of age-0 sandeel availability and age-0 sandeel abundance (age-1 sandeel abundance fixed at the average value) and (b) age-0 sandeel abundance and age-1 sandeel abundance (the measure of overlap between the chick-rearing period and the period of age-0 sandeel availability fixed at the average value). To obtain these figures, stepwise backward selection was applied to the respective generalized linear models until either the best model was selected or the model included only the single effects described above

either support for an effect of mismatch but not abundance (i.e. MMH) on seabird breeding success (Hipfner 2008, Watanuki et al. 2009) or support for the role of prey abundance but not mismatch (Burthe et al. 2012). Beyond supporting the MMAH, the present study indicates (1) how the interaction of asynchrony and prey abundance affects productivity differently in different members of a seabird community, and (2) that interspecific differences in seabird breeding phenology, diet and feeding ecology determined the sensitivity of the different phases of the breeding period to variations in abundance and seasonality of this prey.

Trophic synchrony affected hatching or fledging success in most species. In species where an effect of overlap was found, high synchrony was often reinforced by age-0 sandeel abundance and in some species age-1 abundance. Furthermore, in some cases, low synchrony was compensated for by high age-0 sandeel abundance.

As expected from prior observations on seabird and sandeel phenologies (Burthe et al. 2012, Gibb et al. 2017), the period of age-0 sandeel availability overlapped more with the energy-demanding chick-feeding period than with the incubation period in all species except the kittiwake (Table 3). The late breeding schedules in this species resulted in incubation taking place at a time when both age-0 sandeel and older age groups are actively foraging close to the surface.

As a result, prey abundance was only found to influence hatching success in kittiwakes, with higher hatching success observed when both age-0 and age-1 sandeels were abundant (Table 3). Prey availability is more limiting during the energy-demanding chick-feeding period in kittiwakes, potentially as a result of the late breeding period and limited abilities to dive and use alternative prey (Lewis et al. 2001, Wanless et al. 2018). In accordance, fledging success was maximised in years characterised by high sandeel abundance (age 0 and 1) and, in support of the MMAH, the effect of age-0 sandeel abundance on kittiwake fledging success was reinforced by a good synchrony with the period of age-0 sandeel availability (Table 3). These results are consistent with the findings of earlier studies in which kittiwake breeding success was found to be related to the abundances of age-0 and older age classes (Daunt et al. 2008, Burthe et al. 2012), and poor breeding success was observed in years when kittiwakes struggled to find food at the time of the transition from age-1+ to age-0 sandeels in their diet (Lewis et al. 2001). The combination of high age-0 and age-1 sandeel abundance and a good synchrony with age-0 sandeel availability likely result in a smooth transition between age classes, favouring both self and chick feeding.

In the earlier-breeding puffin, breeding success was found to depend mostly on age-1 sandeel abundance

Table 3. Summary of the effects of overlap and sandeel age-0 and age-1 abundances ('Abd0' and 'Abd1', respectively) on the various components of seabird breeding success. A lack of effect (not significant or effect size not different from 0) is indicated by an empty cell, while positive and negative effects are indicated by '+' and '−', respectively ('overlap' corresponds to overlap.inc for hatching success and overlap.cr for fledging and breeding success; see Eqs. 3 & 4)

Species	Component	Overlap	Abd0	Abd1	Overlap × Abd0	Abd0 × Abd1
Kittiwake	Hatching success			−		+
	Fledging success		+	+	+	−
Puffin	Breeding success	+		+		
Razorbill	Hatching success					
	Fledging success			+		
Guillemot	Hatching success		−		+	
	Fledging success	+	+			
Shag	Hatching success					
	Fledging success				+	

and the synchrony between the chick-rearing period and age-0 sandeel availability (Table 3). The effect of age-1 abundance found in the present study is contrary to earlier findings of a lack of effect of sandeel abundance on breeding success (Daunt et al. 2008). The difference likely results from both the different time scales between the studies (only 4 years in common between the 2 time series) and a measure of sandeel abundance in the earlier study that is more sensitive to seasonal and daily variation in sandeel behaviour. However, this result is in accordance with another study finding that puffin breeding success was higher in the year following a high age-0 sandeel biomass index (i.e. age 1 at the time of the measure, Burthe et al. 2012). Nevertheless, the effect of synchrony on puffin breeding success is contrary to the findings of Burthe et al. (2012), and taken together, the present results are supportive of MMAH with the cost of temporal asynchrony compensated by high sandeel abundance in the earlier-breeding puffin.

In the razorbill, a moderate positive effect of age-1 sandeel abundance was found on fledging success (Table 3), in contrast to earlier studies that found no such effect (Daunt et al. 2008, Burthe et al. 2012). The availability of age-1 sandeels as higher-quality prey may have enhanced fledging success, as this sandeel age class is found in the diet of razorbill chicks (Wanless et al. 2018), and razorbills appear to be sensitive to variation in prey size (Thaxter et al. 2013). However, the lack of effect of synchrony with age-0 sandeels is surprising, since this age class forms a markedly greater proportion in the diet than age-1 sandeels (Wanless et al. 2018), The time series for razorbills was composed of years with consistently high annual fledging success and strong overlap with age-0 sandeel availability. The comparatively small variation in both measures may have precluded the

detection of effects in this species. Additionally, the considerable increase in the proportion of clupeids in chick diet observed over the last 2 decades (Wanless et al. 2018) may indicate a strong ability of this species to switch prey.

Despite similar breeding schedules in guillemots and razorbills, effects differed between the species such that hatching and fledging success in guillemots were both influenced by age-0 sandeel abundance and the synchrony between age-0 sandeel availability (Table 3). The effects of synchrony and prey abundance reinforced each other through a positive interaction for hatching success but more substantially, their additive effects compensated each other for fledging success (Table 3). Guillemots are single-prey loaders and feed their chicks with high-quality prey, mostly comprising age-1 sandeels and clupeids (Wanless et al. 2018). However, guillemot parents also feed on lower-quality prey, mainly age-0 sandeels (Wilson et al. 2004, Thaxter et al. 2013), and high age-0 sandeel availability may benefit both hatching and fledging success by decreasing the pressure on energy budgets (Thaxter et al. 2013, Regular et al. 2014, Wanless et al. 2023) with positive consequences on chick-provisioning rates (Regular et al. 2014). These results are therefore supportive of the MMAH.

We found no effect of sandeel abundance and synchrony on hatching success and very weak effects on fledging success in shags, despite sandeels being prominent in the diet. However, the results support recent findings of Keogan et al. (2021), who reported no apparent relationship between proportion of sandeels in the diet and breeding success. The ability of shags to take a wide variety of prey (Furness & Tasker 2000), as observed on the Isle of May (Howells et al. 2017, 2018, Wanless et al. 2018), may allow them

to compensate for a lack of sandeels as a primary resource. However, the lack of a meaningful relationship found in the present study must be considered with caution, as sandeel abundance data originate from stations outside of the shag foraging range (Bogdanova et al. 2014), and differences in sandeel population dynamics have been found over distances above 29 km (Jensen et al. 2011).

These results deviate from the findings of an earlier study which identified trophic mismatch between age-0 sandeel phenology and seabirds in the same seabird species and colony but found no consequence on breeding success (Burthe et al. 2012). While there is only a 6 yr overlap between the time series used by Burthe et al. (2012) and our study, the present findings are expected to hold for the period covered by Burthe et al. (2012), and the lack of consistency is likely a result of methodological differences, particularly on the sandeel component. The sandeel phenology estimates in the present study are derived from a model providing a more accurate representation of sandeel growth as it uses a greater number of sources covering a larger part of the first year of growth (plankton samples, seabird diet, summer and winter surveys), and the model accounts for the major effect of metamorphosis on sandeel growth. In addition, the mismatch measures used in both studies are not similar. Burthe et al. (2012) measured the difference between the date of the mid-point of the chick-rearing period and the date at which sandeels reach a threshold size of 55 mm, while the present study considers the overlap between the periods of age-0 sandeel availability and both incubation and chick-rearing periods in seabirds.

Taken together, our findings identify the specific links between seasonality in prey availability and the different components of seabird breeding success. The study species showed differing responses in terms of their sensitivity to conditions at different times of the breeding season, and the relative importance of timing and abundance of prey. Notwithstanding some exceptions, our results broadly followed our expectations based on seabird breeding phenology, diet and foraging ecology. We found that the surface-feeding kittiwake was sensitive to overlap and abundance of its sandeel prey, whereas effects on diving species were either limited/absent (razorbill and shag) or were such that abundance could compensate for poor overlap (puffin). The species that contrasted somewhat with expectations was the guillemot, where effects of overlap were reinforced by sandeel abundance on hatching success, as was the case in the kittiwake, but compensated low sandeel abundance on fledging success. Guillemots have the greatest diving capacity of the study species considered here, and they have the ability to switch prey as evidenced by the increasing importance of clupeids in chick diet over the course of the study (Wanless et al. 2018). Our results therefore suggest that the importance of sandeels in self-feeding diet and the constraint of single-prey loading may be critical in explaining the sensitivity of this species to timing and availability of this prey type (Wanless et al. 2023). Differences between these seabird species are therefore related to their foraging traits. This assertion is supported by a study showing that razorbills in the Baltic are often single-prey loaders, and their self-maintenance is more sensitive to variation in high-quality prey during the chick-rearing period than guillemots, potentially because of their more limited diving capacity (Hentati-Sundberg et al. 2021).

Our study suggests that a trophic synchrony measure that accounts for an overlap between periods of prey availability and predator requirements is a more useful measure of predator–prey interactions than those based on distance between peak predator requirements and peak prey availability. Puffins have a protracted chick-rearing period that benefits from conditions promoting an early start and a late end of sandeel availability, while conditions promoting later sandeel availability favour kittiwakes. In contrast, the short chick-rearing period of guillemots results in decreased fledging success when age-0 sandeel availability has an early start.

These findings suggest that, in addition to seabird breeding schedules, the sensitivity of seabird breeding success to variations in prey abundance and availability is also modulated by other life-history traits in the study species. In particular, the effects observed on hatching success or the effect of the abundance and availability of a prey not usually fed to chicks in guillemots suggest that resource availability may alleviate the pressure on parental self-maintenance and energy budget and favour parental care as observed in another study (Regular et al. 2014). The use of alternative prey, particularly by razorbills, guillemots and shags, was found to increase over the last 2 decades (Wanless et al. 2018). While age-0 sandeel abundance and availability affected components of breeding success in guillemots, likely through parental energy budgets (Wanless et al. 2023), no or limited effects were found in razorbills and shags. Therefore, for a more comprehensive understanding of predator–prey interactions in this system, future work should consider not only sandeels but alternative prey such as clupeids.

This study demonstrates the importance of MMH, and specifically MMAH, through the interplay between trophic synchrony and prey abundance in predator—prey dynamics. This is relevant to the development of prey reference points for predators in an ecosystem-based fisheries management approach (Hill et al. 2020), since prey abundance is not the only driving factor that needs to be considered. Our study highlights the value of examining mechanisms in detail, focusing on predator productivity components in relation to their prey dynamics. Relationships were most evident in species reliant on a single prey species. While past studies of prey sensitivity have highlighted the ability of seabirds to dive or switch diet (Furness & Tasker 2000), our study emphasizes the need to account for simultaneous variations in the phenology and abundance of predators and prey. Long-term data-rich studies are needed for accomplishing detailed mechanistic understanding of predator—prey dynamics. Specifically in the North Sea, accounting for variations in the phenology of sandeel on the productivity of their avian predators is essential to understand and assess the efficiency of management measures, since simply promoting prey abundance may not necessarily result in a higher seabird breeding success. For example, the large sandeel year-class of 2009 (ICES 2021) was not reflected by a good breeding success in any of the species considered here. As climate change is likely to lead to further disturbance of sandeel phenology (Régnier et al. 2019), future work should consider how management actions to increase abundance might mitigate these changes in prey that propagate to higher trophic levels.

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