Estimating the size of the UK grey seal population between 1984 and 2015

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Abstract

We fitted a Bayesian state-space model of British grey seal population dynamics to two sources of data: (1) regional estimates of pup production from 1984 to 2014, and (2) two independent estimates assumed to be of total population size just before the 2008 and 2014 breeding seasons. The model allowed for density dependence in pup survival, using a flexible form for the density dependence function, and assumed no movement of recruiting females between regions. This model is identical to that used to provide last year's advice; the same prior distributions were used on model parameters, including a prior on sex ratio and a constraint on adult survival to the range 0.8-0.97.

The 2014 pup production data had not been used in any previous modelling. Like the 2012 estimate, which was the first produced with new survey equipment and revised analysis assumptions, pup production estimates were noticeably higher than what might be expected given the trajectory from 1984-2010. The independent estimate for 2014 was also new; an estimate for 2008 had been used previously but a re-analysis of the data underlying the independent estimates meant the 2008 value was approximately 14% higher than the value used previously, and had a slightly larger coefficient of variation. The estimates used adjust for the fact that the population model is based only on regularly monitored breeding colonies (approx. 94% of the total population).

Estimated adult population size in regularly monitored colonies in 2015 was 127,100 (95% CI 105,900-151,900). The estimated population trajectory is approximately 20% higher than that reported last year. An initial investigation showed that a difference of 14% can be attributed to changes in the independent estimate (the presence of the 2014 estimate and the revised 2008 estimate); the other 6% is presumably caused by the high 2014 pup count.

Introduction

This paper presents estimates of British grey seal population size and related demographic parameters, using identical models and fitting methods to Thomas (2015, and previous years), but incorporating new data in the form of a pup production estimate from 2014, a revised independent estimate of adult population size in 2008 and a new independent estimate from 2014. We project the model forward from the last available data to provide estimates of population size in 2015.

As with past briefing papers, the data are fitted to a population dynamics model within a Bayesian statistical framework using an algorithm called a Monte Carlo particle filter. Previously, multiple models of the population dynamics have been fitted and compared, representing differing hypotheses about the demographic parameter subject to density dependent regulation and about movement of recruiting females between regions. The model where density dependence affects pup survival, and where recruiting females do not move between regions was found to be better supported by the data than one where density dependence affects female fecundity (Thomas 2012); hence only this model is used here. A revised set of priors were suggested by Lonergan (2012), based on updated information and discussions within the Sea Mammal Research Unit; these were further modified in Thomas (2015) to constrain adult female survival to a maximum of 0.97 and the modified priors were used in the SCOS advice in 2015. This set of priors were used here. Hence the only differences in models and methods from Thomas (2015) are the new data.

Materials and Methods

Process model

The population dynamics model is described fully in Thomas and Harwood (2008) and papers cited therein (it is referred to there as the EDDSNM model), except that those models assumed a fixed adult sex ratio. The model was extended to allow estimation of adult sex ratio by Thomas (2012). In summary, the model tracks seal population numbers in 8 age and sex groups (pups, age 1-5 females, which do not pup, and age 6+ females, which may produce a single pup, and age 1+ males) 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 age 5 females between regions, but we assume no movement in the current model.) Age 1+ ("adult") males are not tracked explicitly, but instead are linked to the number of females by a sex ratio parameter. The model has 9 parameters: adult (i.e., age 1 and older) female survival, ϕ_a, maximum pup survival, $\phi_{j\max}$, one carrying capacity parameter-related parameter for each region, β_1 - β_4, a parameter, ρ, that dictates the shape of the density-dependent response, fecundity (i.e., probability that an age 6+ female will birth a pup), α, and adult sex ratio ω.

Data, observation models, and priors

One source of input data was the pup production estimates for 1984-2010, 2012 and 2014 from Duck (2016) covering the regularly surveyed colonies, aggregated into regions. These estimates were assumed to be normally distributed with mean equal to the true pup production in each region and year, and constant coefficient of variation (CV). This CV was estimated from an initial run of the model by Thomas (2014), and for the runs performed here was fixed to this value (10.5%).

The second source of input data was two estimates of adult population size obtained by Russell et al. (2016) from summer haulout counts and telemetry data. Although these data were collected over multiple years, we assumed they were estimates of population size just before the start of the 2008 and 2014 breeding seasons. We scaled the estimates of Russell et al. to account for the fact that their estimate is of the total adult UK population of seals while the pup production model covers only the breeding colonies regularly surveyed – estimated to be 92.34% of total pup production in 2008 (Duck 2009) and 93.40% in 2014 (Russell pers. comm). Uncertainty in the estimates was represented using a right-shifted gamma distribution that was fitted to the nonparametric bootstrap distribution produced by Russel et al., after scaling, using maximum likelihood. We assumed the two estimates were independent of one another, when in fact they are derived partly from the same data (telemetry data used to derive the correction factor turning counts of hauled-out animals to a total population size) – see Discussion.

Prior distributions for the process model parameters were the same as the "revised priors" used in Thomas (2014); these in turn are those suggested by Lonergan (2012, Table 1), except for the prior on adult sex ratio, which was first suggested by Thomas (2014), and the prior on adult female survival, which was constrained to lie between 0.8 and 0.97 as suggested by Thomas (2015). 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. Prior distributions for the states were generated using the 1984 data, as described by Thomas and Harwood (2008).

Fitting method

The fitting method was identical to that of Thomas (2015), again using the particle filtering algorithm of Thomas and Harwood (2008). This involves simulating samples ("particles") from the prior distributions, projecting them forward in time according to the population model, and then resampling and/or reweighting them (i.e., “filtering”) according to their likelihood given the data. An identical algorithm to that of Thomas and Harwood (2008) was used for the pup production data, and the additional adult data was included by reweighting the final output according to the likelihood of the estimated 2008 and 2014 population sizes, using the method described by Thomas (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 2,000 replicate runs of 1,000,000 samples. A technique called 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). The rejection control threshold used was w_c=1000.

Additional investigation: effect of new total population size estimates

An estimate of total population size in 2008, derived by Lonergan et al. (2010) was used in previous year’s analyses. However, the value used here for this year, derived by Russell et al. (2016) from a re-analysis of the data, is higher than the value used previously; the variance is also larger. To determine the effect of this change, and of the new 2014 population size estimate, we re-ran the analysis using the same pup production data, but only the total population estimate for 2008 from Lonergan et al. (2010).

Results

Total population estimates for 2008 and 2014

The bootstrap estimates of total population size from Russell et al. (2016) were well approximated by right-shifted gamma distributions (Figure 1). The mean and SD of the bootstrap data were, after scaling, 94,390 (SD 9,787) for 2008 and 137,639 (SD 14,271) for 2014 (note that these are not identical to the numbers provided by Russell et al. because those are before scaling, have an additional 4% included to account for the proportion of the population in the South-west UK, and are medians not means); the equivalent values from the fitted gamma distributions were 94,399 (SD 9,788) and 137,650 (SD 14,273). (For the record, the right-shifted gamma distribution parameters were 59167.8, 12.9441 and 2719.38 (shift, shape and scale respectively) for 2008 and 86360.5, 12.9136 and 3971.20 for 2014.)

Monte Carlo accuracy

The effective sample size (ESS) of unique particles is a useful measure of the accuracy of the simulation. The ESS based on pup production data alone was 427.8 (Table 2, 1st row), and after inclusion of the independent population estimate was 97.5. ESSs smaller than this have been shown in previous briefing papers to produce population and parameter estimates accurate to around 2-3 significant figures, so we should expect the estimates reported here to be accurate to at least this level.

This latter ESS is larger than in previous briefing papers, likely because the independent population estimates had larger variance and so did not exert such a strong selection effect on the particles. This is confirmed by the fact that the additional investigation ESS (Table 2, 2nd row), which is from the analysis re-run using the Lonergan et al. (2010) total population estimate from 2008 (and excluding the total estimate for 2014) had a much smaller ESS of 7.6. Although population size estimates from this analysis are likely to be less accurate, they were only produced for the purposes of the additional investigation.

Parameter and population estimates

Model fits to pup production estimates are shown in Figure 2. Modelled pup production estimates are almost unchanged by the addition of the two total population size estimates to the model (cf. blue and red lines in Figure 2). The two most recent pup production estimates are higher than expected under the model in all four regions, but the effect is by far stronger in the Hebrides regions than North Sea or Orkney. Nevertheless, in Orkney the two most recent estimates are high, coming after 5 previous estimates that are relatively stable. In North Sea the estimates are somewhat consistent with a strongly increasing pattern, although the modelled pup production is not increasing as strongly as the pup production estimates indicate.

Estimated adult population size is shown in Figure 3. The estimates are significantly affected by the two total population size estimates: the 2015 estimate is 155,300 (95%CI 113,200-215,800) based on the pup production data alone, but is reduced to 127,100 (95%CI 105,900-151,900) with the addition of the total population estimates. Note that of the two estimates, the 2008 estimate is lower than the modelled adult population size in that year while the 2014 estimate is higher, and that in both cases the confidence intervals from the total population size estimates overlap the modelled credible intervals. Prior and posterior parameter estimates are shown in Figure 4. Estimated adult population size by region for 2015 is given in Table 2, and for all years is given in the Appendix. Posterior distributions on demographic parameters are not strongly affected by the addition of the total population size estimates (cf. Figures 4a and 4b).

Additional investigation: effect of new total population size estimates

The estimate of total population size in 2008 from Lonergan et al. (2010) was 14% lower than the estimate from Russell et al. (2016); the variance was also smaller (coefficient of variation, CV, 8.5% as opposed to 10.2%). Using the Lonergan et al. value for 2008 resulted in an estimated adult population size in 2015 that was 14% lower than the one reported above (109,000 with 95%CI 94,000-132,300). Note that this is the effect both of the different estimate for 2008 and of using no total population size estimate for 2014.

Discussion

The revised total population estimate for 2008 more closely matches the modelled population trajectory from pup production data, although the total estimate is still rather lower than that predicted by the model (cf. estimate with 2008 with blue line in Figure 3). The 2014 total estimate is also lower than that predicted by the model, but not as much. When pup production data and total population estimates are combined, the joint trajectory matches both datasets reasonably well. One area of concern, however, is the two most recent pup production estimates, which seem unexpectedly high given previous pup production numbers, especially in the Hebrides. The two most recent pup production estimates were produced after a change in survey methodology (and some analysis assumptions); further investigation of this is warranted. It should be noted that pup production in the North Sea region is partly estimated from ground counts, so these counts will need to be separated out in any statistical investigation.

The estimated population trajectory is somewhat higher than that reported last year: the 2014 estimated adult population size for the same model and priors was 105,200 (95% CI 87,000-128,800), compared with 2014 estimates in this report (Appendix) of 125,800 (95% CI 105,500-149,700) – about 20% higher. Our additional investigation showed that the difference in trajectory caused by the revised and new total population size estimate was 14%; therefore, the difference due to the additional pup count estimate is approximately 6%.

In using the total population estimates, we have assumed the two estimates are statistically independent, when in fact they both used the same multiplier to account for proportion of animals hauled out. It may be possible to account for this correlation in a revised analysis (although we also note that aspects of pup production estimation are the same across years, potentially inducing correlation there also).

The model assumes a fixed CV for pup production estimates, and obtains this value from an initial model run. Ideally, region-level estimates of pup production variance would be produced as part of fitting the pup production model to aerial pup count data; we plan to investigate this in the coming year. One factor that will require consideration is how to incorporate uncertainty on the ground counts made in some North Sea colonies.

Previous briefing papers (e.g., Thomas 2014, 2015) discussed other aspects of the model that could be improved, including a re-examination of the sex ratio prior and the movement of recruiting females between regions.

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Table 1. Prior parameter distributions and summary of posterior distributions. (The two parameters of the gamma distribution specified here are shape and scale respectively.) Posterior summaries are all from analyses that use both 1984-2014 pup production estimates, and the 2008 and 2014 total population estimates.

	Main analysis		
Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)
adult survival ϕ_a	0.8+0.17*Be(1.6,1.2)	0.90 (0.04)	0.95 (0.01)
pup survival ϕ_j	Be(2.87,1.78)	0.62 (0.20)	0.51 (0.08)
fecundity $\alpha_{\max}$	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.90 (0.06)
dens. dep. ρ	Ga(4,2.5)	10 (5)	3.47 (0.79)
NS carrying cap. χ_1	Ga(4,2500)	10000 (5000)	1700 (3900)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3620 (277)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	12700 (693)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	23000 (2470)
observation CV ψ	Fixed	0.89 (0)	-
sex ratio ω	1.6+Ga(28.08, 3.70E-3)	1.7 (0.02)	1.7 (0.02)

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 estimates (ESS_{u2}). For the second row, the last part of the analysis, where the independent population size is introduced, was re-run with only the 2008 estimate from Lonergan et al. (2010).

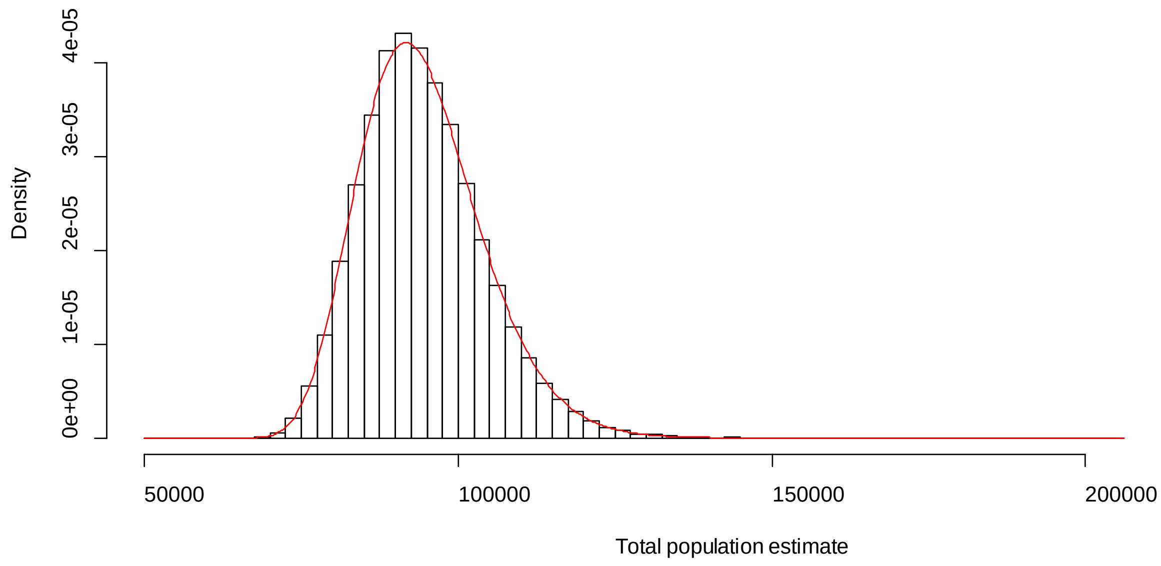
Model	*K* (x10^7)	*K** (x10^6)	*U* (x10^4)	ESS_{u1}	ESS_{u2}
EDDSNM All data	2000	28.5	32.3	427.8	97.5
EDDSNM Old 2014 total pop size estimate	.	.	.	.	7.6

Table 3. Estimated size, in thousands, of the British grey seal population at the start of the 2015 breeding season, derived from models fit to pup production data from 1984-2014 and the additional total population estimates from 2008 and 2014, using the revised parameter priors. Numbers are posterior means with 95% credible intervals in brackets.

	Estimated population size in thousands (95% CI)
North Sea	33.7 (26.2 41.4)
Inner Hebrides	8.7 (7.3 10.3)
Outer Hebrides	30.4 (26.3 35.2)
Orkney	4.3 (46.1 65.1)
Total	127.1 (105.9 151.9)

Figure 1. Histograms of total population estimates from Russell et al. (2016) (scaled to account for colonies not regularly surveyed) with fitted right-shifted gamma distributions (line).

(a) 2008



(b) 2014

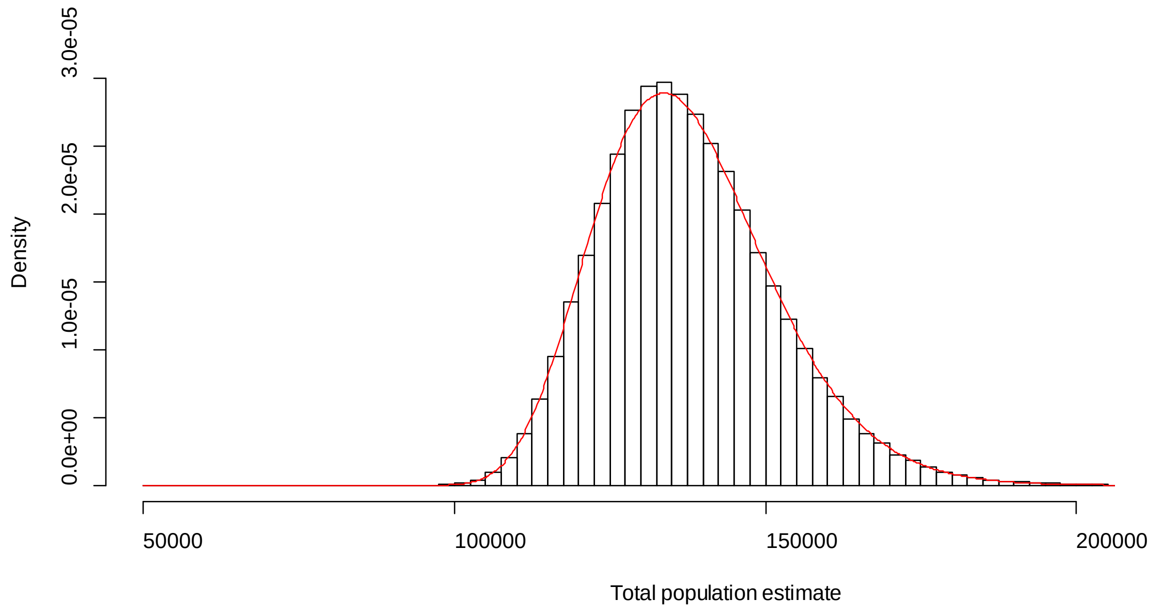


Figure 2. Posterior mean estimates of pup production (solid lines) and 95%CI (dashed lines) from the model of grey seal population dynamics, fit to pup production estimates from 1984-2014 (circles) and the total population estimates from 2008 and 2014. Blue lines show the fit to pup production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

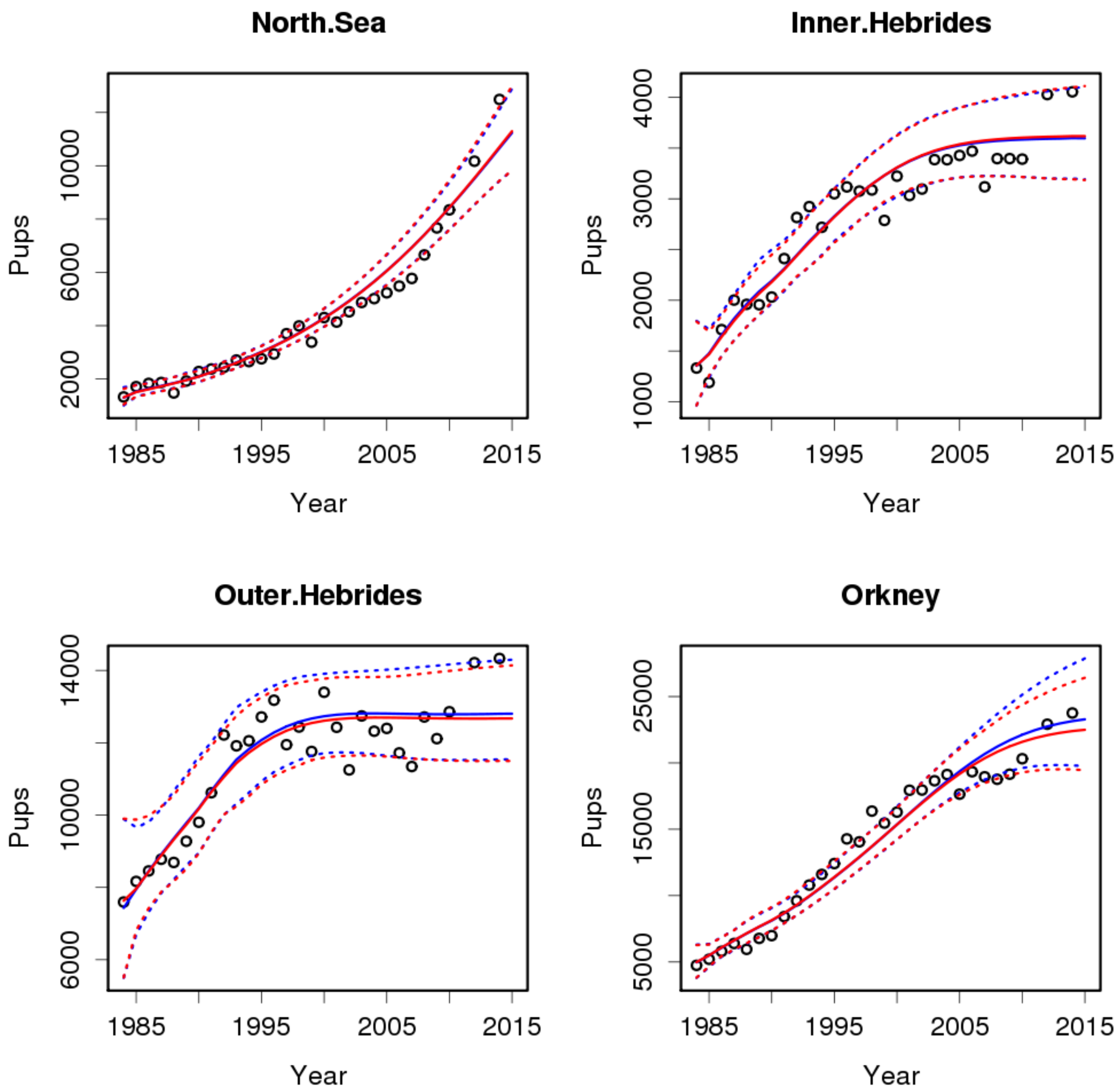


Figure 3. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2015 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2014 and total population estimates from 2008 and 2014 (circles, with vertical lines indicating 95% confidence interval on the estimates). Blue lines show the fit to pup production estimates alone; red lines show the fit to pup production estimates plus the total population estimates.

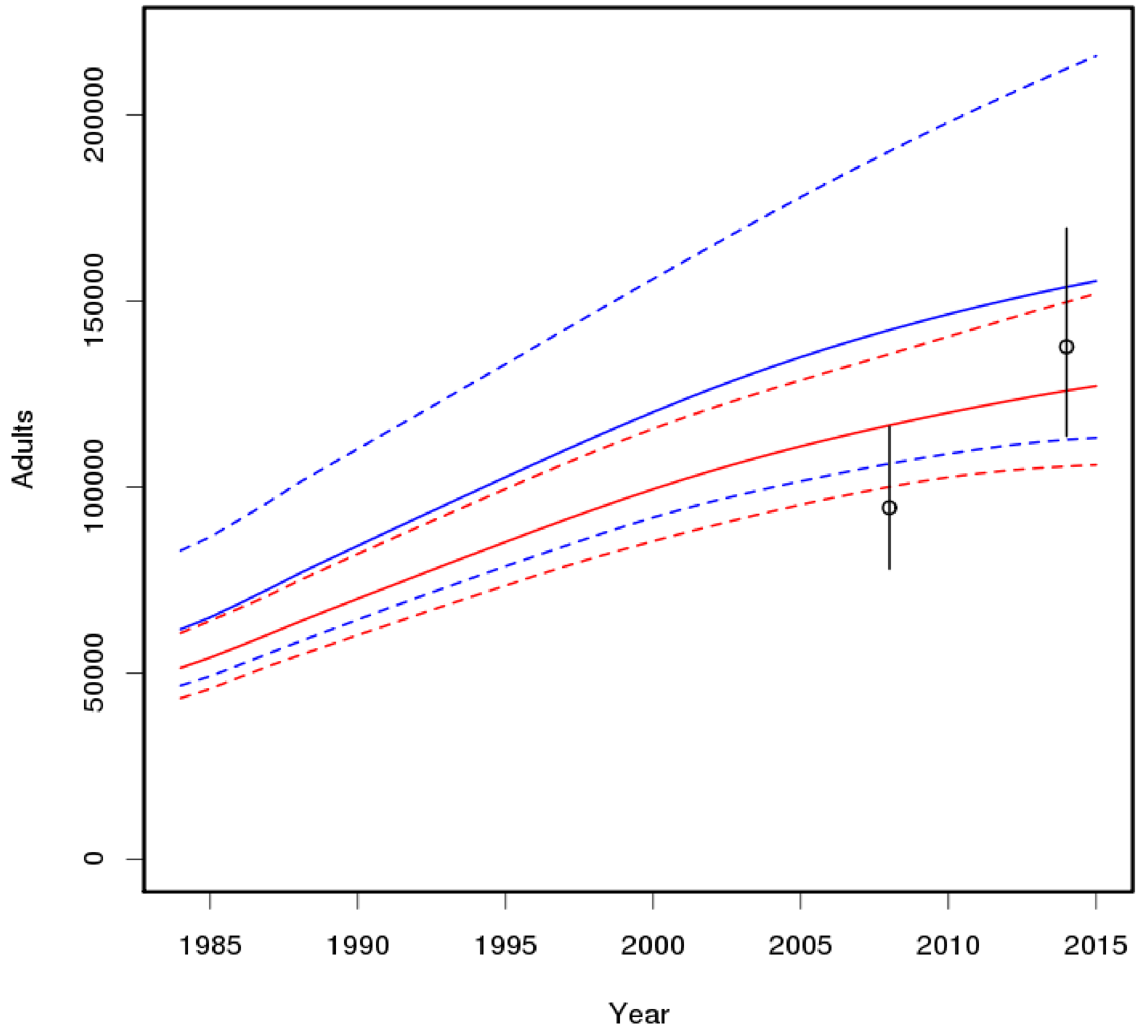
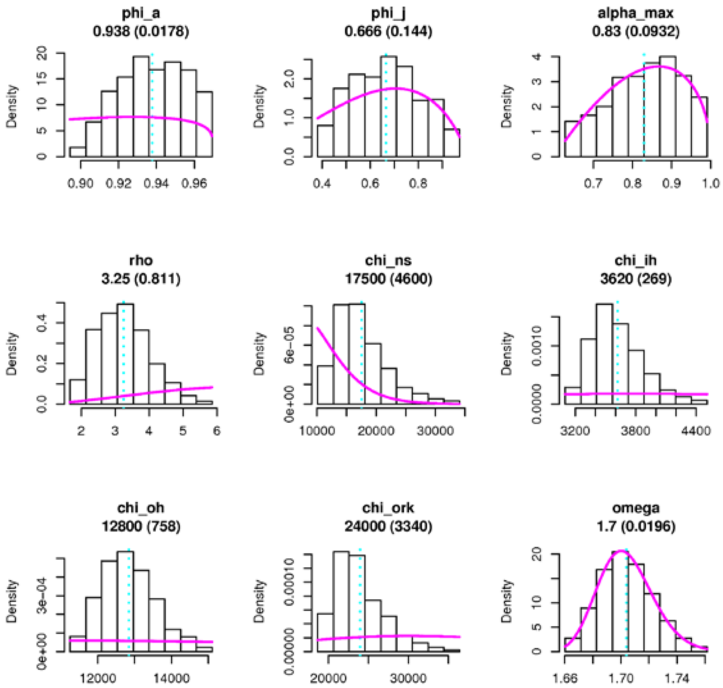
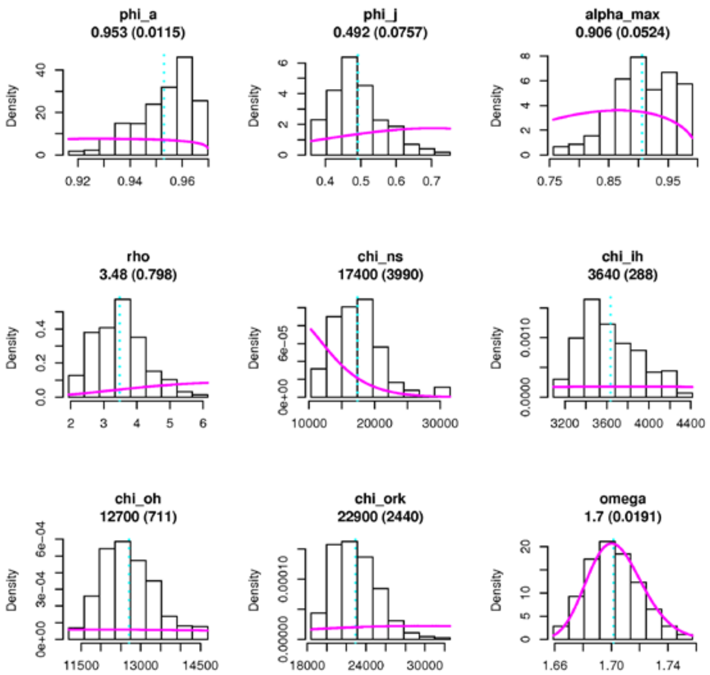


Figure 4. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2014 and total populations estimate from 2008 and 2014. The vertical dashed line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

(a) Pup production data alone



(b) Pup production data and 2008 and 2014 population estimates



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2015, made using the model of British grey seal population dynamics fit to pup production estimates from 1984-2014 and total population estimates from 2008 and 2014. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.7 (4 5.5)	5 (4.2 5.9)	23.3 (19.7 27.6)	18.4 (15.4 21.7)	51.4 (43.2 60.7)
1985	5 (4.2 5.8)	5.2 (4.4 6.2)	24.4 (20.6 29)	19.5 (16.5 23)	54.1 (45.8 64)
1986	5.4 (4.6 6.3)	5.5 (4.7 6.5)	25.5 (21.8 30.3)	20.8 (17.7 24.3)	57.2 (48.9 67.4)
1987	5.8 (5 6.7)	5.8 (5 6.9)	26.5 (22.8 31.4)	22.3 (19.1 25.9)	60.4 (51.9 70.9)
1988	6.3 (5.4 7.2)	6.2 (5.3 7.3)	27.4 (23.5 32.6)	23.9 (20.5 27.7)	63.7 (54.7 74.8)
1989	6.7 (5.8 7.8)	6.5 (5.6 7.7)	28.1 (24.1 33.3)	25.6 (21.9 29.6)	66.9 (57.4 78.4)
1990	7.2 (6.2 8.3)	6.8 (5.9 8)	28.7 (24.6 34)	27.3 (23.4 31.6)	70 (60.2 82)
1991	7.7 (6.7 8.9)	7 (6.2 8.3)	29.2 (25.1 34.5)	29.1 (25 33.7)	73 (62.9 85.6)
1992	8.3 (7.2 9.6)	7.3 (6.4 8.6)	29.6 (25.5 35)	30.9 (26.6 35.8)	76.1 (65.6 89.1)
1993	8.9 (7.7 10.3)	7.5 (6.5 8.9)	29.9 (25.8 35.2)	32.9 (28.2 38)	79.2 (68.2 92.5)
1994	9.6 (8.3 11.1)	7.8 (6.7 9.2)	30.1 (26 35.4)	34.8 (29.8 40.3)	82.2 (70.9 96)
1995	10.3 (8.9 11.9)	7.9 (6.8 9.4)	30.2 (26.2 35.5)	36.8 (31.5 42.6)	85.2 (73.5 99.5)
1996	11 (9.6 12.8)	8.1 (7 9.6)	30.3 (26.4 35.5)	38.8 (33.1 45)	88.2 (76.1 102.9)
1997	11.8 (10.3 13.7)	8.2 (7.1 9.7)	30.4 (26.5 35.5)	40.7 (34.8 47.2)	91.1 (78.6 106.2)
1998	12.6 (11 14.7)	8.3 (7.1 9.9)	30.4 (26.5 35.5)	42.6 (36.3 49.4)	94 (81 109.5)
1999	13.5 (11.8 15.8)	8.4 (7.2 9.9)	30.4 (26.5 35.4)	44.3 (37.8 51.5)	96.7 (83.2 112.6)
2000	14.5 (12.6 16.9)	8.5 (7.2 10)	30.4 (26.5 35.3)	46 (39.1 53.4)	99.4 (85.4 115.6)
2001	15.5 (13.5 18.2)	8.5 (7.3 10)	30.4 (26.5 35.2)	47.4 (40.3 55.1)	101.9 (87.5 118.5)
2002	16.6 (14.4 19.4)	8.6 (7.3 10.1)	30.4 (26.4 35.2)	48.8 (41.5 56.6)	104.4 (89.5 121.2)
2003	17.8 (15.3 20.8)	8.6 (7.3 10.1)	30.4 (26.4 35.1)	49.9 (42.5 57.9)	106.7 (91.5 123.8)
2004	19 (16.3 22.2)	8.6 (7.3 10.1)	30.4 (26.4 35.1)	50.9 (43.4 59)	108.8 (93.4 126.3)
2005	20.2 (17.4 23.6)	8.6 (7.3 10.1)	30.4 (26.4 35)	51.7 (44.2 59.9)	110.9 (95.2 128.7)
2006	21.5 (18.4 25.2)	8.6 (7.3 10.1)	30.3 (26.3 35)	52.4 (44.8 60.7)	112.9 (96.9 131)
2007	22.9 (19.6 26.8)	8.6 (7.3 10.2)	30.3 (26.3 35)	52.9 (45.3 61.4)	114.8 (98.5 133.4)
2008	24.2 (20.7 28.5)	8.7 (7.3 10.2)	30.3 (26.3 35)	53.3 (45.7 62)	116.5 (100 135.7)
2009	25.6 (21.8 30.2)	8.7 (7.3 10.2)	30.3 (26.3 35)	53.6 (46 62.6)	118.3 (101.4 138)
2010	27.1 (22.8 31.9)	8.7 (7.3 10.2)	30.4 (26.3 35.1)	53.9 (46.2 63.2)	119.9 (102.6 140.4)
2011	28.5 (23.7 33.8)	8.7 (7.3 10.2)	30.4 (26.3 35.1)	54 (46.3 63.7)	121.5 (103.6 142.7)
2012	29.9 (24.5 35.6)	8.7 (7.3 10.2)	30.4 (26.3 35.1)	54.1 (46.3 64.1)	123 (104.4 145.1)
2013	31.2 (25.2 37.5)	8.7 (7.3 10.3)	30.4 (26.3 35.1)	54.2 (46.2 64.5)	124.5 (105 147.4)
2014	32.5 (25.8 39.5)	8.7 (7.3 10.3)	30.4 (26.3 35.2)	54.3 (46.1 64.8)	125.8 (105.5 149.7)
2015	33.7 (26.2 41.4)	8.7 (7.3 10.3)	30.4 (26.3 35.2)	54.3 (46.1 65.1)	127.1 (105.9 151.9)