

Incorporating movement into models of grey seal population dynamics

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Summary

1. One of the most difficult problems in developing spatially explicit models of population dynamics is the validation and parameterization of the movement process. We show how movement models derived from capture–recapture analysis can be improved by incorporating them into a spatially explicit metapopulation model that is fitted to a time series of abundance data.

2. We applied multisite capture–recapture analysis techniques to photo-identification data collected from female grey seals at the four main breeding colonies in the North Sea between 1999 and 2001. The best-fitting movement models were then incorporated into state-space metapopulation models that explicitly accounted for demographic and observational stochasticity.

3. These metapopulation models were fitted to a 20-year time series of pup production data for each colony using a Bayesian approach. The best-fitting model, based on the Akaike Information Criterion (AIC), had only a single movement parameter, whose confidence interval was 82% less than that obtained from the capture–recapture study, but there was some support for a model that included an effect of distance between colonies.

4. The state-space modelling provided improved estimates of other demographic parameters.

5. The incorporation of movement, and the way in which it was modelled, affected both local and regional dynamics. These differences were most evident as colonies approached their carrying capacities, suggesting that our ability to discriminate between models should improve as the length of the grey seal time series increases.

Key-words: metapopulations, multisite capture–recapture, photo-identification, sequential importance sampling, state-space models.

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Introduction

The grey seal *Halichoerus grypus* (Fabricius 1791) is a colonially breeding pinniped whose distribution is confined to the North Atlantic and its contiguous seas. It has a world population of about 300 000 individuals, 40% of whom breed around the British Isles (SCOS

2004). The total number of pups born at British colonies has grown steadily since the 1960s (Harwood & Prime 1978). Commercial fishermen are concerned about the impacts of seal predation on depleted fish stocks and conservation agencies about the effects of breeding seals on sensitive terrestrial habitats. It is therefore important to be able to predict the future size and spread of the British population. Individual female grey seals show high levels of fidelity to specific pupping locations at a single colony (Pomeroy *et al.* 1994). This may account for the highly significant differences in microsatellite allele frequency that have been observed between breeding colonies (Allen *et al.* 1995), and suggests that the British grey seal population cannot be modelled as if it is a single, homogeneous unit. Instead,

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we require a spatially explicit model, which accounts for differences in colony dynamics, and the impact of movement between colonies on local and regional dynamics (Gaggiotti *et al.* 2004; Matthiopoulos, Harwood & Thomas 2005; Thomas *et al.* 2005). Grey seal colonies meet all of the assumptions for a metapopulation (Hanski & Gaggiotti 2004): the sites occupied by aggregations are discrete, individuals only occasionally move between these sites, and there is turnover of occupied sites (i.e. previously occupied sites are recolonized following local extinction).

One of the key parameters in the metapopulation approach is the probability of movement between aggregations (in the case of grey seals, between breeding colonies). For grey seals, which spend more than 80% of their time at sea (McConnell *et al.* 1999) and 90% of this time below the surface (Thompson *et al.* 1991), direct observation of movement is impracticable and movement probabilities must be estimated using techniques such as multisite capture–recapture (CR) (Brownie *et al.* 1993).

Individual female grey seals can be ‘marked’ for CR analysis using photo-identification. The Sea Mammal Research Unit has collected a large catalogue of photographs of British grey seals; individuals are identified using the boldly patterned markings on the side of their necks (Hiby & Lovell 1990).

For statistical modelling of multisite CR data the Arnason–Schwarz (AS) model (Brownie *et al.* 1993) – the multisite equivalent of the Cormack–Jolly–Seber model (Lebreton *et al.* 1992) – provides a good starting point. Maximum likelihood estimates of the parameters for this model can be obtained using software packages such as M-SURGE (Choquet *et al.* 2004), but the model is highly parameterized and it may be impossible to estimate all parameters. However, reduced-parameter versions of this model are available and a suitable model can be chosen using standard model selection procedures (Lebreton *et al.* 1992).

During the course of model selection, biological hypotheses relating to the parameters in the models can be tested. M-SURGE utilizes a generalized linear model framework, so it is possible to relate variation in demographic rates to environmental variables (Buckland, Goudie & Borchers 2000).

Annual censuses of the number of pups produced at each breeding colony can also provide movement information, but only if there is some prior knowledge of the species’ population dynamics. For example, if annual pup production increases faster than is feasible as a result of internal recruitment of breeding females, one may infer that net immigration must be taking place. This inference can be formalized by fitting the pup production data to different candidate models for the dynamics of the metapopulation. Model selection criteria can be used to evaluate the different models in much the same way as for the CR data.

An ideal framework is the state-space model (SSM), which takes account of all major sources of uncertainty

(Buckland *et al.* 2004; Thomas *et al.* 2005; Newman *et al.* 2006). A SSM incorporates two parallel and simultaneous processes: the state process, which models the true but unknown state of the population; and the observation process, which links the state process to a time series of observational data.

Inference about which SSM provides the best fit to the available data is usually obtained using computer-intensive Bayesian methods (Ellison 1996; Millar & Meyer 2000; Doucet, Frietas & Gordon 2001; Liu 2001). Prior distributions for the model parameters and the initial states are specified using information from previous experiments and expert knowledge. Thus, CR results can be used to provide informative priors for the population dynamics modelling, combining the strengths of both data sets. Bayesian inference proceeds by interpreting these prior distributions with respect to the pup production data, and generating posterior distributions for the parameters and states of the model. These posterior distributions can be used to project the models forward in time and make predictions about future animal abundances.

Thomas *et al.* (2005) developed a spatially explicit SSM of the British grey seal population, which they divided into four regions. At this spatial scale, there was little evidence for movement of animals between local populations. Here, we develop colony-level SSMs of grey seal population dynamics in one of these regions (the North Sea) and use them to investigate the nature and consequences of movement at this scale.

Methods

CAPTURE–RECAPTURE MODELLING

Study animals, sampling occasions and locations

The locations of the four North Sea colonies (Isle of May, Fast Castle, Farne Islands and Donna Nook) are shown in Fig. 1. Photographs were taken at all four colonies on one or two occasions during the pupping season (between 26 October and 10 December) in 1999, 2000 and 2001. As many adult females as possible were photographed using a Canon EOS 505si 35 mm camera fitted with a 600 mm lens and $\times 1.4$ converter and loaded with Kodak XP2 film.

In total, 1122 individual females were identified from photographs of their left-hand side (LHS), 1181 from their right-hand side (RHS), and 358 by both sides. The LHS and RHS data were analysed separately. However, parameter estimates from these two analyses are not completely independent because an unknown proportion of animals in one data set are also represented in the other.

Recapture detection

Photographs were digitized and then analysed using software developed by Hiby & Lovell (1990). Decisions

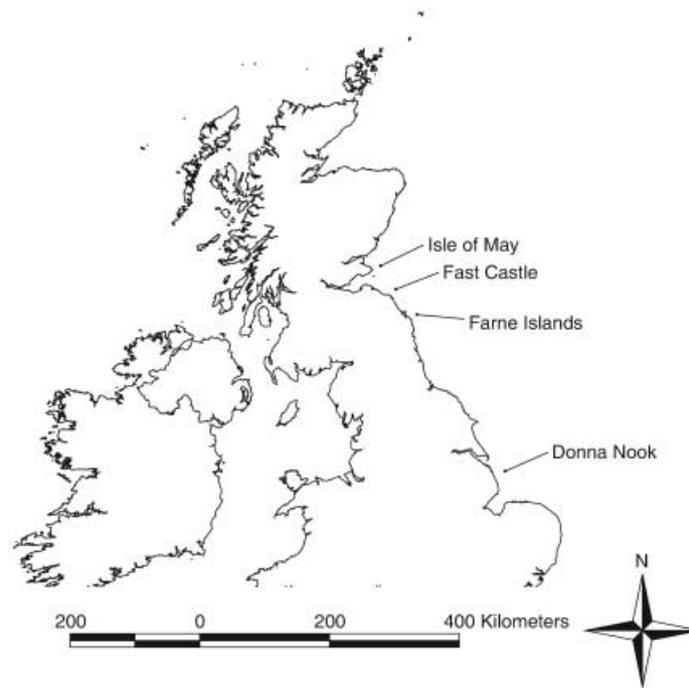


Fig. 1. Map of the UK showing the four North Sea grey seal breeding colonies used in this study.

on which photographs to analyse were based on the exposure, image size on the negative, the amount of blurring, and the distinctness of the pelage pattern (John Watkins, pers. comm.). The software uses a three-dimensional model to derive a numerical description of a specific area on the side of the seal's neck that is compared with all others in the computer library. Pairs of photographs that score above a preset similarity threshold are then compared by eye. This method is robust to changes in orientation and position of the seal, average brightness and contrast (Hiby & Lovell 1990).

Data screening

Seven individuals were photographed at more than one colony in the same year, indicating that within-season movement does occur. Each of these animals was allocated to the breeding colony in which it was photographed around the peak of the pupping season. For instance one seal was photographed at the Isle of May on 26 October 2001 and at Fast Castle on 3 November 2001. It was allocated to Fast Castle because the peak of pupping occurs there in November.

Models, parameters and assumptions

We analysed reduced versions of the time-dependent conditional AS model (CAS – Choquet *et al.* 2004), using the computer package M-SURGE. The model parameters are:

$\Phi_{i,t}$ The probability that a seal alive on colony i in year $t - 1$ survives (and does not permanently leave the four North Sea colonies) until year t , where $i = \text{colony}$ and $t = 2000$ or 2001.

$\Psi_{i \rightarrow j,t}$ The probability that a seal (conditional on surviving) moves from colony i in year $t - 1$ to colony j in year t .

$P_{j,t}$ The probability that a seal photographed in a previous year and alive on colony j at time t , is re-photographed there.

In this parameterization we have used the time step $t - 1$ to t instead of t to $t + 1$, conventionally used in the CR literature (e.g. Brownie *et al.* 1993; Nichols & Kendall 1995), for consistency with the SSM.

Female grey seals are long lived (35–40 years), so > 90% of the photographed animals were expected to survive the entire study period. It was therefore unlikely that $\Phi_{i,t}$ could be estimated precisely (Lebreton *et al.* 1992) and $\Phi_{i,t}$ was fixed at 0.96, based on an extended study of a group of branded and tagged adult females at the Isle of May. The sensitivity of the analysis to uncertainty in this estimate was checked by repeating the analysis using its lower and upper 95% confidence limits (0.896 and 0.985, respectively).

Goodness of fit and variance inflation factors

Lebreton *et al.* (1992) recommend that the fit of the most general model is evaluated first. Pradel, Wintrebert & Giminez (2003) have developed methods for assessing the fit of the CAS model using the variance inflation factor (c), which can be estimated using the program U-CARE (Choquet *et al.* 2003). $\hat{c} = 1$ indicates a perfect fit, $\hat{c} > 1$ indicates overdispersion (Lebreton *et al.* 1992).

Model selection

Lebreton *et al.* (1992) also recommend that the fit of all other models is compared with that of the general

model using Akaike's information criterion (AIC) or quasi-likelihood adjusted AIC (QAIC), which is the AIC adjusted using \hat{c} (Burnham & Anderson 2002). We also calculated the QAIC weight, which can be thought of as the probability that each model is the 'best' approximating model from the models compared (Buckland, Burnham & Augustin 1997; Burnham & Anderson 2002; Cam *et al.* 2004).

To limit the number of models explored, and to focus on the hypotheses of most interest, we followed this route through model space: (1) start from the CAS model with survival fixed to 0.96; (2) explore the effect of time on the movement and recapture probabilities; (3) reduce the number of recapture parameters and test biological hypotheses relating to recapture; (4) repeat step (3) for the movement models. We report only those models with a QAIC weight > 0.05 .

Testing biological hypotheses

The recapture probability in CR analyses can provide interesting insights into the processes that generated the data. We tested whether this probability was related to the proportion of marked seals on a colony in a particular year using a linear-logistic regression:

$$\text{logit}(P_{i,t}) = \ln\left(\frac{P_{i,t}}{1 - P_{i,t}}\right) = \xi_0 + \xi_1 Z_{i,t} \quad \text{eqn 1}$$

where $Z_{i,t} = \frac{m_{6+,i,t}}{y_{0,i,t}}$, such that $m_{6+,i,t}$ represents the number of adult (≥ 6 years old) female seals uniquely identified on colony i in year t . $y_{0,i,t}$, the pup production estimate on colony i in year t , is an estimate of the number of adult females available for photography, because nonbreeding females do not normally visit their colonies. Pup production is estimated every year for all the major grey seal breeding colonies around Great Britain using counts of white-coated pups obtained from aerial photographs or direct census (SCOS 2004). The coefficient of variation of these estimates is generally low (Callan Duck, pers. comm.) and grey seals give birth to only one pup each year, so they should be a close approximation to the number of females present at the colony.

Then we tested the hypothesis that the probability of moving between colonies is related to the distance separating them using the linear-logistic model:

$$\text{logit}(\Psi_{i \rightarrow j,t}) = \alpha_0 + \frac{\alpha_1}{\text{dist}_{i \rightarrow j}} \quad \text{eqn 2}$$

where $\text{dist}_{i \rightarrow j}$ is the distance between colony i and j in kilometres, calculated 'as the seal swims'.

The distance model was then extended to include the difference in abundance between the two colonies such that:

$$\text{logit}(\Psi_{i \rightarrow j,t}) = \alpha_0 + \frac{\alpha_1}{\text{dist}_{i \rightarrow j}} + \alpha_2(y_{0,i,t-1} - y_{0,j,t-1}) \quad \text{eqn 3}$$

The site fidelity parameter, $\Psi_{i \rightarrow i,t}$, i.e. the probability of returning to the colony that was last bred at, was calculated as:

$$\Psi_{i \rightarrow i,t} = 1 - \sum_{j \neq i} \Psi_{i \rightarrow j,t} \quad \text{eqn 4}$$

where $i = 1, \dots, 4$.

STATE-SPACE MODELLING

In this section we describe the SSMs used to represent grey seal population dynamics and outline the methods used to fit these models to the available survey data.

Data and model structure

The available data consisted of annual estimates of pup production (Duck 2003) between 1984 and 2003 derived from aerial surveys (Isle of May and Fast Castle) or ground censuses (Farne Islands and Donna Nook). There were no aerial surveys of Fast Castle prior to 1997.

Annual time steps began just after all pups had been born. We used individual age-classes for pups (age 0) and animals up to 5 years old, and a composite class for adult seals ≥ 6 years. We assumed that only adult females move between colonies, because the capture–recapture data is for these animals. Allowing 5 years-olds (recruiting females) to move made no difference to the results. Age-class 0 included both male and female pups, but the other age-classes are for females only. Four processes are modelled: survival (s), movement (m), ageing (a ; which includes sex determination for pups) and breeding (b). The state vector \mathbf{n}_t representing the state of the population at time t has 28 elements (4 colonies \times 7 age classes), $n_{a,i,t}$ is the number of seals of age a in colony i at time t .

Uncertainty in the progression of animals from \mathbf{n}_{t-1} to \mathbf{n}_t is captured by a series of linked probability density functions (pdfs), in which the input to one pdf is the output from the previous pdf.

$$\mathbf{u}_{s,t} \sim H_{s,t}(\mathbf{n}_{t-1})$$

$$\mathbf{u}_{m,t} \sim H_{m,t}(\mathbf{u}_{s,t})$$

$$\mathbf{u}_{a,t} \sim H_{a,t}(\mathbf{u}_{m,t})$$

$$\mathbf{n}_t \sim H_{b,t}(\mathbf{u}_{a,t}) \quad \text{eqn 5}$$

$H_{x,t}$ is the pdf for subprocess x and $\mathbf{u}_{x,t}$ is a realization of the state vector at time t , after subprocess x has occurred.

Stochastic representation

We assume that survival of females 1 year and older is density independent with binomial probability ϕ_a . Pup survival is assumed to be a density-dependent function of the number of pups (of both sexes) born on that colony in year $t - 1$ (Harwood 1981):

$$\mathbf{u}_{s,0,t} \sim \text{Binomial}(n_{0,i,t-1}, \phi_{p,i,t}) \quad \text{eqn 6}$$

$u_{s,0,i,t}$ is the number of pups surviving and $\phi_{p,i,t}$ is the pup survival probability, modelled using the Beverton–Holt function:

$$\phi_{p,i,t} = \frac{\phi_{pmax}}{1 + \beta_i n_{0,i,t-1}} \quad \text{eqn 7}$$

ϕ_{pmax} represents the survival rate when few pups are present. β_i determines the carrying capacity of colony i , the smaller this parameter the larger the eventual colony size.

Movement of adult females is modelled as a multinomial random variable (Newman *et al.*, unpublished) such that:

$$(u_{m,6+,1,t}, \dots, u_{m,6+,4,t}) \sim \text{Multinomial} \left(\sum_{j=1}^4 (u_{s,6+,j,t}), \rho_{6+,1,t}, \dots, \rho_{6+,4,t} \right) \quad \text{eqn 8}$$

where $\rho_{6+,j,t}$ is the probability that an adult female will be in colony j following movement, given by:

$$\rho_{6+,j,t} = \frac{\sum_{i=1}^4 (u_{s,6+,i,t} \Psi_{6+,i \rightarrow j,t})}{\sum_{i=1}^4 (u_{s,6+,i,t})} \quad \text{eqn 9}$$

and $\Psi_{6+,i \rightarrow j,t}$ is the probability of movement for adult females between colony i and colony j . $\Psi_{i \rightarrow i,t}$ was calculated in the same way as for the CR models (see eqn 4). The structure for the movement probability was determined from the CR analysis.

Ageing of pups includes sex determination: on average, half of the pups are expected to be female:

$$u_{a,1,i,t} \sim \text{Binomial}(u_{m,0,i,t}, 0.5) \quad \text{eqn 10}$$

Ageing is deterministic for all other age categories, all animals age 1 year except for adult females who remain in the same age category.

The number of pups produced in colony i depends on the number of breeding females present there:

$$n_{0,i,t} \sim \text{Binomial}(u_{a,6+,i,t}, \gamma) \quad \text{eqn 11}$$

where γ is both the fecundity and breeding probability of adult females, because grey seals produce a maximum of one offspring per year.

For the observation model, the elements of the vector of pup production estimates at each of the colonies are assumed to be normally distributed. Their coefficient of variation δ is assumed to be a linear function of the true pup production squared:

$$y_{0,i,t} \sim \text{Normal}(n_{0,i,t}, \delta^2 n_{0,i,t}^2) \quad \text{eqn 12}$$

Prior distributions on model parameters

The prior distribution on ϕ_a came from a study of branded and tagged adult females on the Isle of May (see above).

We set broad Beta priors on γ and ϕ_{pmax} with a mean of 0.95 and 0.7, respectively, and a Gamma prior on δ with a mean of 0.1, as in Thomas *et al.* (2005). The β_i parameters were chosen to give an expected carrying capacity of 3000 for the Isle of May, 1000 for Fast Castle, 2500 for the Farne Islands, and 10 000 for Donna Nook, based on the available space at each colony and the assumption that there was no movement between colonies. These values are quite uncertain, so vague Gamma prior distributions were specified to reflect this. The prior distributions on the movement model parameters (α_0 , α_1 and α_2) and their variance–covariance matrices were obtained from the results of the CR analysis. The full prior distributions for the model parameters are available online in Appendix S1 (see Supplementary material).

Initializing the states

The priors for the states were generated using the pup production estimate for 1984 together with the priors for the parameters (Thomas *et al.* 2005) as described online in Appendix S1 (see Supplementary material). For the SSM in which no movement occurred, the number of female seals at Fast Castle was initialized in 1997 (the first year of data for this colony) using the same methods as above. For the other models this was not necessary as seals were able to move to Fast Castle from the established colonies from 1990, the earliest date that pups were observed there by local fishermen (Kevin Rideout, SWT/NTS Ranger, pers. comm.).

Fitting the models

The SSM is completely specified by four classes of pdfs: $g_0(\Theta)$ Prior parameter distribution
 $g_0(\mathbf{n}_0 | \Theta)$ Initial state distribution
 $g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \Theta)$ State process distribution
 $f_t(\mathbf{y}_t | \mathbf{n}_t, \Theta)$ Observation process distribution
 where Θ is a vector of the model parameters, \mathbf{n}_t represents the state at time t and \mathbf{y}_t represents the data observed at time t . Generally, it is the parameters Θ that we want to make inferences about, but we also need to estimate the unknown states. We used sequential importance sampling (SIS) to estimate the model parameters and states because it is well suited to time-series data (Trenkel, Elston & Buckland 2000).

The basic SIS algorithm

- *Step 1: Initializing.* For the year 1984, K particles are drawn from the joint distribution of prior parameters and initial states. A particle can be thought of as one possible population with parameter values that are specific to it. For the models investigated here, $K = 350\,000$.
- *Step 2: Projection.* The particle swarm is projected stochastically forward 1 year using the state process model.

- *Step 3: Correction.* A weight, proportional to the likelihood for the particle given the current data, is calculated for each particle.
- *Step 4: Resampling.* Particles are resampled stochastically according to these weights. This is akin to ‘survival of the fittest’ in a Darwinian analogy: particles with a high weight propagate themselves while those with a low weight are lost.
- *Step 5: Iteration.* Steps 2–4 are repeated until the final time point (2003) is reached.

Particle depletion

The main problem with this SIS algorithm is that the number of particles is rapidly depleted because the variance in the weights increases with time until a few particles have almost all the weight. In effect, Step 4 results in a loss of particle ‘diversity’ (Doucet, Godsill & Andrieu 2000). The resulting posterior distributions show just a few point masses. This is not useful for inference and results in large Monte Carlo error. We used four techniques to combat particle depletion: rejection control (Liu, Chen & Wong 1998; Liu 2001); auxiliary particle filtering (Pitt & Shepherd 1999; Liu & West 2001; Thomas *et al.* 2005); residual resampling (Liu, Chen & Wong 1998; Liu 2001); and kernel smoothing (Trenkel *et al.* 2000; Liu & West 2001; Thomas *et al.* 2005; Newman *et al.* 2006). Details of the four techniques and the augmented SIS algorithm incorporating them are available online in Appendix S1 (see Supplementary material).

Inference and model selection

Smoothed inference (Thomas *et al.* 2005) was used for assessing the fit of the models to the data. Smoothing was done by tracing back through time to find the ‘ancestors’ of the particles that were still present in the particle swarm in the final year. These smoothed estimates were also used to calculate the AIC values for the models. More specifically we calculated Mean Posterior AIC (MPAIC) values as the mean of the AIC values for the fit of the smoothed particles to the time series. We also computed MPAIC weights, so that the models could be compared. However, particle depletion in the early part of the time series can cause substantial Monte Carlo error in the MPAIC values, so we calculated the MPAIC weights using only MPAIC values for the smoothed particles between 1990 and 2003.

Future abundance prediction

The future abundances of pups at each of the colonies were assessed by projecting the models forward using the posterior distributions of states and parameter values. One thousand particles were randomly selected from those that survived until the final time point (2003). These were projected forward stochastically over a time

horizon of 200 years, by which time the colonies were predicted to have reached equilibrium.

All of the models were coded in R Version 2.0.1 (R Development Core Team 2004). Source code is available online in Appendix S2 (see Supplementary material). Each model was run four times in order to assess the level of Monte Carlo variation in the posterior estimates and whether or not the models had converged.

Results

CAPTURE–RECAPTURE MODELLING

The goodness-of-fit tests showed some evidence of lack of fit to the data, so the average value of \hat{c} (2.79) from the LHS and RHS analyses was used. This value is not particularly high for CR models exhibiting overdispersion (Lebreton *et al.* 1992).

The results from the model selection procedure are shown in Table 1. The estimate of the slope parameter ξ_1 for the recapture rate regressions for the LHS models was positive, indicating that the recapture probability increased with the proportion of breeding seals that were photographed. Similarly, the estimate of the slope parameter α_1 was also positive for the models that included effects of distance on movement (L1, L2, R1 and R2), indicating that movement probabilities decreased with increasing distance between colonies. However, for the models that incorporated the effect of both distance and abundance on movement (L1 and R2) the estimate of the slope parameter α_2 was negative, indicating that seals were attracted towards the larger colonies.

Re-running the CR models with the upper and lower bounds on survival had a relatively small effect on the movement probabilities.

Table 1. Number of parameters, Quasi-likelihood adjusted Akaike’s information criteria (QAIC) values and QAIC weights for capture–recapture models applied to photographs of the left-hand side (LHS) and right-hand side (RHS) of North Sea grey seals. Only models with a QAIC weight > 0.05 are shown. Φ = survival probability; Ψ = movement probability; P = Recapture probability. *Model specification:* int = intercept (single parameter estimated); dist = movement probability constrained to be a function distance between colonies; dist & abun = movement probability constrained to be a function of distance and abundance; Z = recapture probability constrained to be a function of $Z_{i,t}$

Model	Model parameters	No. of parameters	QAIC	QAIC weight
LHS				
L1	$\Phi_{(0.96)} \Psi_{(\text{dist \& abun})} P_{(Z)}$	5	374.687	0.586
L2	$\Phi_{(0.96)} \Psi_{(\text{dist})} P_{(Z)}$	4	376.391	0.250
L3	$\Phi_{(0.96)} \Psi_{(\text{int})} P_{(Z)}$	3	377.373	0.153
RHS				
R1	$\Phi_{(0.96)} \Psi_{(\text{dist})} P_{(\text{int})}$	3	362.335	0.570
R2	$\Phi_{(0.96)} \Psi_{(\text{dist \& abun})} P_{(\text{int})}$	4	364.194	0.225
R3	$\Phi_{(0.96)} \Psi_{(\text{int})} P_{(\text{int})}$	2	364.530	0.190

Table 2. Mean posterior Akaike’s information criterion (MPAIC) and MPAIC weight for four different state-space models applied to the North Sea grey seal population. ‘Source of α priors’ refers to the capture–recapture models specified in Table 1

Model	No. of parameters	Movement model form	Source of α priors	MPAIC	MPAIC weight
S1	11	$\text{logit}(\Psi_{i \rightarrow j,t}) = \alpha_0 + \frac{\alpha_1}{\text{dist}_{i \rightarrow j}} + \alpha_2(n_{0,j,t-1} - n_{0,j,t-2})$	L1	603.4	0.052
S2	10	$\text{logit}(\Psi_{i \rightarrow j,t}) = \alpha_0 + \frac{\alpha_1}{\text{dist}_{i \rightarrow j}}$	R1	600.6	0.221
S3	9	$\text{logit}(\Psi_{i \rightarrow j,t}) = \alpha_0$	R3	598.1	0.737
S4	8	No movement	N/A	643.1	0.000

STATE-SPACE MODELLING

The results from the SSM selection are given in Table 2 along with the form of the movement models used and the source of the α priors. The movement probabilities estimated for the LHS and RHS CR analyses were very similar when the same movement model form was used. We therefore used the α priors from the CR analysis that gave the maximum variance in the movement probabilities because it is more important that the priors encompass all likely values than that they have minimum variance. Although all models converged, there was some Monte Carlo error in the MPAIC values, and therefore the average values (across the four runs of each model) were used to calculate the MPAIC weights. Model S3, which assumes a constant movement probability between colonies, had a clear advantage, based on these weights.

Figure 2 shows the performance of model S3. Only two pup production estimates show a poor fit: the Farne Islands in 1999 and Fast Castle in 2003.

The prior and posterior distributions for the parameters in model S3 are shown in Fig. 3. The posteriors on adult survival, ϕ_a , fecundity, γ , the observation model coefficient of variation, δ , and the movement parameter, α_0 , all have a lower variance than the priors, indicative of information content in the data on these parameter values.

Table 3 compares the movement probabilities estimated in the initial CR analyses with those from model S3. The SSM analysis produced a lower estimate for movement than the CR analyses, and consequently a higher site fidelity rate. The width of the confidence interval for the movement probability, obtained from CR model R3, was reduced by 82% when model S3 was fitted to the pup production data. This reduction can also be seen when comparing the prior and posterior distribution widths for the parameter α_0 in Fig. 3.

There was also some support for model S2, and Table 4 compares the movement rates estimated from the CR models that underpin model S2 with the estimates from model S2. Distance has a less pronounced effect in the

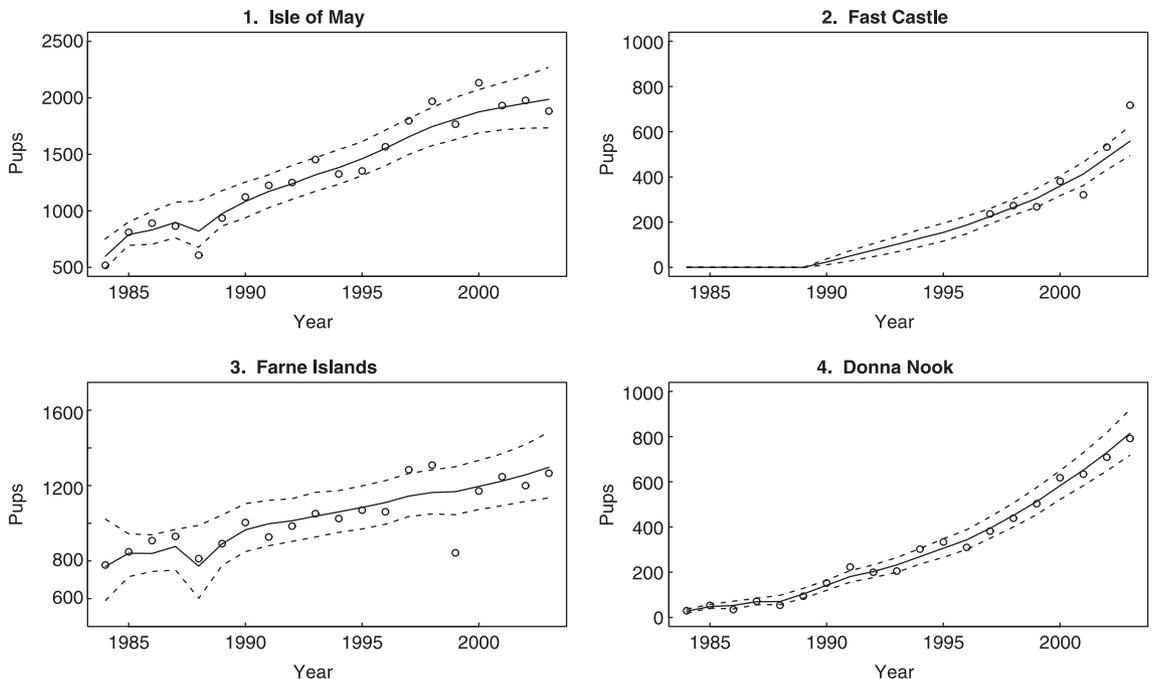


Fig. 2. Pup production data (circles) and smoothed estimates (solid line) for the best-fitting state-space model of the North Sea grey seal population. Dashed lines show the posterior 95% Bayesian credibility intervals.

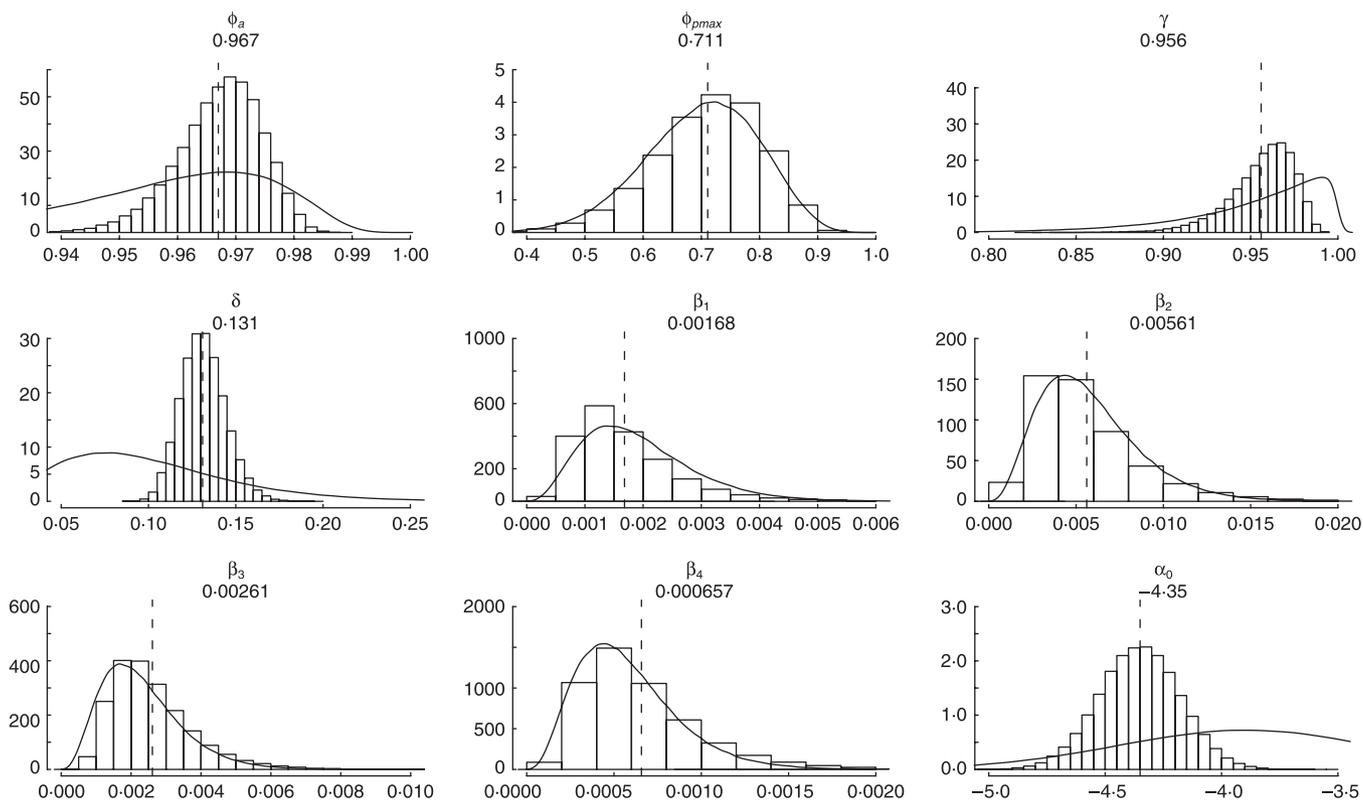


Fig. 3. Prior (solid lines) and posterior (histograms) distributions and posterior means (dotted vertical line) for the best fitting state-space model. ϕ_a , adult survival; ϕ_{pmax} , maximum pup survival; γ , adult fecundity; δ , coefficient of variation in pup production; β , carrying capacity parameters for each colony; α_0 , movement parameter.

Table 3. Movement probability estimates from two different capture–recapture (CR) models and a state-space model incorporating a single movement parameter. The mean, 2.5th and 97.5th percentiles are given. The movement probability, Ψ , is given in terms of the source colony and the destination colony. $i \leftrightarrow i$ is the site fidelity probability and $i \leftrightarrow j$ is the probability of moving to one of the other colonies

Movement probability Ψ	CR model L3	CR model R3 (α prior from this)	SSM S3
$i \leftrightarrow i$	0.933 (0.838, 0.973)	0.940 (0.830, 0.979)	0.961 (0.947, 0.973)
$i \leftrightarrow j$	0.022 (0.009, 0.054)	0.020 (0.007, 0.057)	0.013 (0.009, 0.018)

Table 4. Movement probability estimates from two different capture–recapture (CR) models and a state-space model including the effect of distance between colonies. 1 = the Isle of May, 2 = Fast Castle, 3 = the Farne Islands and 4 = Donna Nook, so $1 \leftrightarrow 1$ is the site fidelity at the Isle of May and $1 \leftrightarrow 2$ represents the probability of movement between the Isle of May and Fast Castle. The mean, 2.5th and 97.5th percentiles are given

Ψ	CR model L2	CR model R1 (α priors from this)	SSM S2
$1 \leftrightarrow 1$	0.924 (0.716, 0.979)	0.916 (0.643, 0.979)	0.961 (0.946, 0.973)
$2 \leftrightarrow 2$	0.912 (0.703, 0.973)	0.903 (0.630, 0.974)	0.959 (0.943, 0.972)
$3 \leftrightarrow 3$	0.955 (0.828, 0.986)	0.967 (0.806, 0.993)	0.964 (0.949, 0.976)
$4 \leftrightarrow 4$	0.981 (0.838, 0.998)	0.992 (0.818, 0.9997)	0.970 (0.948, 0.984)
$1 \leftrightarrow 2$	0.057 (0.016, 0.177)	0.073 (0.019, 0.236)	0.017 (0.010, 0.028)
$1 \leftrightarrow 3$	0.014 (0.003, 0.053)	0.009 (0.001, 0.060)	0.012 (0.008, 0.017)
$1 \leftrightarrow 4$	0.006 (0.0006, 0.054)	0.002 (0.0001, 0.061)	0.010 (0.005, 0.017)
$2 \leftrightarrow 3$	0.025 (0.010, 0.066)	0.022 (0.006, 0.073)	0.014 (0.010, 0.019)
$2 \leftrightarrow 4$	0.006 (0.0007, 0.054)	0.003 (0.0001, 0.061)	0.010 (0.005, 0.017)
$3 \leftrightarrow 4$	0.006 (0.0007, 0.054)	0.003 (0.0001, 0.060)	0.010 (0.005, 0.017)

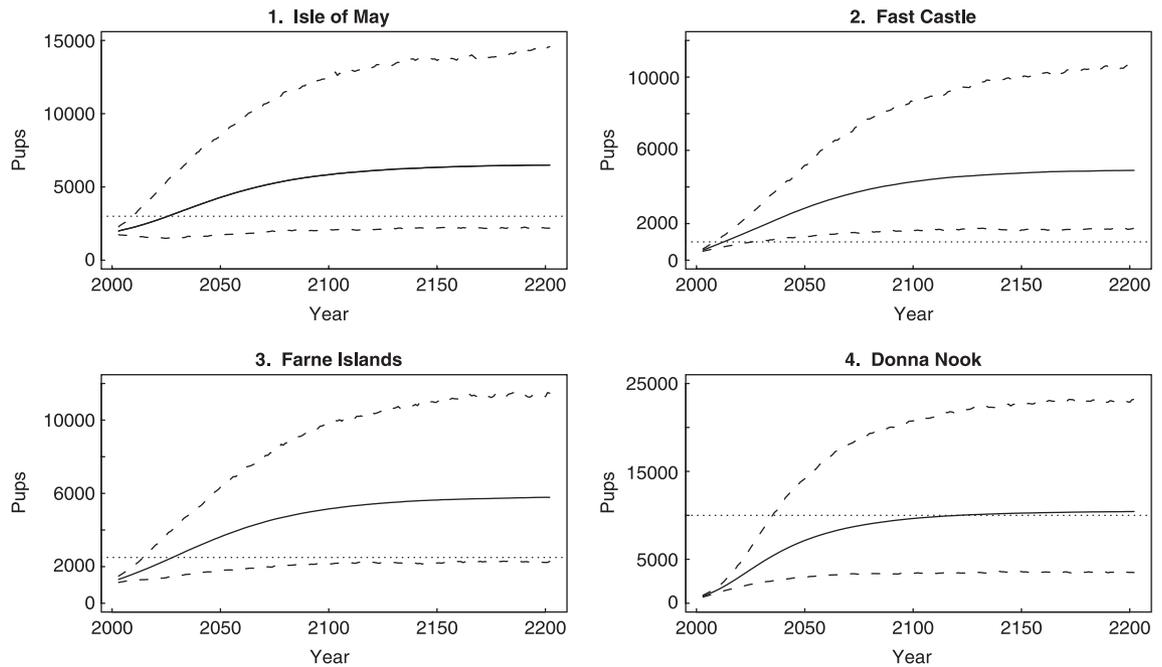


Fig. 4. Predicted future pup productions for North Sea grey seal colonies based on posterior states and parameters from the best-fitting state-space model. Dashed lines show the 95% Bayesian credibility interval, the dotted horizontal line is the prior estimate of carrying capacity at each colony.

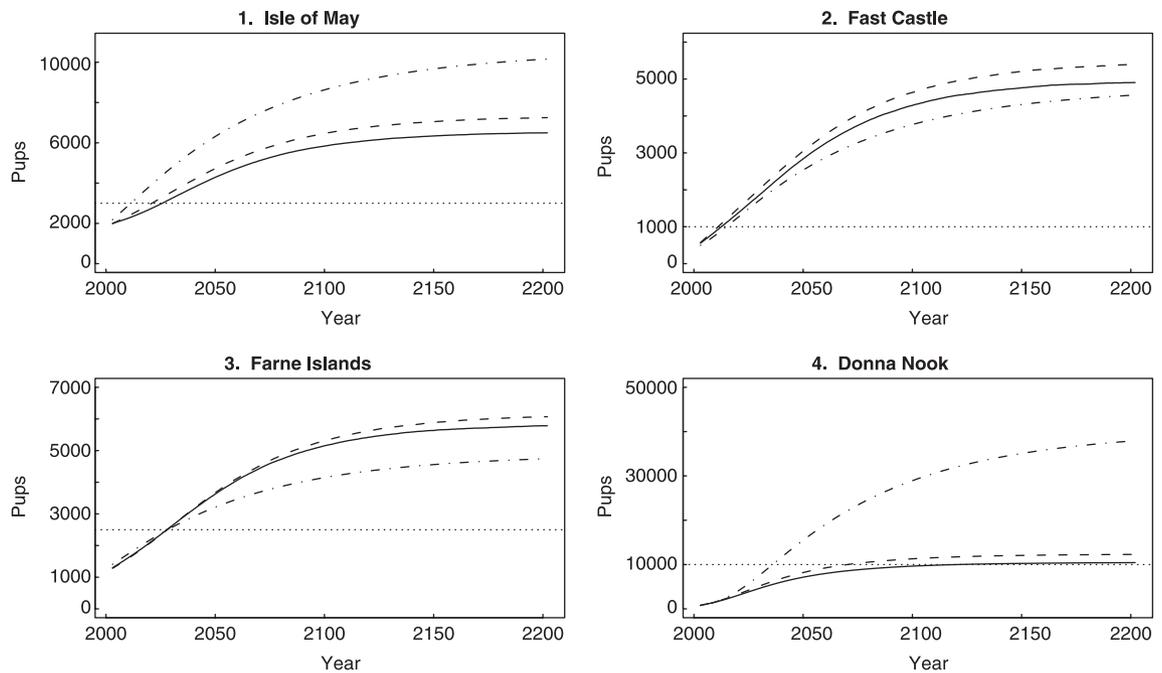


Fig. 5. Predicted future pup productions for North Sea grey seal colonies based on three state-space models (dashed line, movement determined by distance; solid line, fixed probability of movement; dotted and dashed line, no movement). The dotted horizontal line shows the prior estimate of carrying capacity for each colony.

SSM estimates, and the uncertainty in the movement probabilities is much reduced.

Figure 4 shows the predicted pup productions when model S3 is projected forward 200 years. There is wide variation in the equilibrium sizes predicted, but they tend to be greater than our prior estimates for the Isle of May, Fast Castle and the Farne Islands. The 95%

Bayesian credibility intervals are very large after about 100 years (a consequence of projecting forward in time for a long period) but do not become much worse over the next 100 years.

Figure 5 compares the mean predicted future pup abundances from projecting three of the four SSMs forward 200 years. Model S1 produced unstable

behaviour in which all animals were eventually attracted to the two larger colonies. This outcome seems unlikely and the results from this model have not been shown. Although the no-movement model, S4, had a zero MPAIC weight, it has been included for comparison. The two movement models that were supported by the pup production data result in different equilibrium distributions and a different equilibrium size for the whole system than model S4. However, there was considerable overlap in the 95% Bayesian credibility intervals for the trajectories at all four colonies. The model-averaged carrying capacity for each colony (Buckland *et al.* 1997), calculated using the MPAIC weights were: Isle of May 6595 pups, Fast Castle 4809 pups, Farne Islands 5616 pups, and Donna Nook 10 887 pups.

Discussion

POSTERIOR PARAMETER ESTIMATES

The pup production data contained information on adult female survival, ϕ_a , and on δ , the coefficient of variation of the observation model. There was also some information on the fecundity rate, γ . There was, however, no information to refine our estimates of the maximum pup survival rate, ϕ_{pmax} , and the β parameters that affect the equilibrium values at the colonies. This is not surprising, because all four colonies are still growing and must therefore be some way from equilibrium.

GREY SEAL MOVEMENT

There was strong evidence that incorporating movement between the colonies improved model performance. In fact, the model with no movement (S4) had zero MPAIC weight. The estimated movement probability from the SSM was approximately 35% lower than the CR estimate. The upward bias in the CR estimate was probably because some short-term within-season movements were misclassified as permanent moves between colonies. The SSM estimate also had a much tighter confidence interval.

Although this analysis provided strong evidence of movement between colonies, the estimated fidelity of animals to their own colony (0.961) was very high and similar to the value obtained by Pomeroy *et al.* (1994) from a detailed study of permanently marked breeding female grey seals at North Rona. Thomas *et al.* (2005) found little evidence for movement of grey seals between regional populations, but this is unsurprising because even relatively high levels of movement between adjacent colonies would not necessarily generate significant movement between regions.

It has long been held that distances between sub-populations are an important factor in theoretical and empirical movement studies (Serrano & Tella 2003). The CR analysis supported a model that included both distance and colony size as determinants of movement

probability, with seals being attracted from smaller colonies to larger ones. This may have been a result of conspecific attraction (Smith & Peacock 1990; Cam *et al.* 2004) but it may also be an artefact because the smallest colony, Fast Castle, had a much lower fidelity rate than any other colony. This view is supported by the fact that the movement probabilities associated with Fast Castle had wide confidence limits and were highly sensitive to the choice of movement model. There was little support for this movement model when it was incorporated into a SSM (MPAIC weight of 0.052) and it predicted unlikely long-term dynamics, with the largest two colonies acting as sinks that drained all the animals from the other two colonies.

ABUNDANCE PREDICTION

Bowne & Bowers (2004) point out that relatively few metapopulation studies have documented rates of inter-patch movement. Those that did rarely determined the population level consequences of these movements. Our study addressed both aspects. Movement affects not only the dynamics of the individual colonies but also the metapopulation as a whole (Hanski, Kuussaari & Nieminen 1994; Matthiopoulos *et al.* 2005). If there is no movement, the equilibrium size of each colony in our models is entirely determined by the β parameters. When movement is incorporated, some colonies become net suppliers of migrants at equilibrium, while others will be net receivers. The best-fitting model predicted equilibrium sizes for three colonies that were very different from our initial expectations. Donna Nook, the one colony that did not overshoot its prior expectation, continued to act as a source of migrants to the other colonies at equilibrium. However, the available time series provided little information on the equilibrium size of the four colonies. The 95% Bayesian credibility intervals in Fig. 4 indicate that the predictions range from virtually no increase to a continuation of the current growth trend.

The most noticeable difference between the model predictions is for Donna Nook (Fig. 5): the no-movement model (S4) predicts a much larger equilibrium size than the others, probably because the rapid early rise in pup numbers was inconsistent with a smaller equilibrium size. However, when migration into Donna Nook was allowed (as in models S3) the rapid early rise was adequately explained (see Fig. 2).

Conclusions

SSMs provide a valuable framework for combining demographic and time-series information to understand the dynamics of metapopulations. Using this framework, estimates of movement rates between metapopulation units and survival from independent studies can be refined by incorporating them into such a framework and fitting them to a time series of population estimates using computer-intensive Bayesian techniques. The

resulting models provided valuable insights into the potential future dynamics of grey seals in the North Sea. We believe that this approach could have wide applications to many other spatially structured populations.

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Supplementary material

The following supplementary material is available for this article online.

Appendix S1. In-depth description of the sequential importance sampling algorithm used.

Appendix S2. Source code and data to implement model S3, written in R Version 2.0.1 (R Development Core Team 2004). Six text files for running the model and a ReadMe text file listing the contents of the other files and how to use them.