

State-space modelling reveals proximate causes of harbour seal population declines

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Abstract Declines in large vertebrate populations are widespread but difficult to detect from monitoring data and hard to understand due to a multiplicity of plausible biological explanations. In parts of Scotland, harbour seals (*Phoca vitulina*) have been in decline for 10 years. To evaluate the contributions of different proximate causes (survival, fecundity, observation artefacts) to this decline, we collated behavioural, demographic and population data from one intensively studied population in part of the Moray Firth (north-east Scotland). To these, we fit a state-space model comprising age-structured dynamics and a detailed account of observation errors. After accounting for culling (estimated by our model as 14 % of total mortality),

the main driver of the historical population decline was a decreasing trend in survival of young individuals combined with (previously unrecognised) low levels of pupping success. In more recent years, the model provides evidence for considerable increases in breeding success and consistently high levels of adult survival. However, breeding success remains the most volatile demographic component of the population. Forecasts from the model indicate a slow population recovery, providing cautious support for recent management measures. Such investigations of the proximate causes of population change (survival, fecundity and observation errors) provide valuable short-term support for the management of population declines, helping to focus future data collection on those ultimate causal mechanisms that are not excluded by the demographic evidence. The contribution of specific ultimate drivers (e.g. shooting mortality or competitors) can also be quantified by including them as covariates to survival or fecundity.

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Introduction

Many population declines are ecological mysteries, not because of the lack of candidate explanations but due to the superabundance of possible causes and combinations thereof (Caughley 1994). Added to the scientific complexity of these on-going declines are the urgent conservation concerns over those populations' potential extinctions.

Strategically, the two management priorities in any suspected population decline are diagnosis and mitigation. For diagnosis, it is necessary to ascertain whether decreasing patterns in partial counts imply a population decline

and quantify the extinction threat for the population. For mitigation, it is desirable to identify the ultimate drivers of population change. There may be several such underlying mechanisms (e.g. disease, pollution, food quality, food quantity, food accessibility, human disturbance, and predation) and more than one of these can be in operation. Past experiences with heavily researched populations in decline, such as the Alaskan Steller sea lion (*Eumetopias jubatus*), have shown that it is impractical to conduct field or modelling studies for every conceivable mechanistic hypothesis or combination of hypotheses (Fay and Punt 2006; Guénette et al. 2006; Winship and Trites 2006). However, the task of pinpointing the ultimate, mechanistic drivers of a decline can be facilitated by first focusing on its proximate causes: trends in births, deaths, immigration and emigration but, also, possible observational artefacts.

Therefore, an expedient approach is to focus initially on the proximate causes of a decline (Wolf and Mangel 2008). This allows the use of simpler models whose parameters are identifiable from sparse demographic data. It also permits the examination of multifactor mechanisms, such as the possibility of a simultaneous decline in fecundity and survival. These models must be confronted with data in a way that accounts for observation and process uncertainty. The rapid introduction into ecology of state-space models (Clark 2007) and computer-intensive techniques now enables us to perform this type of statistical inference on non-trivial population models. To further elucidate the biological mechanism of a decline, it is then possible to incorporate any available data on ultimate causes as candidate covariates to the fundamental demographic processes. This empowers field investigations to target further data collection on the basis of residual demographic trends remaining after the known mechanisms have been accounted for.

Within the United Kingdom, the decreasing numbers of harbour seals (*Phoca vitulina*) counted in northern and eastern Scottish regions have raised the possibility of an emerging large-scale population decline (Lonergan et al. 2007). Given that the status of harbour seals in the United Kingdom had, until recently, been considered of minimum concern, it is particularly pertinent to investigate this developing issue.

We have focused on a well-studied, clearly defined sub-population of harbour seals in the Moray Firth, Scotland. Since it includes a Special Area of Conservation for harbour seals (Butler et al. 2008), this region is of additional interest as a case study in the implementation and effectiveness of management plans. We sought to answer these questions:

1. Whether the patterns in the monitoring data are due to a population decline and not to observation artefacts.
2. Whether these patterns are primarily explained by trends in known mortality (seal shooting).
3. What the remaining proximate demographic drivers of population change in the area might be.
4. What the projected size of the population is for the years following the end of the observed time series.

Materials and methods

To address the above questions we relied on an integrated analysis of different types of data (partial and seasonal population counts, sparse aggregate population estimates, shooting records, local mark-recapture estimates of survival and fecundity as well as data on haulout behaviour), within a Bayesian state-space model. The Bayesian approach enabled us to supplement the available data with prior information from historical studies and biological first principles. The model attempted to capture several hidden demographic processes and contained different stochastic observation components to enable it to draw information from the diverse data provided to it. The complexity of the resulting model incurred a considerable computational overhead and a penalty in terms of its ability to converge. This needed to be resolved pragmatically by fixing some parameters, limiting the ranges for the priors of others and only using uninformative priors for important parameters. We considered important those parameters to which the model results were sensitive and those which related directly to our four scientific questions. In this section, we begin by an overview of the data used and then describe the structure of the state-space model. We devote several subsections to justifying our treatment of each parameter in the model.

Count data

Harbour seals are one of two resident seal species encountered around the United Kingdom (the other being grey seals, *Halichoerus grypus*). The total United Kingdom population is estimated as 40,000–46,000 (Sea Mammal Research Unit 2010). Females reach reproductive maturity between their 4th and 6th year (Härkönen and Heide-Jørgensen 1990). They breed in early summer when each adult female produces up to one pup. Animals aggregate later in the summer for the moulting season. The onshore sites of aggregation used for resting, nursing pups and moulting are known as ‘haulouts’.

The University of Aberdeen carried out annual land-based counts in the inner Moray Firth between 1988 and 2006. Repeat surveys ($n = 3 - 10$) were conducted each year during both the pupping and moulting seasons. The ground count protocols are detailed in Thompson et al.

(1997, 2007). From 2006 onwards, the University of St Andrews started conducting fixed-wing aerial surveys in the region (four to five annually) during the pupping season, supplementing on-going but less frequent aerial surveys during the moult. Aerial count protocols can be found in Thompson et al. (2005) and Lonergan et al. (2007).

Breeding haulout sites in the inner Moray Firth are clustered into northern and southern areas, which have exhibited slightly different population trends over the last two decades (see Figs. 1 and 4 in Thompson et al. 2007). The ground survey dates in these two areas differed, making it computationally difficult to pool the data for a unified analysis (simultaneous modelling of multiple subpopulations was beyond the scope of this paper). We used data from just the northern area under the assumption that there was no net flux of animals between these regions. Harbour seals are particularly haulout-faithful during the summer months (Thompson et al. 1996) so the effect of movement between haulouts on the survey data from a single year is likely to be negligible (Cordes 2011). Between-haulout movement in the rest of the year is more extensive (Thompson et al. 1996), although a high proportion of individuals are faithful to the same haulout throughout the year. The assumption of no net flux is likely to be better supported for mature females whose breeding haulout fidelity often brings them back to the same region each summer (Härkönen and Harding 2001; Cordes 2011). To a lesser extent, this may also be true for males and immature females as an indirect effect of natal haulout fidelity. Additionally, the pup time series of the two regions were positively correlated, indicating no net movement between them. In broader terms, Thompson et al. (1996) found support for the idea that the harbour seal population of the Moray Firth, as a whole, is not affected by emigration. We therefore treated the northern area as an approximately closed population and hereafter refer to it as the ‘study population’.

Demographic model

We assumed that first reproduction occurs at age 5 and used a state-structured model comprising one pup, three subadult and one adult stage for each sex. Both sexes were included because differences between their haulout patterns may affect the numbers counted on the coast at different times of the year (Härkönen et al. 1999). The model’s ten state variables are specified to a time just following the breeding season, and the deterministic version of the model is:

$$N_{t+1} = R_t N_t \tag{1}$$

where $N_t = (n_{1,t}, \dots, n_{10,t})^T$ is the vector of population classes (the first five classes are males and the remaining are females) in year t . The deterministic transition matrix takes the form:

$$R_t = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}b_{t,sf,t} \\ s_{p,t} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{j,t} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{j,t} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{j,t} & s_{m,t} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}b_{t,sf,t} \\ 0 & 0 & 0 & 0 & 0 & s_{p,t} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{j,t} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{j,t} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{j,t} & s_{f,t} \end{pmatrix} \tag{2}$$

where the subscripts p, j, m, f refer to pups, subadults, adult males or adult females, respectively. Binomial demographic stochasticity is assumed for both fecundity and survival. Fecundity was modelled as a binomial (rather than Poisson) process because twins practically never occur (so, a Poisson would have been overdispersed). We incorporated a Year and Density effect into the fecundity rate by modelling the probability of pupping as a logit-polynomial function:

$$b_t = \frac{\exp(\beta_0 + \sum_{k=1}^3 \beta_k t^k + \beta_N N_t)}{1 + \exp(\beta_0 + \sum_{k=1}^3 \beta_k t^k + \beta_N N_t)} \tag{3}$$

A third-order polynomial in time was used to allow flexibility in describing trends in fecundity that are not due to population density. Survival was similarly modelled:

$$s_{*,t} = \frac{\exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k} t^k + \sigma_{*,N} N_t)}{1 + \exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k} t^k + \sigma_{*,N} N_t)} \tag{4}$$

where $*$ stands for p, j, m, f depending on whether the function refers to pups, subadults, adult males or adult females, respectively. Age-dependence in survival was incorporated by using different parameters for the baseline survival of pups ($\sigma_{p,0}$), subadults ($\sigma_{j,0}$), adult males ($\sigma_{m,0}$) and adult females ($\sigma_{f,0}$). During model fitting, we were able to estimate most of the demographic parameters. However, due to the sparsity of data on juvenile animals, it proved difficult to estimate separate trend parameters for pup and juvenile survival. We therefore combined the trend parameters but estimated baseline survival separately for pups and juveniles.

Observation model

We denote by $p_{i,t}(d)$ the probability that a seal belonging to the i th of ten population classes on shore on a given day ($1 \leq d < 365$) during the year t . Within a day, the number of seals hauled out varies greatly with tide (Thompson et al. 1997), so we specify $p_{i,t}(d)$ to ± 2 h of low tide, consistent with the protocol followed for both ground and

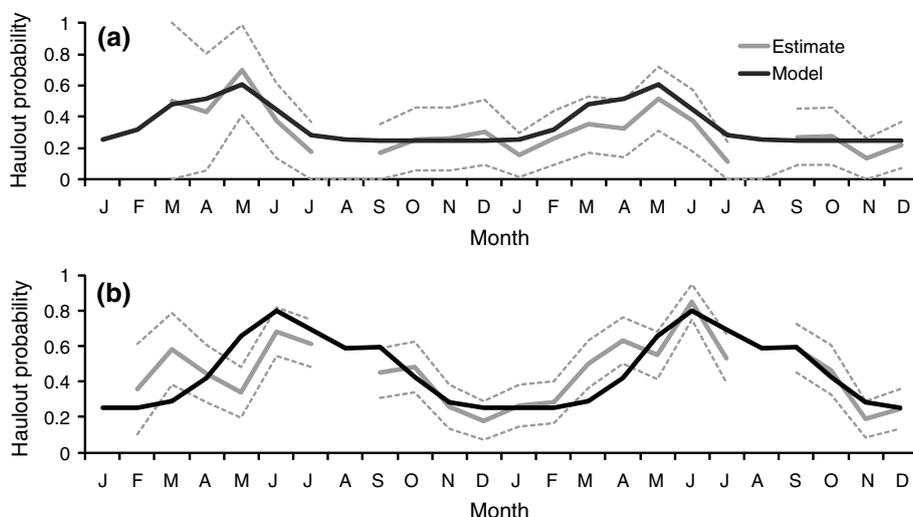
aerial surveys. The haulout probability was formulated as the superposition of three components: a baseline haulout probability and two pulse-like Gaussian components (without their normalizing constant) associated with the pupping and moulting seasons.

$$p_{i,t}(d) = \pi_{i,0} + \pi_{i,1} \exp \left[-\frac{1}{2} \frac{(d - \delta_{i,t,1})^2}{\gamma_{i,1}^2} \right] + \pi_{i,2} \exp \left[-\frac{1}{2} \frac{(d - \delta_{i,t,2})^2}{\gamma_{i,2}^2} \right] \quad (5)$$

Here, parameters with subscripts 1 and 2 refer to the breeding and moulting seasons, respectively. π_0 is the background haulout probability outside of the breeding and moulting seasons. The δ 's determine the timing of breeding and moulting in the year. The remaining parameters determine the duration ($\gamma_{i,1}, \gamma_{i,2}$) and peak ($\pi_{i,1}, \pi_{i,2}$) of the breeding and moulting seasons. Although in this paper we fixed the parameters of Eq. 5 using information from data collected in the region (Fig. 1), application of the model to other regions would have necessitated the use of priors for many of these parameters. For independently selected parameter combinations, Eq. 5 can exceed one. The maximum of such an expression cannot be calculated analytically, so a normalizing term cannot be constructed without numerical approximation. An upper bound can be imposed on Eq. 5 by using a conditional version,

$$p_{i,t}(d) = \min \left\{ 0.95, \pi_{i,0} + \pi_{i,1} \exp \left[-\frac{1}{2} \frac{(d - \delta_{i,t,1})^2}{\gamma_{i,1}^2} \right] + \pi_{i,2} \exp \left[-\frac{1}{2} \frac{(d - \delta_{i,t,2})^2}{\gamma_{i,2}^2} \right] \right\} \quad (6)$$

Fig. 1 Haulout probabilities for **a** adult males and **b** adult females for the period 2009–2010 at Loch Fleet. *Solid grey lines* are the estimates provided by Cordes (2011), *dashed lines* indicate $\pm 2SE$. The *solid black line* shows the parameterisation of Eq. 6 used by the state-space model



Alternatively, a logit transformation can be used to constrain the values between 0 and 1.

The values of the π and γ parameters in Eq. 6 were assumed time-invariant but the peak dates of the breeding/moult seasons were allowed to drift annually at a common rate c

$$\begin{aligned} \delta_{i,t,1} &= c_{i,1} + c_1(t - 22) \\ \delta_{i,t,2} &= c_{i,2} + c_1(t - 22) \end{aligned} \quad (7)$$

Here, $c_{i,1}$ and $c_{i,2}$ are the peak dates of the breeding and moult seasons for the i th class of animals in the year for which information on haulout probabilities was available ($t = 22$, see below). Due to the high daily variation in haulout numbers observed in the species, we allowed this probability to vary stochastically according to a beta distribution with the mean given by Eq. 6. Preliminary estimation attempts for the variance of this beta distribution, as part of the main model, indicated that it needed to be large; however, constant variance values or constant coefficient of variation (CVs) yielded Markov chain Monte Carlo (MCMC) sampling problems when probabilities were too close to 0 or 1. We therefore specified the variance as $0.4p_{i,t}(d)(1 - p_{i,t}(d))$, which was found to provide the maximum possible flexibility in capturing misspecification and daily stochasticity in Eq. 6.

The number of animals observed in an aerial survey depends on the date (d) of the survey. Because pups are distinguishable from a distance, pup and non-pup numbers were separately recorded in the data. We therefore aggregated the hidden population classes into two separate observable components (pups and non-pups, respectively).

$$\begin{aligned} P_t(d) &= n_{1,t}q_1p_{1,t}(d) + n_{6,t}q_6p_{6,t}(d) \\ A_t(d) &= \sum_{i=2}^5 n_{i,t}q_i p_{i,t}(d) + \sum_{i=7}^{10} n_{i,t}q_i p_{i,t}(d) \end{aligned} \quad (8)$$

Here, q_i is the probability of sighting an animal belonging to the i th class conditional on it being onshore. This probability is specific to the survey methodology hence allowing for different sighting abilities from the ground and air. The stochastic version of this observation model is:

$$\begin{aligned}
 Z_i &\sim B(n_{i,t}, q_i p_{i,t}(d)) \\
 P(d) &= Z_1 + Z_6 \\
 A(d) &= \sum_{i=2}^5 Z_i + \sum_{i=7}^{10} Z_i
 \end{aligned}
 \tag{9}$$

Inference

We used the software OpenBugs (<http://www.mrc-bsu.cam.ac.uk/bugs/>) for Bayesian computation (code listed in S1). We consistently ran two MCMC chains for 5×10^5 iterations, removing the first 4×10^5 for burn-in. Each chain was initialised at different points in parameter space. Using the autocorrelation diagnostic tool in OpenBugs, we opted to thin the MCMC trials by retaining every 100th step to save on memory. Mixing was ascertained by visual inspection of the two chains for all parameters and states in the model. Convergence was confirmed by use of the Brooks-Gelman-Rubin diagnostic tool in OpenBugs.

Prior distributions

Due to the large number of parameters in the model, use of unbounded prior distributions invariably led to problems with convergence and mixing. We therefore used re-scaled beta distributions for all informative priors, defined as follows:

$$\begin{aligned}
 Y &\sim \text{Beta}(2,2) \\
 X &= X_{\min} + Y(X_{\max} - X_{\min})
 \end{aligned}
 \tag{10}$$

Here, Y is a dummy variable taking values in the interval $[0, 1]$ with mean 0.5 and variance 0.05, selected to give low likelihood at the values 0 and 1. The values of X_{\min}, X_{\max} define the range of the parameter of interest as dictated by the prior information. If the published information on the parameter was given in the form of a mean and variance, then these values were defined as $X_{\min}, X_{\max} = \mu \pm 2\sigma$.

Trend parameters (i.e. the slope parameters in Eqs. 3, 4, 7) were assigned priors according to Eq. 10 with mean zero, to ensure equal prior weight between negative and positive trends. For these parameters we used a range as wide as would be permitted by computational constraints but no wider than would be required to describe sharp demographic declines during the period of the study. This latter constraint

was explored by separately plotting different parameterisations of the individual demographic curves.

All fixed parameter values and prior distributions are listed in Tables S2.1, S2.2. Model evaluation employed simulated data, sensitivity to priors and exploration of different model specifications (see S3).

Demographic parameters

The only information on adult harbour seal survival in the United Kingdom comes from two mark-recapture studies carried out in the Moray Firth between 1999–2002 (Mackey et al. 2008) and 2006–2010 (Cordes 2011). Analysis of these data provided little evidence for temporal variation in adult survival after 1999, but there was evidence for sex differences. The estimates from Cordes (2011) and their associated confidence intervals allowed us to set the plausible range for baseline female survival to 0.94–1.0. This is in line with recent estimates from other well-studied populations (Hastings et al. 2012). All baseline values refer to a time ~ 22 years after the start of the survey data. Therefore, Eq. 4 was written as follows for adults:

$$s_{*,t} = \frac{\exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k} (t - 22)^k + \sigma_N N_t)}{1 + \exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k} (t - 22)^k + \sigma_N N_t)}
 \tag{11}$$

Our setting of priors on baseline survival ($s_{*,22}$) and the density-dependence parameter (σ_N) with reference to year $t = 22$, yields the following relationship for the implicit prior of the intercept in Eq. 11:

$$\sigma_{*,0} = \ln \left(\frac{s_{*,22}}{1 - s_{*,22}} \right) - \sigma_N N_{22}
 \tag{12}$$

There is considerable evidence to suggest that adult males have a lower survival rate than females (Hastings et al. 2012; Härkönen and Heide-Jørgensen 1990 and references therein). We therefore constructed a joint prior for the baseline survival rates of the two sexes by using the relationship $s_{10,22} = r s_{5,22}$ where the prior for the ratio r was modelled according to Eq. 10, taking values between 0.85 and 0.95. These values were supported by the localised study from the Moray Firth (Cordes 2011) using mark-recapture data from 2006 to 2010.

Information on the survival of subadults and pups was more vague. We motivated our priors from the values discussed in Thompson et al. (2007) and Härkönen and Heide-Jørgensen (1990) but used the wider ranges of 0.7–0.9 for juveniles and 0.6–0.8 for pups.

Regarding births, Cordes (2011) estimated the reproductive rate in a small part of the Moray Firth during the period 2006–2010 as 0.87 (SE 0.02). We therefore used the range

(0.83, 0.91) in the prior for the baseline value b_{22} in the following model for reproductive rate:

$$b_t = \frac{\exp(\beta_0 + \sum_{k=1}^3 \beta_k (t-22)^k + \beta_N N_t)}{1 + \exp(\beta_0 + \sum_{k=1}^3 \beta_k (t-22)^k + \beta_N N_t)} \quad (13)$$

$$\beta_0 = \ln\left(\frac{b_{22}}{1-b_{22}}\right) - \beta_N N_{22}$$

Haulout parameters

Equation 6 implies a maximum of 70 haulout-related parameters (seven for each of ten population classes). Our early work with this model showed that it was not possible to estimate these parameters from the population data at the same time as estimating demographic trends. In particular, we found that when implemented as informative priors, (1) posteriors for these parameters generally returned the prior information, (2) the MCMC chains would occasionally drift away into regions of low and flat likelihood, and (3) the running time of the model increased by two orders of magnitude. There were therefore no estimation advantages and two computational disadvantages to using priors in this instance. We therefore parameterised this part of the model with particular values specified as follows:

1. Estimates of seasonal haulout probabilities of male and female harbour seals were obtained from mark-recapture modelling of individual sightings histories collected through photo-identification surveys carried out monthly (mean = 3 surveys, SE = 0.3) in 2009 and 2010 (Cordes 2011). These omitted the month of August but otherwise covered 2 whole years. We therefore specified the parameters pertaining to adult haulout probabilities in a way that approximated these observations (Fig. 1).
2. It is not clear how the breeding season affects the haulout probabilities of subadults (ages 2–4 years) but a study carried out in Sweden (Härkönen et al. 1999) did not indicate separate peaks in the haulout probabilities of subadults during the summer months. We therefore assumed that the moulting pulse on its own would capture the behaviour of subadults and set the peak of their moult to be half-way between the dates for yearlings and adults.
3. The haulout probability of yearlings is little affected by breeding (Härkönen et al. 1999). We therefore modelled it only in terms of the moult. Moulting in yearlings starts early and lasts for the whole summer (~twice the duration of adults). Hence, the timing of the 2009 moult for yearlings of both sexes ($c_{2,2} = c_{7,2}$) was placed at the middle of the summer and the duration parameters ($\gamma_{2,2} = \gamma_{7,2}$) were assigned twice the value used for adults. We assume that the moult lasts the same for each individual and the difference in the duration of the moult is due to asynchrony between yearlings compared to adults (Thompson and Rothery 1987). This implies that the area under the moulting curve needs to be preserved for all animals. Therefore, for yearlings and adults, we require that:

$$\int \pi_A e^{-\frac{1}{2}\left(\frac{d-\delta_A}{\gamma_A}\right)^2} dd = \int \pi_Y e^{-\frac{1}{2}\left(\frac{d-\delta_Y}{\gamma_Y}\right)^2} dd \quad (14)$$
 which gives the following relationship between the peak of the moult for yearlings as a function of the value for adults:

$$\pi_{2,2} = \pi_{7,2} = \pi_Y = \pi_A \frac{\gamma_A}{\gamma_Y} \quad (15)$$
4. Most pups are born during June and mothers care for individual pups on average for 3 weeks (Cordes and Thompson 2013). Therefore, it is likely that at the peak of the pupping and nursing season (mid-June to mid-July) nearly all the pups will still be associated with their mothers, either staying on the breeding haulout or venturing into the sea together. Therefore, the haulout probability, duration and timing for pups, during the pupping season were set to be equal to the mothers' (i.e. $\pi_{1,1} = \pi_{6,1} = \pi_{10,1}$, $c_{1,1} = c_{6,1} = c_{10,1}$, $\gamma_{1,1} = \gamma_{6,1} = \gamma_{10,1}$).
5. All pups moult in utero, so after the breeding season, young-of-the-year were assumed to haul out according to the baseline probability ($\gamma_{1,2} = \gamma_{6,2} = 1$, $\pi_{1,2} = \pi_{6,2} = \delta_{1,2} = \delta_{6,2} = 0$).
6. The trend parameter (c_1) for the timing of moult and breeding was assumed to be the same for all classes of animals. The prior used Eq. 10 with the range $-1, 1$. This means that the expected peak of the moult and breeding pulses is allowed to drift by a maximum of 1 day each year (or, a total of 22 days during the period of the data).
7. Beyond the mostly deterministic specification of the parameters on haulout probabilities there are several other potential influences that may affect haulout probabilities day to day. We therefore introduced an uncorrelated error term in the daily haulout probabilities to capture misspecification in Eq. 6 and variability in environmental conditions causing these probabilities to fluctuate (see section “[Observation model](#)”, above).

Observation parameters

It was considered likely that the sighting ability for pups and adults varies between survey methodologies (see

description of Eq. 8). We had data from both aerial and ground surveys and the two types of surveys overlapped in 2006. In that year, surveys were carried out by two independent crews simultaneously, to provide direct comparison between the two methods. We therefore asked the model to estimate these sighting rates using uninformative priors (Eq. 10 with range 0.8–1.2). Values >1 were considered to allow for the possibilities that animals were misclassified, or that ground features were mistaken for seals.

Population structure and size

The population’s initial age and sex structure was unknown. Previous studies have tended to assume that a stable-state distribution has been achieved prior to the collection of the count data, implying a period of stability or exponential growth in the population’s recent past. Using this as our starting point, we allowed the model to estimate the initial population structure. If the population has not been affected by catastrophic effects or abrupt waves of migration it would be expected to have a decreasing probability density for the ages within each sex. We described this relationship using the empirical form

$$f(x) = c_* e^{-c_* x} \tag{16}$$

Due to the potential differences in male and female survival, we used two different values of the c_* parameter (c_m, c_f). The corresponding size of any age class in our model can be obtained from Eq. 16 by integrating over the desired age range (e.g. $p_1 = \int_0^1 f(x) = 1 - \exp(-c_m)$, $p_{10} = \int_4^\infty f(x) = \exp(-4c_f)$). These proportions need to be scaled up by the initial number of males $N_{m,1}$ and females $N_{f,1}$ in the population. The demographic model assumes a 1:1 sex ratio at birth and equal male and female survival in the first year of life. Therefore, the number of males can be written as a function of the number of females

$$N_{m,1} = N_{f,1} \frac{p_6}{p_1} \tag{17}$$

The number of females present in the first year was given a uniform prior ranging from 200 to 1,000 individuals. The prior for the parameter c_f was constrained within the range 0.10, 0.24. These values were selected by simulation as plausible descriptions of the age structure given the broad demographic characteristics of this population. The same simulations were used to derive an approximate relationship for the parameter of the male age distribution: $c_m = c_f + 0.03$.

Due to the inclusion of density dependence in the model, information on total population size was necessary for 2009 (the quantity N_{22} in Eqs. 12, 13). Such information was available in 1993 and 2009. For 1993, Thompson et al. (1997)

provided two estimation methods. For our study population, the first method yielded the number 727 and the second, making additional use of telemetry information for haulout rates, estimated the subpopulation to be 20 % higher (~860). Neither of these approaches included pups-of-the-year, indicating that total study population size in 1993 was closer to 900 individuals. The associated CV for these estimates was 0.2. The 2009 estimate was based on mark-recapture data collected by Cordes (2011) for Loch Fleet. The abundance estimate for that location was 117 with associated CV of 0.015. Examination of the counts in Loch Fleet compared to the rest of the outer Firth indicated that, on any given survey date, they could comprise between 20 and 40 % of all animals counted. We used these numbers to scale all aerial counts to provide an estimate of 416 and a CV of 0.16 for our entire study population. We used the estimates $N_5 = 900$ and $N_{22} = 416$ as data whose inherent uncertainty was accounted for by a Gaussian observation model. We treated all the other years as missing population data.

The effect of shooting

Shooting mortality was incorporated into the model by modifying Eq. 11:

$$s_{*,t} = \frac{\exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k}(t - 22)^k + \sigma_N N_t)}{1 + \exp(\sigma_{*,0} + \sum_{k=1}^3 \sigma_{*,k}(t - 22)^k + \sigma_N N_t)} (1 - u_t m) \tag{18}$$

Here, u_t takes values between 0 and 1 and represents the relative strength of shooting effort in different years. Maximum mortality across all years is denoted by m . Both of these quantities were estimated by the model. Approximate information on the number of harbour seals shot in the entire Moray Firth was available for the period 1994–2004, previously analysed by Thompson et al. (2007) to provide estimates of seals shot. These estimates were incorporated into the model to partly account for annual deaths. In this, we faced the following challenges:

1. The estimates cover only part of the period of interest. We therefore treated shooting at the start and end of the time series as missing data and estimated the seals shot in those years from the model.
2. In the absence of specific information about age- or sex-related differences in shooting vulnerability, we assumed that these were the same for all classes.
3. Due to difficulties in identification by the reporters, numbers of harbour seals are confounded with the numbers of grey seals. We used the data provided on the most likely numbers shot to fit the model and the associated maximum and minimum numbers for validation of fit to the shooting data.

4. There was no specific information made available on the spatial distribution of shooting effort. Following consultation with authorities involved in the management of the Moray Firth, we assumed an equal split between subareas. We introduced a division-of-effort parameter that scaled the rate of shooting in our study population to the total for the entire Moray Firth (for computational expediency in the final version of the model this was assigned a narrow prior according to Eq. 10 with a range of 1.99–2.01, but we explored sensitivity to less constrained priors in earlier versions). This rate was used to generate realizations of numbers shot, from a Poisson distribution, which were simultaneously fit to the shooting data along with the rest of the model.
5. Shooting effort underwent two regime changes in the duration of the data. The first in 1999, when shooting effort apparently doubled and the second in 2003, with the implementation of the Moray Firth Seal Management Plan, when shooting effort dropped to about a tenth of immediately preceding years. Because these numbers were both anecdotal and relative to the peak shooting intensity, we allowed the model to fine-tune them by estimating the strengths of pre-1999 and post-2003 shooting mortality, as a proportion of the peak of shooting, which occurred in the intervening years. Peak shooting intensity is estimated by the parameter m . Therefore, setting the interim period to 100 % of this maximum, the priors for the relative shooting intensity were allowed to range between 40 and 60 % for the period 1988–1999 and 5–15 % for the period 2004 onwards:

$$u_t \begin{cases} \sim U(0.4,0.6) & \text{for } 1988 \leq t \leq 1999 \\ = 1 & \text{for } 2000 \leq t \leq 2003 \\ \sim U(0.05,0.15) & \text{for } 2004 \leq t \leq 2014 \end{cases} \quad (19)$$

Results

Irrespective of the initial conditions, the MCMC chains converged, mixed well, and yielded a close fit to the count data from all years (Fig. S4.1), hinting that the model was neither grossly misspecified nor over-parameterised. The model's qualitative results were not sensitive to the variance used for the beta priors and none of the estimated posteriors presented high densities close to their prior bounds. However, replacing these with unbounded (e.g. Gaussian) priors often caused the chains to diverge into extreme regions of parameter space, depending on their initial conditions. In those cases, chains did not mix and they often failed to converge. This behaviour is not unexpected, given the complexity of the model involved.

There was no evidence of a drift in the dates of the moult and breeding season (the dates drifted at most by

1–2 days during the duration of the entire study). This result was robust to changes in model and prior specification. Removal of this feature speeded the model up by an order of magnitude, so runs of the model discussed below did not contain this feature. We were able to obtain estimates for sighting abilities under different survey methodologies. According to these, aerial counts could miss juvenile and adult animals (~90 % sighting ability) whereas ground counts tend to overestimate their numbers (sighting ability ~110 %). By having access to data from both types of surveys, the model was able to automatically correct these biases. Pup sighting abilities were estimated as ~100 % from the air and ~85 % from the ground. The estimated sighting abilities tended to be sensitive on the assumptions made about haulout probabilities, so if these were respecified, we would also expect the sighting abilities to change.

The model estimated low historical levels of fecundity (with an effective reproductive failure in 1990–1991). Estimated demographic trends (Fig. 2) indicate sharp increases in fecundity (Fig. 2a) since then, operating against a background of decreasing survival for younger animals (Fig. 2b, c). Fecundity was by far the most volatile demographic component of this system and forecasts into the future were characterised by high uncertainty and the possibility of declines. The period of peak shooting appears as a dent in the survival trends (Fig. 2b–d). The model provided a good fit to both the pup and non-pup counts (Fig. S4.1) and there was no evidence that the residuals from the observed counts were related to year or date. We found evidence for density dependence in fecundity, but not survival.

The estimated total population size varied between 600 and 1,400 individuals (Fig. 3), presenting two initial periods of decline down to 50 % of the initial size. The model had difficulty in reconciling the 2009 population estimate with the information contained in the pup and moulting counts. Following the curtailment of shooting, the model forecasts a slow recovery based on the prediction of fluctuating fecundity, constant survival and low levels of shooting.

The model was able to fit the shooting data well (Fig. 4). At its maximum, shooting accounted for 14 % of observed mortality. The estimates of shooting mortality before 1999 and after 2003 were 8 and 2 % respectively. The posterior for the parameter ρ provided no evidence that more or fewer animals were shot in our study population compared to the southern inner Moray Firth.

Following sensitivity analysis on the specification of fixed parameters and parameter priors (S3), the following conclusions were found to be robust:

1. The decline in counts is not the result of a drift in the dates of moult and breeding.

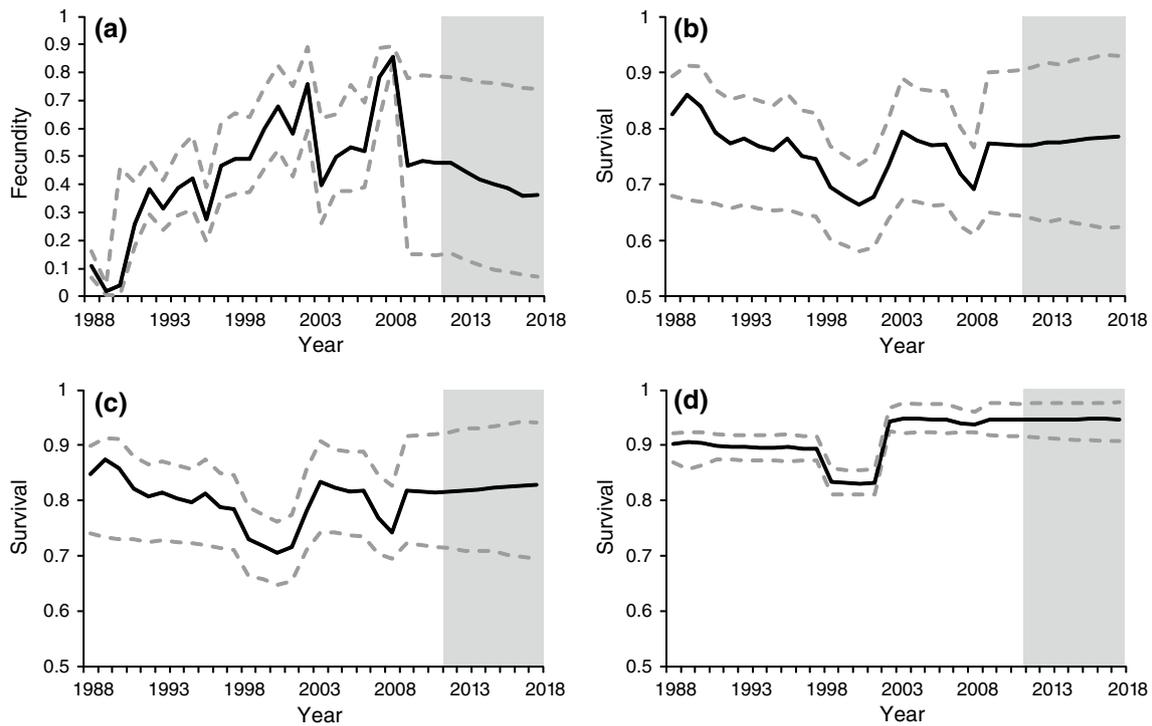


Fig. 2 Four different demographic trends as estimated by the model, with associated 95 % credible intervals: **a** fecundity, **b** first-year survival, **c** juvenile survival, and **d** adult survival. The effect of shooting

can be discerned as a dip in survival between 1999 and 2003. Forecasts outside the range of the survey data are in the shaded area of the plot

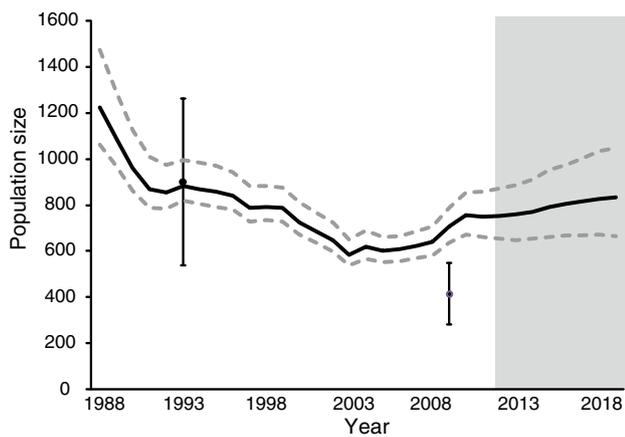


Fig. 3 Estimated total population size for the northern part of the Moray Firth, with 95 % credible intervals. The shaded area represents predictions generated after the end of the survey data. The two circles indicate total population estimates for the region with associated uncertainty

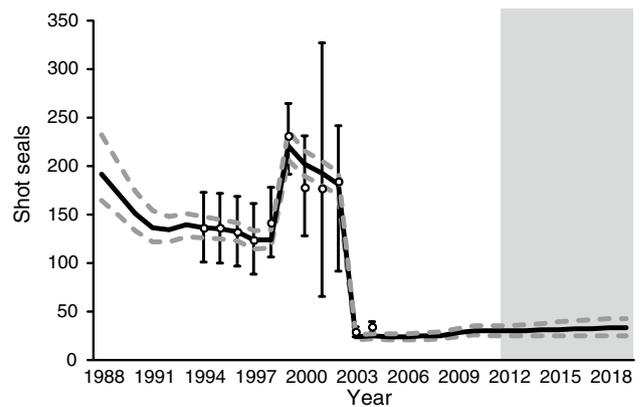


Fig. 4 Fit of the model to the shooting data. The estimated numbers shot in the whole of the Moray Firth according to the model are shown as a solid line accompanied by the shaded 95 % credible intervals. The open circles indicate the most likely numbers of shot harbour seals and the bars are based on the reported maximum and minimum numbers (Table 3 in Thompson et al. 2007)

2. Fecundity has increased dramatically during the study.
3. Adult survival has not been affected greatly by influences other than shooting.
4. Subadult survival is characterised by a slow background decline.

5. Density dependence is evident in fecundity but not survival.

In contrast, the following were sensitive to the model's parameters and assumptions:

1. The population's forecast recovery and the estimated initial population size depended on the estimates of total population size provided to the model for the years 1993 and 2009.
2. The exact proportions of increase in fecundity and decrease in survival depended on the dispersion of priors for the demographic trend parameters.

Discussion

We investigated the underlying causes of the declines observed in many United Kingdom harbour seal monitoring counts, using detailed data from a long-term Scottish study. We sought to evaluate the severity of the underlying population decline, its proximate demographic causes, the effect of historical influences [such as shooting (Thompson et al. 2007)] and the anticipated population trajectory in future years following the introduction of new management measures to reduce fisheries-related mortality (Butler et al. 2008). Our main conclusions are that, since 1989, there was a marked (~50 %) decline in population size caused by a combination of low fecundity in the period 1989–1999 and high shooting mortality during the period 1999–2003. The population has been slowly recovering since, despite the decreasing trend in subadult survival. Assuming that the estimated demographic trends continue for the years following the end of the data, the model forecasts a slow and uncertain recovery. This predicted reversal in the historical downward trend is supported by increasing counts observed at the very end of the time series, combined with slower decreases in recent years. However, the suggestion of recovery must be tempered against the fact that the model does a poor job of explaining the mark-recapture population estimate from 2009. We explored the sensitivity of the estimated trajectory on the value and variance associated with the population estimate. Although the quantitative nature of the recovery is sensitive to both, its occurrence is not. Given that the point and interval population estimate originated from an analysis of independent mark-recapture data, we are forced to conclude that there is some source of model misspecification. In future work, this would best be clarified by gradually replacing some of the polynomial terms in our demographic trends by field data on demographic covariates (such as the abundance of prey, competitors or predators).

The directions of the trends in survival and fecundity are a robust result of this model, indicating that a decreasing number of animals recruit into the adult population, but those that do, have a better chance of surviving and reproducing. These patterns may hint at the possibility of intraspecific competition between adult and young

individuals, or at processes that affect younger animals particularly strongly (for example, because they are less experienced foragers, have lower body mass, or have limited physiological capabilities in diving).

Our conclusions regarding demographic trends are predicated on the functional forms used in the model. However, we believe that the logit-cubic functions, used for both fecundity and survival, are sufficiently flexible to capture non-monotonic trends in demographic processes. Also, estimated rates of mortality and fecundity are dependent on the assumption that the northern area of the inner Moray Firth is a closed population. It is unlikely that influx from remote harbour seal colonies could reverse the estimated trends and there is no evidence of a negative correlation in the counts of the northern and southern Moray Firth (Thompson et al. 2007).

The effect of shooting was quantified from recorded kill data and plausible assumptions about the distribution of shooting effort across regions, time periods and population components. We were able to estimate the temporal and spatial aspects of these assumptions but, due to lack of data on the sex and age of shot animals, we had to assume that all individuals in the population faced the same shooting risk. If shooting tended to affect juveniles more than adults, its overall effect might have been different. However, the observed numbers shot were well explained by the model (Fig. 4), raising no serious concerns about the assumptions pertaining to shooting. Shooting is a good example of a known mortality source for which data were partly available, although factors such as species misidentification result in high levels of uncertainty in these data. Other influences, such as the density of competitors (e.g. grey seals or harbour porpoises), relative abundance of prey and climate trends, may be readily added to the model to try and investigate their importance in shaping the historical decline and predicted recovery. Inclusion of such covariates will simplify the phenomenological parts of the model (by allowing us to reduce the order of the logit polynomials used to describe temporal trends) and thus greatly extend its heuristic value.

Although none of the estimated posteriors presented high densities close to their prior bounds, some of our conclusions may nevertheless be predicated on the bounds used to constrain the parameter priors. Given the parametric complexity of this model our strategy was to be as informative as possible about those parameters that did not directly relate to demographic trends. In the Moray Firth, we are fortunate to have extensive information additional to the counts, such as estimates of vital rates for particular years and estimates of haulout behaviour at different parts of the year. However, any misspecifications of these parameters could give misleading results. For example, if the haulout probabilities are, in reality, greater than their

assumed model values, then our current model would be overestimating population size and hence underestimating the effect of shooting (because the recorded kills would correspond to a larger proportion of the population).

The Moray Firth is a flagship region both in terms of conservation interest and data availability. However, an important question regarding the status of United Kingdom harbour seals is how to generalise from the Moray Firth to the rest of the country. There are three fruitful avenues: first, the model developed here represents a custom-made analysis framework for the historical moult count data obtained by aerial survey from the rest of the country (Sea Mammal Research Unit 2010). Although these data are multi-annual and geographically extensive, haulout-specific surveys are not as frequent (both between and within years) as the Moray Firth ones. Nevertheless, a considerable advantage of the Bayesian specification of the model is that parameter posteriors obtained in the Moray Firth can be used as informative prior distributions for other (less data-rich) regions. Second, hierarchical Bayesian approaches (Clark and Gelfand 2006) may be used to estimate common parameters across regions. This will help decompose the demographic trends into colony-specific, regional and country-wide components. Such investigations will be considerably enhanced by the use of biologically meaningful covariates (such as prey availability or anthropogenic disturbance) in place of phenomenological polynomial terms, in the description of demographic trends. Third, wildlife managers can exploit the species-specific insights already obtained from the present paper, such as the sensitivity of harbour seal populations to culling and the strength of density dependence.

We used an integrated modelling approach to disparate, discontinuous and error-prone data. Our experience with this system illustrates three broader issues relevant for the study of complicated population hypotheses. The first is the issue of parameterisation. The traditional and more expedient approach to complex population models (e.g. in the area of stock assessment) is to supply parameter point and interval estimates from independent analyses, or by trawling through the primary literature (Kuparinen et al. 2012). This is in stark contrast with the more recent Bayesian approaches that advocate the simultaneous estimation of all parameters from population data, using only as informative a set of priors as can be justified by available information (Brooks et al. 2004; Schaub et al. 2007; Newman et al. 2009; Kuparinen et al. 2012). This considerably more painstaking approach may safeguard against many problems of model and parameter misspecification, but may not provide timely results for wildlife managers. Our study is a case in point: disentangling the broader question of harbour seal declines in the United Kingdom is both difficult and urgent. Here, we achieved a compromise between

robustness and expediency by fixing some parameters, providing bounded and informative priors for others and only assigning vague priors to those parameters for which we needed answers. As a result, our final model is certainly less vulnerable to our initial preconceptions about the system and our predictions represent the logical and quantitative consequences of the extent of our current knowledge. Should these be found to disagree with future trends in count data, we will have obtained a falsification of the particular assumptions involved and will have therefore made tangible scientific progress.

The second point is that the emergent properties of stochastic and non-linear population models fit to field data will not always be intuitively obvious. One of the most persistent features of our results is the long-term historical increase in individual fecundity. This is an intriguing finding that is supported by limited field observations from this study area that recorded similar maximum pup counts in 1989 and 2006 despite an approximate halving of counts of other age classes (Cordes et al. 2011). This finding also highlights the potential roles of both intrinsic and extrinsic drivers when assessing the mechanism underlying population change. Particularly given the backdrop of harbour seal population declines (Lonergan et al. 2007) and grey seal population increases (Sea Mammal Research Unit 2010) in the United Kingdom, this modelling approach should now be extended to explore how intra- and inter-specific competition interact with those stressors that are more likely to be considered for mitigation by conservation managers.

Finally, we must stress the importance of identifying proximate demographic causes when managing population declines. A wide range of marine and terrestrial species have exhibited dramatic declines over recent decades (Fewster et al. 2000; Blaustein and Kiesecker 2002; Robinson et al. 2004). However, uncertainty over population drivers often constrains efforts to reverse these declines, some of which may also have important, broader scale ecosystem consequences (Scheffer et al. 2005; Potts et al. 2010). Motivated by precautionary principles, wildlife managers usually prefer to understand a phenomenon before trying to manipulate it. This often leads to the experimental pursuit of specific mechanistic hypotheses, but it has long been recognized that this can be particularly problematic if population processes result from multiple causes (Hilborn and Stearns 1982; Connor and Simberloff 1986). Our approach offers the potential to help focus such issues. In turn, the data from these studies would incrementally crystallise previously vague parts of the population model, offering a smooth transition from purely phenomenological to more mechanistic demographic models. It may, of course, be argued that it does not matter what has caused a decline, as long as we can identify a mechanism for reversing it. This can, for example, be achieved by focusing on demographic

parameters with high elasticity (sensu Caswell 2006). However, even if causal biological insights are not required, elasticity analyses of this kind for management use are best performed on population models with biologically relevant parameters, such as those delivered by integrated model fitting.

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