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RESEARCH ARTICLE

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Environment-sensitive mass changes influence breeding frequency in a capital breeding marine top predator

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Abstract

1. The trade-off between survival and reproduction in resource-limited iteroparous animals can result in some individuals missing some breeding opportunities. In practice, even with the best observation regimes, deciding whether 'missed' years represent real pauses in breeding or failures to detect breeding can be difficult, posing problems for the estimation of individual reproductive output and overall population fecundity.
2. We corrected fecundity estimates by determining whether breeding had occurred in skipped years, using long-term capture–recapture observation datasets with parallel longitudinal mass measurements, based on informative underlying relationships between individuals' mass, breeding status and environmental drivers in a capital breeding phocid, the grey seal.
3. Bayesian modelling considered interacting processes jointly: temporal changes in a phenotypic covariate (mass); relationship of mass to breeding probability; effects of maternal breeding state and mark type on resighting. Full reproductive histories were imputed, with the status of unobserved animals estimated as breeding or non-breeding, accounting for local environmental variation. Overall fecundity was then derived for Scottish breeding colonies with contrasting pup production trends.
4. Maternal mass affected breeding likelihood. Mothers with low body mass at the end of breeding were less likely to bear a pup the following year. Successive breeding episodes incurred a cost in reduced body mass which was more pronounced for North Rona, Outer Hebrides (NR) mothers. Skipping breeding increased subsequent pupping probability substantially for low mass females. Poor environmental conditions were associated with declines in breeding probability at both colonies. Seal mass gain between breeding seasons was (a) negatively associated with lagged North Atlantic Oscillation for seals at NR and (b) positively associated with an index of seal prey (*Ammodytes* spp) abundance at Isle of May, Firth of Forth (IM). Overall fecundity was marginally greater at IM (increasing/stable pup production) than at NR (decreasing). No effects of mass were detected on maternal survival.

5. Skipping breeding in female grey seals appears to be an individual mass-dependent constraint moderated by previous reproductive output and local environmental conditions. Different demographic trends at breeding colonies were consistent with the fecundities estimated using this method, which is general and adaptable to other situations.

KEYWORDS
fecundity, *Halichoerus grypus*, mass, state space model

1 | INTRODUCTION

Resource limitation results in animals making trade-offs between traits such as survival and reproduction: costly expenditure on breeding can impact future survival or reproduction (Stearns, 1992). Iteroparous long-lived species may trade off current and future reproduction when a reproductive episode is sacrificed in favour of survival. True capital breeders must acquire resources in advance of a breeding attempt to provision themselves and their offspring throughout the breeding season. Fasting during reproduction means that maternal resources are finite. Individuals may differ in their ability to acquire resources according to age or experience (Beauplet, Barbraud, Dabin, Küssener, & Guinet, 2006; Desprez, Pradel, Cam, Monnat, & Gimenez, 2011); individual quality (Hamel, Cote, Gaillard, & Festa-Bianchet, 2009); or population density (Hamel, Cote, & Festa-Bianchet, 2010). Moreover, environmental conditions may lead to changing resource availability and individual life-history schedules are more likely to feature missed breeding attempts when conditions are unfavourable (Cubaynes, Doherty, Schreiber, & Gimenez, 2011; Forcada, Trathan, & Murphy, 2008; Parsons, 2008; Soldatini, Albores-Barajas, Massa, & Gimenez, 2016). Skipped breeding episodes may allow individuals to maintain survival, and together, these impact lifetime reproductive output (LRO). Population fecundity is affected when sufficient such events occur.

The probability of a seal giving birth to a pup is associated with individual body condition, which results from foraging success (Ferguson et al., 2017; Guinet, Roux, Bonnet, & Mison, 1998; Stenson, Buren, & Koen-Alonso, 2016). The mass of a mature female at the start of lactation is a proxy for body condition which can vary between years but also sets limits on maternal expenditure (the net change in maternal mass from birth to weaning of the pup) in phocid seals (Arnbom, Fedak, & Boyd, 1997). Few studies have examined the consequences of breeding expenditures between seasons for individuals in capital breeding species. Grey seal (*Halichoerus grypus*) mothers expending substantial resources in one breeding season were less likely to return to breed in the subsequent year (Pomeroy, Fedak, Rothery, & Anderson, 1999). Therefore, a mother's mass in one season may influence the probability that she breeds in the subsequent year, depending on her ability to regain condition through successful foraging. In other marine predators, biotic and/or abiotic environmental fluctuations can influence foraging success by changing prey availability, with consequences for predator condition, reproductive success and survival (Bost et al., 2015; Frederiksen, Lebreton, Pradel, Choquet, & Gimenez, 2014; King, Brooks, Morgan, & Coulson, 2005; McMahon, Harcourt, Burton, Daniel, & Hindell, 2017).

Overall, the UK grey seal population has increased in recent decades. Grey seals breed at ~60 colonies in Scotland and the long-term decline in pup production at North Rona (NR) in the Outer Hebrides contrasts with the growth and stabilization seen at the Isle of May (IM) in the North Sea, reflecting wider regional variation between grey seal breeding colonies (Duck & Morris, 2016; Smout, King, & Pomeroy, 2011a). Currently, an age-structured population model is fitted to pup production data using Bayesian methods to estimate grey seal abundance in UK waters (Thomas et al., 2019). This model is applied to wide geographical areas, each of which includes many breeding colonies. As the model's fit and output are sensitive to prior assumptions concerning vital rates, the accuracy, precision and representativeness of estimates used to inform the priors of the population model are of fundamental importance, with fecundity a key parameter (Øigård, Frie, Nilssen, & Hammill, 2012).

Determining how often animals breed can be challenging, requiring information additional to that needed to estimate survival (Desprez, Gimenez, McMahon, Hindell, & Harcourt, 2017). Ideally, breeding events can be compiled from direct observations on known, representative individuals, occurring over the duration of the animals' lifespan, with individuals equally detectable and breeding state known without error. The latter is problematic even for long-term studies – if an animal is not observed in a given year but is resighted later, is this a failure to detect a breeding episode or a non-breeding year for that animal? In practice, determining animals' breeding status when they are not observed at the main study site is difficult and this has prompted development of statistical methods to account for uncertain state and individual heterogeneity (Desprez et al., 2017; King & McCrea, 2014; Rouan, Gaillard, Guédon, & Pradel, 2009).

Here, we use long-term data from the grey seal breeding colonies on NR and IM including state specific capture–mark–recapture records and a time-varying covariate, body mass, to impute the breeding likelihood of female grey seals in skipped breeding years. Simple estimates of fecundity based on those animals that are observed to attend the colony in a given year can give an inflated fecundity rate as non-breeding animals may be less likely to attend (or even if they attend, be resighted at) a breeding colony compared to breeding

animals. Therefore, in order to obtain realistic fecundity estimates, it is important to consider the breeding status of seals that are not observed, potentially because they are absent from the study colony when observations are collected. Although grey seals are known to show fidelity to their breeding colonies and philopatry (Pomeroy, Anderson, Twiss, & McConnell, 1994; Pomeroy, Smout, Moss, Twiss, & King, 2010), this remains a challenge, because the numerous/inaccessible alternative breeding colonies are difficult to monitor adequately through the breeding season (Harrison et al., 2006). We use a Bayesian state-space approach (Juez, Aldalur, Herrero, Galarza, & Arizaga, 2015; King, 2014; King & McCrea, 2014; Royle, 2008), assuming that changes in individual mass depend on the breeding status of animals and that the probability of subsequent breeding is dependent on body mass (Pomeroy et al., 1999). Using an underlying process model for the trajectory of individual mass over time, we estimate the mass and pupping status of unobserved animals and hence obtain overall estimates of fecundity for grey seals breeding at the NR and IM colonies. Within the same integrated modelling framework, we test for associations between mass, vital rates and environmental drivers (sandeel abundance index for IM and the NAO index for NR) and the predicted impacts of these on individual breeding probability and colony pup production.

2 | MATERIALS AND METHODS

2.1 | Study colonies and individuals

NR (59.12°N, 5.83°W) Outer Hebrides is 65 km north-west of Cape Wrath, Scotland. The pupping season on NR spans mid September to late November (Boyd, Lockie, & Hewer, 1962; Hiby et al., 2013) with peak pupping in early October. Annual pup production declined from around 2,500 in the 1960s to around 500 at present. IM (56.18°N, 2.55°W) lies at the mouth of the Firth of Forth, Scotland. Until the 1970s, few seals bred there, but annual production was over 2,000 pups by the 1990s and has fluctuated around this number since then (Duck & Morris, 2016). The pupping season is from early October to early December, peaking in early November. Researchers were present on NR typically between 25 September and 4 November and on IM from 25 October to 6 December.

Results are based on analysis of data from 584 known adult females at NR covering the period 1993–2013; on the IM, data were available for 273 adult females from 1987 to 2014 (Table 1). At both colonies, individuals were marked with tags or brands or identified using natural pelage patterns (Smout et al., 2011a). Some animals carried combinations of marks, sometimes applied at different times, with new animals added to the dataset throughout the study period (Pomeroy et al., 1999; Smout et al., 2011a). Most study animals at NR were 'marked' as breeding adults, very few tagged pups recruited there (Pomeroy et al., 2010). At IM, up to 25% of known mothers in the early 2000s onwards had retained tags applied when they were pups. Further details of study animals, mark–recapture protocols and the Cormack–Jolly–Seber (CJS) model for the mark–recapture process including tag loss are reported elsewhere (McCrea & Morgan, 2014; Pomeroy et al., 1994; Smout, King, & Pomeroy, 2011b).

TABLE 1 Numbers and categories of study animals at each colony

	NR	IM
Years of data collection	1993–2013	1987–2014
Number of marked animals	584 (394)	273 (1)
Number of marked animals with associated mass data	210	217

Note: In the second row are counts of animals in the mark–recapture dataset, with animals entering the study in different years during the study period at each site (numbers in parentheses represent animals identified by pelage-ID only, while the totals include all animals including those identified with multiple marks for at least some of the years they were observed.) In the third row are animals with associated mass data.

Throughout each breeding season, at each colony, researchers surveyed the main breeding areas daily and the more outlying areas every 3–4 days so that seals were identified as soon as possible after coming ashore. When birth date was not observed directly, it was estimated using age-related pup mass and development characteristics (Kovacs & Lavigne, 1986). Mother/pup pairs were captured and weighed twice, as close to the start and end of lactation as possible to allow estimation of maternal postpartum mass (*M*) directly after the pup is born, and maternal weaning mass (*W*) at the end of lactation, maternal absence defined weaning date (protocol in Pomeroy et al., 1999). Average normal lactation duration was 18 days (range 14–23 days) and we aimed for a minimum of 10d between captures (typically days 3 and 15 of 18). The study included seals that bred regularly, as well as intermittent and rarely sighted breeders. At both colonies, study animals were originally branded or flipper-tagged as adults and their pups tagged (Smout et al., 2011a); additional pups were tagged at weaning (Pomeroy et al., 2010). 'New' animals were added regularly for weighing. Age ranges of mothers from each colony were similar (5–35 NR, 6–34 IM: ages were determined from reading incisor tooth sections, or from resights of recruited tagged pups, Pomeroy et al., 2010). Not all seals captured had a tooth removed for ageing. At NR from 1998 as many animals as possible were identified by natural markings, many of these remained observed but not weighed or aged (Hiby et al., 2013).

2.2 | Environmental correlates

UK grey seals are capital breeders: lactating females fast, relying on body reserves accrued during the preceding foraging period. Food abundance over the year preceding breeding was expected to play an important role in determining grey seal breeding success (Pomeroy et al., 1999). To link between breeding, food abundance and environmental conditions, we selected environmental correlates a priori which were relevant to grey seal regional diets, assuming that both breeding and foraging occurred within the same respective

general areas for each colony (Hammond & Wilson, 2016; Russell et al., 2013).

The North Atlantic Oscillation (NAO) annual winter index offers a broad scale measure of annual meteorological fluctuations, and it has been associated with vital rates of different species (King et al., 2005; Sandvik, Erikstad, Barrett, & Yoccoz, 2005; Thompson & Ollason, 2001). We used 1-year lagged annual winter NAO (i.e., relating to the winter prior to breeding) to index food (1-group forage fish, Hammond & Wilson, 2016) abundance.

In the UK, the sandeel *Ammodytes marinus* is found consistently in grey seal diet samples. This high-energy prey appears to be of particular importance for east coast seal populations (Cury et al., 2011; Hammond & Wilson, 2016). Indices of sandeel abundance are available in some areas of the North Sea including areas close to the IM (ICES, 2016). However, direct estimates of sandeel abundance are not consistently available for west coast areas used by NR seals and sandeels are also less important in west coast seal diets (Hammond, Hall, & Prime, 1994; Hammond & Wilson, 2016). Sandeels are an important dietary component for seals foraging around IM therefore sandeel abundance associated with spring/summer (when sandeels are in the water column and available to fishing) during the year leading up to grey seal breeding was used as a covariate for the IM colony (Hammond & Wilson, 2016; ICES, 2016).

2.3 | Analytical framework

Adapting the CJS model, we assumed animals were identified by unique marks during each breeding season (Lebreton, Burnham, Clobert, & Anderson., 1992). Individuals were recorded as 1 or 0 ('seen' or 'not seen'). Pupping status was recorded similarly. Direct mass measurements were obtained for some of the individuals

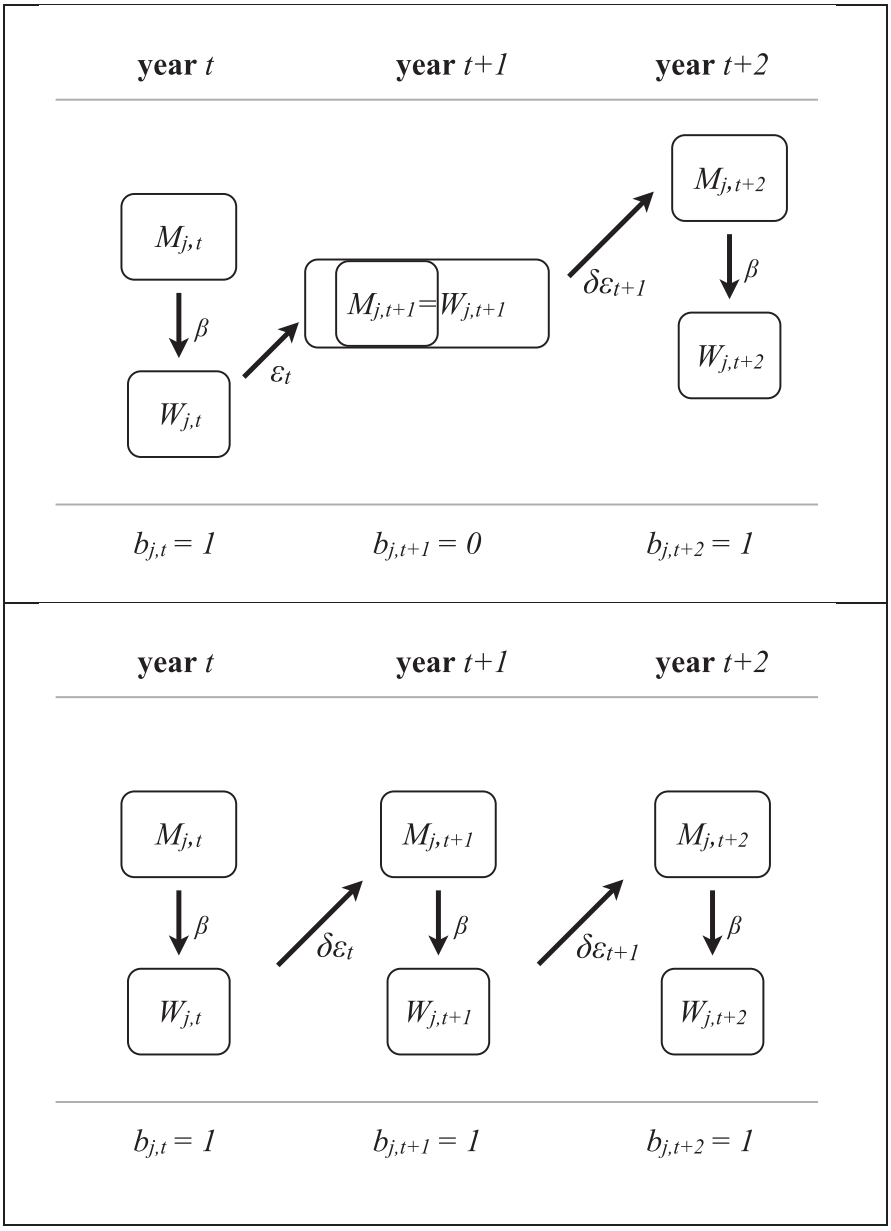

FIGURE 1 For seal *j* her mass at the start of breeding (measured immediately after pupping) is $M_{j,t}$ and mass at the end of the season when the pup is weaned is $W_{j,t} = \beta M_{j,t}$; therefore, $1 - \beta$ represents proportional mass loss by the mother during lactation. A mother's gain in mass after breeding from $M_{j,t}$ to $M_{j,t+1}$ is modelled using two multipliers; a year-specific (environmental) effect ε_t and a pupping-dependent factor δ. In non-breeding years, mothers increase mass only by the year effect ε_t

in the study. We adopted a Bayesian state-space modelling approach, offering some important advantages; for example, the user can include informative priors to constrain the parameter search; and sampling from the posterior distribution of parameters allows for inference about quantities calculated from model parameters. Adapting the CJS model for this framework required us to separate the process model (which includes survival and pupping) from the observation model (animals may or may not have been observed). However, the level of detail that could be included was limited, due to the nature and quantity of the data available. Because the link between phenology, breeding and environment was a primary concern, our modelling focused on this, explicitly including links from environment to individual mass and pupping history, and then to vital rates. This contrasts with models that assume time-dependent survival/breeding/recapture probabilities that are common to all individuals, estimating them separately for each year. In our approach, processes such as foraging success and mark loss drove the state of the individual (its mass, breeding status and marks present) through the study period (King 2014; King, Morgan, Gimenez, & Brooks, 2009). The observation process (whether or not the animal was observed) depended on the state of the animal including its breeding status and identifying marks. After initial exploratory analyses, the initial CMR model in which vital rates depended on mass was further simplified by excluding mass dependence in survival rate for both study systems, as there was little evidence for this dependence structure, and survival was estimated separately for each colony.

2.4 | Process model

Maternal expenditure, represented by mass loss during lactation, was estimated using a general multiplier β acting on maternal postpartum mass (Pomeroy et al., 1999; Wheatley, Bradshaw, Harcourt, & Hindell, 2008; Figure 1). Thus, for a female j pupping in year t, the expected mass of a female at the start of the breeding season $M_{j,t}$ was related to her mass at the end of breeding season

$$W_{j,t} \sim N(\beta M_{j,t}, \sigma_W^2).$$

The true mass of the female was assumed to be Normally distributed around the expected value, reflecting both the individual variation between females, and observation error in mass measurement. The mass of a female j at the end of breeding in year t influenced mass at the beginning of breeding in year $t+1$ subject to an additional colony and year-specific environmental effect ε_t common to all animals, breeders and non-breeders. The effect of pregnancy on expected mass gain was estimated by the factor δ such that for a pregnant female pupping in year $t+1$, with the true mass of the female assumed to be Normally distributed:

$$M_{j,t+1} \sim N\left(\delta\varepsilon_t W_{j,t}, \sigma_M^2\right).$$

Thus, combining the above modelling components, for a female pupping in year $t+1$, the expected relationship between end-of-season masses in year t and $t+1$ is given by

$$E(W_{j,t+1}) = \varepsilon_t \delta\beta W_{j,t}$$

For a non-pupping female, there was no effect of pregnancy on mass gain and no lactation, so $\delta\beta$ were both set to 1. For these non-breeding animals, the expected relationship is described by

$$E(W_{j,t+1}) = \varepsilon_t W_{j,t}$$

The product $\delta\beta$ could be interpreted as a general estimate of the ratio between the end-of-season mass for breeding and non-breeding females. Both constants were estimable because we observe values of both $W_{j,t}$ and $M_{j,t}$ in the dataset, allowing direct estimation of β from data on breeding animals. As previously, maternal masses $W_{j,t}$ were assumed to be Normally distributed with constant variance.

The year-dependent mass-gain ε_t was modelled as a function of the respective environmental variable (1 year lagged NAO for NR, and sandeel abundance for IM) represented here by x_t

$$\varepsilon_t = a + bx_t$$

where a and b were estimated. If the 95% BCI (Bayesian credible interval) around the estimate for the parameter b did not include zero, this was taken as evidence for an association between mass gain and the environmental variable.

Pupping was treated as a Bernouilli process with underlying probability $f_{j,t+1}$. This was associated with maternal weaning mass $W_{j,t}$ in the previous year, scaled by the year effect. A logistic relationship was assumed:

$$f_{j,t+1} = \frac{\exp\left(a_p + b_p \varepsilon_t W_{j,t}\right)}{1 + \exp\left(a_p + b_p \varepsilon_t W_{j,t}\right)}$$

Colony-specific values for a_p and b_p were estimated. If the 95% BCI around the estimate for the b_p did not include zero, this was taken as evidence for an association between pupping probability $f_{j,t+1}$ and $W_{j,t}$. The sign of b_p indicated the type of association.

Because we could not distinguish between animals that died and any that permanently emigrated from the study population we estimated 'apparent survival', abbreviated to 'survival' hereafter. Preliminary investigations into the effects of maternal mass on survival did not find evidence for a strong effect of mass on survival so the model structure was adjusted and survival was estimated as a constant value for each colony (see Appendix S1).

The model included the possibility that some females, referred to here as 'transients', were available to be seen on only one occasion (Hiby et al., 2013; Pradel, Hines, Lebreton, & Nichols., 1997). We estimated the colony-specific probability $p_{\text{transient}}$ that an animal identified for the first time was in this category.

2.5 | Observation model

We estimated distinct parameters p_{pup} representing the resighting probability of breeding females, and $p_{no\,pup}$ for non-breeding females. Seals were marked with brands, flipper tags and pelage markings. Mark-dependent values of resighting probability were estimated during the model-fitting process for NR and IM separately. The probability of tag loss could also be estimated, because some animals carried multiple mark types, for example tags and brands. Brands and pelage-ID were treated as permanent marks (Smout et al., 2011a; Appendix S1).

2.6 | Estimation

The Bayesian fitting algorithm estimated values of female mass where gaps occurred in series (Figure 1). Similarly, the unknown pupping status of unobserved animals was estimated based on observed masses in the previous and subsequent years.

Unknown mass values and model parameters were estimated using the freely available open source software WinBUGS (Lunn, Spiegelhalter, Thomas, & Best, 2009). A model description, equations and priors are detailed in Appendix S1; code is provided in Appendix S2. Convergence was checked based on visual inspection of plots for multiple chains and BGR convergence statistics (Gelman et al., 2013).

2.7 | Checking goodness of fit

With a complex dataset and substantial missing data, it is difficult to directly estimate goodness of fit or to use information criteria such as DIC to carry out model comparison (Celeux, Forbes, Robert, & Titterington, 2006). To address the question of goodness of fit, we have implemented an approach with the same underlying principle as a Bayesian *p*-value, but focused on the estimation of net fecundity – the quantity of particular interest in this study. In particular, our aim is to compare simulated fecundity rates (conditional on the initial sighting and observed mass if any) with estimated rates drawn from the posterior distribution of the parameters (i.e., from the MCMC iterations) to identify whether or not they are comparable. If the estimates are comparable there is no evidence against the model; alternatively, if they are systematically different this suggests a lack of absolute model fit with regard to fecundity. This fecundity rate was then used as the associated 'discrepancy function': we compared the estimated fecundity from the posterior distribution with the associated simulated fecundity given these particular parameter values. This process was repeated for 1,000 random draws from the posterior. We then record the proportion of simulated fecundity rates that were higher than the associated fecundity rate for that posterior sample. As for a formal Bayesian *p*-value, if simulated and fitted rates are similarly distributed, this proportion is expected to be around 0.5, and this then indicates a satisfactory correspondence between model and data; whereas a proportion in the 'tails' (e.g., lower or upper 5% quantiles) would indicate a potential lack of model fit (King et al., 2009).

2.8 | Model predictions for pupping probabilities; the effects of varying environmental conditions

To explore the implications of the fitted model, we estimated the effect of environmental drivers on the probability of pupping. 'Poor environmental conditions', chosen from the original covariate data, were defined as the values of sandeel abundance or NAO that predicted lowest proportional mass gain. 'Good conditions' were those values of environmental covariates for which predicted proportional mass gain was highest. We estimated the 'skipping point maternal weaning mass' W_{50} as the mass of the mother when her pup weaned at which pupping probability in the next year would be 50%, if conditions during the intervening year were poor. This was calculated using the fitted model for each colony. Similarly, the probability of pupping for a female with mass at weaning W_{50} after a year of good conditions was also calculated. Therefore, in effect, we tested a theoretical 'skipping point mother' against the worst and best conditions observed in the data.

The consequences of the variable environment were explored further by estimating pupping probabilities for females starting at W_{50} after two years of good conditions and after two years of poor conditions. These values were calculated either assuming that pupping took place in the breeding season after the first year, or that it did not.

2.9 | Model predictions for local population trends

To explore the consequences of our model estimates for local populations, we used a simple Leslie matrix population simulation for females breeding at IM and NR, assuming no density-dependent effects were acting and accounting for transients. In this model, all animals became fertile aged 6, adult and subadult survival rates were set at the mean estimated values for adults for each colony, and fecundity was set to the mean colony average estimate. Female first-year survival was set at 0.6 for IM (Hall & McConnell, 2007), and for NR, this value was set at $0.6s_{NR}/s_{IM}$ where s_{NR} and s_{IM} were the estimated adult survival rates at NR and IM.

3 | RESULTS

After a 2000 iteration burn-in period, the MCMC for NR and IM appeared to converge with stationary posterior parameter estimates achieved after 100,000 iterations. Breeding parameter estimates are summarized in Table 2; for full parameter table, see Supplementary Material (Appendix S1). The estimated values from

TABLE 2 Mean parameter estimates for the process and observation models (95% Bayesian credible intervals are shown in brackets)

	Meaning	NR value	IM value
s	Overall survival rate (average over all years)	0.89 (0.87, 0.90)	0.94 (0.93, 0.95)
f	General estimate of fecundity for all animals at the colony, including years they are not observed at the colony	0.79 (0.77, 0.81)	0.82 (0.79, 0.84)
β	Ratio of W (maternal mass at weaning) to M (maternal post partum mass)	0.65 (0.64, 0.66)	0.65 (0.65, 0.66)
δ	Maternal mass gain (preg)	1.34 (1.32, 1.36)	1.40 (1.38, 1.42)
p_{pup}	Probability that a female marked with a brand (i.e. highly visible) and pupping is present and will be seen at the colony	0.89 (0.85, 0.93)	0.83 (0.80, 0.86)
$p_{\text{no pup}}$	Probability that an animal marked with a brand which is not pupping will be seen at the colony	0.08 (0.06, 0.11)	0.05 (0.03, 0.08)
$P_{\text{transient}}$	Probability that a female recorded in the dataset for the first time is a 'transient'	0.21 (0.16, 0.27)	0.04 (0.01, 0.09)
P_{tagloss}	Annual probability of tag loss	0.07 (0.05, 0.09)	0.02 (0.01, 0.03)

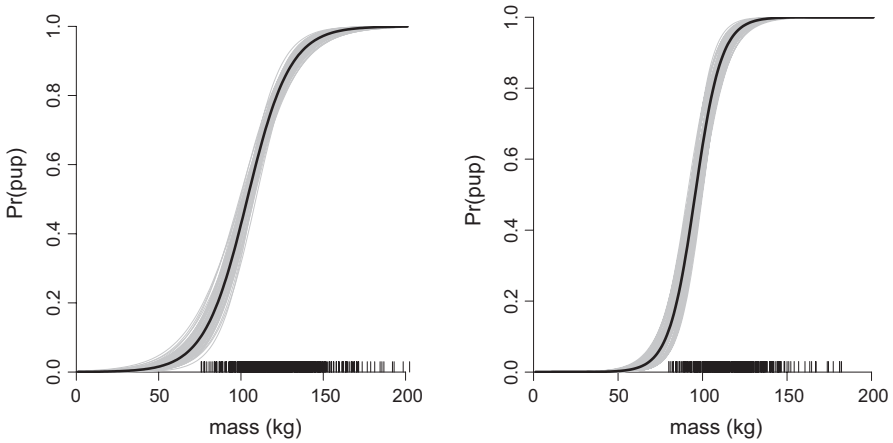

FIGURE 2 The relationship between pupping probability in year t+1 and maternal mass at weaning in year t for NR (left) and IM (right). In each panel, the dark curve is based on mean estimates of the logistic parameters, grey curves are simulations from random samples of the Markov chain. The rug plot indicates the range of the observed mass data $W_{j,t}$ at each colony

our goodness-of-fit tests were 0.307 for NR and 0.284 for IM which were both satisfactory, indicating acceptable model fit for fecundity rate estimation.

3.1 | Parameter estimates

Mean survival rate at NR was lower than at IM, consistent with previous findings (Smout et al., 2011a). There were more mothers estimated as 'transient' at NR than at IM (Table 2).

For both colonies, there was evidence for a positive relationship between pupping probability in year $t+1$ and W_t(maternal mass at the end of breeding in year t) with appreciable effects on pupping probability over the range of mass values observed in the dataset (Figure 2). The IM pupping probability–mass curve shows a steeper relationship than that for NR: at IM, pupping probability doubles from 0.4 to 0.8 over a range of ~13 kg, while at NR, the same change occurs over a range of ~23 kg.

Average net fecundity calculated for NR females was less than that for IM females, but credible intervals overlap for the two sites (Table 2). For comparison, a simple calculation based on the observational data, assuming that all unobserved known animal-years were non-breeding years, gave net fecundity rates of 0.679 at NR and 0.750 at IM, highlighting the importance of accounting for unobserved individuals.

The estimated probability of resighting a non-breeding female was low at both colonies, consistent with the observation that very few non-breeding adult females are seen at these colonies (Table 2).

The postpartum masses of mothers at NR and IM encompassed a similar range, with several at each colony exceeding 250 kg. The estimated value of β (the ratio of maternal mass at the end of lactation to mass at start of lactation) was very similar between IM and NR: on average, a mother expended 35% of her postpartum mass on raising a pup (Table 2). Average proportional mass gain δ for pregnant mothers between end and start of successive breeding seasons was lower for those at NR than for those at IM (Table 2).

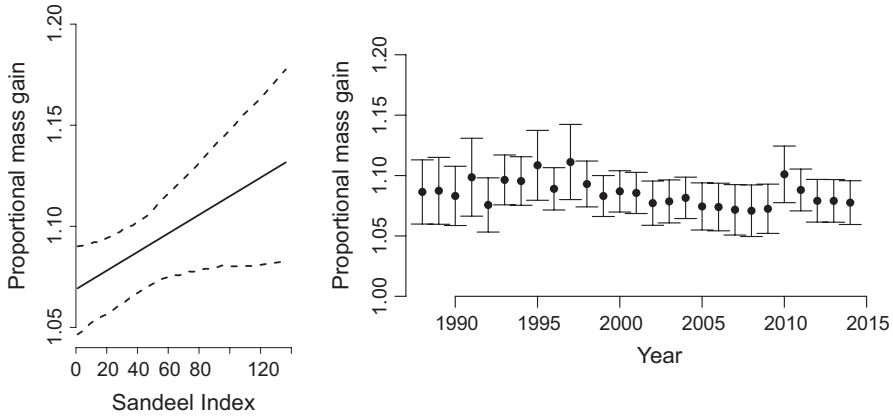

FIGURE 3 The year effect ε_t component of mass gain expressed as a proportion for IM. Left panel: year effect proportional mass gain as a function of sandeel abundance index (dotted lines represent 95% CI). Right panel: time series estimates of year effect proportional mass gain with 95% CI

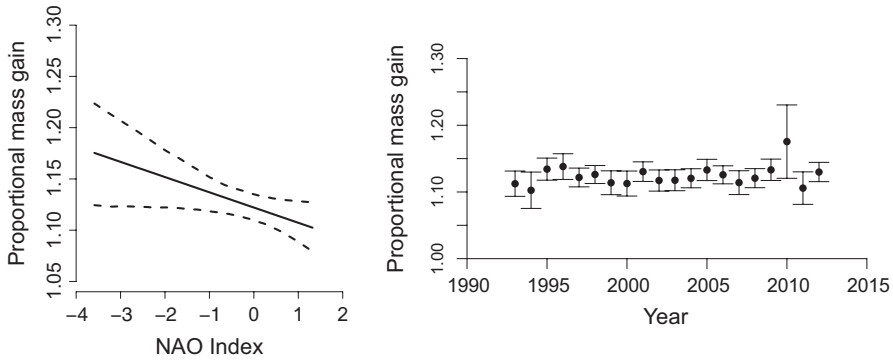

FIGURE 4 The year effect ε_t component of mass gain expressed as a proportion for NR. Left panel: year effect proportional mass gain as a function of NAO winter index (dotted lines represent 95% CI). Right panel: time series estimates of year effect proportional mass gain with 95% CI

3.2 | Environmental variation and breeding probability

There was no evidence for an association between mass gain and NAO at IM, so this was excluded from the final fitted model. The relationship between mass gain and sandeel abundance at IM was positive (Figure 3). For NR, the underlying relationship between mass gain and NAO index was negative (Figure 4).

Year specific proportional mass gains ϵ_t were generally larger at NR than at IM (Figures 3, 4; right panels). Synchronicity of environmental effects at the two colonies was limited; better-than-average mass gains occurred at both colonies in 1995 and 2010.

The predicted effects of environment and breeding on subsequent pupping probability are important for 'skipping point' W_{50} animals at both colonies ($\boldsymbol{p}_{t+1}$ in Table 3). Not breeding had an appreciable effect for skipping point animals, where pupping probability $\boldsymbol{p}_{t+2}$ can either decrease if pupping takes place in year t + 1, or increase if breeding is skipped (Table 3, columns 4 and 5). Mothers at the skipping point were heavier at NR (93.5kg) than at IM (88.5kg).

TABLE 3 The predicted impacts of environmental conditions

	Environmental conditions	p_{t+1}	p_{t+2} (*pupped t*+1)	p_{t+2} (skipped *t*+1)
NR	**Poor** - High NAO	0.500	0.423	0.696
	Good - Low NAO	0.633	0.675	0.884
IM	**Poor** - Low sandeels	0.500	0.426	0.709
	Good - High sandeels	0.620	0.647	0.868

Note: 'Skipping point' mothers of mass W_{50} in year *t* have a 50% probability of pupping in year *t*+1 after a 'poor' year of environmental conditions. If environmental conditions are better (low NAO at NR, high sandeels at IM), then pupping probability in year *t*+1 is improved ($\boldsymbol{p}_{t+1}$ column 3). Predicted pupping probabilities for year *t*+2 are shown after 2 years of consistent environmental conditions (2 good years or 2 bad years), in columns 4 and 5. Column 4 gives values for females if they bred in year *t*+1; Column 5 gives values for females that 'skipped' breeding in year *t*+1.

3.3 | Population trajectory for each colony

The predicted time series of number of females breeding derived from the Leslie model declined at NR and increased at IM (dashed and solid lines respectively, Figure 5). Simple visual comparison suggests that there is a good correspondence with trends in pup production estimates derived from synoptic counts of pups from aerial survey (NR, IM solid and open circles respectively, Duck & Morris, 2016).

4 | DISCUSSION

Intermittent breeding in iteroparous animals acts on LRO and individual fitness and affects demographic rates at the population level. Capital breeding species in fluctuating environments are likely to be particularly prone to skipping breeding episodes when survival takes

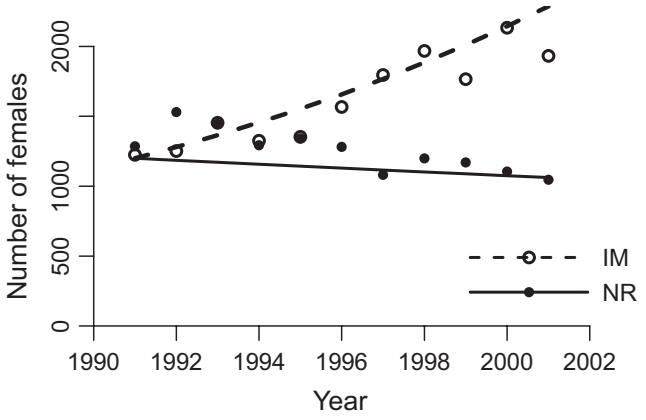

FIGURE 5 Observed and predicted breeding colony trends at IM and NR. The curves show predictions from a Leslie population model using this work's estimates of mean survival and mean fecundity at each colony (NR solid, IM dashed). Starting populations were set to 1,200 at each site, based on observed pup production count estimates in 1991. Points (solid for NR and open for IM) show observed pup production count estimates derived independently from synoptic aerial surveys at each site

precedence over reproduction (Stearns, 1992). Skipped breeding episodes among experienced breeders are known in capital breeding phocid seals, but mechanistic explanations of the process have often relied anecdotally on Boyd's (2000) finding that body mass accounted for more variation in pregnancy rates in capital breeding than income breeding species (Chambert, Rotella, Higgs, & Garrott, 2013; Desprez et al., 2017). Desprez et al. (2017) used resighting records at Macquarie Island to investigate intermittent breeding of southern elephant seals *Mirounga leonina*. Using a multievent model incorporating uncertain reproductive status and categorizing adult females into breeding heterogeneity classes, they found that there was a survival cost to breeding for females in the infrequently breeding class. This latter class they suggested comprised females of lower quality in some phenotypic property positively related to fitness, and while variability in individuals' ability to forage and gain resources were hypothesized to be likely explanatory factors, no phenotypic or other measures of animals were provided to support this (Desprez et al., 2017). Similarly, Chambert, Rotella, and Garrott, (2015) proposed that female Weddell seals (*Leptonychotes weddellii*) that skipped breeding in Erebus Bay, Antarctica were in poorer condition than regular breeders. Here, we provide the empirical evidence for an effect of maternal mass on pupping probability in a capital breeding phocid, the grey seal, and importantly, of the increased pupping probability that low body mass females accrue by skipping a reproductive episode.

Environmental fluctuations are seen to impact long-lived marine species' fecundity rather than survival (Reed, Harris, & Wanless, 2015; Stenson et al., 2016). Our study showed an impact of female mass on the probability of pupping but did not detect an effect on survival. While a female in sufficiently poor condition might be expected to have reduced survival probability, this may be difficult to observe. If low-mass animals miss breeding, are not observed at the colony and are never seen again we may lack the data to define the shape of the descending arm of the logistic curve for the survival–mass relationship. If breeding is costly, animals in poor condition (low body mass) may forego breeding and improve their own chances of survival (Ronget, Garratt, Lemaître, & Gaillard, 2017). We found that impacts of breeding on subsequent pupping probability for grey seals are substantial for seals whose mass at the end of breeding is low (Figure 2). At both colonies our model predicts that in poor environmental conditions, females that 'skip' breeding are more likely to pup in subsequent years (Table 3). Similar skipping breeding sequences were linked with body condition and environmental conditions in Weddell seals (Chambert et al., 2015; Proffitt, Garrott, Rotella, & Wheatley, 2007).

Mass-adjusted fecundity rates suggest that around two-thirds of 'missing' years are indeed non-breeding years (Table 2). Movement away from the natal colony or permanent emigration by adults to different colonies might occur, and cannot be distinguished here from permanent loss of fertility, or death (Harrison et al., 2006). Nevertheless, our analyses suggest breeding occurred in around one third of 'missed' breeding years. Some pupping events of known females at their 'normal' colony could have gone unobserved, but high resight rates (Table 2) suggest these should be few. The remaining 'missed' breeding events must have occurred outwith the prevalent breeding site fidelity pattern (Pomeroy et al., 1994). Genetic differences between NR and IM seals are sufficient to suggest very low effective breeding interchange between distant colonies (Allen, Amos, Pomeroy, & Twiss, 1995), but any breeding colony infidelity would help explain unassigned paternities (Worthington Wilmer, Allen, Pomeroy, Twiss, & Amos, 1999).

Some female grey seals observed for the first time became subsequently unobservable, especially at NR (Table 2). Although termed 'transients', different phenomena can produce such records. Most convincing is the difficulty in making matches between patterns extracted from different photographs of the same grey seal identified by pelage alone (Hiby et al., 2013), as many more females were identified by this method at NR (Table 1). Alternative explanations include: some subset of adult females have lower survival, for example primiparous females; higher tag loss rates directly after application; different tag loss rates between seals at different colonies. Seals may visit a colony once only, then breed elsewhere subsequently – features of a declining colony such as NR may indicate to first time visitors that it is undesirable, resulting in demographic state-dependent colony fidelity.

Intermittent breeding has been described as a tactic employed by poorer quality mothers to optimize LRO (Desprez et al., 2017). True capital breeders rely on accumulated reserves, expending a large proportion of postpartum body mass (grey seals 0.35, Table 2; southern elephant seals 0.35, Arnbom et al., 1997) to sustain a reproductive episode. Average proportional expenditure was the same at NR and IM, despite body mass differences and different vital rates. Pregnant NR seals did not regain as much of their previous MPPM as equivalent mothers at IM (δ = 1.34, 1.40, respectively; Table 2), suggesting that successive pregnancies incur a cost in reduced subsequent MPPM

and that NR mothers experienced this to greater extent, possibly as a result of poorer overall resource availability. Further reductions in mass of small mothers would be unsustainable and in such cases skipping breeding seems likely. While a mother experiences strong selective pressure on raising a pup within resource limits, the future costs of which vary according to initial maternal body mass and reserves, individual and episodic variations in reproductive expenditure occur (Arnbom et al., 1997; Pomeroy et al., 1999). However, even for capital breeders, body mass alone may not be a perfect metric of body reserves, because it masks the availability of all the nutrients required for a successful breeding episode. Often only lipid reserves are used to estimate 'condition' in capital breeders as they provide most of the energetic requirements of mother and offspring, but protein and other nutrients must also be available and in the extreme may be more limiting (Arnbom et al., 1997; Boyd, 2000; Hanson, Smout, Moss, & Pomeroy, 2019; Mellish, Iverson, & Bowen, 1999). Our modelling framework could be adapted to include more complex measures of body condition in future studies, including combining different measures, if such data are available.

Assessing the effects of different demographic rates on populations requires that rates are estimated appropriately: for fecundity, non-breeders and non-breeding episodes must be taken into account (Lee, Reid, & Beissinger, 2017). Here, we found that relatively small differences in colony fecundity rate are associated with very different colony pup production trajectories. Canadian and Norwegian studies of grey seals have reported fecundity estimates similar to our mass-adjusted overall female fecundity rates (Bowen, Iverson, McMillan, & Boness, 2006; Hammill & Gosselin, 1995). Nevertheless, fecundity and adult female survival were both lower for NR seals than those at the growing IM colony, which had similar parameters to those reported from the expanding colony on Sable Island, Canada (den Heyer & Bowen, 2017). Simple Leslie matrix population simulations showed rates of local population growth and decline that are consistent with observed trends in pup production at both colonies for the early years of the study: a decline in pup production at NR, compared with a positive trend at IM (Duck & Morris, 2016). The breeding decline at NR is present at other Hebridean grey seal colonies (Duck & Morris, 2016) and poor recruitment of seals tagged as pups to NR is a likely additional factor in explaining these trends (Pomeroy et al., 2010). Long term declines in measures of grey seal 'condition' at NR compared to IM suggests that colony-level effects are reflected in individual phenotypic covariates and these are a local response to local conditions (Hanson et al., 2019) which likely explains lower fecundity at NR (Boyd, 2000). Longitudinal seabird surveys on NR have shown decadal declines in 9 of 15 species that use the island for breeding, in common with trends reported in such species elsewhere in the North Atlantic (Murray & Wilson, 2013). That many different marine apex predators show contemporaneous regional declines is indicative of the generality of ecosystem change to their detriment in this region.

Grey seals are generalist predators and their diet varies in response to changing prey abundance (Smout, Rindorf, Hammond, Harwood, & Matthiopoulos, 2013). As capital breeders capable of wide-ranging foraging, they are buffered against small scale, short term changes in prey availability. The association between NAO (lagged one year) and grey seal mass change at NR, is explicable if Atlantic atmospheric conditions correlate with the abundance of one or more important prey species with direct consequences for the condition of seals foraging and breeding on the UK's Atlantic fringe. There was no evidence of a similar effect of NAO at IM, consistent with the limited influence of NAO on the North Sea ecosystem where most IM seals forage, compared to west coast waters that are connected directly to the Atlantic (Harris, Edwards, & Olhede, 2014). The appreciable effect of local sandeel abundance reflects the importance of sandeels in seal diets in this area and the wider North Sea where these seals are likely to forage (Hammond & Wilson, 2016; Russell et al., 2013).

The Bayesian modelling approach implemented here using freely available software allowed us to fit a model of the relationship between annual mass gain and environmental drivers, including 'nuisance' processes (tag loss) that might otherwise obscure important effects and a realistic observation model with missing data and unknown states. Our analyses highlighted the consequential nature of breeding events: longitudinal maternal mass trajectories suggested underlying breeding histories, and while skipping breeding was associated with low body mass, females that skipped had a higher probability of breeding subsequently.

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CONFLICT OF INTEREST

The authors have no competing interests.

AUTHORS' CONTRIBUTIONS

P.P. designed and managed the long-term research and carried out fieldwork; P.P. and R.K. conceived of and designed the study; S.S. analysed the data; and S.S. and P.P. led writing of the paper and share first authorship. All authors gave final approval for publication.

ETHICAL APPROVAL

Work involving animals in this study was licensed under UK Home Office project 60/4009 or preceding versions and conformed to the UK Animals (Scientific Procedures) Act, 1986. Research was approved by the University of St Andrews Animal Welfare and Ethics Committee.

DATA AVAILABILITY STATEMENT

Data are lodged in PURE, http://dx.doi.org/10.17630/8b1f33d5-50bf-4631-9e65-fca33d26902f (Smout, King, & Pomeroy, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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