Estimating the size of the UK grey seal population between 1984 and 2012, using established and draft revised priors

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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 2010 (no pup production assessments were made in 2011, and estimates for 2012 were not available at time of writing), and (2) an independent estimate assumed to be of total population size just before the 2008 breeding season. 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 the EDDSNM model used in previous briefing papers, and used the same priors on demographic parameters that have been used since 2005. Estimated adult population size in 2012 was 100,300 (95% CI 80,700-128,100).

In addition, we undertook some additional investigations. First, we fitted the model using a set of revised priors on demographic parameters that were introduced in a 2012 briefing paper. Second, we included a prior on sex ratio, rather than assuming this value is known as in previous analyses. Third, we examined correlation in the parameter estimates. Forth, we fitted the model separately in each region to assess evidence for regionally-varying demography above that allowed by the global model. Fifth, we re-fitted the model using fecundity estimates derived directly from the long-term studies on Isle of May and North Rona to assess the sensitivity of model outputs to prior specification. Results of these investigations are presented in the paper, together with discussion of future research needs.

Introduction

This paper presents estimates of British grey seal population size and related demographic parameters, using identical the models and fitting methods to Thomas (2011), but projecting forward one more year to 2012. Models are specified using a Bayesian state space framework with informative priors on demographic parameters, and fitted using a Monte Carlo particle filter. In past briefing papers, multiple models of the population dynamics have been fitted and compared, representing differing hypotheses about the demographic parameter subject to density dependent regulation. The model where density dependence affects pup survival was found to be better supported by the data than one where density dependence affects female fecundity; hence only the former is used here.

A number of additional investigations are also undertaken, related to the priors used on demographic parameters. Lonergan (2012) introduced a revised set of priors, based on updated information and discussions within the Sea Mammal Research Unit; these were used by Thomas (2012) to assess what difference these make to the population estimates and this study is repeated here. We also investigate the consequences of using a prior on sex ratio, rather than assuming a fixed sex ratio, as in previous analyses. We investigate the use of separate regional models, rather than the current global model, and also the effect of using priors on fecundity that are derived directly from the intensive studies on Isle of May and North Rona. The reason to focus on fecundity is that, as we show, this is the parameter whose specification makes the most difference to the estimate of total population size.

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). In summary, the model tracks seal population numbers in 7 age groups (pups, age 1-5 females, which do not pup, and age 6+ females, which may produce a single pup) 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.) The model has 8 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 and fecundity (i.e., probability that an age 6+ female will birth a pup), α.

The model does not describe the dynamics of adult male seals. To obtain an estimate of total population size we followed previous briefing papers in multiplying 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, and we also obtained results using this prior, as detailed below under Additional investigations.

Data, observation models, and priors

One source of input data was the pup production estimates for 1984-2010 from Duck (2011), aggregated into regions. These 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). We followed Thomas (2011) in assuming a CV of 9.8%. (This is based on an estimate from running a simple model; it could be estimated for the EDDSNM model used here or integrated out if required (see Thomas and Harwood 2008), but previous analyses have shown results to be quite insensitive to the actual value used for observation CV.)

The second source of input data was a single estimate of adult population size of 88,300 (95% CI 75,400-105,700) obtained by Lonergan et al. (2010) from summer haulout counts and telemetry data. We followed previous briefing papers (e.g., Thomas 2012) in assuming the estimate was of population size just before the start of the 2008 breeding season, and by representing the uncertainty in the estimate (which Lonergan obtained via a nonparametric bootstrap) using a right-shifted gamma distribution.

Prior distributions for the process model parameters were the same as those used in previous briefing papers (first introduced in Thomas and Harwood 2005), and are given in Table 1. (We also did runs using alternative priors – see Additional investigations, below.) 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).

In summary, the data and priors used here are almost identical to those used by Thomas (2011), except the observation error CV used here is the one that was estimated in that paper. We therefore expect the estimates for 2010 to be almost identical to those of Thomas (2011); the only difference here is that we are projecting the population forward one additional year, to yield population size estimates for 2012.

Fitting method

We used 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 count data, and the additional adult data was included by reweighting the final output according to the likelihood of the estimated 2008 population size, as 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 1,000 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).

Additional investigations

Revised priors

We re-fitted the model using the revised priors suggested by Lonergan (2012; see Table 1), and assuming a CV on pup production of 8.9% (again, obtained by first fitting a simpler model, see Thomas 2012).

Prior on sex ratio

In calculating total population size, the above models assume a fixed multiplier of 1.73 on the estimated adult female population. However, given the independent estimate of total population size, it is possible to estimate the multiplier value, given a prior distribution. We implemented this, using the prior suggested by Lonergan (2012) (denoted ω in Table 1), which has a prior mean of 1.2 and standard deviation of 0.63. (In practice, this involved re-weighting the outputs from the previous revised priors analysis, so no additional model runs were required.)

Parameter correlations

One way to investigate the sensitivity of the model to changes in priors on the parameters is to examine the correlation in the joint posterior parameter estimates. For example, for parameters that are highly negatively correlated, changing the prior on one by decreasing its value will result in a concomitant increase in the value of the other and hence little difference in model fit or predictions. As an initial investigation we calculated pairwise correlations and produced a scatterplot of the posterior parameter values.

Regional model
The models fit above ("global models") assume that adult survival (ϕ_a), fecundity (α) and the density-dependence shape parameter (ρ) are the same in all four regions. To investigate the support for this, we re-fit the data independently in each region, using the revised priors in Table 1 but assuming a fixed sex ratio. We documented the difference in posterior parameter estimates for these four regional models compared with the global model, and the differences in estimated total population size. In this analysis, we used the pup production data alone; it would be feasible to fit a joint regional model and include the 2008 total population size estimate as data, however including the total population size estimate would reduce any differences in the final estimate of population size between this analysis and the global model analysis. Only 150 runs of 1,000,000 samples were used in each of these analyses, so results will have higher Monte Carlo error than the previous ones.

Prior on fecundity from intensively-studied populations
There are two intensively-studied populations, at Isle of May and North Rona, for which minimum fecundity rate estimates can be derived, as documented in Lonergan (2012). Values are given in Table 3 of that paper, based on unpublished work by P. Pomeroy and S. Smout. These are (for all years of data) 0.63 (95% CI 0.59-0.68) for Isle of May and 0.72 (95% CI 0.69-0.74) for North Rona. These values were fit to scaled shifted beta distributions (using a sum of squares objective function); in the event the shift parameter was estimated as being very close to 0 so beta distributions were used (see Table 1). These fitted distributions were used as priors in re-runs of the North Sea and Outer Hebrides regional models (again with 150 runs of 1,000,000 particles), assuming that the Isle of May and North Rona colonies were representative of these two regions, respectively.

Results

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 count data alone was 572.5 (Table 2), and after inclusion of the independent population estimate was 82.5. ESSs around 5 times lower lower 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.

Parameter and population estimates
Model fits to the pup production estimates are shown in Figure 1. As noted by Thomas (2011), the estimates broadly provide a reasonable fit to the pup production data, but there are some clear deficiencies: the fitted model does not adequately capture the rapid rise and sudden levelling off in pup production in the Hebrides during the early 1990s, nor levelling off in Orkney in the late 1990s; it over-estimates pup production in the North Sea in the late 1990s and early 2000s, and does not track the strong increases in pup production there in the past 3 years. Addition of the 2008

independent estimate makes little difference to this part of the model, except in the last years where the addition of the independent estimate decreases the estimated pup count slightly.

Parameter estimates are shown in Figure 2 and summarized in Table 1. The independent population size estimate causes the estimates of adult survival to increase slightly (to 0.95), maximum juvenile survival to decrease (to 0.5), and fecundity to increase slightly (to 0.96) but stay very close to the prior distribution.

Adult population size estimates are shown in Figure 3; the values for 2012 are also given in Table 3. The independent estimate for 2008 of 88,300 (with 95%CI 75,400-105,700) is lower than the value predicted for that year from pup production data alone (125,500, with 95%CI 93,400-167,400), although the credible/confidence intervals overlap. When the independent estimate is included in the population dynamics model fitting, the estimate for 2008 from this model decreases by 20% to 100,300 (95%CI 80,700-128,100). Estimates for all years from the model fit to both pup production data and the independent estimate are given in Appendix 1. The estimate from 2010 (100,000) is, as expected, very close to the estimate for 2010 (of 99,600) made by Thomas (2011) using the estimated CV that was assumed fixed in this model.

Additional investigations

Revised priors
As might be expected, use of revised priors caused differences in posterior parameter estimates (Figure 4 and Table 1). Adult survival was estimated to be higher, and maximum pup survival lower; fecundity was estimated to be higher but was, just as with the previous analysis, almost completely governed by the prior distribution. Addition of the 2008 independent population estimate caused the estimate of adult survival to increase still further (to an implausible 0.985) and maximum pup survival to decrease further (to an also unlikely 0.3), while fecundity was also slightly higher.

Estimates of total population size are somewhat lower without the independent population estimate (cf. blue lines on Figure 3 and 5), which is unsurprising given the revised prior (and posterior) on fecundity is lower. The addition of the independent population size estimate again lowers the total population size estimate, and the result is slightly lower than with the old priors (cf. red lines on Figures 3 and 5).

Prior on sex ratio
With the addition of a prior on sex ratio, posterior estimates of survival remained closer to more realistic values, even with the addition of the 2008 independent population estimate (Figure 6 and Table 1). The posterior on fecundity also remained close to the prior with the addition of the independent estimate. This is because even without this estimate, the estimated total population size was close to that of the independent estimate (Figure 7, blue line); this meant that little alteration in the demographic parameters was required when the independent estimate was introduced. Note that this includes the posterior on the sex ratio parameter – this could potentially be greatly affected by the independent estimate, but because the estimates of total population size from the population dynamics model and independent estimate were so congruent, it was little changed by introduction of the independent estimate into the analysis. The resulting estimate of total population size was similar to that without the independent estimate (Figure 7), but rather more precise (dashed lines in Figure 7 show 95% posterior CI; see also Table 4).

Parameter correlations

The scatterplot of posterior parameter estimates from the previous analysis is shown in Figure 8. Correlations of greater than 0.7 were observed between adult and pup survival (ϕ_a and ϕ_p, -0.94), carrying capacity in the Inner and Outer Hebrides (ψ_{ih} and ψ_{oh}, 0.83) and between adult survival and carrying capacity in the Inner Hebrides (ϕ_a and ψ_{ih}, 0.71). Other, weaker, relationships were also evident (Figure 8) particularly within the carrying capacity parameters and between these and adult survival.

The fact that adult and juvenile survival are so strongly correlated implies that changes in the prior, and therefore posterior, for one will be compensated for by an opposite change in the posterior for the other, thereby having relatively little effect on estimates of total population size (given the constraint of the independent estimate). This was indeed seen when comparing the old and revised priors analyses. By contrast fecundity is not correlated with other parameter estimates; this coupled with the fact that the prior on fecundity is informative to the extent it is not changed greatly by the data in any of the analyses to date means that the prior chosen for fecundity can be expected to have a very strong influence on the estimates of total population size.

Regional models

Fits to the pup production data from the regional models (not shown) were largely similar to the global model, although the fit to Orkney data was somewhat better, with a more rapid levelling-off of pup production in recent years, better matching the data. Posterior parameter estimates for the survival and fecundity parameters were, on the whole, rather similar to those from the global model (Table 5), although the adult survival estimate was somewhat lower (0.94) than the other regions (0.96-0.97) and the global model (0.96). Estimates of carrying capacity (Table 5) were considerably higher in the North Sea region, and were effectively infinity in the Outer Hebrides – the latter is inexplicable and may indicate an issue with the model fitting that needs to be investigated further.

Estimated adult population sizes by region were not greatly different from the global model (Table 6), with the total population size estimate summed across regions being approximately 2% lower (123,000 for the global model and 120,700 for the regional model).

Prior on fecundity from intensively-studied populations

As might be expected given previous analyses, the posterior estimates on fecundity were close to the priors used in these analyses (Table 5), and these produced corresponding changes in the estimates of adult population size for the two regions affected (Table 6): estimates for North Sea were approximately 15% higher and for Outer Hebrides 10% higher. Since these two regions together comprise around 50-60% of the total population, the effect on total adult population size was more modest – an approximate 7% increase (to 129,500).

Discussion

Main analysis

Estimated total population sizes for 1983-2011 are very similar to those reported by Thomas (2011) for the EDDSNM model, which is to be expected given that the same data and priors were used. Pup counts were undertaken in 2012, and will be included in future model fits once available – we anticipate that these will change our estimates of population trajectory somewhat.

The relative weight of the independent estimate and pup production data depends in part on the coefficient of variation on the pup production data. Here this was assumed fixed, but methods exist to allow this to be a model parameter, with some prior distribution, and then integrate it out of the estimates. Although this is likely to produce very similar results, it is a neater solution, and hence is to be preferred.

Additional investigations

We have made an initial investigation of the sensitivity of the total population size estimate to changes in priors on demographic parameters. The strong inverse correlation between posterior estimates of adult and pup survival means that changes in the priors on these parameters have little effect on estimated total population size. By contrast, the fecundity parameter is not correlated with the other parameters, and the prior is also highly informative in the sense that the posterior is almost identical to the prior in all of the analyses performed here, meaning that the data carry little additional information about this parameter; changes in this parameter have a strong effect on population size estimates. We also found that allowing sex ratio to be a parameter, rather than assuming it to be fixed, had a strong effect on estimated population size. It is interesting to note that the population estimates produced by the population dynamics model fit to pup production data and with revised priors including a prior on sex ratio were very similar to the independent population size estimate – this perhaps provides some confirmation for the choice of priors. More work, however, is required to refine the prior distributions, and future work should focus on the priors for fecundity and sex ratio.

We have not investigated the sensitivity of population size estimates to priors on the carrying capacity parameters – this can be expected to be quite low because these parameters are either reasonably well specified by the data (i.e., the priors are changed considerably by the data) or, in the case of the North Sea region, which does not appear to be close to carrying capacity, the posterior estimate is expected to have little effect on the estimated population size. Nevertheless, these parameters should be investigated.

Apart from simply varying the prior distributions, other means exist for quantifying prior sensitivity. For example, Millar (2004) quantified sensitivity of parameter posteriors using a measure of the differential of the posterior mean with respect to prior parameters; this approach could potentially be extended to quantifying sensitivity of the posterior on measures that are not explicit model parameters, but are derived measures, such as population size.

The regional models did not produce results that were substantially different from the global model, suggesting that further investigation of this topic should be a secondary concern. Despite this, including the four regions within the global model seems useful, not least because regional estimates of total population size are useful for management purposes.

Data on pup production is now collected only every second year, with estimates for 2012 expected to be available in the near future. One potential future refinement would be to incorporate the pup production estimation process within the Bayesian framework used here to fit population dynamics models. This has the potential benefit of allowing the statistical uncertainty arising from pup production estimation to cascade naturally into the population dynamics modelling, rather than through the use of a measurement error parameter as happens currently. It is this measurement error parameter, together with the estimated uncertainty on the independent estimate of population size that controls the relative influence of the population dynamics model and the independent estimate on the final population size estimate. With the revised priors, the population dynamics model and the independent estimate produce similar results, and so the weighting of each is not important. Also, it seems unlikely that the weighting given to the population dynamics model would be much different from that currently used – hence this refinement is also considered to be of secondary importance.

In conclusion, the main priority for future work is to refine the priors on fecundity and sex ratio, and we expect to be able to report on this in future briefing papers.

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Table 1. ***Prior parameter distributions and summary of posterior distribution****. (The two parameters of the gamma distribution specified here are shape and scale respectively.) Posterior summaries are all from analyses that use both 1984-2010 pup production estimates and the 2008 total population estimates.*

	Main analysis			Additional investigations					
	Old priors			Revised priors			Revised priors with sex ratio not fixed		
Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)
adult survival ϕ_a	Be(22.05,1.15)	0.95 (0.04)	0.95 (0.016)	0.8+0.2*Be(1.6,1.2)	0.91 (0.05)	0.99 (0.01)	same as previous		0.95 (0.03)
pup survival ϕ_j	Be(14.53,6.23)	0.70 (0.10)	0.50 (0.10)	Be(2.87,1.78)	0.62 (0.20)	0.30 (0.07)	same as previous		0.57 (0.18)
fecundity $\alpha_{\max}$	Be(22.05,1.15)	0.95 (0.04)	0.96 (0.03)	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.89 (0.06)	same as previous		0.80 (0.09)
dens. dep. ρ	Ga(4,2.5)	10 (5)	4.55 (1.33)	same as previous		7.47 (3.69)	same as previous		4.77 (2.05)
NS carrying cap. χ_1	Ga(4,2500)	10000 (5000)	8900 (2530)	same as previous		10100 (3370)	same as previous		10800 (3270)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3270 (274)	same as previous		3280 (11800)	same as previous		3310 (247)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	12100 (717)	same as previous		11800 (1130)	same as previous		12200 (742)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	19500 (2990)	same as previous		20100 (2670)	same as previous		20800 (2920)
observation CV ψ	Fixed	0.098 (0)	-	Fixed	0.89 (0)	-	same as previous		-
sex ratio ω	Fixed	1.73 (0)	-	same as previous		-	1+Ga(0.1,2)	1.2 (0.63)	1.2 (0.13)

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}). Only the global model runs are shown; sample sizes for the regional models were considerably smaller.***

Model	K ($x10^7$)	K^* ($x10^7$)	U ($x10^4$)	ESS_{u1}	ESS_{u2}
EDDSNM Old priors	1000	12.4	24.0	572.5	82.3
EDDSNM New priors	1000	18.0	18.8	500.7	117.2
EDDSNM New priors, estimated sex ratio	n/a				358.6

Table 3. **Estimated size, in thousands, of the British grey seal population at the start of the 2012 breeding season, derived from models fit to pup production data from 1984-2010 and the additional total population estimate from 2008, using the old parameter priors. Numbers are posterior means with 95% credible intervals in brackets.**

	Pup production data alone	Pup production data and 2008 population estimate
North Sea	26.4 (17.5 36.5)	20.3 (14.5 30.3)
Inner Hebrides	8.9 (7.2 10.9)	7.5 (6.2 9.0)
Outer Hebrides	33.3 (26.8 40.0)	28.0 (24.3 33.2)
Orkney	56.9 (41.9 80.0)	44.4 (35.8 55.6)
Total	125.5 (93.4 167.4)	100.3 (80.7 128.1)

Table 4. **Estimated size, in thousands, of the British grey seal population at the start of the 2012 breeding season, using a variety of parameter priors. Numbers are posterior means with 95% credible intervals in brackets.**

Total	Pup production data alone	Pup production data and 2008 population estimate
Old priors	125.5 (93.4 167.4)	100.3 (80.7 128.1)
Revised priors	123 (83.9 179.5)	94.2 (76.5 117)
Revised priors with estimated sex ratio	85.3 (54.4 133.1)	88.8 (70.9 111.7)
Regional model (using revised priors)	120.7 (no CI calculated)	-
Regional model (using revised priors and priors on fecundity for NS and OH from intensively studied populations)	129.5 (no CI calculated)	-

Table 5. ***Prior parameter distributions and summary of posterior distribution for the regional models****. (The two parameters of the gamma distribution specified here are shape and scale respectively.) Posterior summaries are all from analyses that use only 1984-2010 pup production estimates.*

	Revised priors, global model			Regional model (priors same as "Revised priors" analysis)				Regional model (fecundity priors from intensively studied populations)					
				North Sea	Inner Hebrides	Outer Hebrides	Orkney	North Sea			Outer Hebrides		
Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Posterior mean (SD)	Posterior mean (SD)	Posterior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)
adult survival ϕ_a	0.8+0.2*Be(1.6,1.2)	0.91 (0.05)	0.96 (0.03)	0.94 (0.03)	0.97 (0.03)	0.96 (0.04)	0.97 (0.02)	same as previous		0.95 (0.02)	same as previous		0.96 (0.03)
pup survival ϕ_j	Be(2.87,1.78)	0.62 (0.20)	0.51 (0.20)	0.63 (0.18)	0.61 (0.18)	0.57 (0.20)	0.60 (0.17)	same as previous		0.66 (0.17)	same as previous		0.58 (0.20)
fecundity α_{max}	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.81 (0.09)	0.83 (0.09)	0.83 (0.09)	0.82 (0.09)	0.82 (0.09)	Be(279,161)	0.63 (0.02)	0.64 (0.02)	Be(886,355)	0.71 (0.01)	0.71 (0.01)
dens. dep. ρ	Ga(4,2.5)	10 (5)	5.35 (2.76)	10.5 (5)	4.9 (2.6)	6.93 (3.94)	5.72 (3.25)	same as previous		10 (4.7)	same as previous		7.06 (3.87)
ns carrying cap. χ_1	Ga(4,2500)	10000 (5000)	10800 (3410)	25200 (30100)				same as previous		27000 (37200)	same as previous		
ih carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3300 (266)		3400 (550)			same as previous			same as previous		
oh carrying cap. χ_3	Ga(4,3750)	15000 (7500)	12100 (860)			1E34		same as previous			same as previous		12200 (11700)
ih carrying cap. χ_4	Ga(4,10000)	40000 (20000)	20800 (3100)				19600 (5250)	same as previous			same as previous		
observation CV ψ	Fixed	0.098 (0)	-	-	-	-	-	same as previous		-	same as previous		-
sex ratio ω	Fixed	1.73 (0)	-	-	-	-	-	same as previous		-	same as previous		-

Table 6. **Estimated size, in thousands, of the British grey seal population at the start of the 2012 breeding season by region for the global model and the regional models, using revised priors. Numbers are posterior means with 95% credible intervals in brackets.**

	Global model	Regional model	Regional model, with priors for NS and OH from intensively studied populations
North Sea	26.1 (15.8 39.6)	32.3 (18.2 44)	37.5 (22.1 48.1)
Inner Hebrides	8.8 (6.2 12.1)	8.2 (6 11.5)	same as previous
Outer Hebrides	32.7 (23.5 44.3)	33.3 (21.4 54.8)	36.7 (26.8 58.5)
Orkney	55.5 (38.4 83.5)	46.9 (34.1 64.1)	same as previous
Total	123 (83.9 179.5)	120.7 (CI not calculated)	129.5 (CI not calculated)

Figure 1. 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 1984-2010 (circles) and a total population estimate from 2008, using the old parameter priors. Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

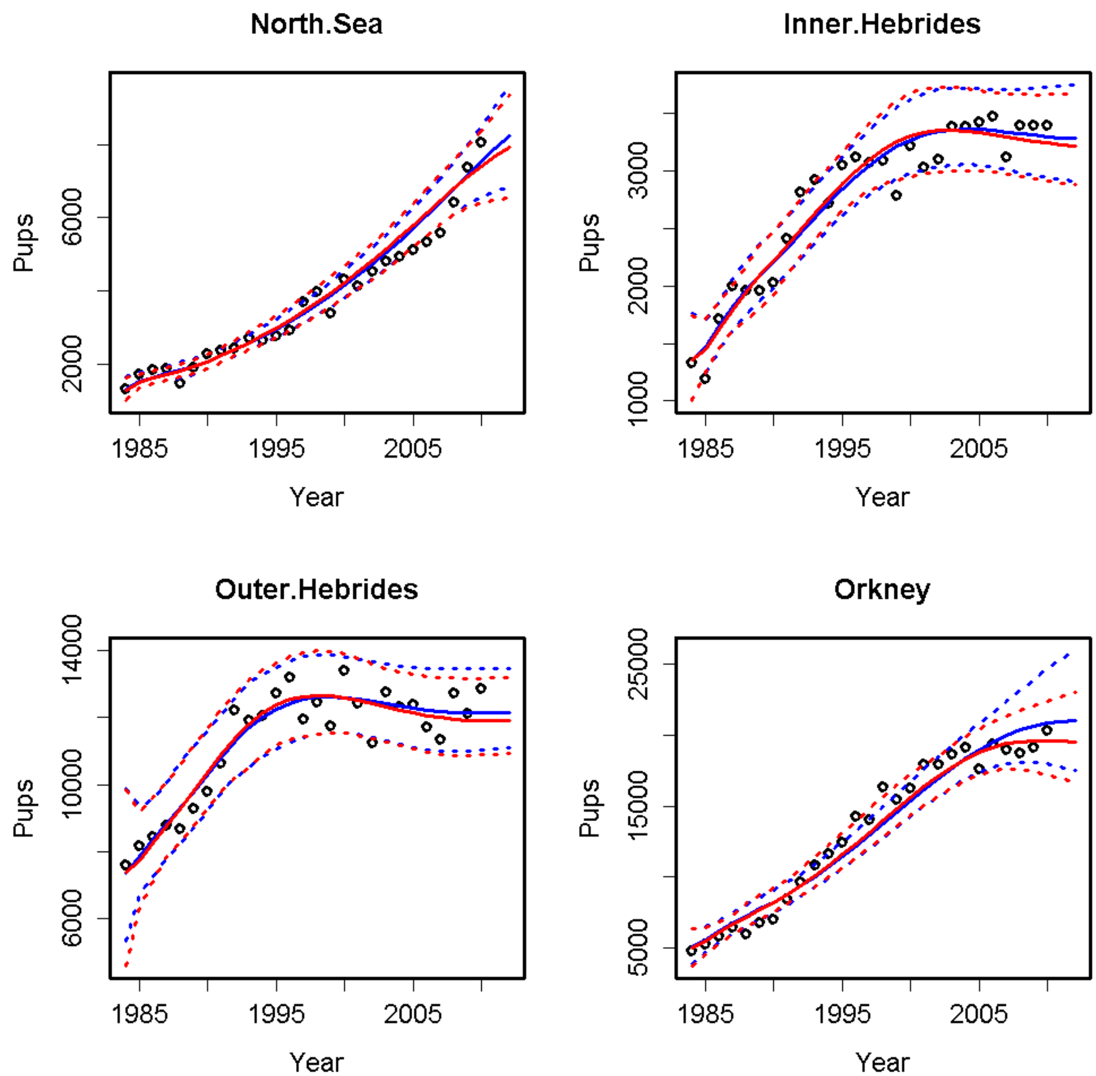
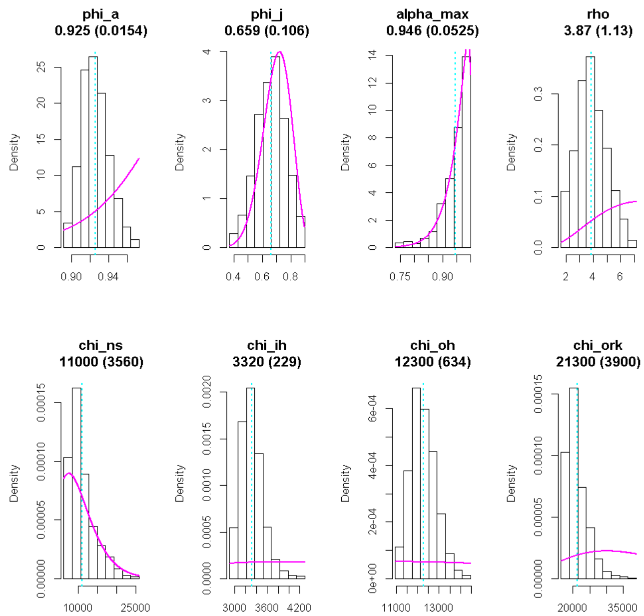


Figure 2. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2010 and a total population estimate from 2008, using the old parameter priors. The vertical line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

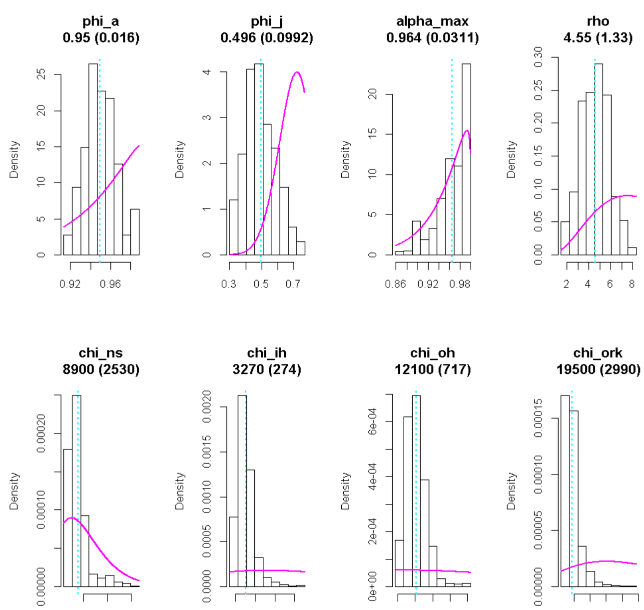


Figure 3. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2012 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2010 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate) , using the old parameter priors. Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

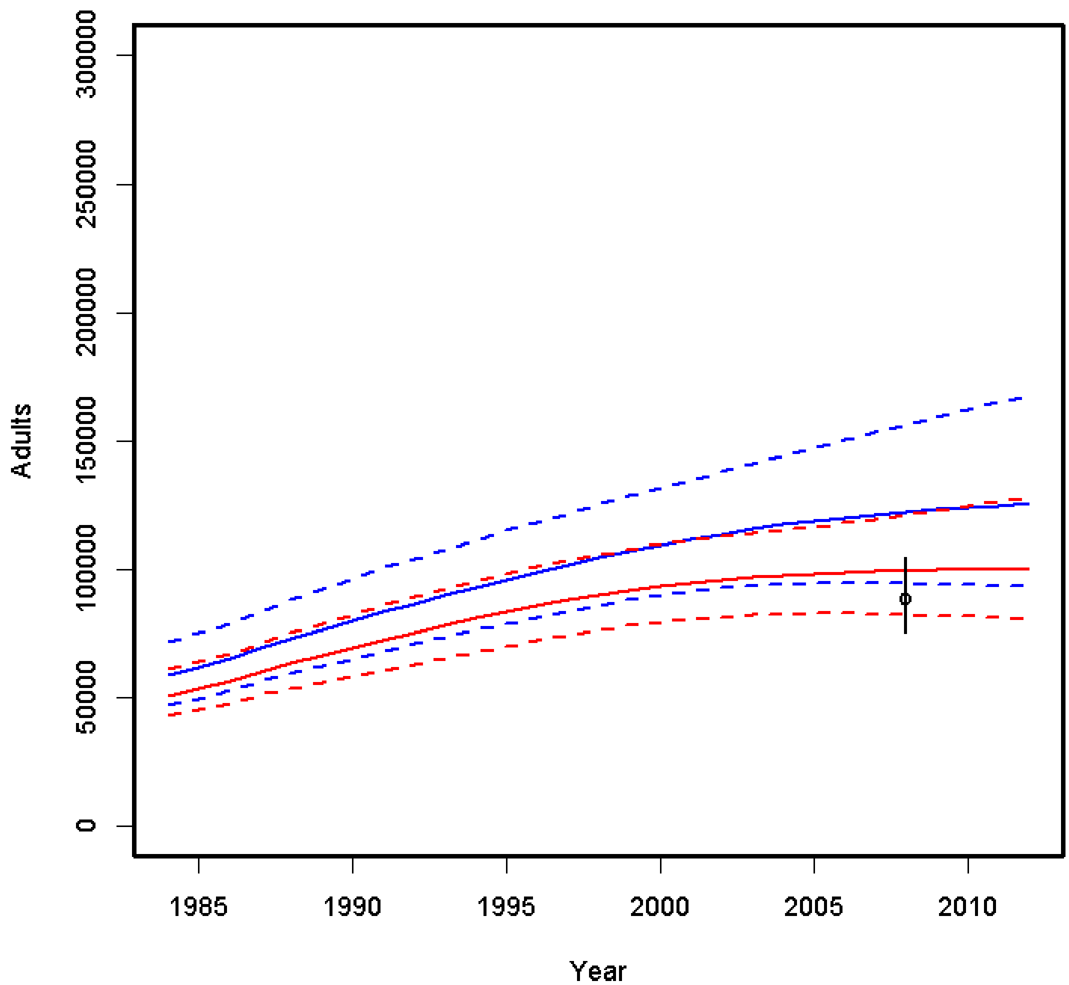
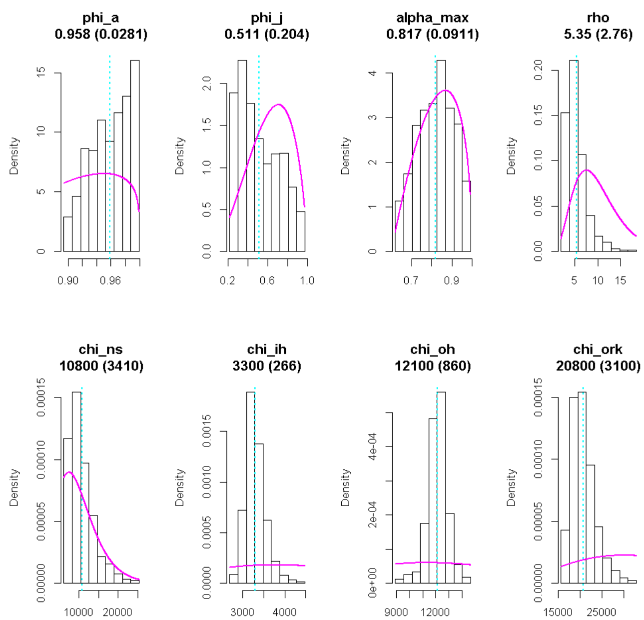


Figure 4. Prior (histograms) and posterior (solid lines) parameter estimates obtained using the revised priors. See Figure 2 legend for further explanation of the plots.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

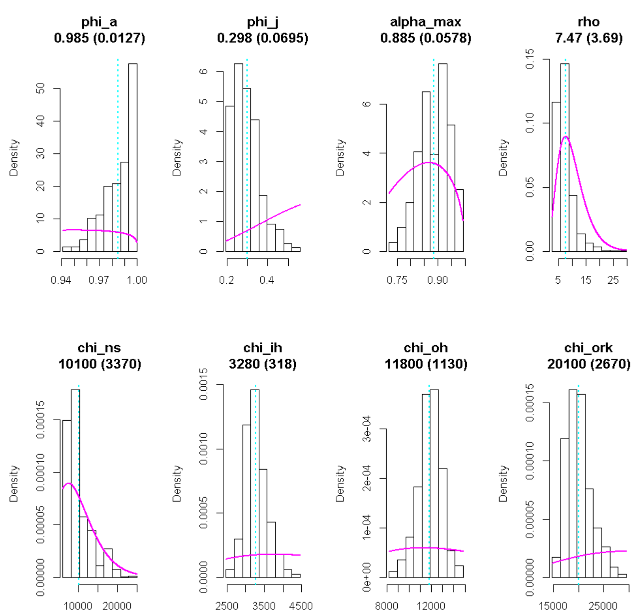


Figure 5. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size obtained using revised priors. See figure 3 legend for further explanation of the plot.

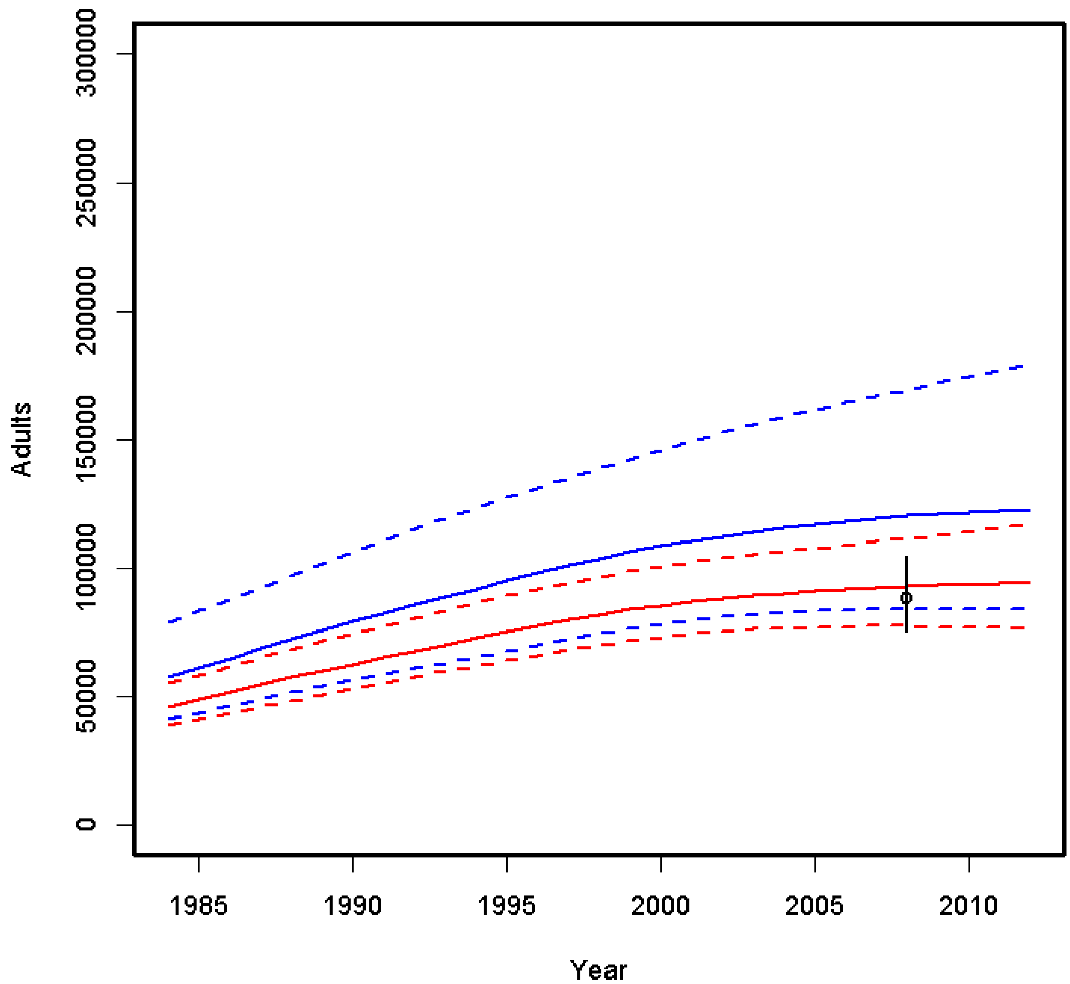
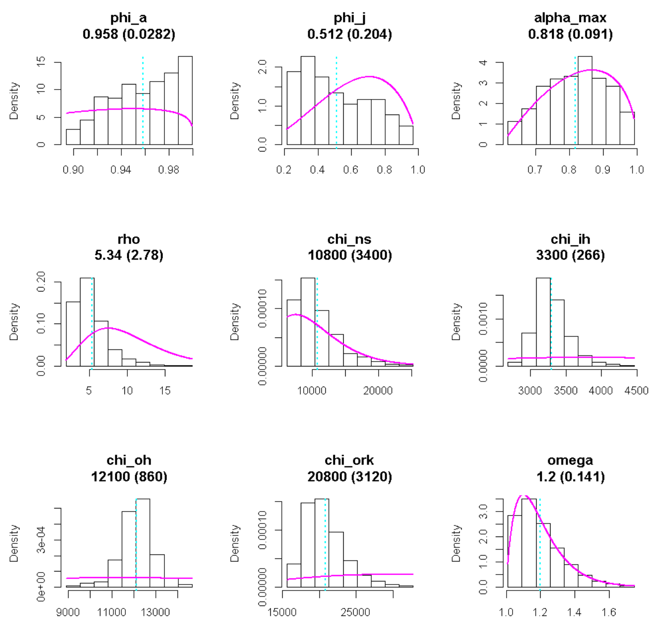


Figure 6. Prior (histograms) and posterior (solid lines) parameter estimates obtained using the revised priors, including a prior on sex ratio. See Figure 2 legend for further explanation of the plots.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

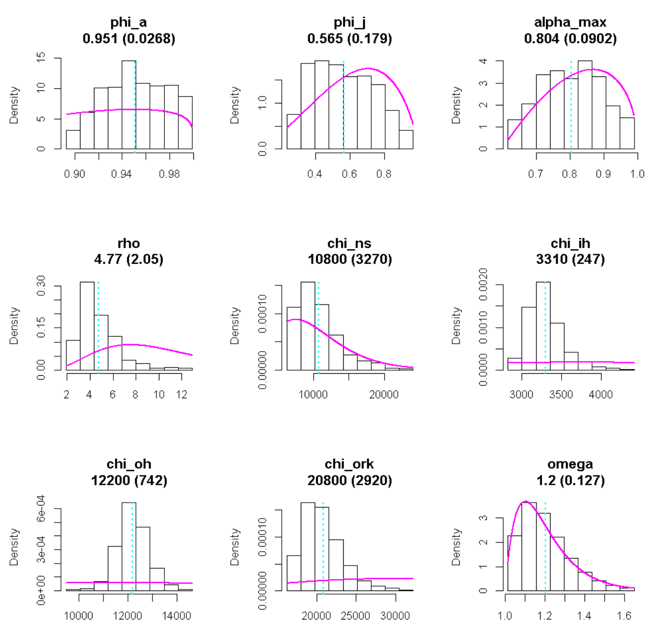


Figure 7. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size obtained using revised priors including a prior on sex ratio. See figure 3 legend for further explanation of the plot.

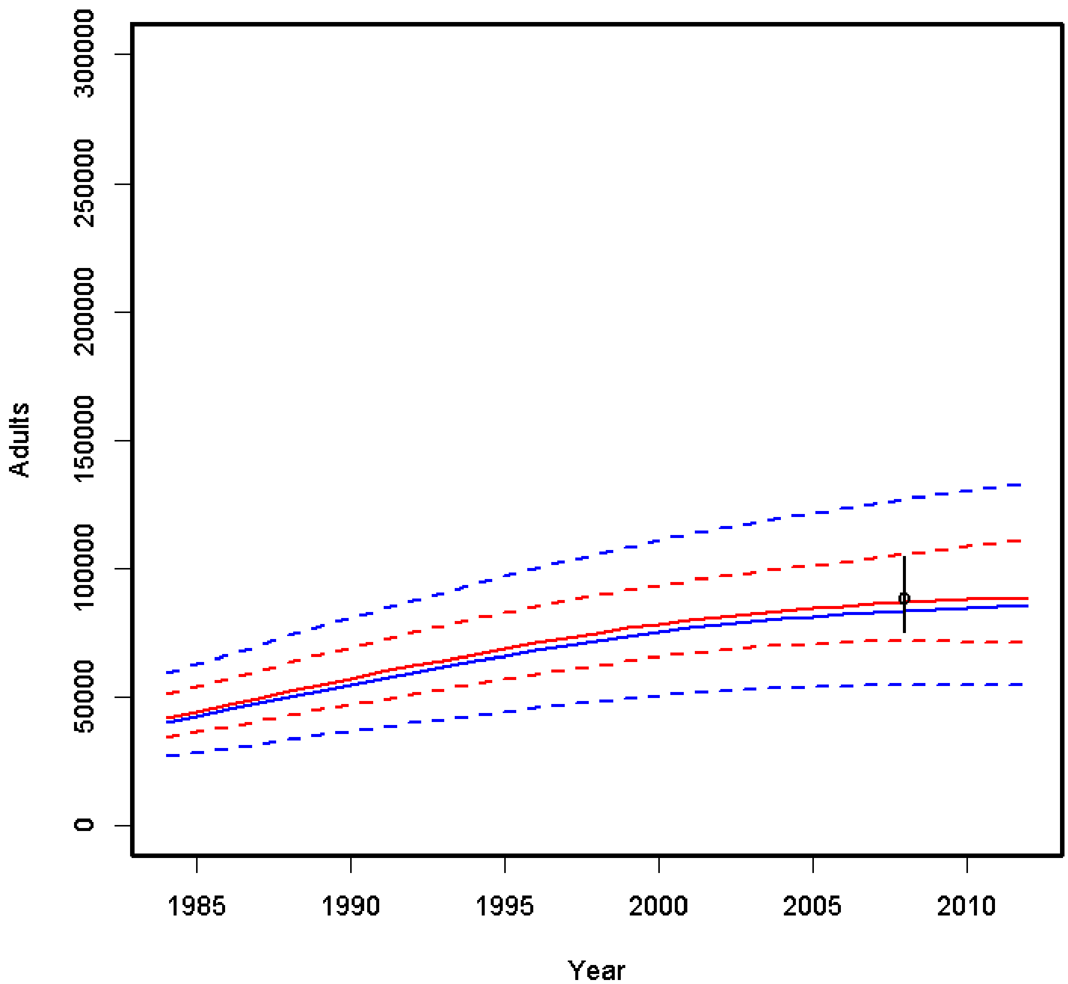
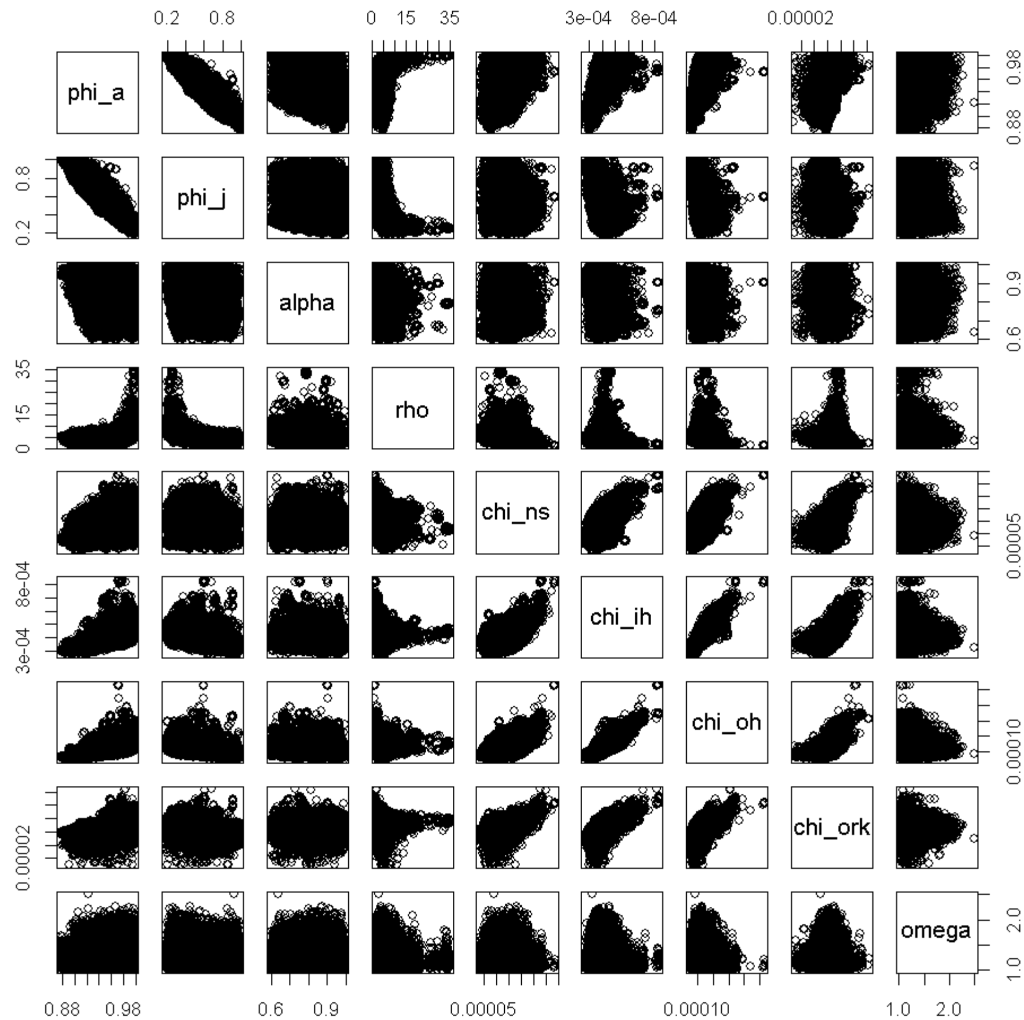


Figure 7. Scatterplot of posterior parameter estimates obtained using the revised priors, including a prior on sex ratio.



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2012, made using the model of British grey seal population dynamics fit to pup production estimates and a total population estimate from 2008, and using the old priors. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.5 (3.9 5.3)	4.9 (4.2 5.9)	22.9 (19.6 28)	17.9 (15.1 21.6)	50.2 (42.7 60.9)
1985	4.8 (4.1 5.7)	5.2 (4.5 6.2)	24.1 (20.6 29.4)	19.1 (16.1 22.8)	53.2 (45.4 64.1)
1986	5.2 (4.5 6.1)	5.5 (4.8 6.5)	25.4 (21.4 30.5)	20.4 (17.2 24)	56.5 (47.8 67.2)
1987	5.6 (4.9 6.6)	5.8 (5 6.8)	26.5 (22.7 31.8)	21.9 (18.4 25.8)	59.8 (51 71)
1988	6.1 (5.2 7.1)	6.1 (5.3 7.2)	27.5 (23 33)	23.5 (19.8 27.6)	63.3 (53.4 75)
1989	6.5 (5.7 7.7)	6.4 (5.5 7.6)	28.3 (23.4 33.8)	25.2 (21.4 29.6)	66.4 (56 78.6)
1990	7 (6.1 8.2)	6.7 (5.7 7.9)	28.8 (23.8 34.6)	27 (22.8 31.6)	69.5 (58.3 82.3)
1991	7.5 (6.5 8.8)	7 (5.8 8.3)	29.2 (24.2 35.1)	28.8 (24.3 33.6)	72.5 (60.7 85.7)
1992	8 (6.9 9.4)	7.2 (5.9 8.6)	29.4 (24.4 35.3)	30.7 (25.8 35.8)	75.4 (63 89.1)
1993	8.6 (7.4 10.1)	7.4 (6 8.8)	29.5 (24.5 35.4)	32.6 (27.4 38)	78.1 (65.3 92.4)
1994	9.2 (7.9 10.8)	7.6 (6.1 9.1)	29.5 (24.7 35.2)	34.5 (29 40.2)	80.8 (67.7 95.3)
1995	9.9 (8.5 11.6)	7.7 (6.1 9.3)	29.3 (24.7 34.9)	36.4 (30.6 42.4)	83.3 (69.9 98.1)
1996	10.5 (9 12.4)	7.8 (6.2 9.4)	29.1 (24.8 34.5)	38.2 (32.2 44.5)	85.7 (72.1 100.8)
1997	11.2 (9.6 13.2)	7.8 (6.2 9.4)	28.9 (24.8 34.1)	39.9 (33.7 46.6)	87.9 (74.3 103.3)
1998	12 (10.1 14.1)	7.8 (6.2 9.4)	28.7 (24.8 33.8)	41.4 (35.1 48.5)	89.9 (76.3 105.7)
1999	12.7 (10.8 14.9)	7.8 (6.2 9.4)	28.4 (24.9 33.4)	42.7 (36.2 50)	91.7 (78.1 107.8)
2000	13.5 (11.4 15.8)	7.8 (6.2 9.3)	28.2 (24.7 33.2)	43.8 (37.1 51.4)	93.3 (79.4 109.7)
2001	14.3 (12 16.7)	7.7 (6.2 9.2)	28.1 (24.5 33)	44.6 (37.7 52.4)	94.7 (80.5 111.3)
2002	15.1 (12.6 17.7)	7.7 (6.2 9.2)	27.9 (24.4 32.8)	45.2 (38.1 53.1)	95.9 (81.3 112.7)
2003	15.8 (13.1 18.6)	7.6 (6.2 9.1)	27.8 (24.3 32.7)	45.5 (38.3 53.6)	96.8 (82 114)
2004	16.6 (13.5 19.6)	7.6 (6.2 9.1)	27.7 (24.3 32.7)	45.7 (38.4 53.9)	97.6 (82.5 115.2)
2005	17.3 (13.8 20.7)	7.6 (6.2 9)	27.7 (24.3 32.6)	45.7 (38.4 54.1)	98.2 (82.7 116.5)
2006	17.9 (14.1 21.8)	7.5 (6.2 9)	27.7 (24.3 32.7)	45.6 (38.1 54.4)	98.7 (82.7 117.9)
2007	18.5 (14.3 23)	7.5 (6.2 9)	27.7 (24.3 32.7)	45.4 (37.7 54.6)	99.1 (82.5 119.3)
2008	19 (14.4 24.3)	7.5 (6.2 9)	27.8 (24.3 32.8)	45.2 (37.2 54.8)	99.5 (82.2 120.9)
2009	19.4 (14.5 25.8)	7.5 (6.2 9)	27.9 (24.3 32.9)	45 (36.7 54.9)	99.7 (81.8 122.6)
2010	19.8 (14.5 27.3)	7.5 (6.2 9)	27.9 (24.3 33)	44.8 (36.3 55.2)	100 (81.4 124.4)
2011	20.1 (14.5 28.8)	7.5 (6.2 9)	28 (24.3 33.1)	44.6 (36 55.4)	100.1 (81 126.3)
2012	20.3 (14.5 30.3)	7.5 (6.2 9)	28 (24.3 33.2)	44.4 (35.8 55.6)	100.3 (80.7 128.1)