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Estimating the size of the UK grey seal population between 1984 and 2011, using revised priors on demographic parameters.

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Summary

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 2010 (no pup production assessments were made in 2011), and (2) an independent estimate assumed to be of total population size just before the 2008 breeding season. The two models allowed for density dependence in either pup survival (EDDSNM) or adult female fecundity (EDDFNM); both used a flexible form for the density dependence function, and assumed no movement of recruiting females between regions. Although the population models are identical to those used in previous briefing papers, the prior distributions on demographic parameters have been revised in light of new research findings as well as re-examination of previous research. In addition, the adult sex ratio, which had previously been assumed known, was included as a model parameter.

The EDDSNM model was strongly favoured over the EDDFNM model, particularly in the light of the independent estimate of adult population size. With the new priors, including a prior on sex ratio, the estimated adult population size using the EDDSNM model with just the pup production data was 84,900 (95%CI 52,600 - 132,000). The 1998 estimate is close to the independent population estimate. Therefore, including this independent estimate did not change the estimated adult population size much, although it did increase precision: the combined estimate was 88,500 (95%CI 70,700-110,900).

Introduction

This paper presents estimates of population size and related demographic parameters, based on the models and fitting methods of Thomas (2010). Models are specified using a Bayesian state space framework, and fitted using a Monte Carlo particle filter. Two models of the population dynamics 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; these priors have been revised compared with previous years, as detailed by Longeran (2012). Generally speaking, the new priors support a broader range of values for survival and fecundity. Also, the adult sex ratio, which has previously been considered fixed, was added as a model parameter. We compare the fit of the two models by calculating posterior model probabilities.

Materials and Methods

The models used and fitting methods are identical to those used in previous years, and so are not repeated here. In summary, the models used are Bayesian state-space models, with the process model component (i.e., the population dynamics model) tracking the population numbers in 7 age categories (pups, age 1-5 females and age 6+ females), and the observation model linking data on estimated pup production to the pup numbers in the process model.

Priors on model parameters are given in Table 1, as well as the priors used in previous briefing papers, for comparison.

Neither the EDDSNM nor EDDFNM models describe the dynamics of adult male seals. To obtain an estimate of total population size, in previous briefing papers, we multiplied the female population size by a fixed value of 1.73, i.e., assuming that females make up 57.8% of the adult population. However, Lonergan (2012) provides a suitable prior for this multiplier, which we denote here as ω, and we here compare runs assuming the previous fixed value, as well as those allowing for an unkown ω, with a prior distribution as given by Longeran.

	New priors			Old priors		
Param	Distribution	Mean	Stdev	Distribution	Mean	Stdev
ϕ_a	0.8+0.2*Be(1.6,1.2)	0.914	0.05	Be(22.05,1.15)	0.95	0.04
$\phi_{j\max}, \phi_j$	Be(2.87,1.78)	0.617	0.20	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5	Ga(4,2.5)	10	5
$\alpha, \alpha_{\max}$	0.6+0.4*Be(2,1.5)	0.828	0.09	Be(22.05,1.15)	0.95	0.04
ψ	Ga(2.1, 66.67)	140	96.6	Ga(2.1, 66.67)	140	96.6
ω	1+Ga(0.1,2)	1.2	0.63	Fixed	1.73	0

Table 1. Prior parameter distributions

Model fitting used a particle filtering algorithm identical to that of Thomas (2010). In essence this involves simulating seal populations according to the prior distribution of model parameters and weighting the simulations according to the data likelihood. Each simulation is called a "particle" and they are "filtered" according to the likelihood. Further details are given in Thomas and Harwood (2008). In this briefing paper, results were generated from 1,000 runs of 1,000,000 samples for the fixed CV model and 500 runs of 1,000,000 samples for the estimated CV model.

Model selection is not straightforward in state-space models when observation error is estimated. Hence, we did an initial set of 135 runs of 1,000,000 samples using the EDDSNM process model (with fixed sex ratio parameter ω), and with the observation error parameter, ψ, sampled from its priors. We then took the posterior mean estimate from of ψ and used for subsequent runs of both the EDDSNM and EDDFNM models. Inferences are based on 1,500 runs of 1,000,000 samples for the EDDSNM model, and 550 runs of the same size for the EDDFNM model.

Results

Monte Carlo accuracy

The effective sample size (ESS) of unique particles is a useful measure of the accuracy of the simulation. For the fixed CV model, the ESS based on pup count data alone was 378.3 (Table 2); this was almost unchanged (to 318.6) by the introduction of the independent estimate when the sex ratio parameter was estimated – this is because the estimated total population size from just pup production data alone is very similar to the independent estimate (see later in *Results*). By contrast, when the sex ratio parameter was fixed (to 1.73), the ESS was substantially reduced (to 72.4), because in this case the estimated total population size from the pup production data was rather different from that of the independent estimate. ESSs in this region have been shown in previous briefing papers to produce population and parameter estimates accurate to around 3 significant figures. The ESS from the EDDFNM model were lower, based on pup production data alone (67.8), and were substantially lower with inclusion of the independent population estimate (<5), because the independent estimate was substantially different. Hence, caution should be exercised in interpreting the estimates from the EDDFNM model.

Observation error CV

Using the EDDSNM model where observation error CV was not fixed, posterior mean CV was 8.9% using pup production data alone, and was almost identical when the independent data was also used (assuming known sex ratio). This was only slightly different from the value found by Thomas (2011) (9.8%) using the old priors. Both numbers are similar to the prior mean of 10.4%. The fixed value of 8.9% was used in subsequent models reported here.

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, assuming fixed sex ratio (ESS_{u2}), or assuming unknown sex ratio (ESS_{u3}).The first model assumed the CV on pup production was estimated; the other models assumed it was fixed (at the posterior mean estimate from the first analysis).*

Model	*K* ($x10^7$)	*K** ($x10^7$)	*U* ($x10^4$)	ESS_{u1}	ESS_{u2}	ESS_{u3}
EDDSNM CV Est.	350	9.7	10.9	62.5	24.3	-
EDDSNM CV Fixed	1500	14.1	16.4	378.3	72.4	318.6
EDDFNM CV Fixed	550	11.7	3.7	67.8	2.9	3.8

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 (assuming sex ratio known). 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 some evidence of Monte-Carlo error in the EDDSNM estimate for pup production error alone, with a slight discontinuity in the estimate around 2005-2007.

The models broadly provide a reasonable fit to these data, but there are some deficiencies, particularly with the EDDFNM model, which does not adequately capture the rapid rise and sudden levelling off in pup production in the Hebrides during the early 1990s, nor the recent levelling off in Orkney; the EDDSNM model both over-fits pup production in the North Sea in the late 1990s and early 2000s, but EDDFNM under-fits the recent increase. Overall, particularly the EDDSNM data fit is better than has been seen previously.

Results when sex ratio is estimate were similar, and are not shown here.

Posterior parameter estimates are shown in Figure 2 (for fixed sex ratio) and Figure 3 (for estimated sex ratio). (Appendix 1 gives estimated pup survival for the EDDSNM model, as requested by SCOS.) Parameter estimates are, for the survival and fecundity parameters, quite different from those reported in previous briefing papers (Thomas 2010, 2011) due to the new priors.

Posterior model probabilities for the two models are shown in Table 3. There appears to be very strong evidence for the EDDSNM model over the EDDFNM, including or excluding the 2008 independent population size estimate.

Table 3. Number of parameters, negative log integrated likelihood (-LnIL) and posterior model probabilities (p(M)) for fit to pup production data from 1984-2010 and the additional total population estimate from 2008.

Model	# params	-LnIL	p(M)
Sex ratio fixed			
Pup production data alone			
EDDSNM	8	1321.41	1.00
EDDFNM	8	1332.08	0.00
Pup production and total population estimate Sex ratio fixed			
EDDSNM	8	1587.54	1.00
EDDFNM	8	2123.97	0.00
Pup production and total population estimate Sex ratio estimated			
EDDSNM	9	1589.29	1.00
EDDFNM	9	1640.27	0.00

Estimates of total population size

Estimates of total population size from the EDDFNM model were more than twice those from the EDDSNM model, based on pup production data alone (Table 4 and Figure 4). As expected, assuming a fixed sex ratio of 1.73 produced higher abundance estimates than allowing for uncertainty in sex ratio, using a prior distribution with a prior mean of 1.2.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2011 breeding season, derived from models fit to pup production data from 1984-2010 and the additional total population estimate from 2008. Numbers are posterior means with 95% credibility intervals in brackets.

	Fixed sex ratio		Estimated sex ratio	
	EDDSNM	EDDFNM	EDDSNM	EDDFNM
Pup production data alone				
North Sea	20.5 (13.8 30.4)	37.1 (27.4 46.9)	17.7 (10.1 28.3)	25.7 (18.2 36.1)
Inner Hebrides	7.2 (5.8 9.6)	24.2 (18.9 31.2)	6.1 (4 9.2)	16.8 (12.4 23.7)
Outer Hebrides	26.7 (21 35.4)	96.4 (75.1 128.6)	22.5 (14.6 33.7)	66.9 (48.9 95.8)
Orkney	44.3 (34 60.5)	122.2 (93.9 155.1)	38.5 (23.9 60.7)	84.8 (62 119.3)
Total	98.7 (74.6 135.9)	279.9 (215.2 361.9)	84.9 (52.6 132)	194.1 (141.5 274.9)
Pup production data and 2008 total population estimate				
North Sea	19.2 (14 27.2)	27 (23.4 34.2)	18.5 (13.3 24.8)	15.3 (13.7 17.7)
Inner Hebrides	6.8 (5.8 8.3)	18.9 (16.9 22.6)	6.4 (5.2 7.7)	11.1 (10 12.5)
Outer Hebrides	25.2 (21.2 30.2)	73.5 (66.7 89.8)	23.5 (19.6 28.3)	42.6 (39.2 48.8)
Orkney	41.7 (35.1 50.6)	91.9 (80.4 111.6)	40.1 (32.6 50.1)	52.7 (47.5 60.7)
Total	93 (76.1 116.3)	211.2 (187.4 258.2)	88.5 (70.7 110.9)	121.7 (110.5 139.8)

Inclusion of the independent estimate of total population size from 2008 brought the estimates down considerably for the EDDFNM model, and for the EDDSNM model with fixed sex ratio. For the EDDSNM model with estimated sex ratio, the estimate based on pup production data alone was very similar to that from the independent estimate, so including the independent estimate did not change the composite result much. In all cases, including the independent estimate resulted in much greater precision on the composite population estimates.

Estimates for all years for the EDDSNM model with sex ratio estimated are given in Appendix 2.

References

Longeran, M. 2012. Priors for grey seal population model. *SCOS Briefing Paper 12/2*.

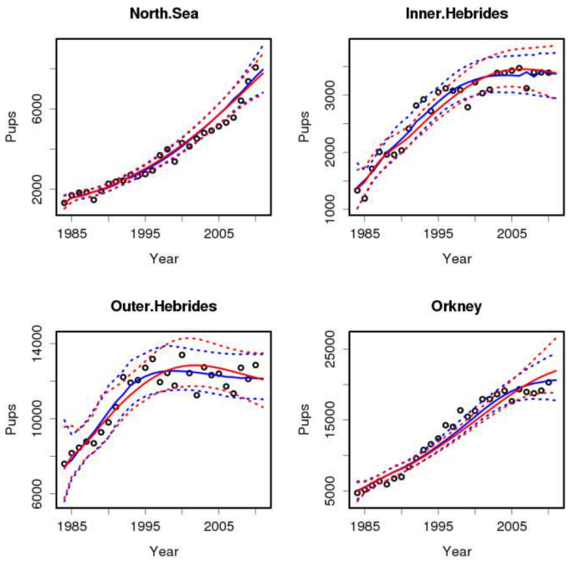
Thomas, L. 2010. Estimating the size of the UK grey seal population between 1984 and 2009. *SCOS Briefing Paper 10/2*. [Updated 16th March 2011.]

Thomas, L. 2011. Estimating the size of the UK grey seal population between 1984 and 2010. *SCOS Briefing Paper 11/2.*

Thomas, L. and J. Harwood. 2009. Estimating the size of the UK grey seal population between 1984 and 2008. *SCOS Briefing Paper 09/2*

Figure 1. Posterior mean estimates of true pup production for 1984-2011 from two models of grey seal population dynamics, fit to pup production estimates from 1984-2010 (circles) and a total population estimate from 2008, assuming the CV of the pup production estimates is 8.9%. 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

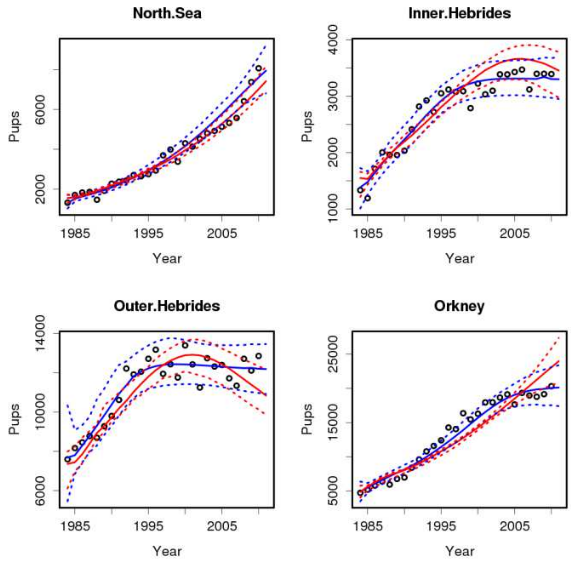
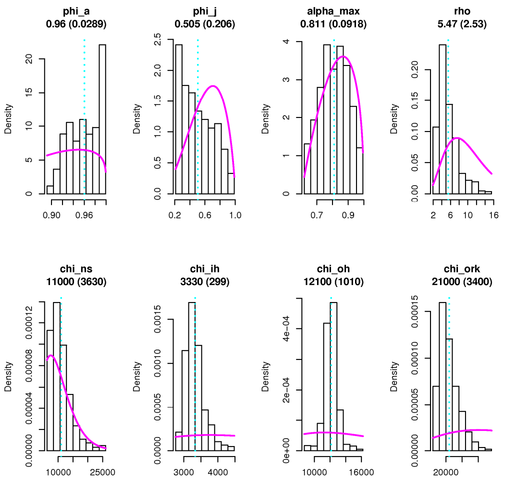


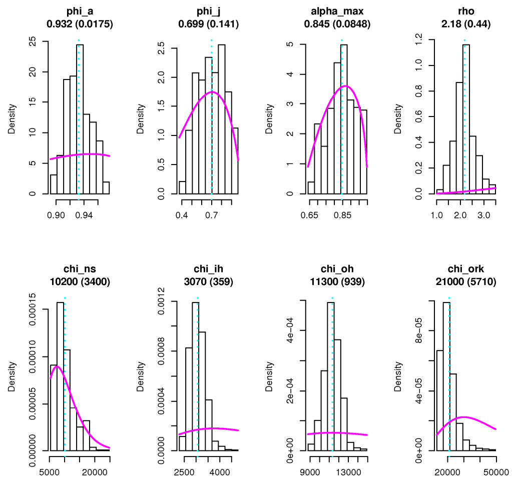
Figure 2. Posterior parameter estimates (histograms) and priors (solid lines) from two models of grey seal population dynamics, fit to pup production estimates from 1984-2010 (circles) and a total population estimate from 2008. Estimates derived assuming a fixed sex ratio. The vertical line shows the 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)

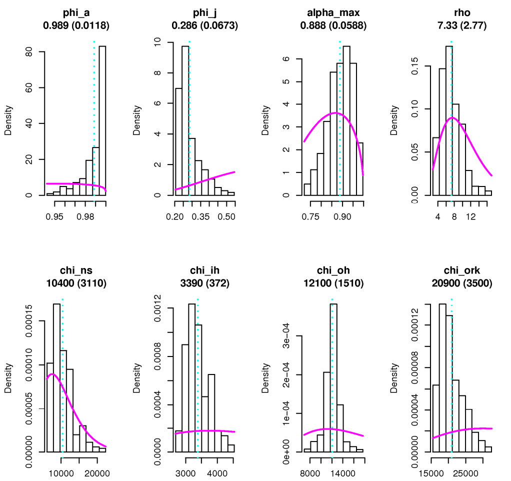


(b) Extended density dependent fecundity no movement (EDDFNM)



Pup production data and 2008 population estimate

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



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

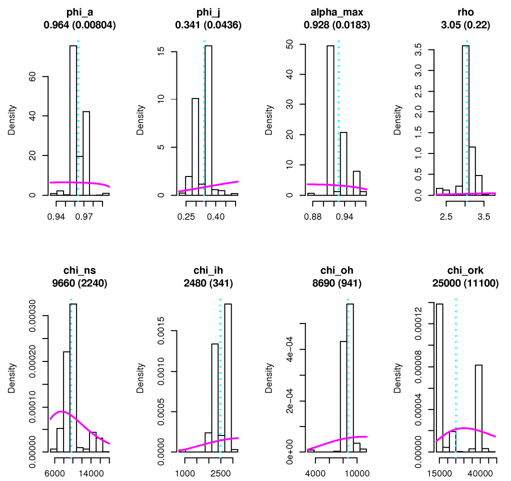
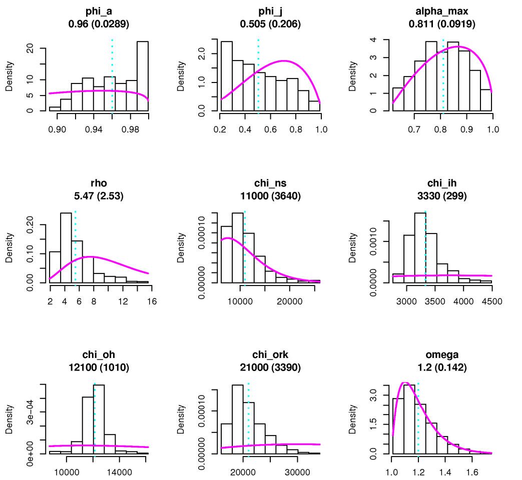


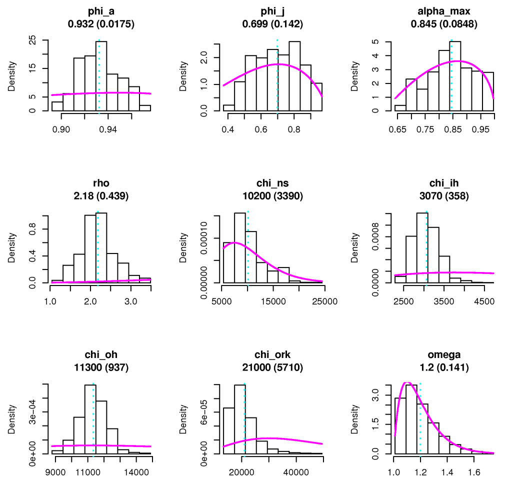
Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from two models of grey seal population dynamics, fit to pup production estimates from 1984-2010 (circles) and a total population estimate from 2008. Estimates derived using estimated sex ratio (ω). The vertical line shows 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)

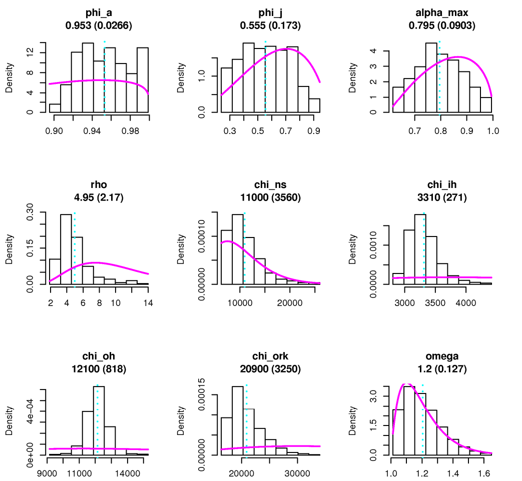


(b) Extended density dependent fecundity no movement (EDDFNM)



Pup production data and 2008 population estimate

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



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

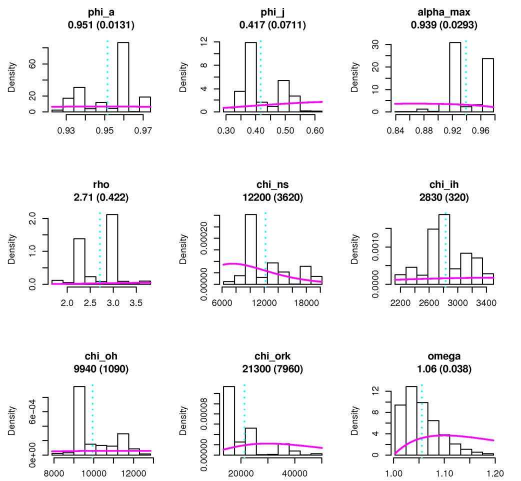
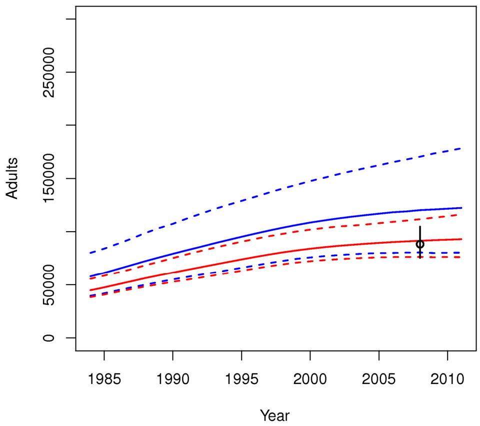
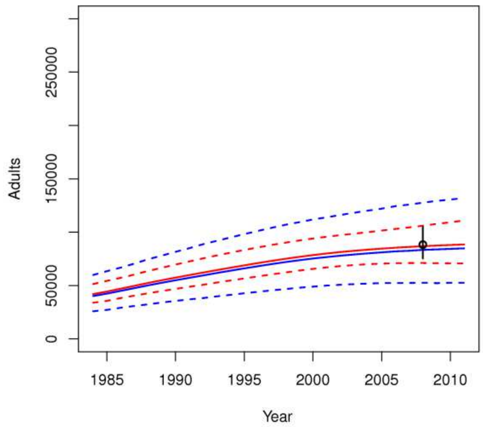


Figure 3. Posterior mean estimates of total population size in 1984-2011 from two models of grey seal population dynamics, fit to pup production estimates from 1984-2010 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate), assuming the CV of the pup production estimates is 8.9%. Lines show the posterior mean bracketed by the 95% credibility intervals for the pup production data only (blue) and pup production data plus the 2008 total population estimate (red).

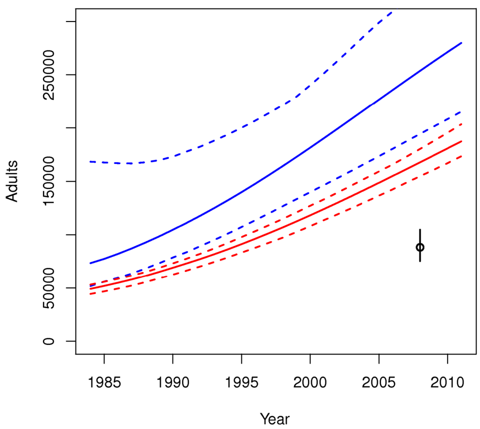
(a) EDDSNM, fixed sex ratio



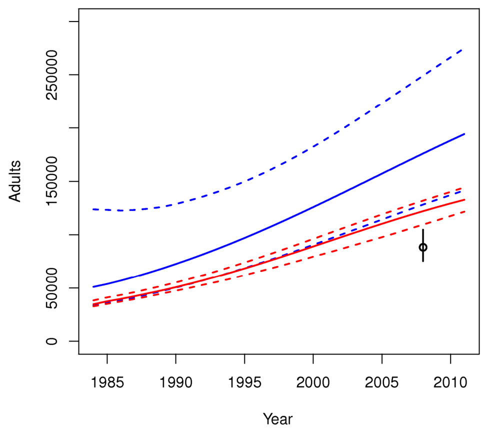
(b) EDDSNM, estimated sex ratio



(c) EDDFNM, fixed sex ratio



(d) EDDFNM, estimated sex ratio



Appendix 1

Estimates of pup survival from the EDDSNM model, using both pup production and 1998 total population estimate, and with sex ratio estimated. Because these were produced quickly at the request of SCOS, corresponding uncertainty values are not given, but these can be readily generated on request.

	North.Sea	Inner.Hebrides	Outer.Hebrides	Orkney
1984	0.55	0.54	0.45	0.55
1985	0.55	0.53	0.42	0.55
1986	0.55	0.51	0.39	0.55
1987	0.55	0.49	0.35	0.55
1988	0.55	0.46	0.32	0.55
1989	0.55	0.43	0.28	0.54
1990	0.55	0.40	0.25	0.54
1991	0.55	0.37	0.21	0.54
1992	0.55	0.33	0.19	0.53
1993	0.55	0.30	0.16	0.52
1994	0.55	0.27	0.15	0.51
1995	0.55	0.24	0.14	0.49
1996	0.55	0.21	0.14	0.47
1997	0.55	0.19	0.13	0.44
1998	0.55	0.18	0.13	0.41
1999	0.55	0.16	0.13	0.38
2000	0.54	0.16	0.13	0.35
2001	0.54	0.15	0.13	0.31
2002	0.53	0.15	0.13	0.28
2003	0.53	0.14	0.14	0.25
2004	0.52	0.14	0.14	0.22
2005	0.50	0.14	0.14	0.20
2006	0.49	0.14	0.14	0.19
2007	0.47	0.14	0.15	0.18
2008	0.44	0.15	0.15	0.17
2009	0.42	0.15	0.15	0.16
2010	0.39	0.15	0.15	0.16
2011	0.36	0.15	0.15	0.15

Appendix 2

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2011, 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. In this model, sex ratio is estimated. Numbers are posterior means followed by 95% credibility intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	3.8 (3.1 4.6)	4.1 (3.3 5)	19.1 (15.4 23.5)	15 (12.1 18.3)	42 (33.9 51.4)
1985	4.1 (3.3 4.9)	4.3 (3.5 5.3)	20 (15.9 24.8)	15.9 (12.8 19.4)	44.4 (35.6 54.4)
1986	4.4 (3.6 5.2)	4.5 (3.7 5.5)	21.1 (17 25.9)	17 (13.9 20.6)	47 (38.2 57.2)
1987	4.7 (3.9 5.6)	4.8 (3.9 5.8)	22 (17.8 26.9)	18.2 (14.9 21.9)	49.7 (40.5 60.3)
1988	5.1 (4.2 6.1)	5.1 (4.2 6.1)	22.8 (18.4 28)	19.4 (15.9 23.5)	52.4 (42.7 63.6)
1989	5.4 (4.5 6.5)	5.3 (4.4 6.4)	23.4 (18.9 28.6)	20.8 (17.1 25.1)	54.9 (44.8 66.6)
1990	5.8 (4.8 6.9)	5.6 (4.6 6.7)	23.8 (19.3 29.2)	22.2 (18.2 26.8)	57.4 (46.8 69.6)
1991	6.2 (5.1 7.4)	5.8 (4.7 7)	24.2 (19.6 29.6)	23.7 (19.4 28.6)	59.8 (48.8 72.6)
1992	6.6 (5.5 8)	6 (4.9 7.3)	24.3 (19.7 29.8)	25.2 (20.7 30.4)	62.1 (50.7 75.5)
1993	7.1 (5.8 8.5)	6.2 (5 7.5)	24.4 (19.9 29.9)	26.7 (22 32.2)	64.4 (52.8 78.2)
1994	7.6 (6.2 9.1)	6.3 (5.1 7.7)	24.5 (20 29.9)	28.3 (23.4 34.1)	66.7 (54.7 80.8)
1995	8.1 (6.7 9.7)	6.4 (5.2 7.8)	24.4 (20.1 29.7)	30 (24.8 36)	68.9 (56.7 83.3)
1996	8.6 (7.1 10.4)	6.5 (5.2 7.9)	24.3 (20.1 29.5)	31.6 (26.2 37.9)	71 (58.6 85.7)
1997	9.2 (7.6 11.1)	6.6 (5.3 8)	24.2 (20.1 29.3)	33.1 (27.5 39.7)	73.1 (60.4 88)
1998	9.8 (8.1 11.8)	6.6 (5.3 8)	24.1 (20 29.1)	34.5 (28.8 41.3)	75 (62.2 90.2)
1999	10.4 (8.6 12.6)	6.5 (5.3 8)	24 (20 28.8)	35.9 (30.1 42.8)	76.8 (64 92.2)
2000	11.1 (9.2 13.4)	6.5 (5.3 7.9)	23.9 (19.9 28.6)	37 (31.2 44.1)	78.5 (65.6 94)
2001	11.8 (9.7 14.2)	6.5 (5.3 7.9)	23.8 (19.9 28.4)	38 (32.1 45.2)	80 (67 95.7)
2002	12.5 (10.3 15)	6.5 (5.3 7.9)	23.7 (19.8 28.3)	38.7 (32.8 46)	81.4 (68.2 97.2)
2003	13.2 (10.9 15.9)	6.5 (5.3 7.8)	23.6 (19.8 28.2)	39.3 (33.2 46.7)	82.6 (69.2 98.6)
2004	13.9 (11.4 16.8)	6.4 (5.3 7.8)	23.5 (19.7 28.1)	39.7 (33.5 47.3)	83.6 (70 100)
2005	14.7 (11.9 17.8)	6.4 (5.3 7.7)	23.5 (19.7 28.1)	40 (33.6 47.8)	84.6 (70.5 101.5)
2006	15.4 (12.3 18.9)	6.4 (5.3 7.7)	23.5 (19.7 28.1)	40.1 (33.6 48.3)	85.4 (70.9 103)
2007	16.1 (12.7 20)	6.4 (5.3 7.7)	23.5 (19.7 28.1)	40.2 (33.5 48.7)	86.2 (71.1 104.5)
2008	16.7 (12.9 21.1)	6.4 (5.3 7.7)	23.5 (19.6 28.1)	40.2 (33.3 49.1)	86.9 (71.1 106)
2009	17.3 (13.1 22.3)	6.4 (5.3 7.7)	23.5 (19.6 28.3)	40.2 (33 49.5)	87.5 (70.9 107.7)
2010	17.9 (13.2 23.5)	6.4 (5.2 7.7)	23.5 (19.6 28.2)	40.1 (32.8 49.8)	88 (70.8 109.3)
2011	18.5 (13.3 24.8)	6.4 (5.2 7.7)	23.5 (19.6 28.3)	40.1 (32.6 50.1)	88.5 (70.7 110.9)