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Estimating the size of the UK grey seal population between 1984 and 2009.

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Summary¹

We fitted two Bayesian state-space models of British grey seal population dynamics to two sources of data: (1) regional estimates of pup production from 1984 to 2009, and (2) an independent estimate assumed to be of total population size just before the 2008 breeding season. One model (EDDSNM) allowed for density dependence in pup survival, while the other (EDDFNM) allowed for density dependence in female fecundity. Both models had flexible forms of density dependence, but allowed no movement of recruiting females between regions. Including the independent estimate of population size influenced estimates of population size for the entire time series in both models, and strongly facilitated model selection. The estimated adult population size in 2009 was 96,600 (95% CI 77,600-120,500) for the EDDSNM model and 157,100 (95% CI 147,800-185,700) for the EDDFNM model. The posterior model probabilities were 1.0 and 0.0 respectively; hence the model-averaged estimate of total population size was identical to that for the EDDSNM model. These results assume an adult sex ratio of 57.8% females. If, instead, a uniform prior of between 50% and 100% females is used, then the estimated adult population size becomes closer to the independent estimate, particularly for the EDDSNM model, but the posterior estimated adult sex ratio becomes unfeasibly female-biased (79% (95% CI 59-98%) for EDDSNM and 97% (90-100%) for EDDFNM).

Introduction

This paper presents updated estimates of population size and related demographic parameters, based on the models and fitting methods of Thomas and Harwood (2009), but

updated to include 2009 pup count estimates (Duck 2010), and additional data from an independent estimate of population size obtained from summer haulout counts and telemetry data (Loneragan *et al.* 2010). Models are specified using a Bayesian state space framework, and fitted using a Monte Carlo particle filter. Only the two best models from previous years' briefing papers are used: one assumes density dependent pup survival and the other density dependent fecundity. Both allow extended forms of Beverton-Holt-like density dependence and assume no movement of females between regions; hence they are abbreviated EDDSNM and EDDFNM respectively. Informative priors are used on many model parameters. We compare the fit of the two models by calculating posterior model probabilities, and make joint inference about population size from the two models combined. We also investigate the consequences of allowing for uncertainty in the adult sex ratio, a quantity that has been assumed to be fixed in previous analyses.

Materials and Methods

Process Models

The population dynamics models are described fully in Thomas and Harwood (2008) and papers cited therein. In summary, they track seal population numbers in 7 age groups (pups, age 1-5 females and age 6+ females) in each of four regions (North Sea, Inner Hebrides, Outer Hebrides and Orkney). There are three population sub-processes: (1) survival, (2) ageing and pup sexing and (3) breeding. (The models of Thomas and Harwood 2008 also included movement of recruiting females between regions, but we assume no movement in the current models.) The two models each have 8 parameters. They share 6: adult survival, ϕ_a , one carrying capacity parameter-related parameter for each region, $\beta_1 - \beta_4$, and a parameter, ρ , that dictates the shape of the density-dependent response. The model with density dependent survival (EDDSNM) has a

¹ This report (dated 16 March 2011) is an update of that presented at the 2010 SCOS meeting. The population estimates have been recalculated to reflect updated estimates of 2008 total population size provided after the meeting.

parameter for maximum pup survival $\phi_{j\max}$ and another for constant fecundity α , while the model with density dependent fecundity (EDDFNM) has a parameter for maximum fecundity α_{\max} and constant pup survival ϕ_j .

Neither model describes the dynamics of adult male seals. To obtain an estimate of total adult population size, we follow previous briefing papers in multiplying the estimate of adult female population size by a fixed value of 1.73 (Hiby and Duck, unpublished) – i.e., assuming that females make up 57.8% of the adult population. For this briefing paper, we also have available an independent estimate of total population size, potentially allowing the sex ratio to be estimated. We make some initial steps in this direction, as detailed in a later section.

Data, Observation Models, and Priors

One source of input data was the pup production estimates for 1984-2009 from Duck (2010), aggregated into regions. This was assumed to be normally distributed with mean equal to the true pup production in each region and year, and constant coefficient of variation (CV). In previous briefing papers, the value for this CV was first estimated based on a run of a simple model (DDS), and then fixed at the estimated value to facilitate model comparison. For this paper, we used the estimated CV value of 10.64% from Thomas and Harwood (2009) to save time.

The second source of input data was the estimate of adult population size obtained by Lonergan *et al.* (2010) from summer haulout counts and telemetry data. The haulout data were collected between 2007 and 2009, with the majority from 2008. The telemetry data was collected between 1995-2008. Since it is not possible reliably to relate regional estimates of population size from the haulouts to regional estimates during breeding, only the total population estimate was used. This had to be attached to one year, and so we assumed it corresponded to the population size in 2008. For simplicity (and since mortality rates between summer and the start of the breeding season is likely very low) we assumed the estimate was of population size just before the start of the 2008 breeding season. Lonergan *et al.* (2010) gave an estimate of 88,300 with 95% CI 75,400-105,700. We approximated this by assuming the estimate comes from a right-

shifted gamma distribution, with a shift of 57,949.67, a scale parameter of 1,861,16 and a shape parameter of 16.3035. This gave a distribution with the correct mean, and with lower and upper 2.5% lower and upper quantiles of 75,400 and 104,700 respectively. This distribution implies a CV on the total population size estimate of 8.49%.

Prior distributions for the process model parameters were the same as those of Thomas and Harwood (2009) and are given in Table 1. We followed previous briefing papers 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.

Prior distributions for the states were generated using the 1984 data, as described by Thomas and Harwood (2008).

Fitting Method

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{j\max}, \phi_j$	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
α, α_{\max}	Be(22.05,1.15)	0.95	0.04

We used the particle filtering algorithm of Thomas and Harwood (2008). This involves simulating samples from the prior distributions, projecting them forward in time according to the population model, and then resampling and/or reweighting them according to their likelihood given the data. An identical algorithm to that of Thomas and Harwood (2008) was used for the pup count data, and the additional adult data was included by reweighting the final output according to the likelihood of the estimated 2008 population size given the estimate of Lonergan *et al.* (2010).

The final output is a weighted sample from the posterior distribution. Many samples are required for accurate estimation of the posterior, and we generated 750 runs of 1,000,000 samples

for each model (Table 2). Rejection control was used to reduce the number of samples from the posterior that were required to be stored, and the effective sample size of unique initial samples was calculated to assess the level of Monte Carlo error, as detailed in Thomas and Harwood (2008). As an additional check, we divided the samples into 3 sets of 250 runs and examined the difference in results among these 3 sets.

Model comparison and model outputs

We calculated the posterior model probability for each model, assuming equal prior weights. (Since both models had the same number of parameters, the two prior weighting schemes used in Thomas and Harwood (2009) would both produce equal weights.)

We also present posterior estimates of the model parameters and estimated pup production from 1984-2009. Lastly, we present model averaged estimates of adult population size, combining the models according to their posterior model probabilities.

To evaluate the effect of the additional independent estimate of total population size, we calculated results both with and without this datum. These are based on the same set of particles, either reweighted to include the additional data or not.

Estimating the adult sex ratio

The population dynamics model fitted to pup production data allows estimation of the number of adult females, but this must be scaled by an assumed adult sex ratio to produce an estimate of total population size. In previous briefing papers, it was assumed the female proportion of the adult population was 0.58. The presence of an independent estimate of total population size potentially allows the sex ratio to be estimated. To illustrate this, we re-processed the simulation outputs for both models, allowing the female proportion to be a random variable with a uniform prior distribution with limits 0.5 (equal sex ratio) and 1.0 (all adults are females).

Results

Unique ancestral particle numbers

The number of particles retained and effective sample sizes (ESS) when only the pup count data was used (Table 2) were rather greater than those used in recent briefing papers, due to the larger number of simulations performed. However effective sample size was dramatically reduced

by inclusion of the independent adult population size estimate, particularly for the EDDFNM model. This is not surprising given that the estimate was some distance from that implied by the pup count data and priors alone, especially

Table 2. Number of particles simulated (K), number saved after final rejection control step (K), number of unique ancestral particles (U), effective sample size of unique particles from pup count data alone (ESS_{u1}), and with pup production data and the independent total population estimate (ESS_{u2}).*

Model	K (x10 ⁷)	K* (x10 ⁷)	U (x10 ⁴)	ESS _{u1}	ESS _{u2}
EDDSNM	750	7.38	5.97	630.9	75.15
EDDFNM	750	3.53	2.22	372.5	2.16

for the EDDFNM model (see later in *Results*).

Despite the small ESS, for the EDDSNM model, when the data was divided into three and key results examined, they were all found to be identical to 2-3 significant figures. However, this was not the case for the EDDFNM model, where differences even in the second significant figure were noted – for example, total population size was estimated to be 150.8, 177.7 and 179.5 in the three subsets. Hence population estimates from the EDDFNM model after inclusion of the independent data should be treated with caution. An exception was the posterior model probabilities, which were stable across all three subsets, as showing effectively no support for the EDDFNM model (see later section).

Comparison of models for density dependence with and without the total population estimate

Smoothed posterior means and 95% credible intervals for the two models are shown in Figure 1, both with and without the additional total population estimate. Both models showed similar fits to the pup production data alone; the addition of the total population estimate affected the fit of the EDDFNM model somewhat. There is evidence that the EDDSNM model tracks the observations slightly better than the EDDFNM, particularly after the addition of the total population estimate, but there is also evidence of some Monte-Carlo error in the EDDFNM model estimates – for example the clearly incorrect credibility intervals for Orkney in the 1980s. The models broadly provide a reasonable fit to these data, but there are some clear deficiencies: neither adequately captures the rapid rise and sudden levelling off in pup production in the

Hebrides during the early 1990s, nor the recent levelling off in Orkney; both over-fit pup production in the North Sea in the late 1990s and early 2000s.

Posterior parameter estimates are shown in Figure 2. Addition of the 2008 adult data changed the posterior estimates somewhat; there is also strong evidence that not enough particles have been run in the non-smoothness of the posterior histograms for the EDDFNM model.

Posterior model probabilities for the two models are shown in Table 3. Based on pup production data alone, there appears to be strong support for the EDDSNM model (difference in negative log integrated likelihood, $-\text{LnIL}$, of 5.3; posterior model probability 0.99), although there is some Monte Carlo error associated with this figure: dividing the simulations into three parts yielded changes in posterior model probability of up to 10 percentage points. When the total population estimate is included, support for the EDDSNM model becomes extremely strong, with the $-\text{LnIL}$ values differing by 154 points and posterior model probability for the EDDSNM model of 1.0. With such a large difference in $-\text{LnIL}$, the posterior model probabilities are unlikely to be affected by Monte Carlo error, and indeed we obtained a weighting of 1.0 for EDDSNM in all three subsets of the simulations.

Table 3. Number of parameters, negative log integrated likelihood ($-\text{LnIL}$) and posterior model probabilities ($p(M)$) for fit to pup production data from 1984-2009 2009 and the additional total population estimate from 2008

Model	# params	$-\text{LnIL}$	$p(M)$
Pup production data alone			
EDDSNM	8	796.79	0.99
EDDFNM	8	802.09	0.01
Pup production and total population estimate			
EDDSNM	8	1080.43	1.00
EDDFNM	8	1234.03	0.00

Estimates of total population size

Estimates of total population size from the EDDFNM model were approximately twice those from the EDDSNM model, based on pup production data alone (Table 4 and Figure 3). Inclusion of the independent estimate of total population size from 2008 brought the estimates down by approximately 20% for the EDDSNM model and 35% for the EDDFNM model; it also

narrowed the posterior credibility intervals, particularly of the EDDFNM model (Figure 3). Because the posterior model probability for the EDDSNM model was effectively 1.0, the model-averaged estimates of population size were identical to the EDDSNM estimates.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2009 breeding season, derived from models fit to pup production data from 1984-2009 and the additional total population estimate from 2008. Numbers are posterior means with 95% credibility intervals in brackets.

Pup production data alone		
	EDDSNM	EDDFNM
North Sea	22.4 (14.6 30.6)	30.7 (23.9 41.0)
Inner Hebrides	8.8 (6.9 10.7)	21.8 (17.7 29.7)
Outer Hebrides	32.3 (25.7 38.8)	87.0 (69.4 128.6)
Orkney	56.3 (40.7 83.4)	107.7 (86.6 145.2)
Total	119.8 (87.9 163.5)	247.1 (197.6 344.4)
Pup production and total population estimate		
	EDDSNM	EDDFNM
North Sea	17.7 (12.7 25.2)	17.3 (15.5 22.3)
Inner Hebrides	7.5 (6.1 8.9)	14.0 (13.1 17.0)
Outer Hebrides	27.4 (23.5 32.7)	58.5 (56.0 66.0)
Orkney	44.0 (35.1 53.7)	67.3 (63.3 80.4)
Total	96.6 (77.6 120.5)	157.1 (147.8 185.7)

Estimating the adult sex ratio

For both population models, when adult sex ratio is not assumed fixed, the posterior sex ratio was considerably more female-based than the prior (Figure 4), and also than the previously-assumed value of 0.57: posterior mean (and 95%CI) was 0.79 (0.59-0.98) and 0.97 (0.90-1.00) for the EDDSNM and EDDFNM models respectively. Population size was thus made closer to the independent estimate: posterior mean (and 95% CI) total population size in 2009 was 88.0 (69.5-112.2) and 121.9 (109.7-138.3) thousand seals for the two models.

Discussion

Previous (unpublished) work has suggested that pup production data alone is not sufficient to distinguish between models of density dependent survival and fecundity. Yet, results given here show that given these models and priors, there is strong support for the EDDSNM model based on pup production data alone. Although Monte-Carlo error in model selection statistics may be a factor, this deserves further investigation.

Including the independent estimate of total population size caused the model selection to unambiguously favour the EDDSNM model. Population estimates were also reduced substantially from those under that model based on pup production data alone, so that the posterior mean estimate for 2008 from the model was only approximately 8,000 seals higher than the independent estimate. The extent to which the posterior estimates of total population size move towards the independent 2008 estimate depends upon the precision of this estimate relative to the precision of the estimate of total population size arising from the population dynamics model and pup production data. The latter is governed by the assumed precision of the pup production data and the amount of information about total population size contained in the priors on model parameters.

The posterior estimates of population sizes and model parameters from the EDDFNM model after addition of the independent 2008 total population estimate had significant Monte-Carlo uncertainty attached to them. This was a consequence of the fitting algorithm used, which generated simulations (particles) from the prior distributions, and filtered them first on the pup production data alone, yielding a set of simulations with a wide range of population sizes, almost all larger than the independent estimate. Hence, very few simulations survived the next step of filtering by the independent estimate. This problem could be remedied by starting the simulations with a weighted sample that emphasizes those with low population sizes, running the particle filtering algorithm, and then re-weighting appropriately. Such strategies will be investigated in future research. In the meantime, we do not anticipate that this will affect the conclusion that the EDDFNM model has effectively no weight given the independent estimate, so that Monte Carlo error in the population estimates from this model do not affect any of the conclusions.

One obvious flaw in the initial models fitted here is that no uncertainty is attributed to the multiplier used to scale up adult female numbers to total population size. When the sex ratio parameter is estimated, rather than assumed fixed, the total population estimates for the two models more closely match the independent estimate – however, because the prior on sex ratio was wide (female proportion 0.5 to 1.0), quite unrealistic posterior estimates are required to produce move the population estimates even close to the independent estimate, particularly for the EDDFNM model. Careful thought will be required to specify appropriate priors on sex ratio. Until this is done, we should not investigate the effect of an uncertain sex ratio on model selection.

New estimates of other population parameters are becoming available – for example of fecundity at two intensively-monitored colonies (Smout et al. 2010). These could potentially be incorporated by revising the priors, or as observation data – the latter being more appropriate for parameters that vary through time such as through density dependence.

Other potential changes to the models have been discussed in previous briefing papers (e.g., allowing annual fluctuation in fecundity), but it is not clear what effect these would have on the model-based estimates of total population size.

Acknowledgement

Thanks to Mike Lonergan for suggesting a scaled gamma distribution to approximate the total population size estimate.

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Figure 1. Posterior mean estimates of true pup production from two models of grey seal population dynamics, fit to pup production estimates from 1984-2009 (circles) and a total population estimate from 2008. Lines show the posterior mean bracketed by the 95% credibility intervals for the EDDSNM (blue) and EDDFNM models (red).

(a) Pup production data only

(b) Pup production data and 2008 total population estimate

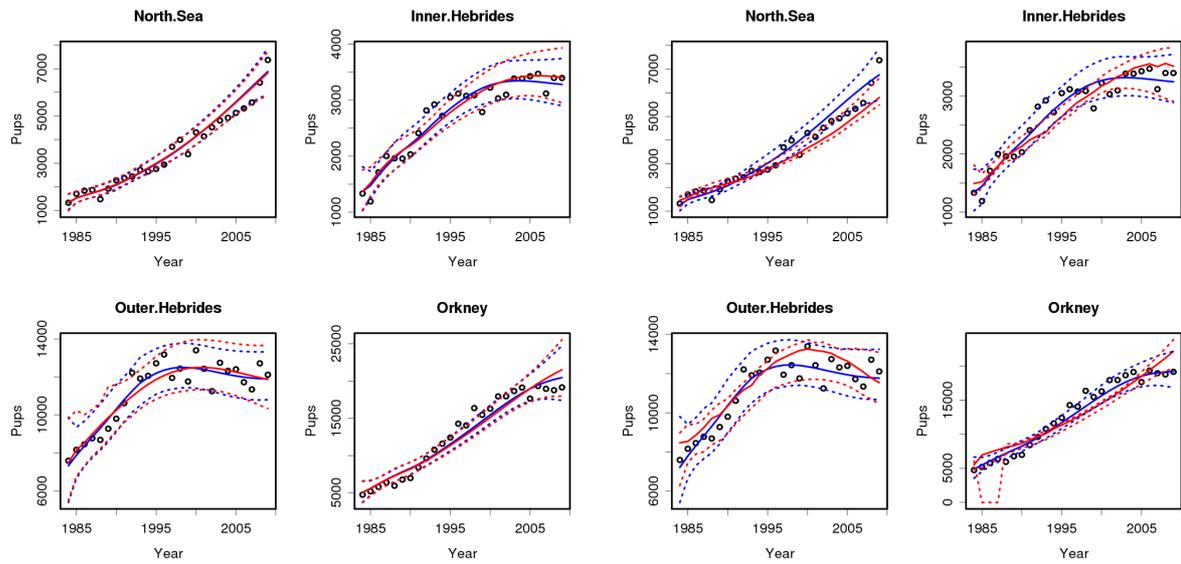
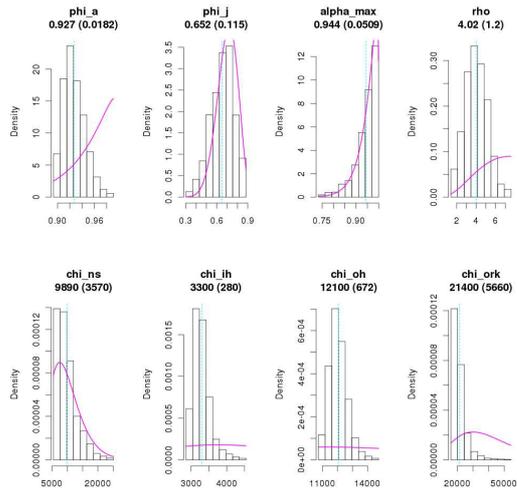


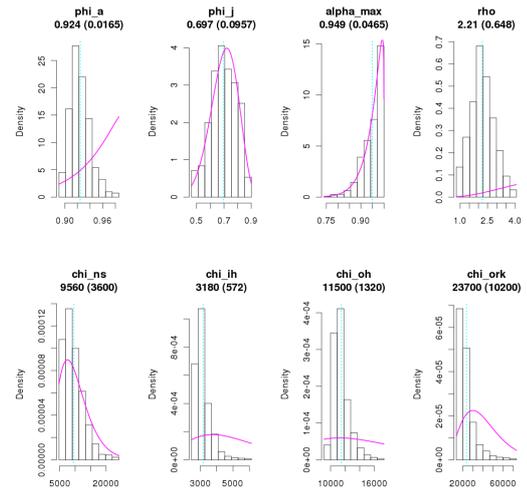
Figure 2. Posterior parameter estimates (histograms) and priors (solid lines) from two models of grey seal population dynamics, fit to pup production estimates from 1984-2009 (circles) and a total population estimate from 2008. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

Pup production data only

(a) Extended density dependent survival no movement (EDDSNM)

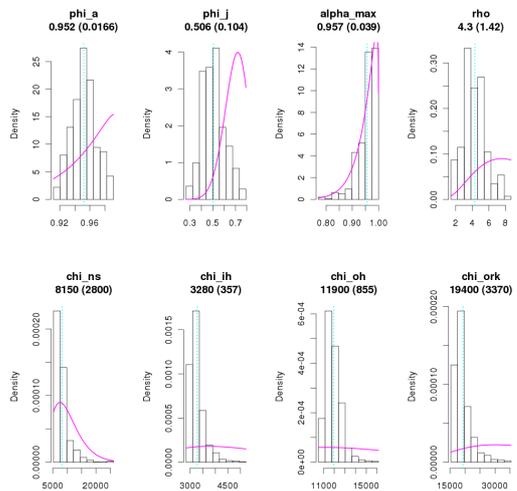


(b) Extended density dependent fecundity no movement (EDDFNM)



Pup production data and 2008 population estimate

(c) Extended density dependent survival no movement (EDSSNM)



(d) Extended density dependent fecundity no movement (EDDFNM)

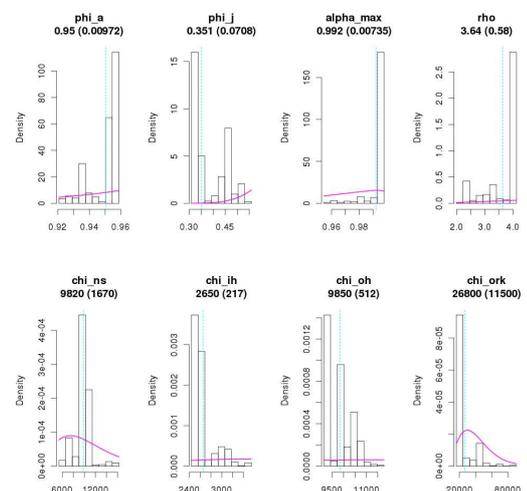


Figure 3. Posterior mean estimates of total population size from two models of grey seal population dynamics, fit to pup production estimates from 1984-2009 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate). Lines show the posterior mean bracketed by the 95% credibility intervals for the EDDSNM (blue) and EDDFNM models (red).

(a) Pup production data only

(b) Pup production data and 2008 total population estimate

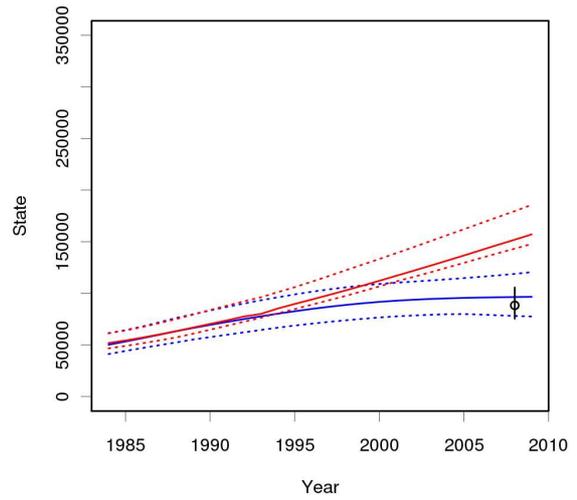
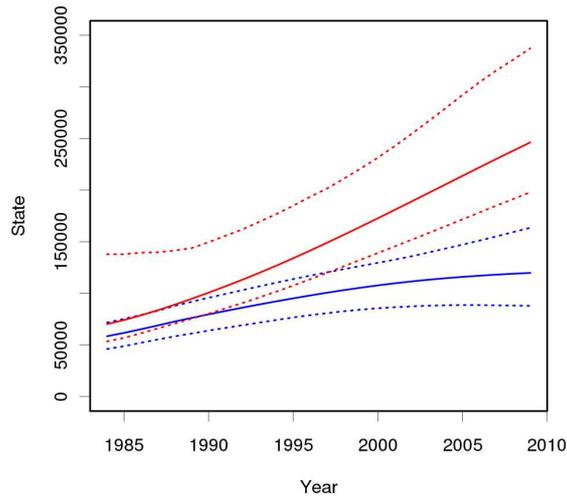
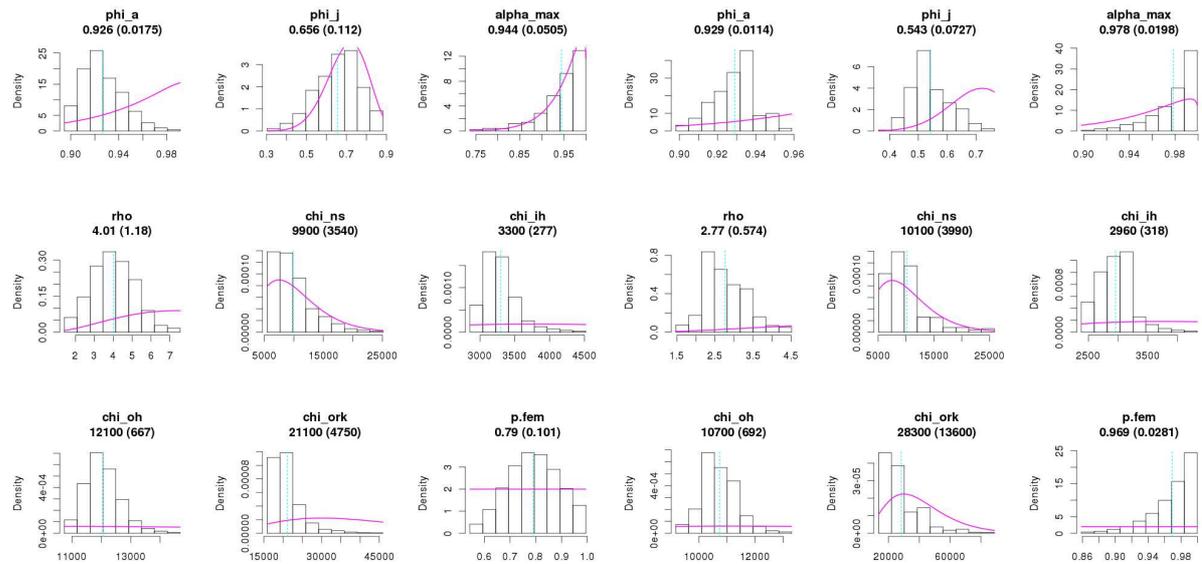


Figure 4. Posterior parameter estimates (histograms) and priors (solid lines) from two models of grey seal population dynamics, fit to pup production estimates from 1984-2009 (circles) and a total population estimate from 2008. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses. The models here differ from those in Figure 2 in that here the proportion of adult females in the population ($p.fem$) is an estimated parameter, while in the runs reported in Figure 2 it was assumed fixed.

(a) Extended density dependent survival no movement (EDDSNM)

(b) Extended density dependent fecundity no movement (EDDFNM)



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2009, made using the EDDSNM (extended density dependent survival with no movement) model of British grey seal population dynamics fit to pup production estimates and a total population estimate from 2008. Numbers are posterior means followed by 95% credibility intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.5 (3.7 5.5)	4.8 (4 5.9)	22.9 (18.9 27.8)	18 (14.5 22.2)	50.2 (41.1 61.3)
1985	4.8 (4 5.8)	5.1 (4.3 6.2)	24.1 (20.1 29.1)	19.2 (15.8 23.2)	53.3 (44.2 64.4)
1986	5.2 (4.4 6.3)	5.4 (4.6 6.5)	25.3 (21.1 30.5)	20.5 (17 24.6)	56.5 (47 67.9)
1987	5.7 (4.7 6.7)	5.8 (4.9 6.9)	26.4 (21.8 31.9)	22.1 (18.4 26.4)	59.9 (49.8 71.9)
1988	6.1 (5.1 7.2)	6.1 (5.1 7.3)	27.4 (22.3 33.2)	23.7 (20 28.4)	63.3 (52.4 76.2)
1989	6.6 (5.5 7.8)	6.4 (5.3 7.7)	28 (22.9 33.9)	25.4 (21.5 30.4)	66.4 (55.2 79.7)
1990	7 (5.9 8.3)	6.7 (5.5 8)	28.5 (23.2 34.5)	27.2 (23 32.5)	69.4 (57.6 83.4)
1991	7.5 (6.4 8.9)	7 (5.7 8.4)	28.8 (23.3 35)	29 (24.5 34.6)	72.3 (59.9 86.9)
1992	8.1 (6.9 9.6)	7.2 (5.8 8.7)	28.9 (23.5 35.2)	30.9 (26 36.7)	75.1 (62.2 90.1)
1993	8.7 (7.4 10.2)	7.4 (5.9 8.9)	29 (23.7 35.2)	32.7 (27.4 38.9)	77.7 (64.5 93.2)
1994	9.3 (7.9 10.9)	7.5 (6 9.2)	28.9 (23.8 35)	34.6 (28.9 41)	80.2 (66.7 96.1)
1995	9.9 (8.5 11.7)	7.6 (6.1 9.3)	28.7 (23.8 34.7)	36.4 (30.4 43.2)	82.6 (68.8 98.9)
1996	10.5 (9 12.5)	7.7 (6.2 9.4)	28.5 (23.8 34.3)	38.1 (31.6 45.3)	84.9 (70.6 101.5)
1997	11.2 (9.5 13.2)	7.7 (6.2 9.5)	28.3 (23.9 33.9)	39.6 (32.7 47.1)	86.9 (72.3 103.8)
1998	11.9 (10 14)	7.7 (6.2 9.5)	28.1 (23.9 33.5)	41 (33.8 48.7)	88.7 (73.8 105.8)
1999	12.6 (10.4 14.9)	7.7 (6.2 9.4)	27.9 (23.9 33.2)	42.1 (34.7 50.1)	90.3 (75.3 107.6)
2000	13.2 (11 15.7)	7.7 (6.3 9.4)	27.7 (23.8 32.8)	43 (35.5 51.2)	91.7 (76.6 109)
2001	13.9 (11.5 16.6)	7.6 (6.2 9.3)	27.6 (23.8 32.5)	43.7 (36.2 51.9)	92.8 (77.7 110.3)
2002	14.5 (11.8 17.4)	7.6 (6.2 9.2)	27.4 (23.7 32.4)	44.2 (36.8 52.4)	93.8 (78.5 111.3)
2003	15.1 (12.1 18.4)	7.6 (6.2 9.1)	27.4 (23.6 32.2)	44.4 (37.3 52.7)	94.5 (79.2 112.4)
2004	15.7 (12.3 19.4)	7.5 (6.2 9)	27.3 (23.6 32.2)	44.6 (37.6 52.9)	95.1 (79.7 113.5)
2005	16.2 (12.4 20.5)	7.5 (6.2 9)	27.3 (23.6 32.2)	44.6 (37.7 53.1)	95.5 (79.9 114.7)
2006	16.7 (12.5 21.5)	7.5 (6.2 8.9)	27.3 (23.6 32.3)	44.5 (37.1 53.3)	95.9 (79.4 116)
2007	17 (12.6 22.7)	7.5 (6.2 8.9)	27.3 (23.5 32.4)	44.3 (36.3 53.4)	96.2 (78.7 117.4)
2008	17.4 (12.7 23.9)	7.5 (6.2 8.9)	27.4 (23.5 32.5)	44.2 (35.7 53.5)	96.4 (78.1 118.8)
2009	17.7 (12.7 25.2)	7.5 (6.2 8.9)	27.4 (23.5 32.7)	44 (35.1 53.7)	96.6 (77.6 120.5)