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4   **Environment-sensitive mass changes influence breeding frequency in a**

5   **capital breeding marine top predator**

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20   **Abstract**

21   1. The trade-off between survival and reproduction in resource-limited iteroparous animals

22   can result in some individuals missing some breeding opportunities. In practice, even with

23   the best observation regimes, deciding whether 'missed' years represent real pauses in

24   breeding or failures to detect breeding can be difficult, posing problems for the estimation

25   of individual reproductive output and overall population fecundity.

26   2. We corrected fecundity estimates by determining if breeding had occurred in skipped

27   years, using long term capture-recapture observation datasets with parallel longitudinal

28   mass measurements, based on informative underlying relationships between individuals'

29   mass, breeding status and environmental drivers in a capital breeding phocid, the grey seal.

30   3. Bayesian modelling considered interacting processes jointly: temporal changes in a

31   phenotypic covariate (mass); relationship of mass to breeding probability; effects of

32   maternal breeding state and mark type on resighting. Full reproductive histories were

33   imputed, with the status of unobserved animals estimated as breeding or non-breeding,

34   accounting for local environmental variation. Overall fecundity was then derived for Scottish

35   breeding colonies with contrasting pup production trends.

36   4. Maternal mass affected breeding likelihood. Mothers with low body mass at the end of

37   breeding were less likely to bear a pup the following year. Successive breeding episodes

38   incurred a cost in reduced body mass which was more pronounced for North Rona, Outer

39   Hebrides (NR) mothers. Skipping breeding increased subsequent pupping probability

40   substantially for low mass females. Poor environmental conditions were associated with

41   declines in breeding probability at both colonies. Seal mass gain between breeding seasons

42   was: (i) negatively associated with lagged North Atlantic Oscillation for seals at NR, ; (ii)

43   positively associated with an index of seal prey (*Ammodytes* spp) abundance at Isle of May,

44   Firth of Forth (IM).   Overall fecundity was marginally greater at IM (increasing/stable pup

45   production) than at NR (decreasing). No effects of mass were detected on maternal survival.

46   5. Skipping breeding in female grey seals appears to be an individual mass-dependent

47   constraint moderated by previous reproductive output and local environmental conditions.

48   Different demographic trends at breeding colonies were consistent with the fecundities

49   estimated using this method, which is general and adaptable to other situations.

50   **Introduction**

51

52   Resource limitation results in animals making trade-offs between traits such as survival and

53   reproduction: costly expenditure on breeding can impact future survival or reproduction

54   (Stearns, 1992). Iteroparous long-lived species may trade off current and future

55   reproduction when a reproductive episode is sacrificed in favour of survival. True capital

56   breeders must acquire resources in advance of a breeding attempt to provision themselves

57   and their offspring throughout the breeding season. Fasting during reproduction means that

58   maternal resources are finite. Individuals may differ in their ability to acquire resources

59   according to age or experience (Beauplet, Barbraud, Dabin, Küssener & Guinet, 2006;

60   Desprez, Pradel, Cam, Monnat & Gimenez, 2011); individual quality (Hamel, Cote, Gaillard

61   & Festa-Bianchet , 2009) or population density (Hamel, Côté & Festa-Bianchet, 2010).

62   Moreover, environmental conditions may lead to changing resource availability and

63   individual life history schedules are more likely to feature missed breeding attempts when

64   conditions are unfavourable (Cubaynes, Doherty, Schreiber & Gimenez, 2011; Forcada,

65   Trathan & Murphy, 2008; Parsons 2008; Soldatini, Albores-Barajas, Massa & Gimenez,

66   2016). Skipped breeding episodes may allow individuals to maintain survival and together

67   these impact Lifetime Reproductive Output. Population fecundity is affected when sufficient

68   such events occur.

69

70   The probability of a seal giving birth to a pup is associated with individual body condition,

71   which results from foraging success (Guinet, Roux, Bonnet & Mison 1998; Stenson, Buren &

72   Koen-Alonso 2016; Ferguson *et al.* 2017). The mass of a mature female at the start of

73   lactation is a proxy for body condition which can vary between years but also sets limits on

74   maternal expenditure (the net change in maternal mass from birth to weaning of the pup) in

75   phocid seals (Arnbom, Fedak & Boyd 1997).   Few studies have examined the consequences

76   of breeding expenditures between seasons for individuals in capital breeding species.   Grey

77   seal (*Halichoerus grypus*) mothers expending substantial resources in one breeding season

78   were less likely to return to breed in the subsequent year (Pomeroy, Fedak, Rothery &

79   Anderson 1999). Therefore a mother's mass in one season may influence the probability

80   that she breeds in the subsequent year, depending on her ability to regain condition

81   through successful foraging.   In other marine predators, biotic and/or abiotic environmental

82   fluctuations can influence foraging success by changing prey availability, with consequences

83   for predator condition, reproductive success and survival (Frederiksen, Lebreton, Pradel,

84   Choquet & Gimenez, 2014; King, Brooks, Morgan & Coulson, 2005; Bost et al., 2015,

85   McMahon, Harcourt Burton, Daniel & Hindell, 2017).

86

87   Overall, the UK grey seal population has increased in recent decades. Grey seals breed at

88   approximately 60 colonies in Scotland and the long term decline in pup production at North

89   Rona (NR) in the Outer Hebrides contrasts with the growth and stabilization seen at the Isle

90   of May (IM) in the North Sea, reflecting wider regional variation between grey seal breeding

91   colonies (Duck & Morris, 2016; Smout, King & Pomeroy, 2011a).   Currently, an age-

92   structured population model is fitted to pup production data using Bayesian methods to

93   estimate grey seal abundance in UK waters (Thomas *et al.*, in press). This model is applied to

94   wide geographical areas, each of which includes many breeding colonies. As the model's fit

95   and output are sensitive to prior assumptions concerning vital rates, the accuracy, precision

96   and representativeness of estimates used to inform the priors of the population model are

97   of fundamental importance, with fecundity a key parameter (Øigård, Frie, Nilssen &

98   Hammill 2012).

99

100   Determining how often animals breed can be challenging, requiring information additional

101   to that needed to estimate survival (Desprez, Gimenez, McMahon, Hindell & Harcourt,

102   2017). Ideally, breeding events can be compiled from direct observations on known,

103   representative individuals, occurring over the duration of the animals' lifespan, with

104   individuals equally detectable and breeding state known without error. The latter is

105   problematic even for long term studies – if an animal is not observed in a given year but is

106   resighted later, is this a failure to detect a breeding episode or a non-breeding year for that

107   animal?   In practice determining animals' breeding status when they are not observed at

108   the main study site is difficult and this has prompted development of statistical methods to

109   account for uncertain state and individual heterogeneity (Rouan, Gaillard, Guédon and

110   Pradel 2009; King & McCrea 2014; Desprez *et al.* 2017).

111

112   Here we use long-term data from the grey seal breeding colonies on NR and IM including

113   state specific capture-mark-recapture records and a time-varying covariate, body mass, to

114   impute the breeding likelihood of female grey seals in skipped breeding years. Simple

115   estimates of fecundity based on those animals that are observed to attend the colony in a

116   given year can give an inflated fecundity rate as non-breeding animals may be less likely to

117   attend (or even if they attend, be re-sighted at) a breeding colony compared to breeding

118   animals. Therefore, in order to obtain realistic fecundity estimates, it is important to

119   consider the breeding status of seals that are not observed, potentially because they are

120   absent from the study colony when observations are collected. Although grey seals are

121   known to show fidelity to their breeding colonies and philopatry (Pomeroy, Anderson, Twiss

122   & McConnell 1994; Pomeroy, Smout, Moss, Twiss & King 2010) this remains a challenge,

123   because the numerous/inaccessible alternative breeding colonies are difficult to monitor

124   adequately through the breeding season (Harrison *et al.* 2006).   We use a Bayesian state-

125   space approach (Royle 2008; King 2012; King & McCrea 2014; Juez, Aldalur, Herrero,

126   Galarza & Arizaga 2015), assuming that changes in individual mass depend on the breeding

127   status of animals, and that the probability of subsequent breeding is dependent on body

128   mass (Pomeroy et al., 1999). Using an underlying process model for the trajectory of

129   individual mass over time, we estimate the mass and pupping status of unobserved animals,

130   and hence obtain overall estimates of fecundity for grey seals breeding at the NR and IM

131   colonies. Within the same integrated modeling framework we test for associations between

132   mass, vital rates, and environmental drivers (sandeel abundance index for IM, and the NAO

133   index for NR) and the predicted impacts of these on individual breeding probability and

134   colony pup production.

135

136   **Methods**

137

138   *Study colonies and individuals*

139   NR (59.12° N, 5.83° W) Outer Hebrides is 65 km north-west of Cape Wrath, Scotland. The

140   pupping season on NR spans mid September to late November (Boyd, Lockie & Hewer 1962;

141   Hiby *et al.* 2013) with peak pupping in early October. Annual pup production declined from

142   around 2500 in the 1960s to around 500 at present. IM (56.18°N, 2.55°W) lies at the mouth

143   of the Firth of Forth, Scotland. Until the 1970's few seals bred there, but annual production

144   was over 2000 pups by the 1990s and has fluctuated around this number since then (Duck &

145   Morris 2016). The pupping season is from early October to early December, peaking in early

146   November.   Researchers were present on NR typically between 25 Sep-4 Nov and on IM

147   from 25 Oct-6 Dec.

148

149   Results are based on analysis of data from 584 known adult females at NR covering the

150   period 1993-2013; on the IM, data were available for 273 adult females from 1987-2014

151   (Table 1). At both colonies, individuals were marked with tags or brands, or identified using

152   natural pelage patterns (Smout *et al.*, 2011a). Some animals carried combinations of marks,

153   sometimes applied at different times, with new animals added to the data set throughout

154   the study period (Pomeroy *et al*. 1999; Smout *et al*. 2011a). Most study animals at NR were

155   'marked' as breeding adults, very few tagged pups recruited there (Pomeroy *et al*. 2010). At

156   IM, up to 25% of known mothers in the early 2000s onwards had retained tags applied

157   when they were pups. Further details of study animals, mark-recapture protocols and the

158   Cormack-Jolly-Seber (CJS) model for the mark-recapture process including tag loss are

159   reported elsewhere (Pomeroy *et al.* 1994; Smout, King & Pomeroy 2011b; McCrea &

160   Morgan 2014).

161

Table 1.	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

162

163   Table 1: Numbers and categories of study animals at each colony. In the second row are counts of animals in

164   the mark-recapture data set, with animals entering the study in different years during the study period at each

165   site (numbers in parentheses represent animals identified by pelage-ID only, while the totals include all

166   animals including those identified with multiple marks for at least some of the years they were observed.) In

167   the third row are animals with associated mass data.

168

169   Throughout each breeding season, at each colony, researchers surveyed the main breeding

170   areas daily and the more outlying areas every 3-4d so that seals were identified as soon as

171   possible after coming ashore. When birth date was not observed directly, it was estimated

172   using age-related mass and development characteristics (Kovacs & Lavigne 1986).

173   Mother/pup pairs were captured and weighed twice, as close to the start and end of

174   lactation as possible to allow estimation of maternal postpartum mass (M) directly after the

175   pup is born, and maternal weaning mass (W) at the end of lactation, maternal absence

176   defined weaning date (protocol in Pomeroy *et al*., 1999). Average normal lactation duration

177   was 18d (range 14-23d) and we aimed for a minimum of 10d between captures (typically

178   days 3 and 15 of 18). The study included seals that bred regularly, as well as intermittent

179   and rarely-sighted breeders. At both colonies, study animals were originally branded or

180   flipper-tagged as adults and their pups tagged (Smout et al. 2011a); additional pups were

181   tagged at weaning (Pomeroy *et al.*, 2010). "New" animals were added regularly for

182   weighing. Age ranges of mothers from each colony were similar (5-35 NR, 6-34 IM: ages

183   were determined from reading incisor tooth sections, or from resights of recruited tagged

184   pups, Pomeroy *et al.*, 2010). Not all seals captured had a tooth removed for ageing. At NR

185   from 1998 as many animals as possible were identified by natural markings, many of these

186   remained observed but not weighed or aged (Hiby *et al.*, 2013).

187

188   *Environmental correlates*

189   UK grey seals are capital breeders: lactating females fast, relying on body reserves accrued

190   during the preceding foraging period. Food abundance over the year preceding breeding

191   was expected to play an important role in determining grey seal breeding success (Pomeroy

192   *et al.,* 1999). To link between breeding, food abundance and environmental conditions, we

193   selected environmental correlates *a priori* which were relevant to grey seal regional diets,

194   assuming that both breeding and foraging occurred within the same respective general

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

196

197   The North Atlantic Oscillation (NAO) annual winter index offers a broad scale measure of

198   annual meteorological fluctuations, and it has been associated with vital rates of different

199   species (Thompson & Ollason 2001; King *et al.* 2005; Sandvik, Erikstad, Barrett and Yoccoz

200   2005). We used 1-year lagged annual winter NAO (i.e. relating to the winter prior to

201   breeding) to index food (1-group forage fish, Hammond & Wilson 2016) abundance.

202   In the UK, the sandeel *Ammodytes marinus* is found consistently in grey seal diet samples.

203   This high-energy prey appears to be of particular importance for east coast seal populations

204   (Cury *et al.* 2011; Hammond & Wilson 2016). Indices of sandeel abundance are available in

205   some areas of the North Sea including areas close to the IM (ICES 2016). However, direct

206   estimates of sandeel abundance are not consistently available for west coast areas used by

207   NR seals and sandeels are also less important in west coast seal diets (Hammond, Hall &

208   Prime 1994; Hammond & Wilson 2016). Sandeels are an important dietary component for

209   seals foraging around IM therefore sandeel abundance associated with spring/summer

210   (when sandeels are in the water column and available to fishing) during the year leading up

211   to grey seal breeding was used as a covariate for the IM colony (ICES 2016; Hammond &

212   Wilson 2016) .

213

Analytical framework

215   Adapting the CJS model, we assumed animals were identified by unique marks during each

216   breeding season (Lebreton, Burnham, Clobert & Anderson. 1992). Individuals were recorded

217   as 1 or 0 ('seen' or 'not seen'). Pupping status was recorded similarly. Direct mass

218   measurements were obtained for some of the individuals in the study. We adopted a

219   Bayesian state-space modeling approach, offering some important advantages e.g. the user

220   can include informative priors to constrain the parameter search; and sampling from the

221   posterior distribution of parameters allows for inference about quantities calculated from

222   model parameters. Adapting the CJS model for this framework required us to separate the

223   process model (which includes survival and pupping) from the observation model (animals

224   may or may not have been observed). However, the level of detail that could be included

225   was limited, due to the nature and quantity of the data available. Because the link between

226   phenology, breeding and environment was a primary concern, our modelling focused on

227   this, explicitly including links from environment to individual mass and pupping history, and

228   then to vital rates. This contrasts with models that assume time-dependent

229   survival/breeding/recapture probabilities that are common to all individuals, estimating

230   them separately for each year. In our approach, processes such as foraging success and

231   mark loss drove the state of the individual (its mass, breeding status and marks present)

232   through the study period (King 2014; King, Morgan, Gimenez & Brooks 2009). The

233   observation process (whether or not the animal was observed) depended on the state of

234   the animal including its breeding status and identifying marks. After initial exploratory

235   analyses the initial CMR model in which vital rates depended on mass was further simplified

236   by excluding mass-dependence in survival rate for both study systems, as there was little

237   evidence for this dependence structure, and survival was estimated separately for each

238   colony.

239

240   *Process model*

241

242   Maternal expenditure, represented by mass loss during lactation, was estimated using a

243   general multiplier β acting on maternal postpartum mass (Pomeroy *et al.*, 1999; Wheatley,

244   Bradshaw, Harcourt & Hindell, 2008; Figure1) . Thus for a female j pupping in year t the

245   expected mass of a female at the start of the breeding season $M_{j,t}$ was related to her mass

246   at the end of breeding season

247
248     $W_{j,t} \sim N(\beta M_{j,t}, \sigma_W^2)$
249

250   The true mass of the female was assumed to be Normally distributed around the expected

251   value, reflecting both the individual variation between females, and observation error in

252   mass measurement.The mass of a female j at the end of breeding in year t influenced mass

253   at the beginning of breeding in year $t+1$ subject to an additional colony and year-specific

254   environmental effect ε_t common to all animals, breeders and non-breeders. The effect of

255   pregnancy on expected mass gain was estimated by the factor δ such that for a pregnant

256   female pupping in year $t+1$, with the true mass of the female assumed to be Normally

257   distributed:

258

259     $M_{j,t+1} \sim N(\delta \varepsilon_t W_{j,t}, \sigma_M^2)$
260

261

262   Thus combining the above modelling components, for a female pupping in year $t + 1$ the

263   expected relationship between end-of-season masses in year t and $t + 1$ is given by:

264

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

266

267   For a non-pupping female, there was no effect of pregnancy on mass gain and no lactation,

268   so $\delta \; \beta$ were both set to 1. For these non-breeding animals the expected relationship is

269   described by:

270

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

272

273   The product $\delta \; \beta$ could be interpreted as a general estimate of the ratio between the end-

274   of-season mass for breeding and non-breeding females. Both constants were estimable

275   because we observe values of both $W_{j,t}$ and $M_{j,t}$ in the data set, allowing direct estimation

276   of β from data on breeding animals. As previously, maternal masses $W_{j,t}$

277   were assumed to be Normally distributed with constant variance.

278

279   The year-dependent mass-gain ε_t was modelled as a function of the respective

280   environmental variable (1 year lagged NAO for NR, and sandeel abundance for IM)

281   represented here by x_t

282

283    $\varepsilon_t = a + bx_t$

284

285   where a and b were estimated. If the 95% BCI (Bayesian Credible Interval) around the

286   estimate for the parameter b did not include zero, this was taken as evidence for an

287   association between mass gain and the environmental variable.

288

289   Pupping was treated as a Bernouilli process with underlying probability $f_{j,t+1}$. This was

290   associated with maternal weaning mass $W_{j,t}$ in the previous year, scaled by the year-effect.

291   A logistic relationship was assumed:

292

293    $f_{j,t+1} = \dfrac{\exp(a_p + b_p\, \varepsilon_t\, W_{j,t})}{1+\exp(a_p + b_p\, \varepsilon_t\, W_{j,t})}$

294

295   Colony-specific values for a_p and b_p were estimated. If the 95% BCI around the estimate for

296   the b_p did not include zero, this was taken as evidence for an association between pupping

297   probability $f_{j,t+1}$ and $W_{j,t}$. The sign of b_p indicated the type of association.

298

299   Because we could not distinguish between animals that died and any that permanently

300   emigrated from the study population we estimated 'apparent survival', abbreviated to

301   'survival' hereafter. Preliminary investigations into the effects of maternal mass on survival

302   did not find evidence for a strong effect of mass on survival so the model structure was

303   adjusted and survival was estimated as a constant value for each colony (see S1).

304

305   The model included the possibility that some females, referred to here as 'transients', were

306   available to be seen on only one occasion (Pradel, Hines, Lebreton & Nichols. 1997; Hiby *et*

307   *al.* 2013). We estimated the colony-specific probability $p_{transient}$ that an animal identified

308   for the first time was in this category.

309

310   *Observation model*

311

312   We estimated distinct parameters p_{pup} representing the re-sighting probability of breeding

313   females, and $p_{no\ pup}$ for non-breeding females. Seals were marked with brands, flipper tags,

314   and pelage markings. Mark-dependent values of re-sighting probability were estimated

315   during the model-fitting process for NR and IM separately. The probability of tag loss could

316   also be estimated, because some animals carried multiple mark types e.g. tags and brands.

317   Brands and pelage-ID were treated as permanent marks (Smout *et al.* 2011a; S1).

318

319   *Estimation*

320

321   The Bayesian fitting algorithm estimated values of female mass where gaps occurred in

322   series (Figure 1). Similarly, the unknown pupping status of unobserved animals was

323   estimated based on observed masses in the previous and subsequent years.

324   Unknown mass values and model parameters were estimated using the freely-available

325   open source software WinBUGS (Lunn, Speigelhalter Thomas & Best 2009). A model

326   description, equations and priors are detailed in Supplementary Material (S1); code is

327   provided in (S2). Convergence was checked based on visual inspection of plots for multiple

328   chains and BGR convergence statistics (Gelman *et al.* 2013).

329

330   *Checking goodness-of-fit*

331   With a complex data set and substantial missing data, it is difficult to directly estimate

332   goodness of fit or to use information criteria such as DIC to carry out model comparison

333   (Celeux, Forbes, Robert & Titterington 2006). To address the question of goodness of fit we

334   have implemented an approach with the same underlying principle as a Bayesian *p*-value,

335   but focused on the estimation of net fecundity - the quantity of particular interest in this

336   study. In particular our aim is to compare simulated fecundity rates (conditional on the

337   initial sighting and observed mass if any) with estimated rates drawn from the posterior

338   distribution of the parameters (i.e. from the MCMC iterations) to identify whether or not

339   they are comparable. If the estimates are comparable there is no evidence against the

340   model; alternatively, if they are systematically different this suggests a lack of absolute

341   model fit with regard to fecundity. This fecundity rate was then used as the associated

342   "discrepancy function": we compared the estimated fecundity from the posterior

343   distribution with the associated simulated fecundity given these particular parameter

344   values. This process was repeated for 1000 random draws from the posterior. We then

345   record the proportion of simulated fecundity rates that were higher than the associated

346   fecundity rate for that posterior sample. As for a formal Bayesian *p*-value, if simulated and

347   fitted rates are similarly distributed, this proportion is expected to be around 0.5, and this

348   then indicates a satisfactory correspondence between model and data; whereas a

349   proportion in the "tails" (e.g. lower or upper 5% quantiles) would indicate a potential lack of

350   model fit (King *et al*., 2009).

351

352   *Model predictions for pupping probabilities; the effects of varying environmental conditions*

353

354   To explore the implications of the fitted model, we estimated the effect of environmental

355   drivers on the probability of pupping. 'Poor environmental conditions', chosen from the

356   original covariate data, were defined as the values of sandeel abundance or NAO that

357   predicted lowest proportional mass gain. 'Good conditions' were those values of

358   environmental covariates for which predicted proportional mass gain was highest. We

359   estimated the 'skipping point maternal weaning mass' W_{50} as the mass of the mother when

360   her pup weaned at which pupping probability in the next year would be 50%, if conditions

361   during the intervening year were poor. This was calculated using the fitted model for each

362   colony. Similarly the probability of pupping for a female with mass at weaning W_{50} after a

363   year of good conditions was also calculated. Therefore, in effect we tested a theoretical

364   'skipping point mother' against the worst and best conditions observed in the data.

365

366   The consequences of the variable environment, were explored further by estimating

367   pupping probabilities for females starting at W_{50} after two years of good conditions, and

368   after two years of poor conditions. These values were calculated either assuming that

369   pupping took place in the breeding season after the first year, or that it did not.

370

371   *Model predictions for local population trends*

372   To explore the consequences of our model estimates for local populations, we used a simple

373   Leslie matrix population simulation for females breeding at IM and NR, assuming no density-

374   dependent effects were acting and accounting for transients. In this model all animals

375   became fertile aged 6, adult and sub-adult survival rates were set at the mean estimated

376   values for adults for each colony, and fecundity was set to the mean colony average

377   estimate. Female first-year survival was set at 0.6 for IM (Hall & McConnell 2007) and for

378   NR this value was set at $0.6s_{NR}/s_{IM}$ where s_{NR} and s_{IM} were the estimated adult survival

379   rates at NR and IM.

380

381   **Results**

382

383   After a 2000 iteration burn-in period, the MCMC for NR and IM appeared to converge with

384   stationary posterior parameter estimates achieved after 100,000 iterations. Breeding

385   parameter estimates are summarized in Table 2, for full parameter table see Supplementary

386   Material (S1). The estimated values from our Goodness of Fit tests were 0.307 for NR and

387   0.284 for IM which were both satisfactory, indicating acceptable model fit for fecundity rate

388   estimation.

389   *Parameter estimates*

Table 2.	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)
$p_{no\ pup}$	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)
$P_{transient}$	Probability that a female recorded in the data set 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)

390
391   Table 2: Mean parameter estimates for the process and observation models (95% Bayesian credible
392   intervals are shown in brackets).

393

394   Mean survival rate at NR was lower than at IM, consistent with previous findings (Smout *et*

395   *al.* 2011a). There were more mothers estimated as 'transient' at NR than at IM (Table 2).

396

397   For both colonies there was evidence for a positive relationship between pupping

398   probability in year $t + 1$ and W_t (maternal mass at the end of breeding in year t) with

399   appreciable effects on pupping probability over the range of mass values observed in the

400   data set (Figure 2). The IM pupping probability-mass curve shows a steeper relationship

401   than that for NR: at IM, pupping probability doubles from 0.4 to 0.8 over a range of

402   approximately 13kg while at NR the same change occurs over a range of approximately

403   23kg.

404

405   Average net fecundity calculated for NR females is less than that for IM females, but

406   credible intervals overlap for the two sites. For comparison, a simple calculation based on

407   the observational data, assuming that all unobserved known animal-years were non-

408   breeding years, gave net fecundity rates of 0.679 at NR and 0.750 at IM, highlighting the

409   importance of accounting for unobserved individuals.

410

411   The estimated probability of re-sighting a non-breeding female was low at both colonies,

412   consistent with the observation that very few non-breeding adult females are seen at these

413   colonies (Table 2).

414

415   The postpartum masses of mothers at NR and IM encompassed a similar range, with several

416   at each colony exceeding 250kg. The estimated value of β (the ratio of maternal mass at the

417   end of lactation to mass at start of lactation) was very similar between IM and NR: on

418   average, a mother expended 35% of her postpartum mass on raising a pup (Table 2).

419   Average proportional mass gain δ for pregnant mothers between end and start of

420   successive breeding seasons was lower for those at NR than for those at IM (Table 2).

421

422   *Environmental variation and breeding probability*

423

424   There was no evidence for an association between mass gain and NAO at IM, so this was

425   excluded from the final fitted model. The relationship between mass gain and sandeel

426   abundance at IM was positive (Figure 3). For NR, the underlying relationship between mass

427   gain and NAO index was negative (Figure 4).

428

429   Year specific proportional mass gains ε_t were generally larger at NR than at IM (Figures 3,4;

430   right panels). Synchronicity of environmental effects at the two colonies was limited; better

431   than average mass gains occurred at both colonies in 1995 and 2010.

432

433   The predicted effects of environment and breeding on subsequent pupping probability are

434   important for 'skipping point' W_{50} animals at both colonies (p_{t+1} in Table 3). Not breeding

435   has an appreciable effect for skipping point animals, where pupping probability p_{t+2} can

436   either decrease if pupping takes place in year t+1, or increase if breeding is skipped (Table 3,

437   columns 4 and 5).   Mothers at the skipping point were heavier at NR (93.5kg) than at IM

438   (88.5kg).

439

440

Table 3.	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

441

442   Table 3: The predicted impacts of environmental conditions. 'Skipping point' mothers of mass W_{50} in year t

443   have a 50% probability of pupping in year $t+1$ after a 'poor' year of environmental conditions. If

444   environmental conditions are better (low NAO at NR, high sandeels at IM) then pupping probability in year $t+1$

445   is improved (p_{t+1} column 3). Predicted pupping probabilities for year $t+2$ are shown after 2 years of consistent

446   environmental conditions (2 good years or 2 bad years), in columns 4 and 5. Column 4 gives values for females

447   if they bred in year $t+1$; Column 5 gives values for females that 'skipped' breeding in year $t+1$.

448

449   *Population trajectory for each colony*

450

451   The predicted time series of number of females breeding derived from the Leslie model

452   declined at NR and increased at IM (dashed and solid lines respectively, Figure 5). Simple

453   visual comparison suggests that there is a good correspondence with trends in pup

454   production estimates derived from synoptic counts of pups from aerial survey (NR, IM solid

455   and open circles respectively, Duck & Morris 2016).

456

457   **Discussion**

458

459   Intermittent breeding in iteroparous animals acts on LRO and individual fitness, and affects

460   demographic rates at the population level. Capital breeding species in fluctuating

461   environments are likely to be particularly prone to skipping breeding episodes, when

462   survival takes precedence over reproduction (Stearns, 1992). Skipped breeding episodes

463   among experienced breeders are known in capital breeding phocid seals, but mechanistic

464   explanations of the process have often relied anecdotally on Boyd's (2000) finding that body

465   mass accounted for more variation in pregnancy rates in capital breeding than income

466   breeding species (e.g. Chambert, Rotella, Higgs & Garrott, 2013; Desprez et al., 2017).

467   Desprez et al. (2017) used resighting records at Macquarie Island to investigate intermittent

468   breeding of southern elephant seals *Mirounga leonina.* Using a multi-event model

469   incorporating uncertain reproductive status and categorizing adult females into breeding

470   heterogeneity classes, they found that there was a survival cost to breeding for females in

471   the infrequently breeding class. This latter class they suggested comprised females of lower

472   quality in some phenotypic property positively related to fitness, and while variability in

473   individuals' ability to forage and gain resources were hypothesized to be likely explanatory

474   factors, no phenotypic or other measures of animals were provided to support this (Desprez

475   et al., 2017). Similarly, Chambert, Rotella & Garrott, (2015) proposed that female Weddell

476   seals (*Leptonychotes weddellii*) that skipped breeding in Erebus Bay, Antarctica were in

477   poorer condition than regular breeders. Here, we provide the empirical evidence for an

478   effect of maternal mass on pupping probability in a capital breeding phocid, the grey seal,

479   and importantly, of the increased pupping probability that low body mass females accrue by

480   skipping a reproductive episode.

481

482   Environmental fluctuations are seen to impact long-lived marine species' fecundity rather

483   than survival (Reed, Harris & Wanless, 2015; Stenson et al*.,* 2016).   Our study showed an

484   impact of female mass on the probability of pupping but did not detect an effect on survival.

485   While a female in sufficiently poor condition might be expected to have reduced survival

486   probability, this may be difficult to observe. If low-mass animals miss breeding, are not

487   observed at the colony and are never seen again we may lack the data to define the shape

488   of the descending arm of the logistic curve for the survival-mass relationship. If breeding is

489   costly, animals in poor condition (low body mass) may forego breeding and improve their

490   own chances of survival (Ronget, Garratt, Lemaître & Gaillard 2017). We found that impacts

491   of breeding on subsequent pupping probability for grey seals are substantial for seals whose

492   mass at end of breeding is low (Figure 2). At both colonies our model predicts that in poor

493   environmental conditions, females that 'skip' breeding are more likely to pup in subsequent

494   years (Table 3). Similar skipping breeding sequences were linked with body condition and

495   environmental conditions in Weddell seals (Proffitt, Garrott, Rotella & Wheatley 2007;

496   Chambert et al., 2015).

497

498   Mass-adjusted fecundity rates suggest that around two-thirds of "missing" years are indeed

499   non-breeding years (Table 2). Movement away from the natal colony or permanent

500   emigration by adults to different colonies might occur, and cannot be distinguished here

501   from permanent loss of fertility, or death (Harrison et al., 2006). Nevertheless, our analyses

502   suggest breeding occurred in around one third of "missed" breeding years. Some pupping

503   events of known females at their "normal" colony could have gone unobserved, but high

504   resight rates (Table 2) suggest these should be few. The remaining 'missed' breeding events

505   must have occurred outwith the prevalent breeding site fidelity pattern (Pomeroy et al.

506   1994). Genetic differences between NR and IM seals are sufficient to suggest very low

507   effective breeding interchange between distant colonies (Allen, Amos, Pomeroy & Twiss,

508   1995), but any breeding colony infidelity would help explain unassigned paternities

509   (Worthington Wilmer, Allen, Pomeroy, Twiss & Amos 2003).

510

511   Some female grey seals observed for the first time became subsequently unobservable,

512   especially at NR (Table 2). Although termed "transients", different phenomena can produce

513   such records. Most convincing is the difficulty in making matches between patterns

514   extracted from different photographs of the same grey seal identified by pelage alone (Hiby

515   *et al.* 2013), as many more females were identified by this method at NR (Table 1).

516   Alternative explanations include: some subset of adult females have lower survival e.g.

517   primiparous females; higher tag loss rates directly after application; different tag loss rates

518   between seals at different colonies. Seals may visit a colony once only, then breed

519   elsewhere subsequently - features of a declining colony such as NR may indicate to first time

520   visitors that it is undesirable, resulting in demographic state-dependent colony fidelity.

521

522   Intermittent breeding has been described as a tactic employed by poorer quality mothers to

523   optimize LRO (Desprez et al., 2017).   True capital breeders rely on accumulated reserves,

524   expending a large proportion of postpartum body mass (grey seals 0.35, Table 2; southern

525   elephant seals 0.35, Arnbom et al., 1997) to sustain a reproductive episode. Average

526   proportional expenditure was the same at NR and IM, despite body mass differences and

527   different vital rates. Pregnant NR seals did not regain as much of their previous MPPM as

528   equivalent mothers at IM ($\delta = 1.34$, 1.40 respectively, Table 2), suggesting that successive

529   pregnancies incur a cost in reduced subsequent MPPM and that NR mothers experienced

530   this to greater extent, possibly as a result of poorer overall resource availability. Further

531   reductions in mass of small mothers would be unsustainable and in such cases skipping

532   breeding seems likely. While a mother experiences strong selective pressure on raising a

533   pup within resource limits, the future costs of which vary according to initial maternal body

534   mass and reserves, individual and episodic variations in reproductive expenditure occur

535   (Arnbom et al., 1997; Pomeroy et al., 1999).   However, even for capital breeders, body

536   mass alone may not be a perfect metric of body reserves, because it masks the availability

537   of all the nutrients required for a successful breeding episode. Often only lipid reserves are

538   used to estimate "condition" in capital breeders as they provide most of the energetic

539   requirements of mother and offspring, but protein and other nutrients must also be

540   available and in the extreme may be more limiting (eg Arnbom et al., 1997; Boyd, 2000;

541   Mellish, Iverson & Bowen, 1999; Hanson, Smout, Moss & Pomeroy, in press). Our modelling

542   framework could be adapted to include more complex measures of body condition in future

543   studies, including combining different measures, if such data are available.

544

545   Assessing the effects of different demographic rates on populations requires that rates are

546   estimated appropriately: for fecundity, non-breeders and non-breeding episodes must be

547   taken into account (Lee, Reid & Beissinger 2017). Here, we found that relatively small

548   differences in colony fecundity rate are associated with very different colony pup

549   production trajectories. Canadian and Norwegian studies of grey seals have reported

550   fecundity estimates similar to our mass-adjusted overall female fecundity rates (Bowen,

551   Iverson, McMillan & Boness 2006; Hammill & Gosselin 1995).   Nevertheless, fecundity and

552   adult female survival were both lower for NR seals than those at the growing IM colony,

553   which had similar parameters to those reported from the expanding colony on Sable Island,

554   Canada (den Heyer & Bowen, 2017).   Simple Leslie matrix population simulations showed

555   rates of local population growth and decline that are consistent with observed trends in pup

556   production at both colonies for the early years of the study: a decline in pup production at

557   NR, compared with a positive trend at IM (Duck & Morris 2016).   The breeding decline at

558   NR is present at other Hebridean grey seal colonies (Duck & Morris 2016) and poor

559   recruitment of seals tagged as pups to NR is a likely additional factor in explaining these

560   trends (Pomeroy *et al.*, 2010). Long term declines in measures of grey seal "condition" at

561   NR compared to IM suggests that colony-level effects are reflected in individual phenotypic

562   covariates and these are a local response to local conditions (Hanson *et al.*, in press) which

563   likely explains lower fecundity at NR (Boyd, 2000). Longitudinal seabird surveys on NR have

564   shown decadal declines in 9 of 15 species that use the island for breeding, in common with

565   trends reported in such species elsewhere in the North Atlantic (Murray & Wilson 2013).

566   That many different marine apex predators show contemporaneous regional declines is

567   indicative of the generality of ecosystem change to their detriment in this region.

568

569   Grey seals are generalist predators and their diet varies in response to changing prey

570   abundance (Smout, Rindorf, Hammond, Harwood & Matthioupolos 2013). As capital

571   breeders capable of wide-ranging foraging, they are buffered against small scale, short term

572   changes in prey availability. The association between NAO (lagged one year) and grey seal

573   mass change at NR, is explicable if Atlantic atmospheric conditions correlate with the

574   abundance of one or more important prey species with direct consequences for the

575   condition of seals foraging and breeding on the UK's Atlantic fringe. There was no evidence

576   of a similar effect of NAO at IM, consistent with the limited influence of NAO on the North

577   Sea ecosystem where most IM seals forage, compared to west coast waters that are

578   connected directly to the Atlantic (Harris, Edwards & Olhede 2014). The appreciable effect

579   of local sandeel abundance reflects the importance of sandeels in seal diets in this area and

580   the wider North Sea where these seals are likely to forage (Russell *et al.*, 2013; Hammond &

581   Wilson 2016).

582

583   The Bayesian modelling approach implemented here using freely available software allowed

584   us to fit a model of the relationship between annual mass gain and environmental drivers,

585   including 'nuisance' processes (tag loss) that might otherwise obscure important effects and

586   a realistic observation model with missing data and unknown states. Our analyses

587   highlighted the consequential nature of breeding events: longitudinal maternal mass

588   trajectories suggested underlying breeding histories, and while skipping breeding was

589   associated with low body mass, females that skipped had a higher probability of breeding

590   subsequently.

591

592   **Ethics**

593   Work involving animals in this study was licensed under UK Home Office project 60/4009 or

594   preceding versions and conformed to the UK Animals (Scientific Procedures) Act, 1986.

595   Research was approved by the University of St Andrews Animal Welfare and Ethics

596   Committee.

597   **Data accessibility**

598   Data are lodged in PURE, http://dx.doi.org/10.17630/8b1f33d5-50bf-4631-9e65-

599   fca33d26902f.

600   **Authors' contributions**

601   PP designed and managed the long term research and carried out fieldwork; PP and RK

602   conceived of and designed the study; SCS analyzed the data; SCS and PP led writing of the

603   paper and share first authorship. All authors gave final approval for publication.

619

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