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Estimating the size of the UK grey seal population between 1984 and 2005, and related research.

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Summary

We used the same Bayesian state-space modelling framework employed in our 2005 briefing paper to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2005. The models allowed 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. As in our 2005 report, there were only small differences between models in model selection criterion values (adjusted posterior log-likelihoods), although the model with simple density dependent fecundity fit slightly better and also produced more believable parameter estimates than the next best model (simple density dependent pup survival). The estimated adult population size in 2005 for these two models was 240,000 (95% CI 171-361,000) and 105,000 (80-142,000) respectively, with the other two models taking intermediate values.

In joint work with various researchers, we are investigating various improvements and alternatives to the model-fitting methods. These include: (i) improving the particle filtering algorithm we currently use; (ii) comparing the performance of the particle filter with a custom-written Markov chain Monte-Carlo (MCMC) sampler; (iii) testing the limits of generic, but accessible MCMC samplers available in the WinBUGS software; and (iv) investigating the utility of the Kalman Filter on various simplified models. One conclusion from this and previous work is that it is very difficult to distinguish between different population models based on pup count data alone, and there is therefore a strong need for additional comprehensive data on either a population vital rate or adult population size.

Introduction

In this paper, we present updated estimates of population size and related demographic

parameters using the modelling framework of Thomas and Harwood (2005) fitted to pup production data from 1984-2005. The biological system is represented using a state-space model – a stochastic time-series model that includes a “state process” for the evolution of the true but unknown state of the population through time, and an “observation process” that describes the measurements taken on the population (Buckland *et al.* 2004, Thomas *et al.* 2005, Newman *et al.* 2006).

We fitted and compared the same four models used by Thomas and Harwood (2005). Two allow for density dependent pup survival (DDS) and density dependent fecundity (DDF). In both cases, the density dependent relationship follows a Beverton-Holt function. Two further models extend this function by adding an extra parameter that allows the effect of density dependence to be lessened until the population is close to carrying capacity (see Thomas and Harwood 2005). We refer to these as extended density dependent pup survival (EDDS) extended density dependent fecundity (EDDF).

To fit the models, we use the same computer-intensive algorithm as Thomas and Harwood (2005), a type of Monte-Carlo particle filter (Liu 2001). We also discuss current research on alternative approaches.

Materials and Methods

Models

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:

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

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:

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

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% (see Discussion).

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 $\beta_1 - \beta_4$, and three movement parameters γ_{sf} , γ_{dd} , and γ_{dist} . They differ in two parameters: the DDS model has maximum pup survival ϕ_{pmax} 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 1984-2005 from Duck and Mackey (2006), aggregated into regions. Estimates for recent years in North Sea region are slightly higher than those used previously as a new colony at Blakeney Point has been included.

Prior distributions for each parameter are given in Table 1, and are shown on Figure 2. We followed Thomas and Harwood (2005) in using a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region, denoted χ_r for region r , rather than directly on the β s.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
ϕ_{pmax}, ϕ_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, as described by Thomas and Harwood (2005).

Fitting Method

We used the same particle filtering algorithm as Thomas and Harwood (2004, 2005), implemented in the C programming language. An introduction to particle filtering algorithms in the context of wildlife studies is given by Newman *et al.* (2006), 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 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 1984-2005. 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 (AIC) using the same method as Thomas and Harwood (2004, 2005). 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.

Since the observations are assumed to be normally distributed random variables, there is an argument for using the bias-adjusted version of AIC, denoted AICc (Burnham and Anderson, 1998, p51). This criterion contains an extra term that imposes a stronger penalty on models with more parameters, with the effect of this extra term decreasing as the number of observations increases.

Results

Effective sample size (ESS)

Using our relatively simple particle filtering algorithm, an extremely large number of particles were required to achieve a unit increase in ESS (Table 2). Because of time constraints, we did not achieve our target of $ESS \geq 1000$ for any model. Nevertheless, the Monte-Carlo error in our results is likely to be reasonably small – for example, dividing the particles from the EDDS model into two, estimated mean adult population size in 1984 is 60.1×10^4 from the first half ($ESS=114$) and 60.8×10^4 from the second ($ESS=148$).

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 ($\times 10^7$)	ESS	ESS/K ($\times 10^7$)
DDS	6.75	747	110.7
EDDS	13.50	254	18.8
DDF	6.75	575	85.2
EDDF	59.40	191	3.2

Comparison of models for density dependence

Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the four models are shown in Figure 1. The estimates are quite similar between models, although 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 and continuing growth in the North Sea. However, none of the models’ estimates can reproduce the rapid increase in pup production in the Hebrides and Orkney in the early 1990s.

There was little difference in posterior likelihood, AIC or AICc between the models (Table 3). The model with the minimum AIC and AICc is the DDF model, but the next best model (DDS) has a mean posterior AIC only 1.70 higher (1.79 higher for AICc). All four models are within 4 AIC and AICc points of one another, meaning there is not strong support for one model over another (Burnham and Anderson 1998, p63).

Although the models produce similar estimates of pup production, they give substantially different estimates of total predicted population size (Table 4 and Appendix 1). The DDF model estimates that there are 2.3 times as many seals as the DDS model, with the other two falling in between.

Posterior parameter estimates for the models are shown in Figure 2. 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 (0.91) in the extended density dependence models. 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. Posterior mean carrying capacities for the Outer Hebrides were rather greater than the prior means for the DDS and DDF models (Figure 2), and this is reflected in the fit of the pup production estimates (Figure 1), which fail to reflect the levelling off of pup production since the mid-1990s. 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 just outside the 95% credibility interval of the posterior.

Table 3. Mean posterior log-likelihood, AIC, AICc and Akaike weights for models fit to data from 1984-2005.

Model	LnL	AIC	Δ AIC	Akaike (AIC) weight	AICc	Δ AICc	Akaike (AICc) weight
DDS	-719.55	1459.01	1.70	0.21	1461.96	1.79	0.22
EDDS	-718.67	1459.35	2.04	0.18	1462.82	2.66	0.14
DDF	-718.65	1457.31	0.00	0.50	1460.17	0.00	0.55
EDDF	-719.21	1460.41	3.10	0.10	1463.89	3.72	0.09

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2005 breeding season, derived from models fit to data from 1984-2005. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	EDDS
North sea	12.0 (9.3 16.3)	18.2 (9.9 26.2)
Inner Hebrides	8.9 (6.9 11.7)	10.5 (7 14.3)
Outer Hebrides	32.2 (23.8 43.3)	41.3 (27.4 55.2)
Orkney	52.2 (39.2 70.4)	74.1 (44.3 98.4)
Total	105.2 (79.3 141.7)	144.1 (88.6 194.1)
	DDF	EDDF
North sea	26.6 (19.3 38.6)	21.9 (16.4 29.7)
Inner Hebrides	21.9 (15.3 33.4)	15.2 (11.5 25.6)
Outer Hebrides	85.8 (58.1 135.8)	59.5 (44.5 95.6)
Orkney	106.6 (77.9 153.1)	83.8 (64.4 119.4)
Total	240.9 (170.5 361)	180.3 (136.9 270.3)

Posterior estimates of the derived parameters (pup survival for the DDS and EDDS models and fecundity for the DDF and EDDF models) are given for each year and region in Appendix 2. Estimated pup survival is very low under the DDS model (as low as 0.19 for Outer Hebrides in 2005), but is higher in the EDDS model (the corresponding estimate is 0.42), likely due to the lower estimate of adult survival in the EDDS model. Estimated fecundity is as low as 0.45 in the DDF model (for Outer Hebrides 2005), and again is higher in the EDDF model (corresponding estimate 0.80), for the same reason.

Discussion

Implications and reliability of results

Our results are very similar to those given last year (Thomas and Harwood 2005), as would be expected when 21 of the 22 years of data are in common and the same analysis methods were used. We again found little to choose among the candidate models, but large differences in estimated total population size. Although our analysis methods can be improved (see below), we believe that an additional source of information about one or more of the population parameters, population age structure, or numbers of one or more adult age class is required before it will be possible to unambiguously distinguish between the models.

The particle filtering algorithm that we used is simple and reliable (without bias), but inefficient in the sense that a large amount of computer time is required to produce an acceptable level of Monte-Carlo error. To obtain results in a reasonable timescale, we fixed observation CV at 25%, a value considerably higher than the 7% estimated for individual colonies by Hiby and Duck (unpublished). It is therefore possible that both the precision of our estimates and our ability to distinguish between models could be improved. We are in the process of amending our fitting algorithms to increase efficiency using tools such as auxiliary particle filtering, limited kernel smoothing and integrating out the observation error parameter (Doucet *et al.* 2001, Lui 2001, Thomas *et al.* 2005, Newman *et al.* submitted).

Other related work

We have completed a study comparing the performance of particle filtering with a custom-written MCMC sampler, using a complex, but tractable model of US Pacific west coast salmon and then a seal model very similar to the DDS model presented above (Newman *et al.*

submitted). The particle filtering algorithm included the tools mentioned above, while the MCMC sampler was highly tuned to the exact state-space model used. We found that while the particle filter produced similar posterior mean estimates to MCMC, it was much less efficient (more computer time required for the same accuracy). However, the particle filtering algorithm used can easily be adapted to work with many population dynamics models, while the MCMC algorithm would need to be re-derived if changes were made to the model, and deriving the sampler used was very challenging. Even for the highly optimized MCMC sampler, convergence was very slow for the seal example, underlining the difficulties associated with fitting models based on pup count data alone.

We have also been investigating the potential for using the off-the-shelf MCMC software WinBUGS (Spiegelhalter *et al.* 2005) to fit state-space models, giving the potential advantage that developing code to fit several plausible models is simplified. This is joint work with Richard Parker (St Andrews) and Lara Jamieson (Cambridge). We have been able to fit Bayesian versions of the autoregressive models used by Thomas *et al.* (2004), and have used a recently-released reversible-jump (RJ) MCMC add-in for WinBUGS to perform model selection via estimating posterior model probabilities. We have validated our results using data from the North American Breeding Waterfowl Survey against results obtained by Jamieson and Brooks (2004) using custom-written RJMCMC code. We are currently investigating the feasibility of fitting more complex models to seal data that track both numbers of pups and breeding females, and include density dependence but not movement. Preliminary results indicate that both update times and convergence in WinBUGS are very slow.

We are also continuing work that investigates how the Kalman filter might be applied to these models. This is joint work with Panagotis Besbeas and Byron Morgan (Kent). We have fit various state-space models to pup production data from the colonies at Isle of May (exponential growth) and Faray (sigmoid growth), together with survival estimates from mark-recapture data, and are comparing results obtained from the Kalman filter with those from a particle filter. One difficulty for the Kalman filter is that the single colony state-space models based on pup-count data are technically non-

observable, meaning that pup counts alone cannot be used to infer the adult states. For particle filters, we use a Bayesian paradigm, and the models are rendered observable by the use of prior information. The non-observability of the models based on pup production data alone in the likelihood context further underlines the need to obtain additional data.

Acknowledgements

We thank Mike Lonergan for suggesting the use of AICc.

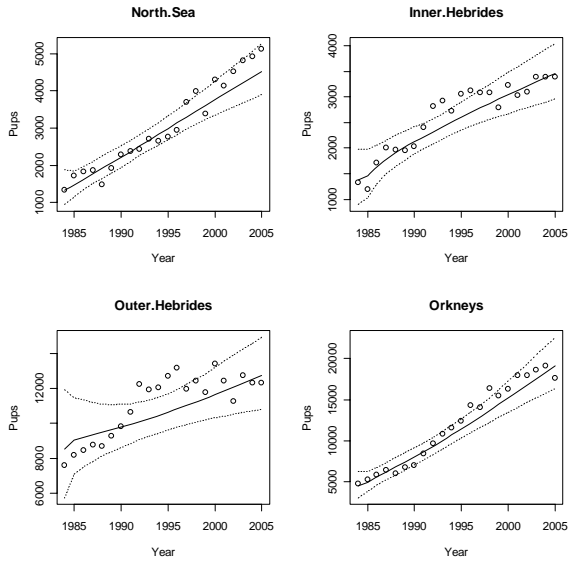
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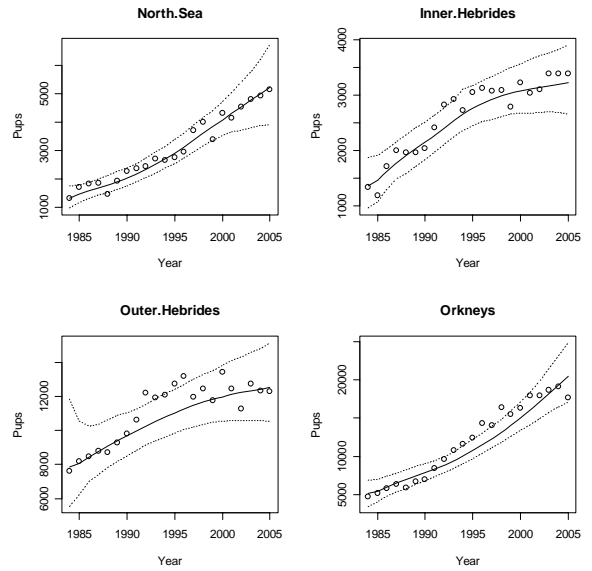
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Figure 1. Estimates of true pup production from four models of grey seal population dynamics fit to pup production estimates from 1984-2005. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

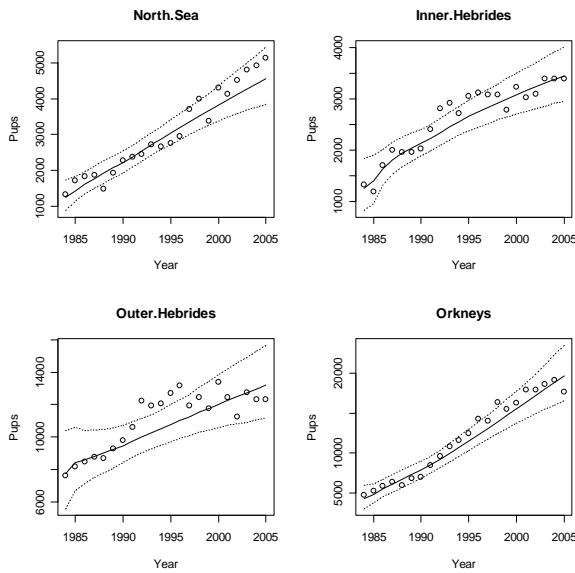
(a) Density dependent survival (DDS)



(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)

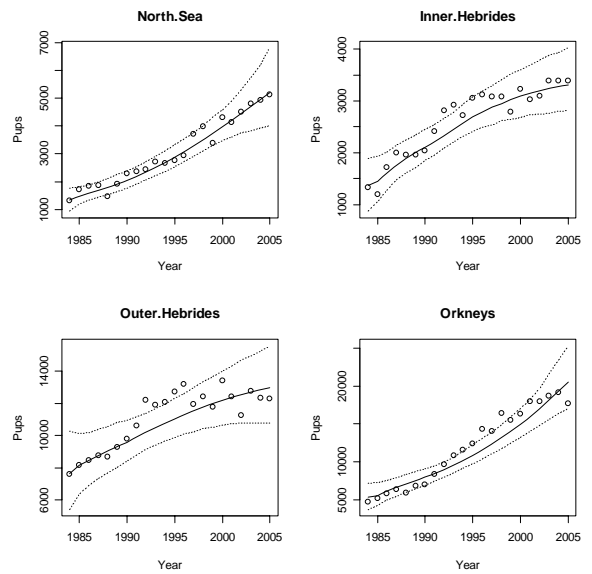
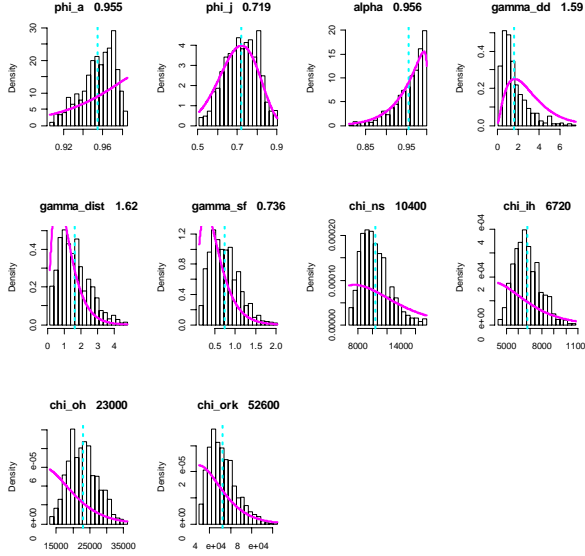
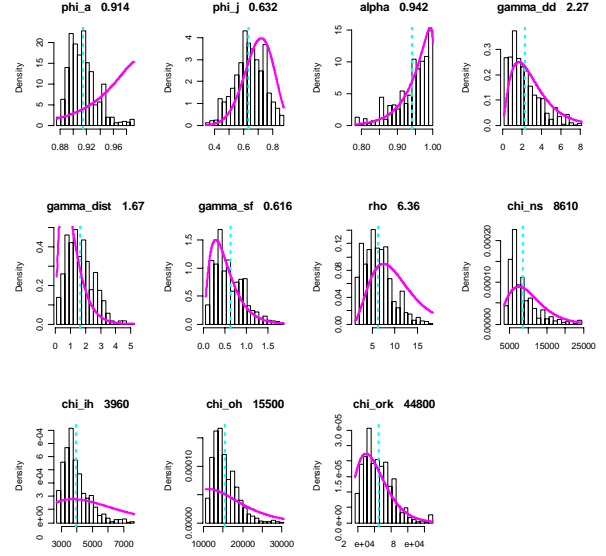


Figure 2. Posterior parameter estimates (histograms) and priors (solid lines) from four models of grey seal population dynamics fit to pup production estimates from 1984-2005. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name.

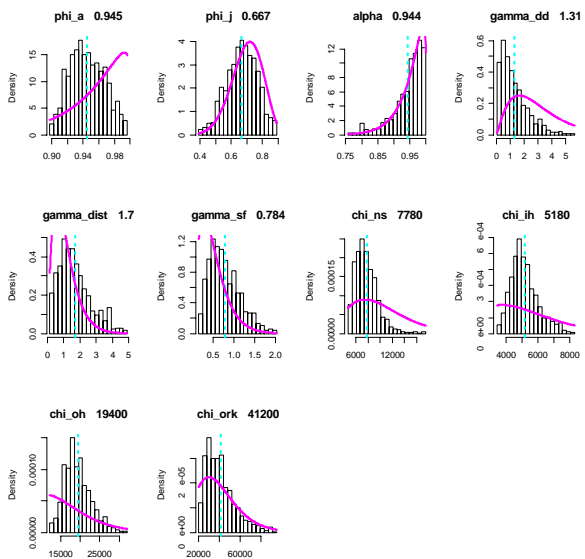
(a) Density dependent survival (DDS)



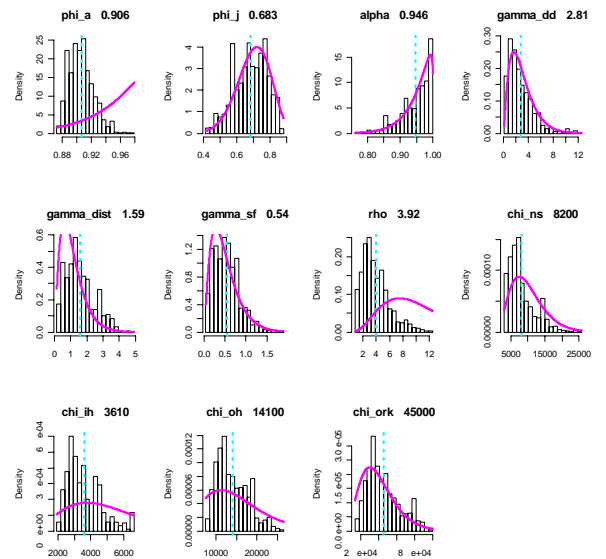
(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)



Appendix 1

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2005, made using four models 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	4.3 (3.4 5.7)	4.3 (3.1 5.9)	24.2 (18.9 32.2)	15.6 (11.6 20.7)	48.5 (37 64.5)
1985	4.7 (3.8 6.1)	4.6 (3.6 6.1)	24.4 (19.3 31.9)	17 (13.2 22.2)	50.7 (39.8 66.2)
1986	5.1 (4.2 6.5)	4.9 (3.9 6.4)	24.6 (19.7 31.9)	18.5 (14.8 23.7)	53 (42.6 68.4)
1987	5.5 (4.5 6.9)	5.2 (4.2 6.6)	24.8 (20.1 32)	20.1 (16.3 25.3)	55.5 (45.2 70.9)
1988	5.9 (4.9 7.3)	5.4 (4.5 6.9)	25.1 (20.4 32.2)	21.7 (17.8 27.1)	58.1 (47.6 73.6)
1989	6.2 (5.2 7.8)	5.7 (4.7 7.2)	25.4 (20.7 32.6)	23.4 (19.5 29)	60.7 (50.1 76.6)
1990	6.6 (5.5 8.3)	5.9 (4.9 7.5)	25.8 (21 33.1)	25.1 (20.9 31)	63.4 (52.3 79.9)
1991	7 (5.8 8.8)	6.2 (5.1 7.8)	26.1 (21.3 33.6)	26.8 (22.4 33)	66.1 (54.5 83.2)
1992	7.4 (6.1 9.3)	6.4 (5.2 8.1)	26.5 (21.5 34)	28.6 (23.8 35.2)	68.8 (56.6 86.6)
1993	7.8 (6.4 9.8)	6.6 (5.4 8.4)	26.9 (21.7 34.6)	30.4 (25.1 37.5)	71.6 (58.6 90.2)
1994	8.1 (6.7 10.3)	6.8 (5.5 8.7)	27.3 (21.9 35.2)	32.2 (26.4 39.8)	74.4 (60.5 94)
1995	8.5 (6.9 10.8)	7 (5.7 9)	27.7 (22.1 35.8)	34 (27.7 42.1)	77.2 (62.4 97.7)
1996	8.9 (7.2 11.3)	7.2 (5.8 9.3)	28.1 (22.3 36.3)	35.9 (29 44.6)	80.1 (64.3 101.6)
1997	9.2 (7.4 11.9)	7.4 (5.9 9.6)	28.5 (22.4 37.1)	37.7 (30.2 47.3)	82.9 (66 105.8)
1998	9.6 (7.7 12.4)	7.6 (6.1 9.9)	29 (22.6 37.7)	39.5 (31.4 49.8)	85.7 (67.8 109.8)
1999	9.9 (7.9 12.9)	7.8 (6.2 10.1)	29.4 (22.8 38.5)	41.4 (32.6 52.3)	88.6 (69.5 113.8)
2000	10.3 (8.2 13.5)	8 (6.3 10.4)	29.9 (23 39.3)	43.2 (33.8 55.2)	91.4 (71.3 118.3)
2001	10.6 (8.4 14.1)	8.2 (6.5 10.8)	30.4 (23.1 40.1)	45 (34.9 57.9)	94.2 (72.9 122.9)
2002	11 (8.6 14.6)	8.3 (6.6 11.1)	30.8 (23.3 40.9)	46.8 (36 60.9)	97 (74.5 127.5)
2003	11.3 (8.8 15.3)	8.5 (6.7 11.3)	31.3 (23.4 41.8)	48.6 (37.1 64.4)	99.7 (76.1 132.8)
2004	11.6 (9.1 15.8)	8.7 (6.8 11.5)	31.8 (23.6 42.5)	50.4 (38.2 67.4)	102.5 (77.7 137.2)
2005	12 (9.3 16.3)	8.9 (6.9 11.7)	32.2 (23.8 43.3)	52.2 (39.2 70.4)	105.2 (79.3 141.7)

Extended density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.1 (3.8 6.7)	5.4 (3.8 7.4)	28.9 (20.4 38)	21 (13.9 27.8)	60.4 (42 79.8)
1985	5.4 (4.2 7)	5.7 (4.1 7.6)	29.9 (21.3 38.4)	22 (15.4 28.6)	63.1 (45 81.6)
1986	5.8 (4.6 7.3)	6.1 (4.5 7.9)	30.9 (21.8 39.1)	23.2 (16.9 29.5)	66 (47.8 83.8)
1987	6.2 (4.9 7.7)	6.5 (4.9 8.3)	32 (22.2 40)	24.5 (18.6 30.9)	69.2 (50.6 86.9)
1988	6.6 (5.3 8.2)	6.9 (5.1 8.8)	33 (22.8 41.1)	26 (20.2 32.6)	72.6 (53.4 90.7)
1989	7.1 (5.6 8.7)	7.4 (5.5 9.3)	34 (23.1 42.1)	27.7 (21.7 34.4)	76.2 (55.8 94.5)
1990	7.6 (5.9 9.3)	7.8 (5.7 9.9)	35 (23.7 43.1)	29.4 (23.1 36.4)	79.8 (58.4 98.7)
1991	8.1 (6.2 9.9)	8.3 (5.9 10.5)	35.9 (24.1 44.3)	31.3 (24.7 38.3)	83.5 (60.9 103)
1992	8.7 (6.7 10.7)	8.7 (6.1 10.8)	36.7 (24.5 45.6)	33.3 (26.5 40.5)	87.3 (63.8 107.6)
1993	9.3 (7.1 11.4)	9.1 (6.3 11.2)	37.4 (24.9 46.4)	35.4 (28.2 42.9)	91.2 (66.5 111.9)
1994	10 (7.6 12.3)	9.4 (6.3 11.7)	38 (25.4 47.2)	37.7 (30.1 45.4)	95.1 (69.5 116.7)
1995	10.7 (7.8 13.2)	9.7 (6.5 12.1)	38.6 (25.8 48.2)	40.1 (31.9 48.4)	99.1 (72 121.9)
1996	11.5 (8.1 14.2)	9.9 (6.6 12.4)	39 (26 49)	42.8 (33.4 51.7)	103.2 (74.1 127.3)
1997	12.3 (8.3 15.2)	10 (6.7 12.6)	39.4 (26.3 49.8)	45.7 (35.3 55.5)	107.3 (76.7 133.1)
1998	13 (8.5 16.2)	10.1 (6.9 12.8)	39.7 (26.3 50.5)	48.7 (36.9 59.7)	111.6 (78.7 139.3)
1999	13.8 (8.8 17.3)	10.2 (6.9 13.1)	40 (26.5 51.5)	51.9 (38.6 64.2)	115.9 (80.8 146.1)
2000	14.6 (9 18.5)	10.2 (6.9 13.3)	40.2 (26.3 52.2)	55.3 (40.1 68.9)	120.3 (82.4 153)
2001	15.4 (9.2 19.7)	10.3 (6.9 13.5)	40.4 (26.3 53)	58.8 (41.3 74)	124.8 (83.7 160.2)
2002	16.1 (9.3 21)	10.3 (7 13.7)	40.6 (26.4 53.6)	62.5 (42.2 80)	129.5 (85 168.3)
2003	16.8 (9.5 22.6)	10.4 (7 13.8)	40.8 (26.7 54.1)	66.3 (43.2 86.1)	134.3 (86.3 176.5)
2004	17.5 (9.7 24.3)	10.5 (6.9 14)	41 (26.8 54.7)	70.2 (43.7 92)	139.2 (87.2 185.1)
2005	18.2 (9.9 26.2)	10.5 (7 14.3)	41.3 (27.4 55.2)	74.1 (44.3 98.4)	144.1 (88.6 194.1)

Density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4 7.7)	6.1 (3.9 9.3)	40.5 (28.1 59.5)	18.5 (13.3 24.8)	70.7 (49.4 101.3)
1985	6.2 (4.6 8.3)	6.7 (4.8 9.8)	41.8 (30 61)	20.4 (15.1 26.6)	75.1 (54.5 105.8)
1986	6.8 (5.2 9.1)	7.5 (5.6 10.4)	43.5 (32 62.6)	22.5 (16.9 28.8)	80.2 (59.7 110.9)
1987	7.5 (5.8 9.9)	8.2 (6.2 11.1)	45.1 (33.6 64.7)	24.9 (19.1 31.5)	85.8 (64.8 117.2)
1988	8.3 (6.4 10.9)	9 (6.9 12)	46.9 (35.3 66.4)	27.6 (21.3 34.7)	91.7 (69.9 124)
1989	9.1 (7 11.9)	9.7 (7.5 12.8)	48.7 (37 69.5)	30.5 (23.6 38.5)	98 (75.2 132.6)
1990	10 (7.7 13.1)	10.5 (8.1 13.8)	50.6 (38.4 71)	33.6 (26 42.5)	104.7 (80.2 140.4)
1991	10.9 (8.4 14.3)	11.2 (8.7 14.8)	52.5 (39.9 72.8)	36.9 (28.5 47.3)	111.5 (85.5 149.1)
1992	11.8 (9.1 15.6)	12 (9.3 15.8)	54.5 (41.2 75.6)	40.4 (31.2 52.4)	118.7 (90.8 159.4)
1993	12.8 (9.8 17)	12.7 (9.8 16.6)	56.5 (42.2 78.8)	44.2 (33.8 57.9)	126.2 (95.7 170.3)
1994	13.8 (10.6 18.4)	13.5 (10.4 17.9)	58.6 (43.6 83.1)	48.2 (37.1 63.7)	134.1 (101.6 183.1)
1995	14.9 (11.3 19.9)	14.2 (10.9 19)	60.8 (44.9 87.1)	52.5 (40.3 70)	142.4 (107.4 196.1)
1996	15.9 (12.1 21.5)	15 (11.4 20.3)	63.1 (46.2 90.7)	57 (43.7 76.9)	151 (113.4 209.4)
1997	17 (12.9 23.1)	15.7 (11.8 21.6)	65.4 (47.5 94.8)	61.7 (47.2 84.4)	159.9 (119.4 223.9)
1998	18.2 (13.7 24.8)	16.5 (12.3 22.9)	67.8 (48.6 99.5)	66.6 (51.1 92)	169.1 (125.7 239.3)
1999	19.3 (14.5 26.6)	17.2 (12.8 24.3)	70.3 (49.9 104.9)	71.8 (54.4 100)	178.6 (131.6 255.8)
2000	20.5 (15.3 28.4)	18 (13.2 25.8)	72.7 (51.5 110.9)	77.1 (58.2 107.9)	188.4 (138.1 273.1)
2001	21.7 (16.2 30.4)	18.8 (13.6 27.3)	75.3 (52.8 115.7)	82.7 (62.3 116)	198.4 (144.9 289.4)
2002	22.9 (17.1 32.4)	19.5 (14 28.8)	77.8 (54.1 120.2)	88.4 (65.7 125.4)	208.7 (151 306.8)
2003	24.1 (17.9 34.6)	20.3 (14.4 30.3)	80.5 (55.4 124.8)	94.3 (69.7 134.5)	219.2 (157.4 324.1)
2004	25.4 (18.5 36.6)	21.1 (14.8 31.8)	83.1 (56.7 130.3)	100.4 (73.8 143.3)	230 (163.7 342.1)
2005	26.6 (19.3 38.6)	21.9 (15.3 33.4)	85.8 (58.1 135.8)	106.6 (77.9 153.1)	240.9 (170.5 361)

Extended density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.5 (4.2 7.4)	5.8 (4.2 7.8)	32.2 (23.7 45.9)	22.3 (16 28.2)	65.7 (48 89.3)
1985	5.8 (4.5 7.7)	6.1 (4.7 8)	33.4 (25.1 47.9)	23.4 (17.3 29.3)	68.8 (51.5 92.9)
1986	6.2 (5 8)	6.5 (5.1 8.5)	34.7 (26.4 49.8)	24.7 (18.6 30.6)	72.1 (55.1 97)
1987	6.6 (5.4 8.5)	7 (5.5 9.6)	36 (27.8 52.2)	26.2 (20 32.1)	75.8 (58.7 102.4)
1988	7.1 (5.8 9.5)	7.5 (6 10.7)	37.4 (29.1 53.9)	27.8 (21.6 33.8)	79.8 (62.5 107.9)
1989	7.6 (6.2 10.5)	8 (6.4 11.7)	38.8 (30.4 55.5)	29.6 (23.2 36.8)	84.1 (66.2 114.5)
1990	8.2 (6.6 11.3)	8.5 (6.8 12.5)	40.2 (31.8 56.4)	31.6 (24.9 40.6)	88.5 (70.2 120.8)
1991	8.7 (7.1 12.5)	9.1 (7.3 13.1)	41.6 (33.1 58.9)	33.6 (26.8 43)	93 (74.3 127.5)
1992	9.4 (7.6 13.5)	9.6 (7.7 14)	43 (34.1 60.7)	35.8 (28.7 45.4)	97.7 (78.2 133.5)
1993	10.1 (8.1 14.4)	10.1 (8.2 14.4)	44.4 (35.4 63.2)	38.1 (30.6 49.4)	102.7 (82.3 141.4)
1994	10.8 (8.7 15.3)	10.7 (8.6 15.1)	45.7 (36.5 66)	40.6 (32.7 54.2)	107.8 (86.6 150.6)
1995	11.5 (9.3 16.4)	11.2 (9 15.8)	47.1 (37.7 68.1)	43.3 (34.9 59.3)	113.2 (90.9 159.6)
1996	12.4 (9.9 17.3)	11.7 (9.4 16.7)	48.5 (38.8 70.8)	46.2 (37.1 63.8)	118.8 (95.2 168.6)
1997	13.3 (10.7 18.5)	12.2 (9.7 17.8)	49.9 (39.5 73.6)	49.4 (39.9 68.9)	124.7 (99.9 178.8)
1998	14.2 (11.5 19.9)	12.7 (10 18.9)	51.2 (40.2 76)	52.7 (42.3 75.3)	130.8 (104 190.1)
1999	15.2 (12.3 21.4)	13.1 (10.3 20.1)	52.5 (41.2 78.5)	56.3 (44.7 81)	137.2 (108.5 201)
2000	16.2 (13 23)	13.5 (10.6 21.1)	53.8 (42 81)	60.2 (47.5 85.9)	143.8 (113.1 211)
2001	17.3 (13.8 24.5)	13.9 (10.8 22)	55 (42.6 83.7)	64.4 (50.5 91.4)	150.6 (117.7 221.6)
2002	18.4 (14.6 25.8)	14.3 (11 23)	56.2 (43.1 86.4)	68.8 (53.9 99)	157.7 (122.6 234.2)
2003	19.5 (15.4 27.1)	14.6 (11.1 23.9)	57.3 (43.6 88.6)	73.5 (57.5 104.8)	164.9 (127.6 244.4)
2004	20.7 (16 28.4)	14.9 (11.3 24.8)	58.4 (44.1 92.1)	78.5 (60.9 112.6)	172.5 (132.4 258)
2005	21.9 (16.4 29.7)	15.2 (11.5 25.6)	59.5 (44.5 95.6)	83.8 (64.4 119.4)	180.3 (136.9 270.3)

Appendix 2

Estimates of derived, time and region-varying population parameters in 1985-2005 for the four models of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival model – estimated annual pup survival $\phi_{p,r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.417 (0.251 0.65)	0.342 (0.172 0.575)	0.249 (0.098 0.479)	0.48 (0.304 0.693)
1986	0.401 (0.238 0.632)	0.331 (0.169 0.554)	0.239 (0.092 0.46)	0.464 (0.301 0.677)
1987	0.383 (0.226 0.619)	0.312 (0.162 0.531)	0.236 (0.091 0.457)	0.444 (0.283 0.664)
1988	0.368 (0.215 0.605)	0.297 (0.153 0.518)	0.233 (0.091 0.456)	0.427 (0.267 0.653)
1989	0.355 (0.203 0.589)	0.286 (0.147 0.507)	0.23 (0.09 0.451)	0.412 (0.252 0.645)
1990	0.342 (0.193 0.58)	0.276 (0.142 0.497)	0.228 (0.09 0.446)	0.398 (0.239 0.637)
1991	0.331 (0.185 0.567)	0.269 (0.138 0.489)	0.226 (0.089 0.442)	0.385 (0.227 0.627)
1992	0.32 (0.178 0.56)	0.262 (0.133 0.481)	0.223 (0.089 0.439)	0.373 (0.216 0.618)
1993	0.31 (0.17 0.551)	0.255 (0.129 0.472)	0.221 (0.087 0.434)	0.36 (0.205 0.609)
1994	0.3 (0.163 0.538)	0.249 (0.126 0.462)	0.218 (0.087 0.43)	0.348 (0.195 0.599)
1995	0.291 (0.157 0.529)	0.243 (0.122 0.454)	0.216 (0.087 0.426)	0.337 (0.187 0.59)
1996	0.282 (0.151 0.521)	0.237 (0.119 0.449)	0.213 (0.086 0.422)	0.326 (0.179 0.581)
1997	0.274 (0.146 0.51)	0.232 (0.116 0.441)	0.211 (0.085 0.418)	0.316 (0.172 0.572)
1998	0.267 (0.141 0.501)	0.227 (0.113 0.431)	0.208 (0.085 0.414)	0.306 (0.165 0.564)
1999	0.26 (0.137 0.494)	0.223 (0.111 0.425)	0.205 (0.084 0.408)	0.297 (0.158 0.557)
2000	0.253 (0.132 0.484)	0.219 (0.108 0.419)	0.203 (0.083 0.403)	0.288 (0.152 0.549)
2001	0.247 (0.129 0.476)	0.215 (0.107 0.415)	0.2 (0.082 0.401)	0.28 (0.146 0.538)
2002	0.241 (0.124 0.465)	0.211 (0.104 0.409)	0.198 (0.082 0.397)	0.272 (0.141 0.525)
2003	0.235 (0.121 0.457)	0.207 (0.102 0.402)	0.195 (0.081 0.394)	0.265 (0.136 0.516)
2004	0.23 (0.118 0.45)	0.204 (0.1 0.399)	0.193 (0.08 0.389)	0.258 (0.132 0.509)
2005	0.225 (0.115 0.443)	0.2 (0.099 0.393)	0.191 (0.079 0.386)	0.251 (0.128 0.5)

Extended density dependent survival model – estimated annual pup survival $\phi_{p,r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.616 (0.338 0.83)	0.604 (0.325 0.826)	0.567 (0.184 0.82)	0.622 (0.338 0.832)
1986	0.614 (0.338 0.83)	0.6 (0.293 0.826)	0.57 (0.187 0.818)	0.62 (0.338 0.832)
1987	0.612 (0.338 0.829)	0.595 (0.278 0.824)	0.565 (0.179 0.81)	0.618 (0.338 0.831)
1988	0.61 (0.316 0.829)	0.588 (0.241 0.822)	0.559 (0.175 0.806)	0.616 (0.338 0.831)
1989	0.607 (0.286 0.828)	0.58 (0.215 0.818)	0.551 (0.169 0.797)	0.615 (0.338 0.831)
1990	0.605 (0.264 0.826)	0.573 (0.199 0.809)	0.543 (0.159 0.793)	0.613 (0.338 0.831)
1991	0.603 (0.24 0.826)	0.565 (0.194 0.802)	0.535 (0.157 0.789)	0.611 (0.338 0.83)
1992	0.6 (0.227 0.826)	0.555 (0.179 0.798)	0.526 (0.154 0.777)	0.609 (0.315 0.829)
1993	0.597 (0.214 0.824)	0.54 (0.172 0.788)	0.514 (0.151 0.767)	0.608 (0.296 0.829)
1994	0.593 (0.206 0.823)	0.521 (0.163 0.769)	0.503 (0.147 0.754)	0.605 (0.274 0.828)
1995	0.589 (0.194 0.821)	0.5 (0.143 0.752)	0.491 (0.14 0.745)	0.603 (0.251 0.827)
1996	0.583 (0.183 0.817)	0.482 (0.121 0.739)	0.479 (0.137 0.739)	0.601 (0.23 0.827)
1997	0.576 (0.174 0.815)	0.466 (0.104 0.726)	0.468 (0.123 0.73)	0.598 (0.209 0.826)
1998	0.568 (0.163 0.812)	0.453 (0.092 0.727)	0.459 (0.108 0.724)	0.595 (0.192 0.824)
1999	0.558 (0.152 0.809)	0.441 (0.087 0.727)	0.45 (0.115 0.721)	0.592 (0.18 0.823)
2000	0.548 (0.145 0.8)	0.431 (0.08 0.719)	0.444 (0.113 0.717)	0.588 (0.165 0.823)
2001	0.538 (0.135 0.796)	0.426 (0.083 0.709)	0.438 (0.108 0.716)	0.583 (0.155 0.823)
2002	0.527 (0.131 0.796)	0.423 (0.1 0.705)	0.434 (0.104 0.713)	0.578 (0.146 0.823)
2003	0.517 (0.125 0.794)	0.421 (0.101 0.701)	0.431 (0.106 0.708)	0.571 (0.137 0.819)
2004	0.506 (0.12 0.789)	0.419 (0.098 0.702)	0.43 (0.113 0.703)	0.564 (0.129 0.814)
2005	0.494 (0.114 0.784)	0.415 (0.096 0.7)	0.428 (0.111 0.701)	0.555 (0.124 0.811)

Density dependent fecundity model – estimated annual fecundity $\alpha_{r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.805 (0.658 0.909)	0.747 (0.553 0.871)	0.63 (0.416 0.793)	0.851 (0.704 0.94)
1986	0.787 (0.633 0.899)	0.718 (0.534 0.851)	0.62 (0.407 0.782)	0.838 (0.695 0.933)
1987	0.771 (0.607 0.89)	0.692 (0.519 0.835)	0.611 (0.399 0.775)	0.825 (0.676 0.926)
1988	0.756 (0.586 0.881)	0.673 (0.496 0.824)	0.603 (0.39 0.769)	0.813 (0.656 0.921)
1989	0.741 (0.563 0.875)	0.657 (0.476 0.814)	0.594 (0.38 0.765)	0.801 (0.636 0.919)
1990	0.727 (0.546 0.866)	0.643 (0.458 0.805)	0.586 (0.371 0.757)	0.79 (0.617 0.914)
1991	0.712 (0.522 0.858)	0.63 (0.44 0.796)	0.576 (0.359 0.752)	0.777 (0.596 0.908)
1992	0.696 (0.502 0.853)	0.615 (0.42 0.788)	0.566 (0.347 0.747)	0.764 (0.573 0.903)
1993	0.68 (0.477 0.846)	0.6 (0.402 0.779)	0.557 (0.337 0.743)	0.749 (0.547 0.897)
1994	0.665 (0.455 0.836)	0.585 (0.386 0.771)	0.547 (0.329 0.74)	0.735 (0.523 0.889)
1995	0.649 (0.433 0.826)	0.571 (0.37 0.76)	0.538 (0.317 0.735)	0.72 (0.503 0.881)
1996	0.634 (0.41 0.815)	0.559 (0.356 0.751)	0.529 (0.305 0.731)	0.705 (0.48 0.874)
1997	0.619 (0.391 0.805)	0.547 (0.337 0.743)	0.52 (0.295 0.726)	0.69 (0.456 0.867)
1998	0.605 (0.371 0.797)	0.535 (0.321 0.736)	0.51 (0.288 0.716)	0.675 (0.435 0.859)
1999	0.59 (0.353 0.789)	0.523 (0.307 0.727)	0.501 (0.278 0.709)	0.66 (0.418 0.85)
2000	0.576 (0.337 0.779)	0.512 (0.294 0.718)	0.492 (0.269 0.703)	0.645 (0.396 0.842)
2001	0.562 (0.322 0.769)	0.501 (0.281 0.711)	0.484 (0.259 0.695)	0.63 (0.373 0.835)
2002	0.549 (0.307 0.76)	0.491 (0.269 0.703)	0.475 (0.246 0.688)	0.615 (0.354 0.827)
2003	0.536 (0.293 0.752)	0.481 (0.259 0.697)	0.467 (0.237 0.682)	0.601 (0.336 0.819)
2004	0.523 (0.279 0.744)	0.471 (0.248 0.689)	0.458 (0.23 0.674)	0.586 (0.318 0.81)
2005	0.511 (0.267 0.735)	0.461 (0.238 0.682)	0.45 (0.224 0.668)	0.572 (0.303 0.803)

Extended density dependent fecundity model – estimated annual fecundity $\alpha_{r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.934 (0.732 0.998)	0.921 (0.668 0.997)	0.898 (0.52 0.993)	0.939 (0.75 0.998)
1986	0.932 (0.732 0.998)	0.917 (0.629 0.997)	0.895 (0.512 0.993)	0.937 (0.736 0.998)
1987	0.93 (0.72 0.997)	0.912 (0.597 0.996)	0.892 (0.535 0.992)	0.936 (0.732 0.998)
1988	0.929 (0.702 0.997)	0.908 (0.57 0.994)	0.889 (0.529 0.991)	0.935 (0.732 0.998)
1989	0.927 (0.687 0.997)	0.904 (0.553 0.994)	0.885 (0.521 0.989)	0.934 (0.725 0.998)
1990	0.926 (0.668 0.997)	0.9 (0.538 0.994)	0.882 (0.514 0.987)	0.933 (0.712 0.998)
1991	0.923 (0.652 0.997)	0.895 (0.552 0.992)	0.877 (0.504 0.986)	0.932 (0.7 0.998)
1992	0.921 (0.634 0.997)	0.89 (0.55 0.99)	0.872 (0.487 0.985)	0.93 (0.692 0.998)
1993	0.918 (0.618 0.996)	0.883 (0.53 0.987)	0.867 (0.472 0.983)	0.929 (0.682 0.998)
1994	0.915 (0.602 0.996)	0.876 (0.506 0.984)	0.861 (0.457 0.981)	0.927 (0.666 0.998)
1995	0.912 (0.586 0.995)	0.868 (0.485 0.982)	0.855 (0.445 0.979)	0.925 (0.65 0.998)
1996	0.909 (0.569 0.995)	0.859 (0.466 0.98)	0.848 (0.436 0.978)	0.924 (0.635 0.998)
1997	0.905 (0.554 0.995)	0.851 (0.447 0.977)	0.841 (0.429 0.976)	0.921 (0.612 0.998)
1998	0.9 (0.539 0.995)	0.843 (0.436 0.974)	0.834 (0.422 0.974)	0.919 (0.597 0.998)
1999	0.895 (0.525 0.994)	0.833 (0.425 0.972)	0.826 (0.415 0.971)	0.917 (0.577 0.998)
2000	0.89 (0.512 0.993)	0.824 (0.415 0.968)	0.818 (0.409 0.969)	0.914 (0.558 0.998)
2001	0.883 (0.497 0.992)	0.814 (0.406 0.966)	0.81 (0.403 0.968)	0.911 (0.54 0.998)
2002	0.877 (0.485 0.992)	0.805 (0.396 0.963)	0.802 (0.397 0.966)	0.908 (0.523 0.998)
2003	0.87 (0.473 0.992)	0.796 (0.386 0.965)	0.794 (0.39 0.964)	0.904 (0.507 0.997)
2004	0.863 (0.46 0.99)	0.786 (0.379 0.961)	0.787 (0.384 0.962)	0.9 (0.492 0.997)
2005	0.854 (0.446 0.989)	0.776 (0.374 0.959)	0.779 (0.373 0.96)	0.895 (0.476 0.997)