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Estimating the size of the UK grey seal population between 1984 and 2004: model selection, survey effort and sensitivity to priors.

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Summary

We used a Bayesian state space modelling framework to fit and compare models of British grey seal population dynamics using regional estimates of pup production from 1984 to 2004. The models allow for a number of different forms of density dependence in either pup survival or fecundity, as well as fitness-dependent movement of recruiting females between regions. There was little difference between models in the adjusted posterior log-likelihoods, meaning that none of the models was obviously best at describing the data. However, this could be a result of the fitting methods used. The estimated adult population size in 2004 varied from 105,000 (95% CI 78-141,000) for the simplest density-dependent survival model to 234,000 (95% CI 167-344,000) for the simplest density-dependent fecundity model, the other models having intermediate estimates.

The estimates of adult survival and pup production at carrying capacity were relatively insensitive to the prior distributions that we chose. However, estimates of juvenile survival, fecundity and movement were almost completely determined by their priors.

Reducing the frequency of pup production estimates to one every second year had little effect on the posterior mean estimates of population size and model parameters, but the variance of the estimates of population size increased as did the sensitivity of the parameters to their prior distributions.

Including a fabricated independent estimate of population size in 2004 for each region enhanced our ability to distinguish between the models. We discuss how such an actual estimate of this variable might be obtained.

Introduction

In this paper, we expand on the methodology that has been used to estimate the size of the grey

seal population associated with those UK colonies that are surveyed each year by SMRU (Thomas and Harwood 2003, 2004). The underlying models are formulated in a state-space framework (Buckland *et al.* 2004, Thomas *et al.* 2005, Newman *et al.* in press). A state-space model is composed of a state process, which models the true but unknown state of the population (i.e., the number of animals in each age group and region in each time period), and an observation process, which models how the survey data are generated given the true states.

Previous versions of this model have used a simple Beverton-Holt function to describe the relationship between pup survival or fecundity and population size. This function predicts that most of the changes in these parameters occur at population sizes well below carrying capacity, whereas the conventional wisdom is that, for large vertebrates, these changes are unlikely to occur until the population is close to its carrying capacity. To capture this we used an extended version of the Beverton-Holt function, first suggested by Shepherd (1982), which has similar properties to the generalised logistic function. We refer to this as “extended density dependence”.

We used an analytic approach to investigate the sensitivity of the posterior parameter estimates to the priors that we used, and we examined the effects of reduced survey effort by removing every other year of data from the time series we analysed..

Materials and Methods

Models

We compared models that incorporate density dependent pup survival (DDS) with models incorporating density dependent fecundity (DDF). The basic DDS model is identical to that presented previously (Thomas and Harwood 2003, 2004), while the basic DDF model is a slight modification of that presented by Thomas and Harwood (2004). Both basic models were

also extended (EDDS and EDDF) to include an extra parameter governing the relationship between density dependence and population size.

In constructing the state processes, we divide the seal population in each region into 7 age classes: pups (age 0), age 1 – age 5 adult females (pre-breeding), and age 6 and older females. Note that our models do not include adult males.

The time step for the process models is 1 year, beginning just after the breeding season. The models are made up of four sub-processes: survival, age incrementation, movement of recruiting females and breeding.

Survival is modelled as a binomial random process. For the DDS model, we assume that pup survival follows a Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p \max}}{1 + \beta_r n_{0,r,t-1}}$$

where $n_{0,r,t-1}$ is the number of pups born in region r in year $t-1$, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p \max}$ is maximum pup survival rate, and $1/\beta_r$ is proportional to the carrying capacity of the region. The EDDS model includes an extra parameter, ρ , that can alter the shape of the relationship between pup survival and pup numbers:

$$\phi_{p,r,t} = \frac{\phi_{p \max}}{1 + (\beta_r n_{0,r,t-1})^\rho} \quad (1)$$

Figure 1 shows the effect of different levels of ρ . For the DDF and EDDF models, we assume pup survival is constant across regions and times, i.e., $\phi_{p,r,t} = \phi_p$.

Since half of the pups born will be male, the expected number of female pups surviving in both models will be $0.5 \phi_{p,r,t} n_{0,r,t-1}$. For all models, we assume that adult female survival rate, ϕ_a is constant across regions and time.

Age incrementation is deterministic – all seals age by one year (although those in the age 6+ category remain there).

To model movement, we assume that only females breeding for the first time may move from their natal region. Once a female has started breeding she remains faithful to that region. We

assume that movement is fitness dependent (Ruxton and Rohani 1998), such that females will only move if the value of the density dependent parameter (pup survival or fecundity) is higher elsewhere, and the probability of movement is proportional to the difference in the density dependent parameter between regions. In addition, we assume that females are more likely to move among regions that are close together, and that females show some degree of site fidelity – that is, they may not move even if conditions for their offspring will be better elsewhere. We model movement from each region as a multinomial random variable where probability of movement from region r to region i at time t is:

$$\rho_{r \rightarrow i,t} = \begin{cases} \frac{\theta_{r \rightarrow i,t}}{\sum_{j=1}^4 \theta_{j \rightarrow i,t}} & : \sum_{j=1}^4 \theta_{j \rightarrow i,t} > 0 \\ I_{i=r} & : \sum_{j=1}^4 \theta_{j \rightarrow i,t} = 0 \end{cases}$$

where $I_{i=r}$ is an indicator that is 1 when $i=r$ and 0 otherwise, and

$$\theta_{r \rightarrow i,t} = \begin{cases} \gamma_{sf} & : i = r \\ \frac{\gamma_{dd} \max(\Delta_{i,r,t}, 0)}{\exp(\gamma_{dist} d_{r,i})} & : i \neq r \end{cases}$$

where γ_{sf} , γ_{dd} , and γ_{dist} are three movement parameters that index the strength of the site fidelity, density dependence and distance effects respectively, $\Delta_{i,r,t}$ is the difference in the density dependent parameter between regions i and r (see below), and $d_{r,i}$ is the 20% trimmed mean of the distances between colonies in regions r and those in region i (standardized so that the largest distance is 1.0). For the DDS and EDDS models,

$$\Delta_{i,r,t} = \phi_{p,i,t} - \phi_{p,r,t}$$

while for the DDF and EDDF models,

$$\Delta_{i,r,t} = \alpha_{i,t} - \alpha_{r,t}$$

where $\alpha_{r,t}$ is the fecundity rate in region r at time t , as defined below.

We model breeding by assuming that the number of pups produced is a binomial random variable, with rate $\alpha_{r,t}$. For the DDS and EDDS models, we assume this value is constant across regions and times, i.e., $\alpha_{r,t} = \alpha$. For the DDF model, we assume this value follows a Beverton-Holt function of the form:

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1 + \beta_r n_{6+,r,t}}$$

This implies that the probability of a female breeding in a particular year is influenced by the number of age 6+ females in that year. Note that this is slightly different from the DDF model of Thomas and Harwood (2004), in which fecundity was a function of the number of pups in the previous breeding season. This resulted in increasing oscillations in pup production under some parameter combinations (there is some evidence of this in the upper confidence limit for the DDF model in Figure 2 of that paper). A viable alternative would be to model breeding probability as a function of the number of age 6+ females in the previous year. The EDDF model is similar, with

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1 + (\beta_r n_{6+,r,t})^\rho} \quad (2)$$

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV) which we assume to be a known value. In the runs reported here, we fixed this CV at 25%.

In summary, the DDS and DDF models have 10 parameters. They share 8: adult survival ϕ_a , one carrying capacity parameter-related parameter for each region β_1 - β_4 , and three movement parameters γ_{sf} , γ_{dd} , and γ_{dist} . They differ in two parameters: the DDS model has maximum pup survival $\phi_{p\max}$ and constant fecundity α , while the DDF model has constant pup survival ϕ_p and maximum fecundity α_{\max} . The EDDS and EDDF models have one additional parameter, ρ , for the shape of the density-dependent response.

Data and Priors

Our input data were the pup production estimates for 1984-2004 from Duck and Mackey (2005), aggregated into regions. Unlike last year, we did not include the Helmsdale colony in the North Sea region as it was not surveyed in 2004, so our totals for the North Sea are slightly lower than those used last year.

In previous years, we have used independent prior distributions on each parameter, but the introduction of the ρ parameter makes this inadvisable. Carrying capacity is strongly

affected by ρ (Figure 1), so a prior on the carrying capacity parameters β that would be reasonable at one level of ρ would be unfeasible at a different ρ . Hence, instead of setting priors on the β s independently of the values of the other parameters, we used a re-parameterization to set priors on the numbers of pups at carrying capacity in each region and then generated values for the β s conditional on the realized values of ρ and the other model parameters. We denote the number of pups at carrying capacity in region r as χ_r . For the EDDS model, it can be shown that

$$\beta_r = \frac{1}{\chi_r} \left[\frac{0.5\alpha\phi_{p\max}\phi_a^5}{1-\phi_a} - 1 \right]^{1/\rho} \quad (3)$$

(values of $\beta_r < 0$ are set to 0). Similarly, for the EDDF model,

$$\beta_r = \frac{[\alpha_{\max}\tau - 1]^{1/\rho}}{\chi_r\tau}$$

where $\tau = 0.5\phi_p\phi_a^5/(1-\phi_a)$. For the DDS and DDF models, the formulae are the same, except that $\rho = 1$.

Prior distributions for each parameter are given in Table 1, and are shown on Figures 3 and 5.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}, \phi_p$	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5
γ_{sf}	Ga(2.25,1.33)	0.5	0.33
γ_{dd}	Ga(2.25,0.49)	3	2
γ_{dist}	Ga(2.25,0.22)	ln(3)	ln(2)
α, α_{\max}	Be(22.05,1.15)	0.95	0.04

Prior distributions for the states in the DDS and EDDS models were generated using the priors for the parameters in conjunction with the 1984 data, as described by Thomas *et al.* (2005). Prior states for the DDF and EDDF model were generated in a similar manner, except that the number of age 6+ females was sampled from a

Poisson distribution, with mean equal to the solution of the equation

$$n_{0,r,0} = \frac{\alpha_{\max}}{1 + (\beta_r n_{6+,r,0})^\rho} n_{6+,r,0}$$

for $n_{6+,r,0}$ given the other values. This can lead to unfeasibly large or small values for the mean, so values were bounded by $n_{0,r,0}$ as a lower bound and $n_{5,r,0} \phi_a / (1 - \phi_a)$ as an upper bound.

Fitting Method

We used the same particle filtering algorithm as described in Thomas and Harwood (2004), although the algorithm has now been ported from SPlus to C, enabling far larger runs to be undertaken. Particle filtering (also called sequential importance sampling or SIS) is a computer-intensive method for estimating the posterior distribution of the parameters and states of a state-space model. It is well suited to the analysis of time series data, as data points are introduced one year at a time into the algorithm, making it potentially more efficient than other computer-intensive techniques such as Markov chain Monte Carlo (MCMC). Particle filtering methods were first developed for engineering applications and have only recently been applied to biological problems. Consequently, much methodological work is still required. An introduction to particle filtering algorithms in the context of wildlife studies is given by Newman *et al.* (in press), and a detailed description of a similar algorithm to the one used here, applied to a similar model of seals, is given by Thomas *et al.* (2005). The differences between the algorithm of Thomas *et al.* (2005) and the one used here are outlined by Thomas and Harwood (2004).

Model outputs and comparison

The output from a particle filter is a set of weighted samples (particles) taken from the prior distributions on the parameters and states and projected forward stochastically through the time series. The weights relate to the manner in which the particles were sampled, how they were projected forward and the likelihood of the observed pup production given the simulated pup numbers. We can use these particles to estimate quantities of interest such as posterior means or credibility (confidence) intervals on parameters and states. One issue that arises is the accuracy of the estimates, in terms of Monte-Carlo error.

We can calculate the effective sample size of the particles as

$$ESS = \frac{K}{1 + [CV(w)]^2}$$

where K is the number of particles and $CV(w)$ is the coefficient of variation of the weights of these particles. Our aim was to simulate enough particles to achieve an ESS of at least 1000, although that was not possible for some models in the time available. We report ESS achieved in the Results section.

For all four models, we present posterior estimates of the model parameters and estimated pup production from 1984-2004. The models also estimate adult female numbers, but do not include adult males. We therefore calculated total pre-breeding population sizes by assuming that the number of adult males is 73% of the number of adult females (Hiby and Duck, unpublished).

To compare the models, we calculated the mean posterior Akaike Information Criterion (MPAIC) using the same method as Thomas and Harwood (2003, 2004). This criterion is a form of penalized likelihood, which recognizes the fact that models with more parameters are expected to fit better *a priori* by adding a penalty proportional to the number of model parameters. It is similar in spirit to the Bayesian Deviance Information Criterion (Spiegelhalter *et al.* 2002). Models were compared using Akaike weights (Burnham and Anderson 1998, p124), which can be thought of in the Bayesian context as the posterior probability of each model being the best approximating model.

Sensitivity to priors

Since we used informative prior distributions on the parameters, it is of interest to determine how sensitive our results are to the choice of prior. We used the methods developed by Millar (2004) and implemented by Newman (2005, pers. comm.) to determine local sensitivity – that is sensitivity of results to changes in the hyperparameters of the prior distributions (as opposed to changes in the choice of distribution, for example). Specifically, we estimated the sensitivity of the posterior mean of each parameter with respect to changes in the two hyperparameters that specify the prior, by estimating

$$\frac{dE[\theta | y] / da_i}{dE[\theta] / da_i}$$

from the sample of particles, where $E[\theta | y]$ is the posterior expected value of the parameter (i.e., the expected value given the data y), $E[\theta]$ is the prior value of the parameter, a_i is the value of hyperparameter i ($i = 1, 2$), and dx/dy indicates the first differential of x with respect to y . Despite the complex-seeming formulation, the output has a nice interpretation: it is a measure of the relative contribution to the posterior coming from the data and prior (see Results).

Effect of reduced survey effort

We investigated the effect of reducing the frequency of pup production estimates by re-fitting using only every second year of data. Since our fitting algorithm makes use of the first year of data to set priors on the states, and the second year to implement an efficiency-enhancing method called rejection control (Thomas and Harwood 2004), we retained both 1984 and 1985 data, the first “missing” data point being 1986.

Effect of an independent estimate of adult population size

We investigated the effect of obtaining an independent estimate of the adult population size on our ability to distinguish between the models by re-calculating the particle weights for each model, after including one additional piece of data: regional estimates of adult female population size in 2004 (which we assumed to have a CV of 25%). The value we used for these “fabricated” data was the posterior mean estimates of adult population size from the DDF model (which was the model with the lowest posterior AIC value – see Results). Based on these additional data, we re-calculated the particle weights, and then the posterior AIC and Akaike weights.

Results

Effective sample size (ESS)

For some models, an extremely large number of particles were required to achieve a unit increase in ESS (Table 2). The worst was the EDDF model where 222.2×10^4 particles were required for each unit of ESS. Hence we did not achieve our target of $ESS \geq 1000$ for all models (Table 2). Nevertheless, the Monte-Carlo error in our results is likely to be small. For example, dividing the particles from the EDDF model into two, estimated mean adult population size in 1984 is 64.3×10^4 from the first half and 64.2×10^4 from the second.

Table 2. Number of particles (K) and effective sample size (ESS) for the results presented here. Note that number of particles is before rejection control, ESS is afterwards (see Thomas and Harwood 2004 for details).

Model	K ($\times 10^6$)	ESS	ESS/K ($\times 10^4$)
All data			
DDS	60	795	7.5
EDDS	424	514	82.4
DDF	160	1034	15.4
EDDF	614	276	222.4
Alternate years removed			
DDS	60	12103	0.5
EDDS	60	2230	2.6
DDF	60	8275	0.7
EDDF	32	906	3.5

Comparison of models for density dependence

Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the four models are shown in Figure 2. The estimates are very similar, and there is little difference in posterior likelihood or AIC between the models (Table 2). The model with the minimum AIC is the DDF model, but the next best model (EDDS) has a mean posterior AIC only 1.57 higher. All four models are within 3 AIC points of one another.

Subjectively, the extended density dependence models appear to do a better job of capturing the recent levelling-off of pup production in the Inner and Outer Hebrides. However none of the models’ estimates can reproduce the rapid increase in pup production in the Hebrides and Orkney in the early 1990s.

Although the models produce similar estimates of pup production, they give substantially different estimates of total predicted population size (Table 3 and Appendix 1). The DDF model estimates that there are 2.25 times as many seals as the DDS model, with the other two falling in between.

Table 2. Mean posterior log-likelihood, AIC and Akaike weights for models fit to data from 1984-2004.

Model	LnL	AIC	Δ AIC	Akaike weight
DDS	-685.08	1390.16	1.91	0.19
EDDS	-683.91	1389.82	1.57	0.22
DDF	-684.12	1388.25	0.00	0.48
EDDF	-684.59	1391.20	2.95	0.11

Table 3. Estimated size, in thousands, of the British grey seal population at the start of the 2004 breeding season, derived from models fit to data from 1984-2004. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	EDDS
North sea	11.6 (8.9-15.8)	17.0 (9.5-24.8)
Inner Hebrides	8.9 (6.8-11.6)	10.6 (6.8-14.5)
Outer Hebrides	32.7 (24.0-44.2)	41.8 (27.0-57.4)
Orkney	51.5 (38.6-69.8)	74.5 (45.7-94.4)
Total	104.7 (78.3-141.4)	143.5 (89.0-191.1)
	DDF	EDDF
North sea	25.3 (18.5-36.1)	20.4 (15.6-26.6)
Inner Hebrides	21.4 (15.1-32.3)	14.6 (11.3-20.0)
Outer Hebrides	84.9 (58.7-131.5)	57.5 (43.9-77.3)
Orkney	102.5 (75.3-144.4)	78.7 (61.8-101.5)
Total	234.1 (167.6-344.2)	171.1 (132.5-225.4)

Posterior parameter estimates for the models are given in Figure 3. For the DDS and DDF models, the posterior mean adult survival (ϕ_a) is similar to the prior of 0.95 (although the variance is much reduced), but it is substantially lower in the extended density dependence models (0.91 in EDDS and 0.90 in EDDF). The juvenile survival and fecundity parameters (ϕ_j and α) are almost unchanged relative to the prior in all four models. Similarly, the movement parameters (γ s) are also little changed, except for the density dependence parameter γ_{dd} , which has a posterior mean that is half the prior mean in the DDS and DDF models. Posterior distributions of the carrying capacity parameters (χ s) are somewhat tighter than the priors, with posterior mean estimates that vary between models. In the extended density dependence models, the posterior for ρ has lower mean and variance than the prior – in particular for the EDDF model, where the prior mean of 10 is outside the 95% credibility interval of the posterior.

Sensitivity to priors

Results for the four models are shown in Table 4. The sensitivity values can be interpreted as a

measure of the relative contribution to the posterior coming from the data and the prior: low values mean there is a strong influence of the data while high values mean there is a strong influence of the prior. Millar (2004) has suggested a quantitative interpretation of these sensitivities: for example the value of 0.15 for hyperparameter 1 of ϕ_a in the DDS model means that the posterior mean of ϕ_a is influenced 15% by the prior value of this hyperparameter (which is 22.05) and 85% by the data. However, it is unclear how sensitivities of greater than 1 can be interpreted in this way.

Table 4. Sensitivity of the posterior mean of each parameter to changes in the two hyperparameters that specify the prior on that parameter, under four models of British grey seal population dynamics fit to pup production data from 1984-2004.

	1	2	1	2
	DDS		EDDS	
ϕ_a	0.15	0.16	0.23	0.19
$\phi_{p\max}, \phi_p$	0.73	0.81	1.31	1.06
χ_1	0.19	0.21	0.62	0.61
χ_2	0.16	0.22	0.15	0.13
χ_3	0.27	0.42	0.18	0.20
χ_4	0.32	0.47	0.75	0.94
ρ	-	-	0.66	0.42
γ_{sf}	0.86	1.25	1.05	1.29
γ_{dd}	0.68	0.34	1.14	0.92
γ_{dist}	1.21	1.67	1.26	1.84
α, α_{\max}	0.83	0.95	1.26	1.07
	DDF		EDDF	
ϕ_a	0.25	0.31	0.13	0.08
$\phi_{p\max}, \phi_p$	1.07	0.98	1.04	0.94
χ_1	0.19	0.16	0.64	0.63
χ_2	0.14	0.16	0.23	0.18
χ_3	0.21	0.29	0.30	0.30
χ_4	0.49	0.57	0.70	0.84
ρ	-	-	0.43	0.21
γ_{sf}	0.83	1.28	0.92	0.92
γ_{dd}	0.60	0.28	1.03	0.91
γ_{dist}	1.27	1.84	1.04	1.24
α, α_{\max}	1.22	1.09	0.98	1.02

In general, the sensitivity values confirm the impressions gained from the plots of prior and posterior distributions (Figure 3): ϕ_a has low sensitivity, ρ has reasonably low sensitivity (particularly for the EDDF model), the χ s have moderate sensitivity except for some parameters in some models (e.g., χ_4 in the EDDS and EDDF modes), and the other parameters have high sensitivity. The ϕ_j and α parameters are almost completely determined by their prior, as are the movement parameters, except for γ_{ad} in the DDS and DDF models.

Effect of reduced survey effort

Fitting the models with approximately half the data had relatively little effect on either the estimates of true pup production (Figure 4) or parameters (Figure 5), although the estimates of pup production had wider credibility intervals, particularly at the beginning and end of the time series, and the parameter estimates were generally closer to their prior distributions.

DDF still had the lowest AIC, with the difference between that and the other models (especially EDDF) being slightly greater (Table 5). The predicted total population sizes for 2004 (Table 6) were broadly similar to the estimates using the entire dataset (Table 3), but note that the values in Table 6 are predictions, not estimates, because the 2004 data were excluded. However, the posterior credibility intervals were noticeably wider.

Table 5. Mean posterior log-likelihood, AIC and Akaike weights for models fit to data from 1984, 1985, 1987, 1989, 1991, 1993, 1995, 1997, 1999, 2001 and 2003.

Model	LnL	AIC	Δ AIC	Akaike weight
DDS	-356.43	732.87	1.63	0.24
EDDS	-355.84	733.68	2.44	0.16
DDF	-355.62	731.24	0.00	0.55
EDDF	-357.28	736.56	5.32	0.04

Sensitivities of the parameters were almost all greater (Table 7), indicating a stronger influence of the prior as would be expected with less data. For example, in the EDDS model, sensitivity of the two hyperparameters for the gamma prior on ρ was 0.66 and 0.42 with the full dataset, but 0.95 and 0.69 with the reduced dataset. The posterior mean estimate of this parameter was

6.24 with the whole dataset, but 7.23 with the reduced dataset – closer to the prior mean of 10.

Table 6. Predicted size, in thousands, of the British grey seal population at the start of the 2004 breeding season, derived from models fit to a subset of the data from 1984-2003 (see Table 5 legend). Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	EDDS
North sea	11.0 (8.0-15.5)	17.5 (8.7-27.3)
Inner Hebrides	8.8 (6.4-12.1)	11.4 (6.9-18.0)
Outer Hebrides	31.8 (21.6-45.1)	45.0 (26.8-69.7)
Orkney	49.3 (35.0-69.1)	72.6 (40.2-99.8)
Total	101 (71.1-141.8)	146.6 (82.6-214.8)
	DDF	EDDF
North sea	25.3 (17.2-38.6)	19.8 (14.3-28.8)
Inner Hebrides	21.7 (14.4-34.1)	15.6 (11.0-22.7)
Outer Hebrides	82.5 (54.2-140.2)	62.3 (43.4-88.0)
Orkney	104.7 (71.1-157.3)	74.3 (55.4-102.6)
Total	237.2 (156.9-370.2)	172.1 (124.0-242.1)

Effect of an independent estimate of adult population size

Including an independent estimate of adult population size created a clear distinction between the models (Table 8), with the DDF model having 96% of the posterior Akaike weight, and the EDDF model (which had the closest adult population size estimates to the DDF model) having the remaining 4%.

Discussion

For the runs reported here, we fixed the CV of the pup production estimates at 25%. This value is higher than the only available estimate (Hiby and Duck, unpublished) of 7% for individual colonies. The effect of using a higher CV is to reduce the influence of the data on the posterior states and parameters, relative to the priors. We therefore regard our results as preliminary, especially those regarding the sensitivity of the parameters to the priors and the comparison of models.

Table 7. Sensitivity of the posterior mean of each parameter to changes in the two hyperparameters that specify the prior on that parameter, under four models of British grey seal population dynamics fit to a subset of the data from 1984-2003 (see Table 5 legend).

	1	2	1	2
	DDS		EDDS	
ϕ_a	0.18	0.19	0.28	0.24
$\phi_{p\max}, \phi_p$	0.77	0.85	1.26	1.04
χ_1	0.20	0.20	0.71	0.71
χ_2	0.22	0.31	0.25	0.25
χ_3	0.35	0.54	0.29	0.37
χ_4	0.37	0.49	0.77	0.93
ρ	-	-	0.95	0.69
γ_{sf}	0.90	1.25	1.00	1.14
γ_{dd}	0.74	0.48	1.01	0.88
γ_{dist}	1.20	1.51	1.21	1.44
α, α_{\max}	0.84	0.91	1.21	1.06
	DDF		EDDF	
ϕ_a	0.29	0.36	0.14	0.09
$\phi_{p\max}, \phi_p$	1.15	1.01	1.15	1.02
χ_1	0.22	0.18	0.89	0.91
χ_2	0.19	0.21	0.58	0.57
χ_3	0.26	0.37	0.50	0.56
χ_4	0.50	0.55	0.79	0.89
ρ	-	-	1.19	0.89
γ_{sf}	0.87	1.24	1.03	1.04
γ_{dd}	0.72	0.42	1.06	1.02
γ_{dist}	1.25	1.64	1.14	1.27
α, α_{\max}	1.29	1.12	1.15	1.04

Table 8. Mean posterior log-likelihood, AIC and Akaike weights for models fit to pup production data from 1984-2004 and fabricated regional estimates of adult female population size in 2004.

Model	LnL	AIC	Δ AIC	Akaike weight
DDS	-690.57	1401.14	12.86	0.00
EDDS	-691.40	1404.80	16.52	0.00
DDF	-684.14	1388.28	0.00	0.96
EDDF	-686.40	1394.80	6.52	0.04

We are actively working on improving the fitting methods. The current algorithm is simple (and therefore reliable) but inefficient. We expect to be able to improve efficiency, while at the same time maintaining reliability, using tools such as auxiliary particle filtering, simulated annealing and tempering, and limited kernel smoothing (Doucet *et al.* 2001, Lui 2001, Thomas *et al.* 2005, Newman *et al.* in press). We are also working with K. Newman, C. Fernandez and S. Buckland on a comparison of MCMC and particle filtering for a model similar to the DDS one (Newman *et al.* in prep). Preliminary results indicate that judicious application of tools such as kernel smoothing can result in large gains in efficiency with little bias and that, in cases like this where there is relatively little information in the data relative to the priors, for some parameters, particle filtering appears to be more efficient than MCMC.

Our results from the DDS model are comparable with those of Thomas and Harwood (2004), although the estimated total population sizes presented here are slightly higher for comparable years. The difference is explained by the change in prior on the density dependence parameters. The priors on the β parameters used by Thomas and Harwood (2004) translate into expected numbers of pups at carrying capacity of 5000, 3500, 14000 and 18000 for the North Sea, Inner Hebrides, Outer Hebrides and Orkneys respectively. Here we used priors with higher means (the χ parameters, Table 1: 10000, 5000, 15000, 40000) because they seemed better justified. In both cases, the prior distributions had large variances (coefficient of variation of 50%) and the sensitivity of the posteriors to the prior values was not high – especially for the DDS model (Table 4) – so even a large change in the prior had only a small effect on the estimated adult population size.

Our estimated total population sizes from the DDF model are substantially lower than those of Thomas and Harwood (2004), and much more plausible. Thomas and Harwood noted a problem with oscillations in estimated pup production under their DDF model, and we have rectified that by making fecundity dependent on current 6+ female numbers rather than the previous years pup production. The change appears also to have caused our estimates of population size to decrease.

The estimates of total population size from the new extended density dependence models are intermediate between the DDF and DDS models. Although our model selection criterion did not indicate that they provide a more parsimonious fit than the simple density dependence models after taking the additional parameter into account, the pup production trajectories correspond more closely to our biological understanding of the system. The extended models may prove superior if a lower CV is used for the observation process

None of the models we have used to date have provided an adequate fit to the rapid increase in pup production in the Inner and Outer Hebrides (and, to a lesser extent, in Orkney) observed in the early 1990s. A rapid increase in one region could be a consequence of density dependent movement, but a rapid increase in three out of four cannot. It may be fruitful to investigate the use of covariates such as food supply or climatic conditions that may influence fecundity or juvenile survival in a time-dependent manner. An EPSRC-funded PhD student will be investigating this over the next 3 years.

Our analysis of prior sensitivity has been useful in supplementing the impressions gained by comparing prior and posterior parameter plots. This work can be extended in two ways. Firstly, it would be more useful to estimate the sensitivity of the posterior parameter mean to variation in the prior mean (and its variance) rather than looking at sensitivity with respect to variation in the prior hyperparameters. Secondly, an important output of our modelling is the total population size estimate, and it would be useful to estimate sensitivity of this estimate to variation in the priors on the parameters. We plan to do both of these.

We found little evidence in the pup production estimates to support one model over another, although we acknowledge that this may be a result of the high CV used in the observation model. Introducing a single estimate of adult population size was enough to enable us to unambiguously distinguish between the models. Clearly, a more comprehensive assessment will be required, but there may be merit in reducing the frequency of the pup production surveys in order to finance a new survey designed to estimate total population size.

A total population survey would not be easy to achieve, but one possibility is to attach transponders to the flippers of a large sample of seals. Signals from these seals could then be detected by an aeroplane-mounted receiver during subsequent pup production survey, allowing a mark-recapture estimate of population size. If the ages of tagged seals could be determined at the time of marking, this would provide age-specific population estimates. If a subsequent aerial survey was performed during the moult, a further estimate of population size could be obtained that included size of the male population. However, the necessary tagging and receiving technology for such an exercise is not yet commercially available. It would also be important to determine a protocol for tagging seals that avoids any correlation between probability of marking and recapturing animals. An alternative approach for estimating population size is to combine estimates of numbers of seals hauled out during moult with estimates of the proportion hauled out. Such an approach has its own set of problems. Nevertheless, consideration should be given to this and all other potential approaches.

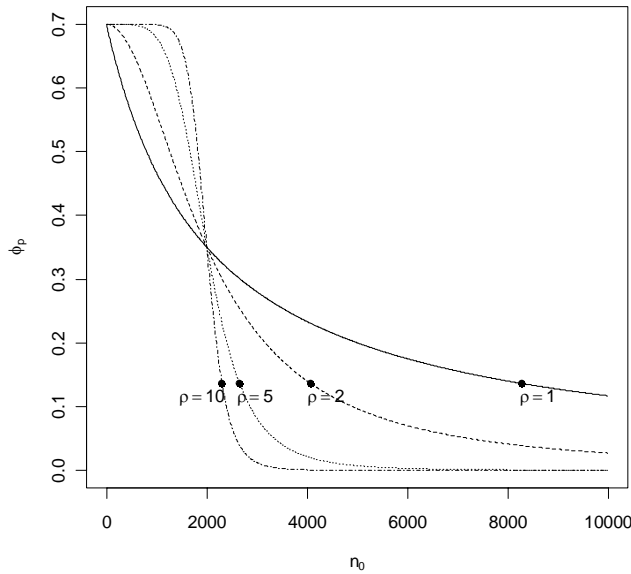
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Figure 1. Relationship between pup survival (ϕ_p) and number of pups (n_0) at different levels of ρ in the extended density dependent survival (EDDS) model (formula 1 in text). $\rho = 1$ corresponds with the standard Beverton-Holt density dependent function. The relationship between fecundity and number of 6+ females has the same shape in the extended density dependent fecundity (EDDF) model (formula 2).

(a) Filled circles show the number of pups at carrying capacity at the given level of ρ (formula 3) with the other model parameters fixed ($\beta = 0.0005$, $\alpha = 0.95$, $\phi_{p\max} = 0.7$, and $\alpha_a = 0.95$).



(b) Labels show the level of β required for a fixed carrying capacity of 8000 (formula 3, $\chi = 8000$, $\alpha = 0.95$, $\phi_{p\max} = 0.7$, and $\alpha_a = 0.95$).

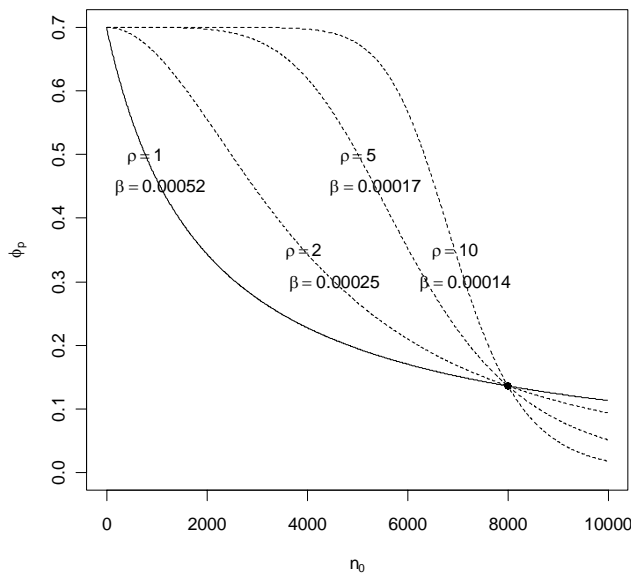
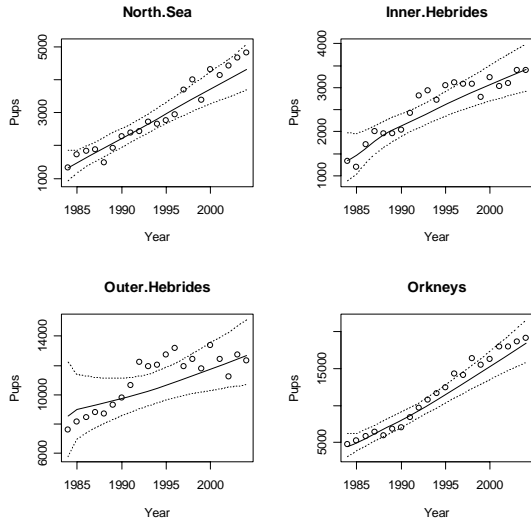
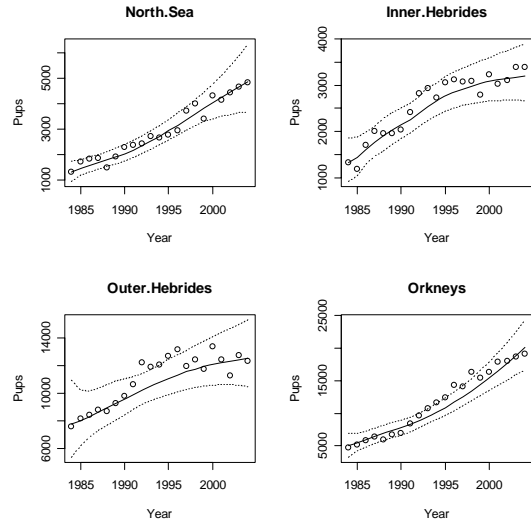


Figure 2. Estimates of true pup production from four models of grey seal population dynamics fit to pup production estimates from 1984-2004. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

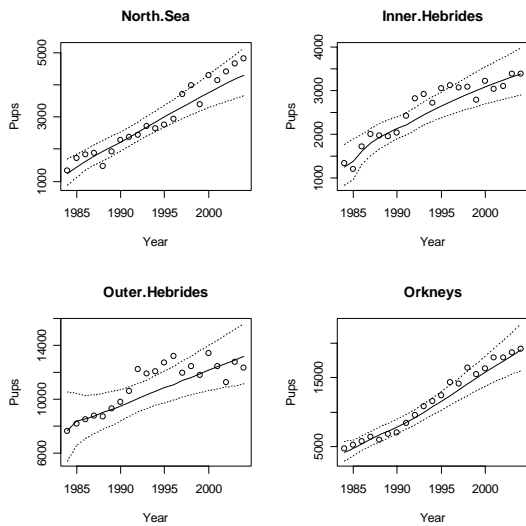
(a) Density dependent survival (DDS)



(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)

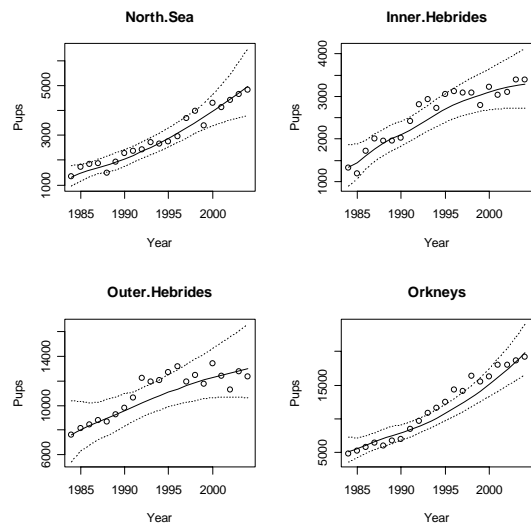


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from four models of grey seal population dynamics fit to pup production estimates from 1984-2004. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name.

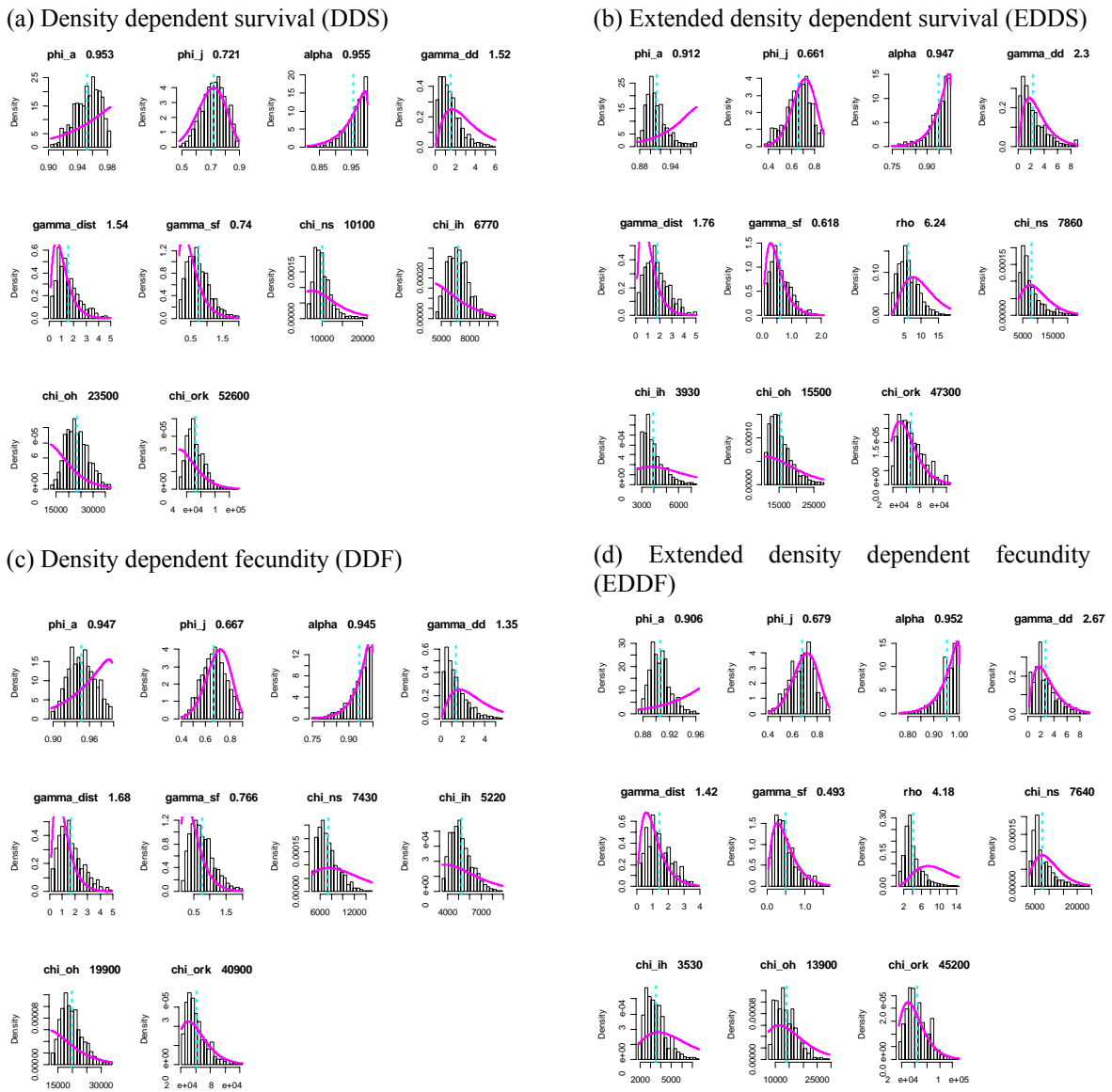
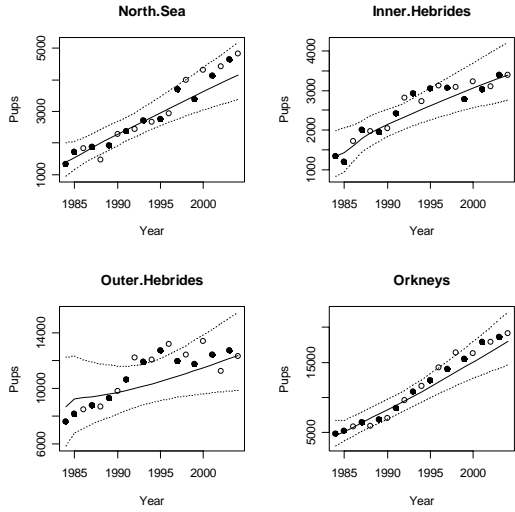
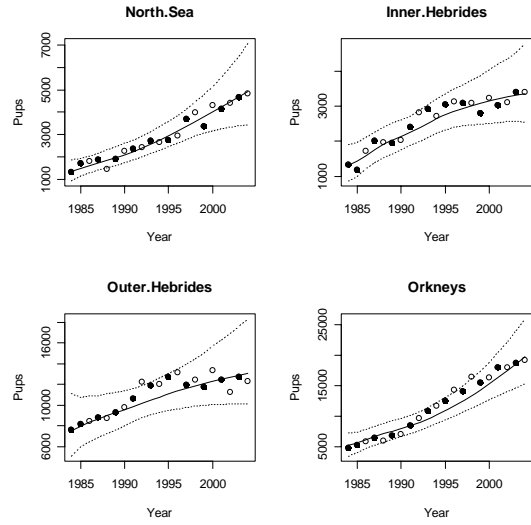


Figure 4. Estimates of true pup production from four models of grey seal population dynamics, fit to pup production estimates from 1984, 1985, 1987, 1989, 1991, 1993, 1995, 1997, 1999, 2001 and 2003. Input data are shown as filled circles and excluded data as empty circles. Lines show the posterior mean bracketed by the 95% credibility interval.

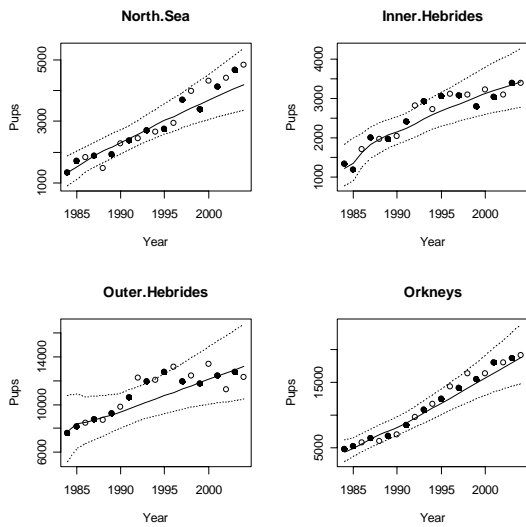
(a) Density dependent survival (DDS)



(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)

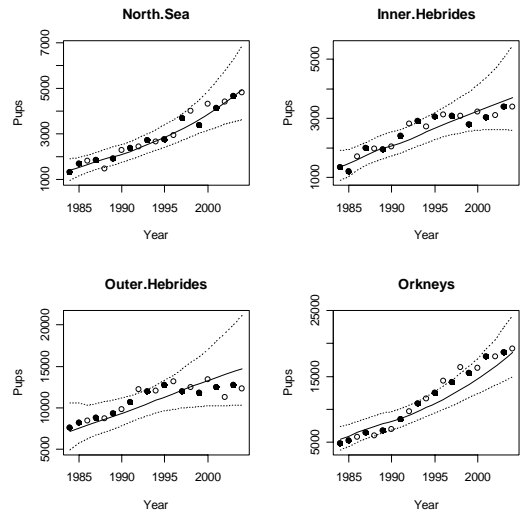
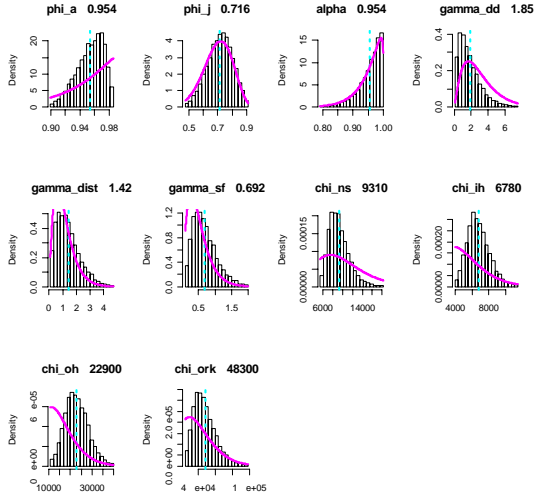
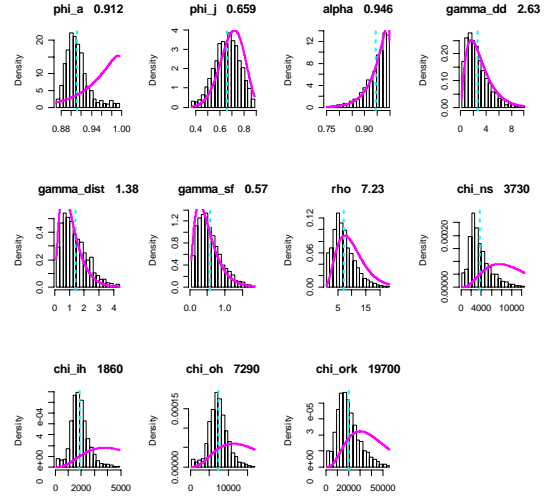


Figure 5. Posterior parameter estimates (histograms) and priors (solid lines) from four models of grey seal population dynamics fit to pup production estimates from 1984, 1985, 1987, 1989, 1991, 1993, 1995, 1997, 1999, 2001 and 2003. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name.

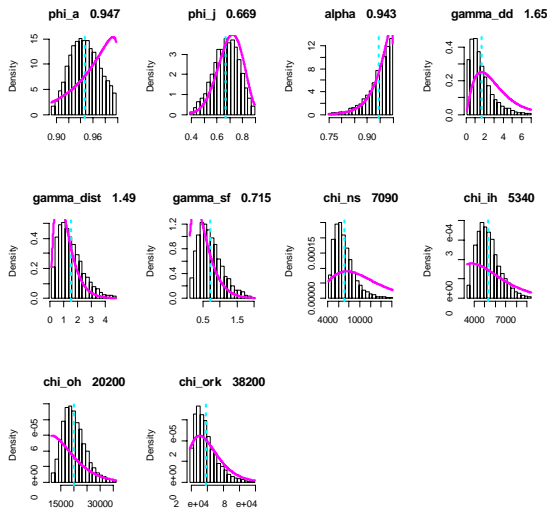
(a) Density dependent survival (DDS)



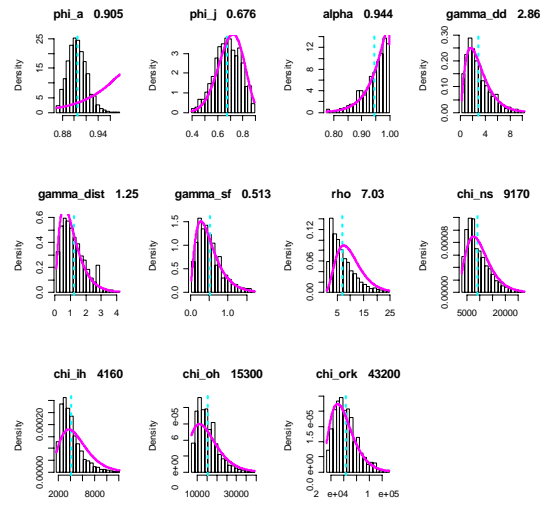
(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2004, made using four model of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	4.4 (3.4 5.8)	4.4 (3.1 6)	24.4 (19 32.7)	15.8 (12 20.9)	49 (37.5 65.3)
1985	4.8 (3.8 6.1)	4.7 (3.6 6.2)	24.6 (19.5 32.4)	17.2 (13.5 22.2)	51.2 (40.3 66.8)
1986	5.2 (4.2 6.5)	5 (3.9 6.4)	24.8 (19.9 32.4)	18.7 (15 23.6)	53.6 (43 68.8)
1987	5.5 (4.5 6.9)	5.3 (4.2 6.7)	25.1 (20.2 32.7)	20.3 (16.5 25.5)	56.2 (45.5 71.8)
1988	5.9 (4.8 7.4)	5.5 (4.4 7.1)	25.4 (20.5 32.8)	22 (17.9 27.3)	58.8 (47.7 74.5)
1989	6.3 (5.1 7.8)	5.8 (4.7 7.3)	25.8 (20.8 33.1)	23.7 (19.3 29.1)	61.5 (50 77.3)
1990	6.7 (5.4 8.3)	6 (4.9 7.7)	26.2 (21.1 33.4)	25.4 (20.8 31.5)	64.3 (52.2 80.8)
1991	7 (5.7 8.8)	6.3 (5.1 8)	26.5 (21.3 33.7)	27.2 (22.3 33.7)	67.1 (54.4 84.1)
1992	7.4 (6 9.3)	6.5 (5.2 8.3)	27 (21.6 34.2)	29 (23.7 35.9)	69.9 (56.5 87.7)
1993	7.8 (6.3 9.8)	6.7 (5.4 8.5)	27.4 (21.8 34.9)	30.9 (25.1 38.4)	72.8 (58.5 91.5)
1994	8.2 (6.6 10.3)	7 (5.5 8.8)	27.8 (22 35.5)	32.7 (26.4 40.7)	75.6 (60.5 95.4)
1995	8.5 (6.8 10.8)	7.2 (5.7 9.1)	28.3 (22.1 36.4)	34.6 (27.8 43.5)	78.6 (62.5 99.8)
1996	8.9 (7.1 11.3)	7.4 (5.8 9.4)	28.7 (22.3 37.2)	36.5 (29.1 46.1)	81.5 (64.4 104.1)
1997	9.2 (7.3 11.9)	7.6 (6 9.7)	29.2 (22.6 38.2)	38.4 (30.4 49)	84.4 (66.2 108.9)
1998	9.6 (7.6 12.5)	7.8 (6.1 10)	29.7 (22.8 38.9)	40.3 (31.7 52.1)	87.3 (68.1 113.4)
1999	9.9 (7.8 13.1)	8 (6.2 10.2)	30.2 (22.9 39.9)	42.2 (32.9 54.9)	90.3 (69.8 118.1)
2000	10.3 (8 13.6)	8.2 (6.3 10.5)	30.7 (23.2 40.9)	44.1 (34.1 57.8)	93.2 (71.6 122.8)
2001	10.6 (8.2 14.2)	8.4 (6.5 10.8)	31.2 (23.4 41.8)	46 (35.3 60.6)	96.1 (73.3 127.3)
2002	10.9 (8.5 14.7)	8.5 (6.6 11)	31.7 (23.6 42.7)	47.8 (36.4 63.7)	99 (75.1 132.1)
2003	11.3 (8.7 15.3)	8.7 (6.7 11.3)	32.2 (23.8 43.4)	49.7 (37.5 66.7)	101.9 (76.7 136.7)
2004	11.6 (8.9 15.8)	8.9 (6.8 11.6)	32.7 (24 44.2)	51.5 (38.6 69.8)	104.7 (78.3 141.4)

Extended density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.3 (3.8 6.7)	5.4 (3.7 7.2)	28.7 (20 37.7)	21 (14.1 27.6)	60.4 (41.6 79.1)
1985	5.6 (4.2 7)	5.8 (4.1 7.5)	29.8 (20.7 38.3)	22.1 (15.4 28.5)	63.2 (44.5 81.3)
1986	5.9 (4.5 7.4)	6.1 (4.5 7.9)	30.9 (21.7 39.3)	23.3 (16.9 29.5)	66.3 (47.5 84.1)
1987	6.3 (4.9 7.8)	6.5 (4.8 8.2)	32.1 (22.4 40.4)	24.7 (18.3 30.9)	69.7 (50.4 87.3)
1988	6.8 (5.2 8.3)	7 (5.1 8.7)	33.2 (22.7 41.5)	26.3 (19.9 32.5)	73.3 (52.9 91)
1989	7.2 (5.6 8.8)	7.5 (5.5 9.2)	34.3 (23.1 42.6)	28 (21.4 34.4)	77.1 (55.5 95)
1990	7.7 (6 9.4)	7.9 (5.7 9.7)	35.4 (23.3 43.6)	29.9 (23.2 36.4)	80.9 (58.2 99.2)
1991	8.3 (6.3 10.1)	8.4 (6 10.3)	36.3 (23.7 44.7)	31.8 (24.9 38.7)	84.8 (60.9 103.8)
1992	8.9 (6.8 10.7)	8.8 (6.1 10.9)	37.2 (24.3 46)	33.9 (26.6 41.1)	88.8 (63.8 108.7)
1993	9.5 (7.1 11.5)	9.2 (6.3 11.5)	38 (24.8 47)	36.2 (28.3 43.7)	92.8 (66.5 113.7)
1994	10.2 (7.6 12.4)	9.5 (6.5 11.9)	38.7 (25.2 48.2)	38.6 (30.1 46.7)	97 (69.3 119.2)
1995	10.9 (7.9 13.3)	9.8 (6.6 12.4)	39.3 (25.4 49.5)	41.3 (32.1 50)	101.2 (71.9 125.1)
1996	11.6 (8.1 14.2)	10 (6.7 12.6)	39.8 (25.8 50.6)	44.2 (34.1 53.7)	105.5 (74.7 131.2)
1997	12.4 (8.3 15.3)	10.1 (6.8 12.9)	40.2 (26.1 51.8)	47.3 (35.9 57.4)	109.9 (77.2 137.3)
1998	13.2 (8.6 16.4)	10.2 (6.8 13.2)	40.5 (26.3 52.5)	50.6 (37.8 61.8)	114.4 (79.5 143.8)
1999	13.9 (8.7 17.5)	10.3 (6.8 13.4)	40.7 (25.8 53.1)	54.2 (39.7 66.2)	119 (81 150.2)
2000	14.6 (9 18.8)	10.3 (6.8 13.6)	40.9 (26.1 54)	57.9 (41.3 70.9)	123.7 (83.2 157.3)
2001	15.2 (9.1 20.2)	10.4 (6.8 13.9)	41.2 (26.2 54.7)	61.8 (42.8 75.9)	128.6 (84.9 164.7)
2002	15.9 (9.3 21.6)	10.4 (6.8 14)	41.4 (26.3 55.6)	65.9 (44.1 81.4)	133.6 (86.4 172.6)
2003	16.5 (9.4 23.1)	10.5 (6.8 14.3)	41.6 (26.5 56.5)	70.2 (44.7 87.7)	138.7 (87.5 181.5)
2004	17 (9.5 24.8)	10.6 (6.8 14.5)	41.8 (27 57.4)	74.5 (45.7 94.4)	143.9 (89 191.1)

Density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.7 (4.1 7.9)	6 (3.8 8.9)	40.1 (27.6 60.1)	18.2 (13.3 24.4)	70 (48.8 101.3)
1985	6.2 (4.7 8.5)	6.6 (4.7 9.4)	41.4 (29.2 60.9)	20.1 (15.1 26.5)	74.4 (53.7 105.3)
1986	6.9 (5.3 9.2)	7.4 (5.4 10)	43 (31.2 61.8)	22.3 (17.1 28.7)	79.6 (59 109.8)
1987	7.7 (5.9 10.1)	8.1 (6.1 10.7)	44.8 (33.1 62.6)	24.8 (19.4 31.6)	85.3 (64.5 115.1)
1988	8.4 (6.5 11)	8.9 (6.9 11.6)	46.6 (35 64.2)	27.5 (21.6 35.1)	91.4 (69.9 121.9)
1989	9.3 (7.2 12)	9.6 (7.5 12.5)	48.5 (36.7 66.5)	30.5 (24 38.8)	97.9 (75.3 129.8)
1990	10.1 (7.9 13.1)	10.4 (8.2 13.4)	50.4 (38.3 69)	33.7 (26.4 42.9)	104.6 (80.9 138.4)
1991	11 (8.6 14.3)	11.2 (8.8 14.6)	52.4 (39.8 71.1)	37.1 (29.1 47.4)	111.7 (86.2 147.4)
1992	11.9 (9.3 15.7)	11.9 (9.4 15.7)	54.5 (41.2 74.9)	40.7 (31.9 52.4)	119.1 (91.8 158.7)
1993	12.9 (10.1 17)	12.7 (9.9 16.9)	56.6 (42.6 77.9)	44.6 (34.9 57.9)	126.9 (97.5 169.8)
1994	13.9 (10.9 18.5)	13.5 (10.4 18.1)	58.9 (44.1 81.5)	48.8 (37.9 64.3)	135 (103.3 182.3)
1995	14.9 (11.7 20.1)	14.2 (10.9 19.4)	61.2 (45.6 85.6)	53.2 (41.3 70.7)	143.5 (109.5 195.8)
1996	16 (12.5 21.8)	15 (11.4 20.6)	63.6 (47.6 89.1)	57.8 (44.6 78.3)	152.4 (116.1 209.8)
1997	17.1 (13.1 23.5)	15.8 (11.9 21.9)	66.1 (49.1 93.3)	62.6 (48 85.2)	161.6 (122.2 223.9)
1998	18.2 (14 25.3)	16.6 (12.4 23.4)	68.6 (50.7 97.6)	67.7 (51.5 93.2)	171.1 (128.5 239.5)
1999	19.3 (14.7 27.1)	17.4 (12.8 24.9)	71.1 (52.1 102.5)	73 (55 101.1)	180.9 (134.6 255.6)
2000	20.5 (15.4 28.9)	18.2 (13.3 26.3)	73.8 (53.4 107.8)	78.6 (59 109.1)	191 (141.1 272.1)
2001	21.6 (16.2 30.7)	19 (13.8 27.8)	76.5 (54.5 113.3)	84.3 (62.6 116.7)	201.4 (147 288.5)
2002	22.8 (16.9 32.5)	19.8 (14.2 29.3)	79.2 (56.1 119.3)	90.2 (66.6 125.4)	212.1 (153.9 306.6)
2003	24 (17.7 34.2)	20.6 (14.7 30.8)	82 (57.3 124.9)	96.3 (71 134.4)	222.9 (160.7 324.3)
2004	25.3 (18.5 36.1)	21.4 (15.1 32.3)	84.9 (58.7 131.5)	102.5 (75.3 144.4)	234.1 (167.6 344.2)

Extended density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.4 (3.9 7)	5.7 (4.1 7.8)	31.3 (22.7 43.1)	21.8 (16 28.8)	64.3 (46.8 86.8)
1985	5.7 (4.2 7.4)	6.1 (4.6 8)	32.5 (24.1 44)	22.9 (17.6 29.6)	67.2 (50.5 89)
1986	6.1 (4.6 7.8)	6.4 (5 8.5)	33.8 (25.5 45.2)	24.1 (19 30.8)	70.5 (54.1 92.3)
1987	6.6 (5 8.3)	6.9 (5.5 8.9)	35.1 (27 46.2)	25.6 (20.6 32.4)	74.2 (58.1 95.9)
1988	7.1 (5.4 8.9)	7.4 (5.9 9.5)	36.5 (28.4 47)	27.2 (22 34.2)	78.2 (61.7 99.5)
1989	7.6 (5.8 9.5)	7.9 (6.4 10)	37.9 (29.8 48.4)	29 (23.5 36.1)	82.3 (65.5 104)
1990	8.1 (6.3 10.3)	8.4 (6.8 10.5)	39.3 (31.2 50)	30.9 (25.2 38.4)	86.7 (69.4 109.3)
1991	8.7 (6.7 11)	8.9 (7.2 11.2)	40.7 (32.5 51.5)	32.9 (26.9 40.5)	91.2 (73.3 114.2)
1992	9.3 (7.1 11.8)	9.4 (7.6 11.7)	42.1 (33.8 52.8)	35 (28.8 42.6)	95.8 (77.3 118.8)
1993	9.9 (7.6 12.6)	10 (8.1 12.3)	43.5 (35.1 54.3)	37.3 (30.9 45.2)	100.8 (81.6 124.4)
1994	10.7 (8.2 13.6)	10.5 (8.5 12.9)	44.9 (36.4 56)	39.8 (32.9 47.9)	105.9 (86 130.4)
1995	11.4 (8.9 14.5)	11 (8.9 13.6)	46.3 (37.6 58)	42.6 (35.1 51.2)	111.3 (90.5 137.3)
1996	12.3 (9.7 15.5)	11.5 (9.3 14.3)	47.7 (38.6 59.6)	45.5 (37.3 55)	116.9 (94.9 144.5)
1997	13.1 (10.5 16.6)	12 (9.7 15.1)	49.1 (39.5 61.8)	48.7 (39.8 59.6)	122.9 (99.5 153)
1998	14 (11.3 17.6)	12.4 (10 15.7)	50.4 (40.4 63.8)	52.1 (42.5 64.5)	129 (104.2 161.6)
1999	15 (12.1 18.6)	12.9 (10.2 16.3)	51.7 (41.2 65.7)	55.7 (44.9 69.6)	135.4 (108.4 170.2)
2000	16 (12.8 19.8)	13.3 (10.5 17.1)	53 (42 68.3)	59.7 (48 74.9)	142 (113.3 180.1)
2001	17.1 (13.7 21.3)	13.6 (10.7 17.9)	54.2 (42.6 70.5)	64 (51.4 80.9)	148.9 (118.4 190.5)
2002	18.1 (14.4 23)	14 (10.9 18.7)	55.3 (43.3 72.6)	68.6 (54.8 86.8)	156 (123.4 201)
2003	19.2 (15.1 24.6)	14.3 (11.1 19.3)	56.5 (43.7 75.1)	73.5 (58.1 94.4)	163.5 (128 213.3)
2004	20.4 (15.6 26.6)	14.6 (11.3 20)	57.5 (43.9 77.3)	78.7 (61.8 101.5)	171.2 (132.5 225.4)