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

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Keywords: *Halichoerus grypus*, fecundity, mass, state space model

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19 **Abstract**

20 1. The trade-off between survival and reproduction in resource-limited iteroparous animals
21 can result in some individuals missing some breeding opportunities. In practice, even with
22 the best observation regimes, deciding whether ‘missed’ years represent real pauses in
23 breeding or failures to detect breeding can be difficult, posing problems for the estimation
24 of individual reproductive output and overall population fecundity.

25 2. We corrected fecundity estimates by determining if breeding had occurred in skipped
26 years, using long term capture-recapture observation datasets with parallel longitudinal
27 mass measurements, based on informative underlying relationships between individuals’
28 mass, breeding status and environmental drivers in a capital breeding phocid, the grey seal.

29 3. Bayesian modelling considered interacting processes jointly: temporal changes in a
30 phenotypic covariate (mass); relationship of mass to breeding probability; effects of
31 maternal breeding state and mark type on re-sighting. Full reproductive histories were
32 imputed, with the status of unobserved animals estimated as breeding or non-breeding,
33 accounting for local environmental variation. Overall fecundity was then derived for Scottish
34 breeding colonies with contrasting pup production trends.

35 4. Maternal mass affected breeding likelihood. Mothers with low body mass at the end of
36 breeding were less likely to bear a pup the following year. Successive breeding episodes
37 incurred a cost in reduced body mass which was more pronounced for North Rona, Outer
38 Hebrides (NR) mothers. Skipping breeding increased subsequent pupping probability
39 substantially for low mass females. Poor environmental conditions were associated with
40 declines in breeding probability at both colonies. Seal mass gain between breeding seasons
41 was: (i) negatively associated with lagged North Atlantic Oscillation for seals at NR, ; (ii)
42 positively associated with an index of seal prey (*Ammodytes* spp) abundance at Isle of May,

43 Firth of Forth (IM). Overall fecundity was marginally greater at IM (increasing/stable pup
44 production) than at NR (decreasing). No effects of mass were detected on maternal survival.
45 5. Skipping breeding in female grey seals appears to be an individual mass-dependent
46 constraint moderated by previous reproductive output and local environmental conditions.
47 Different demographic trends at breeding colonies were consistent with the fecundities
48 estimated using this method, which is general and adaptable to other situations.

49 Introduction

50

51 Resource limitation results in animals making trade-offs between traits such as survival and
52 reproduction: costly expenditure on breeding can impact future survival or reproduction
53 (Stearns, 1992). Iteroparous long-lived species may trade off current and future
54 reproduction when a reproductive episode is sacrificed in favour of survival. True capital
55 breeders must acquire resources in advance of a breeding attempt to provision themselves
56 and their offspring throughout the breeding season. Fasting during reproduction means that
57 maternal resources are finite. Individuals may differ in their ability to acquire resources
58 according to age or experience (Beauplet, Barbraud, Dabin, Küssener & Guinet, 2006;
59 Desprez, Pradel, Cam, Monnat & Gimenez, 2011); individual quality (Hamel, Cote, Gaillard
60 & Festa-Bianchet, 2009) or population density (Hamel, Côté & Festa-Bianchet, 2010).
61 Moreover, environmental conditions may lead to changing resource availability and
62 individual life history schedules are more likely to feature missed breeding attempts when
63 conditions are unfavourable (Cubaynes, Doherty, Schreiber & Gimenez, 2011; Forcada,
64 Trathan & Murphy, 2008; Parsons 2008; Soldatini, Albores-Barajas, Massa & Gimenez,
65 2016). Skipped breeding episodes may allow individuals to maintain survival and together
66 these impact Lifetime Reproductive Output. Population fecundity is affected when sufficient
67 such events occur.

68

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

214 *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

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

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

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

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 Bernoulli 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

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

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, Spiegelhalter 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).

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

439

440 Table 3: The predicted impacts of environmental conditions. ‘Skipping point’ mothers of mass W_{50} in year t
 441 have a 50% probability of pupping in year $t+1$ after a ‘poor’ year of environmental conditions. If
 442 environmental conditions are better (low NAO at NR, high sandeels at IM) then pupping probability in year $t+1$
 443 is improved (p_{t+1} column 3). Predicted pupping probabilities for year $t+2$ are shown after 2 years of consistent
 444 environmental conditions (2 good years or 2 bad years), in columns 4 and 5. Column 4 gives values for females
 445 if they bred in year $t+1$; Column 5 gives values for females that ‘skipped’ breeding in year $t+1$.

446

447 *Population trajectory for each colony*

448

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

454

455 **Discussion**

456

457 Intermittent breeding in iteroparous animals acts on LRO and individual fitness, and affects
 458 demographic rates at the population level. Capital breeding species in fluctuating
 459 environments are likely to be particularly prone to skipping breeding episodes, when
 460 survival takes precedence over reproduction (Stearns, 1992). Skipped breeding episodes
 461 among experienced breeders are known in capital breeding phocid seals, but mechanistic

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

479

480 Environmental fluctuations are seen to impact long-lived marine species' fecundity rather
481 than survival (Reed, Harris & Wanless, 2015; Stenson et al., 2016). Our study showed an
482 impact of female mass on the probability of pupping but did not detect an effect on survival.
483 While a female in sufficiently poor condition might be expected to have reduced survival
484 probability, this may be difficult to observe. If low-mass animals miss breeding, are not
485 observed at the colony and are never seen again we may lack the data to define the shape

486 of the descending arm of the logistic curve for the survival-mass relationship. If breeding is
487 costly, animals in poor condition (low body mass) may forego breeding and improve their
488 own chances of survival (Ronget, Garratt, Lemaître & Gaillard 2017). We found that impacts
489 of breeding on subsequent pupping probability for grey seals are substantial for seals whose
490 mass at end of breeding is low (Figure 2). At both colonies our model predicts that in poor
491 environmental conditions, females that ‘skip’ breeding are more likely to pup in subsequent
492 years (Table 3). Similar skipping breeding sequences were linked with body condition and
493 environmental conditions in Weddell seals (Proffitt, Garrott, Rotella & Wheatley 2007;
494 Chambert et al., 2015).

495

496 Mass-adjusted fecundity rates suggest that around two-thirds of “missing” years are indeed
497 non-breeding years (Table 2). Movement away from the natal colony or permanent
498 emigration by adults to different colonies might occur, and cannot be distinguished here
499 from permanent loss of fertility, or death (Harrison et al., 2006). Nevertheless, our analyses
500 suggest breeding occurred in around one third of “missed” breeding years. Some pupping
501 events of known females at their “normal” colony could have gone unobserved, but high
502 resight rates (Table 2) suggest these should be few. The remaining ‘missed’ breeding events
503 must have occurred outwith the prevalent breeding site fidelity pattern (Pomeroy et al.
504 1994). Genetic differences between NR and IM seals are sufficient to suggest very low
505 effective breeding interchange between distant colonies (Allen, Amos, Pomeroy & Twiss,
506 1995), but any breeding colony infidelity would help explain unassigned paternities
507 (Worthington Wilmer, Allen, Pomeroy, Twiss & Amos 2003).

508

509 Some female grey seals observed for the first time became subsequently unobservable,
510 especially at NR (Table 2). Although termed “transients”, different phenomena can produce
511 such records. Most convincing is the difficulty in making matches between patterns
512 extracted from different photographs of the same grey seal identified by pelage alone (Hiby
513 *et al.* 2013), as many more females were identified by this method at NR (Table 1).
514 Alternative explanations include: some subset of adult females have lower survival e.g.
515 primiparous females; higher tag loss rates directly after application; different tag loss rates
516 between seals at different colonies. Seals may visit a colony once only, then breed
517 elsewhere subsequently - features of a declining colony such as NR may indicate to first time
518 visitors that it is undesirable, resulting in demographic state-dependent colony fidelity.
519
520 Intermittent breeding has been described as a tactic employed by poorer quality mothers to
521 optimize LRO (Desprez *et al.*, 2017). True capital breeders rely on accumulated reserves,
522 expending a large proportion of postpartum body mass (grey seals 0.35, Table 2; southern
523 elephant seals 0.35, Arnborn *et al.*, 1997) to sustain a reproductive episode. Average
524 proportional expenditure was the same at NR and IM, despite body mass differences and
525 different vital rates. Pregnant NR seals did not regain as much of their previous MPPM as
526 equivalent mothers at IM ($\delta = 1.34, 1.40$ respectively, Table 2), suggesting that successive
527 pregnancies incur a cost in reduced subsequent MPPM and that NR mothers experienced
528 this to greater extent, possibly as a result of poorer overall resource availability. Further
529 reductions in mass of small mothers would be unsustainable and in such cases skipping
530 breeding seems likely. While a mother experiences strong selective pressure on raising a
531 pup within resource limits, the future costs of which vary according to initial maternal body
532 mass and reserves, individual and episodic variations in reproductive expenditure occur

533 (Arnbom et al., 1997; Pomeroy et al., 1999). However, even for capital breeders, body
534 mass alone may not be a perfect metric of body reserves, because it masks the availability
535 of all the nutrients required for a successful breeding episode. Often only lipid reserves are
536 used to estimate “condition” in capital breeders as they provide most of the energetic
537 requirements of mother and offspring, but protein and other nutrients must also be
538 available and in the extreme may be more limiting (eg Arnbom et al., 1997; Boyd, 2000;
539 Mellish, Iverson & Bowen, 1999; Hanson, Smout, Moss & Pomeroy, in press). Our modelling
540 framework could be adapted to include more complex measures of body condition in future
541 studies, including combining different measures, if such data are available.

542

543 Assessing the effects of different demographic rates on populations requires that rates are
544 estimated appropriately: for fecundity, non-breeders and non-breeding episodes must be
545 taken into account (Lee, Reid & Beissinger 2017). Here, we found that relatively small
546 differences in colony fecundity rate are associated with very different colony pup
547 production trajectories. Canadian and Norwegian studies of grey seals have reported
548 fecundity estimates similar to our mass-adjusted overall female fecundity rates (Bowen,
549 Iverson, McMillan & Boness 2006; Hammill & Gosselin 1995). Nevertheless, fecundity and
550 adult female survival were both lower for NR seals than those at the growing IM colony,
551 which had similar parameters to those reported from the expanding colony on Sable Island,
552 Canada (den Heyer & Bowen, 2017). Simple Leslie matrix population simulations showed
553 rates of local population growth and decline that are consistent with observed trends in pup
554 production at both colonies for the early years of the study: a decline in pup production at
555 NR, compared with a positive trend at IM (Duck & Morris 2016). The breeding decline at
556 NR is present at other Hebridean grey seal colonies (Duck & Morris 2016) and poor

557 recruitment of seals tagged as pups to NR is a likely additional factor in explaining these
558 trends (Pomeroy *et al.*, 2010). Long term declines in measures of grey seal “condition” at
559 NR compared to IM suggests that colony-level effects are reflected in individual phenotypic
560 covariates and these are a local response to local conditions (Hanson *et al.*, in press) which
561 likely explains lower fecundity at NR (Boyd, 2000). Longitudinal seabird surveys on NR have
562 shown decadal declines in 9 of 15 species that use the island for breeding, in common with
563 trends reported in such species elsewhere in the North Atlantic (Murray & Wilson 2013).
564 That many different marine apex predators show contemporaneous regional declines is
565 indicative of the generality of ecosystem change to their detriment in this region.

566

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

580

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

589

590 **Ethics**

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

595 **Data accessibility**

596 Data are lodged in PURE, [http://dx.doi.org/10.17630/8b1f33d5-50bf-4631-9e65-](http://dx.doi.org/10.17630/8b1f33d5-50bf-4631-9e65-fca33d26902f)
597 [fca33d26902f](http://dx.doi.org/10.17630/8b1f33d5-50bf-4631-9e65-fca33d26902f).

598 **Authors' contributions**

599 PP designed and managed the long term research and carried out fieldwork; PP and RK
600 conceived of and designed the study; SCS analyzed the data; SCS and PP led writing of the
601 paper and share first authorship. All authors gave final approval for publication.

602 Competing interests

603 The authors have no competing interests.

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