Estimating the size of the UK grey seal population between 1984 and 2014

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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 2012, 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 that used to provide last year's advice, and the same "revised" priors were used, including a prior on adult sex ratio. One small change in data was that the total population size estimate was adjusted to account for the fact that the population model is based only on regularly monitored breeding colonies (approx. 94% of the total population). We used the model to predict past the last data point (2012) to give estimates of population size in 2014. Estimated adult population size in 2014 was 95,200 (95% CI 76,400-127,500).

The model assumes constant adult (i.e., aged 6+) female survival. The prior distribution has support in the range (0.8, 1.0) with a prior mean of 0.91 (SD 0.05); the posterior mean is an implausibly high 0.99 (SD 0.01). We investigated the effect of constraining the prior to the range (0.8, 0.97). Posterior mean adult survival with this revised prior was 0.95 (SD 0.03); estimated population size with this revised prior was 105,200 (95% CI 87,000-128,800).

Female survival is currently assumed to be the same for all ages. We investigated the possible effect of including survival senescence, and concluded that adding it would make no practical difference to the modelled population dynamics.

Sex ratio is an important parameter in the model, scaling estimates of adult female population size from the population dynamics model to total population size. The current prior is highly informative (prior mean on ratio of total population:adult females 1.7 SD 0.02). We investigated the consequences of using a less informative prior suggested in a previous briefing paper (prior mean 1.2 SD 0.63). With this prior (and the revised prior on adult female survival), total population size was estimated to be much lower (88,600 with 95%CI 70,200-111,700), but the ratio of total population:adult females was an implausibly low 1.14 (SD 0.09).

Introduction

This paper presents estimates of British grey seal population size and related demographic parameters, using identical models and fitting methods to Thomas (2014, and previous years), but projecting forward two years from the last pup production estimate (2012) to estimate population size in 2014. 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 (Thomas 2012); hence only the former is used here.

A revised set of priors were suggested by Longeran (2012), based on updated information and discussions within the Sea Mammal Research Unit; these were used by Thomas (2012, 2013, 2014) to assess what difference these make to the population estimates compared to the priors previously used (note that a different prior on adult sex ratio was used in the 2014 analysis); the revised priors were adopted for use in the SCOS advice in 2014. We therefore use these revised priors here.

Two additional investigations are carried out: (1) the impact of using a revised prior on adult female survival, so that survival is constrained to maximum of 0.97; (2) the potential impact of including survival senescence.

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 and 2012 from Duck (2014) 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 a single estimate of adult population size obtained by Lonergan et al. (2010) from summer haulout counts and telemetry data. We followed previous briefing papers 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. However, one important change is that we did not previously account for the fact that this adult population estimate covers the whole 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). We therefore scaled the adult estimate to make it comparable with the pup production model outputs, from 88,300 (95% CI 75,400-105,700) to 81,530 (95% CI 69,650- 96,690).

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 Longeran (2012, Table 1), except for the prior on adult sex ratio, which was first suggested by Thomas (2014). 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 priors used here are identical to those used by Thomas (2014); the data were identical except the total population estimate was revised down by 7.66%.

Fitting method

The fitting method was identical to that of Thomas (2014), 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 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 1,750 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: revised prior on survival

The model population dynamics model assumes constant adult (i.e., aged 6+) female survival. The prior distribution was a scaled beta (0.8+0.2xbeta(1.6,1.2)) with support in the range (0.8, 1.0), which has a prior mean of 0.91 (SD 0.05). However, given this prior and the available data, Thomas (2014) obtained a posterior distribution that was implausibly high: the posterior mean was 0.99 (SD 0.01). At the request of SCOS, we therefore investigated the effect of an alternative prior, with the upper bound constrained to 0.97. A prior with support in the range (0.8, 0.97) and the same mean and SD (0.8+0.17xbeta(0.988,0.482)) had an implausible shape (Figure 1b); we therefore obtained a prior by scaling the previous one from the range (0.8,1.0) to (0.8,0.97), i.e., 0.8+0.17xbeta(1.6,1.2) (Figure 1c). This gave a prior with a mean of 0.90 (SD 0.04). We re-fit the model using this revised prior, using 3,000 replicate runs of 1,000,000 samples.

Additional investigation: effect of survival senescence on population dynamics

In the current population dynamics model, female survival is assumed to be the same for all ages. Age 6+ seals are modelled together, in an "absorbing" age class, which implies that some very old seals may be present in this age class. SCOS asked us to investigate the possible effect of including age senescence in the model. This could be done by expanding the number of age classes followed in the model (e.g., to 50) and by making survival a decreasing function of age. We undertook a preliminary investigation of the potential effect of survival senescence by parameterizing a plausible survival function and calculating the proportion of adults that would likely be in the senescent age classes.

The survival function was based on the Gompertz-Makeham function (Makeham 1860), which describes the instantaneous hazard of mortality at age x as

$$H(x) = \lambda + \nu\exp(\delta x) \qquad (1)$$

where λ (>0) is a baseline mortality hazard, and ν (<0) and δ (>0) index how survival declines with age. The population model used here is a discrete-time (annual) model; therefore eqn. (1) was integrated to derive the cumulative probability of survival between two annual time points

$$\phi_x = \phi_{base}\exp\left[\frac{\nu}{\delta}(\exp[\delta x] \quad \exp[\delta(x+1)])\right] \qquad (2)$$

where ϕ_x is survival from age x to age $x+1$ and $\phi_{base} = \exp(\lambda)$ is the baseline survival for young animals.

A range of plausible values were used for baseline survival (ϕ_{base}): 0.97, 0.95 and 0.90. Values for the other two parameters (ν and δ) were derived by least-squares fitting to preliminary adult female survival estimates from Sable Island, Canada (Don Bowen, pers. comm.). Given the fitted functions, we calculated the relative proportion of adults expected in each age class, assuming a stable age structure.

Additional investigation: revised prior on sex ratio

Sex ratio is an important parameter in the model, scaling estimates of adult female population size from the population dynamics model to total population size. The current prior, introduced by Thomas (2014) is highly informative, with a prior mean on the ratio of total population:adult females of 1.7 and standard deviation of 0.02 – almost all of the prior mass lies between 1.66 and 1.76. Longeran (2012) suggested a much less informative prior, which also had a rather lower mean (prior mean 1.2 SD 0.63), and this prior was used by Thomas (2013). For the purposes of demonstration, we repeated the analysis using that less informative prior, coupled with the above 0.8-0.97 bounded prior on adult survival.

Results

Parameter and population estimates

Model fits to pup production estimates are shown in Figure 2, and the estimated adult population size is shown in Figure 3, together with the scaled independent estimate. Posterior parameter estimates are shown in Figure 4 and Table 1. As with Thomas (2014), the posterior mean adult survival is very high (0.99) when the pup production data and independent estimate are used, with the mode being even higher (Figure 4b); conversely maximum juvenile survival is very low (0.282).

Adult population size estimates by region for 2014 are given in Table 2; the posterior mean total population size was 99,500 (95% CI 81,500-124,100). Estimates for all years are given in Appendix 1.

Additional investigation: revised prior on survival
Model fits to the pup production estimates (not shown) were almost identical to those from the main analysis described above. Estimated population size was approximately 10% lower (Figure 5 and Table 2). The posterior distribution on adult population size was bounded at 0.97, with a mode close to 0.97 but a lower mean of 0.96 (Figure 6). Mean maximum juvenile survival was nearly 50% higher than in the main analysis (0.39) and fecundity was slightly higher (0.95).

Additional investigation: effect of survival senescence on population dynamics
The fitted age-specific survival function is shown in Figure 7 (assuming a baseline survival of 1.0). Survival is 90% of baseline at age 33 and drops to 10% of baseline by age 44. Life tables, showing the relative numbers of adults at each age given baseline survival of 0.97, 0.95 and 0.90, are shown in Figure 8. The proportion of the population that is older than 33 given these three baseline survival rates is 4%, 3% and 1%, respectively. Hence, even when baseline survival is high, very few adults in the population are estimated to be old enough to be exhibiting senescence.

Additional investigation: revised prior on sex ratio
The wider prior on sex ratio led to a much wider posterior on adult population size without the independent estimate (blue line in Figure 9); this in turn led to more weight being placed on the independent estimate when it was included in the analysis and hence the final population trajectory (red line in Figure 9) passing very close to the independent estimate. The revised sex ratio prior was also lower, meaning that less change was required to the demographic parameter estimates to accommodate the independent estimate (i.e., the top and bottom panels of Figure 10 are more similar than those of Figures 4 and 6). Although the posterior distributions of many parameters were sensible, the posterior on sex ratio was implausible: the ratio of total population size to adult females was estimated at 1.14 (SD 0.09)

Discussion
The population size estimated in this briefing paper is essentially a projection of the stochastic population dynamics model fit to data from 2012 and earlier. The posterior mean adult population size of 94,500 for 2013 is slightly lower than that for 2013 given by Thomas (2014) (which was 98,800), reflecting the amended independent of total population size used. In all other ways, the fit of the model to the data is nearly identical to that shown in Thomas (2014).

Thomas (2014) documents some inadequacies of the model fit: the fitted model does not capture all features of the pup production data, with clear runs of positive or negative residuals and particular lack of fit to the last data point; the implausible posterior estimate of adult and maximum pup survival also noted above. It is not surprising that high estimated adult survival and low maximum pup survival should occur in the same model, since the two estimates are strongly correlated (Thomas 2013). If the estimates are truly considered infeasible, then consideration should be given to revising the priors to restrict posteriors to feasible regions.

We are investigated a model where the prior range on adult population size, φ_a, is restricted to a maximum of 0.97. This produced a more realistic posterior mean φ_a, although the mode was close to the upper bound of the prior. The estimate of maximum pup survival was higher, as we would expect given the strong correlation between the two parameters; estimated fecundity was also slightly higher. Together, the change in parameter estimates produced a higher estimate of total population size from the population dynamics model (compare blue lines in Figures 3 and 5), which in turn led to a higher total population size estimate when the independent estimate was factored in (red line in Figure 5). Population size estimates using this revised prior on φ_a are approximately 10% higher than those using the previous prior.

Our initial analysis of the importance of senescence appears to show that ignoring it is unlikely to have any practical impact on the dynamics or parameter estimates of the population model. Even using a high baseline adult survival estimate, a very small proportion of the adult population are estimated to be at the age where senescence begins to have a significant effect on survival – assuming the preliminary information provided about survival senescence in Canadian grey seals applies also to UK grey seals.

Using a wider and lower prior on sex ratio had a significant impact on posterior parameter distributions and estimates of total population size. The lower prior mean meant that the estimate from the pup production and population dynamics model was closer to the independent estimate; the wider prior meant that the population dynamics-based estimate was given less weight relative to the independent estimate. Although the posterior on sex ratio was implausible (suggesting there are approximately 7 adult females per adult male), it does suggest that a re-examination of the current sex ratio prior may be helpful in bringing the output from the population dynamics model closer to the independent estimate.

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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 1984-2010 and 2012 pup production estimates, and the 2008 total population estimates.*

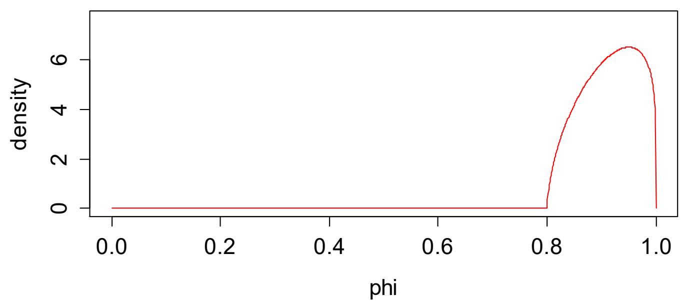
	Main analysis			Additional investigation on adult survival			Additional investigation on sex ratio		
Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)	Prior distribution	Prior mean (SD)	Posterior mean (SD)
adult survival ϕ_a	0.8+0.2*Be(1.6,1.2)	0.91 (0.05)	0.99 (0.01)	0.8+0.17*Be(1.6,1.2)	0.90 (0.04)	0.96 (0.01)	0.8+0.17*Be(1.6,1.2)	0.90 (0.04)	0.95 (0.02)
pup survival ϕ_j	Be(2.87,1.78)	0.62 (0.20)	0.27 (0.05)	same as main analysis	0.62 (0.20)	0.37 (0.06)	same as main analysis	0.62 (0.20)	0.57 (0.11)
fecundity $\alpha_{\max}$	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.90 (0.05)	same as main analysis	0.83 (0.09)	0.95 (0.03)	same as main analysis	0.83 (0.09)	0.87 (0.08)
dens. dep. ρ	Ga(4,2.5)	10 (5)	6.12 (2.31)	same as main analysis	10 (5)	4.24 (0.9)	same as main analysis	10 (5)	3.47 (0.9)
NS carrying cap. χ_1	Ga(4,2500)	10000 (5000)	15800 (7540)	same as main analysis	10000 (5000)	13700 (4440)	same as main analysis	10000 (5000)	14400 (4150)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3760 (448)	same as main analysis	5000 (2500)	4390 (213)	same as main analysis	5000 (2500)	3600 (295)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	13200 (1650)	same as main analysis	15000 (7500)	12300 (628)	same as main analysis	15000 (7500)	12700 (775)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	23300 (3510)	same as main analysis	40000 (20000)	20800 (2270)	same as main analysis	40000 (20000)	23200 (3530)
observation CV ψ	Fixed	0.89 (0)	-	same as main analysis	0.89 (0)	-	same as main analysis	0.89 (0)	-
sex ratio ω	1.6+Ga(28.08, 3.70E-3)	1.7 (0.02)	1.7 (0.02)	same as main analysis	1.7 (0.02)	1.7 (0.02)	1+Ga(0.1,2)	1.2 (0.63)	1.14 (0.09)

Table 2. **Estimated size, in thousands, of the British grey seal population at the start of the 2014 breeding season, derived from models fit to pup production data from 1984-2012 and the additional total population estimate from 2008, using the revised parameter priors. Numbers are posterior means with 95% credible intervals in brackets.**

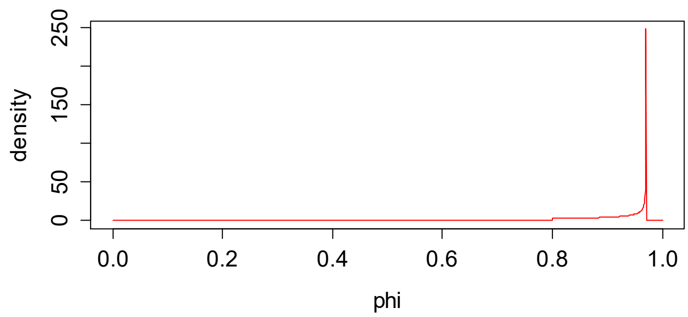
	Estimated population size in thousands (95% CI)		
	Main analysis	Additional investigation on adult survival	Additional investigation on sex ratio
North Sea	22.5 (16 29.7)	25.6 (18.6 33.5)	20.8 (15.1 27.9)
Inner Hebrides	6.9 (5.7 8.1)	7.6 (6.6 8.9)	6.2 (5.1 7.7)
Outer Hebrides	24.4 (20.9 29)	26.8 (23.9 30.8)	22 (18.3 26.4)
Orkney	41.4 (33.8 50.7)	45.2 (37.9 55.7)	39.6 (31.7 49.7)
Total	95.2 (76.4 117.5)	105.2 (87 128.8)	88.6 (70.2 111.7)

Figure 1. Prior distributions on adult female survival.

(a) Prior used in main analysis.



(b) Prior with same mean and standard deviation as (a), but constrained to a maximum of 0.97.



(c) Prior based on (a) scaled so that the maximum is 0.97 – this is the prior used in the additional investigation.

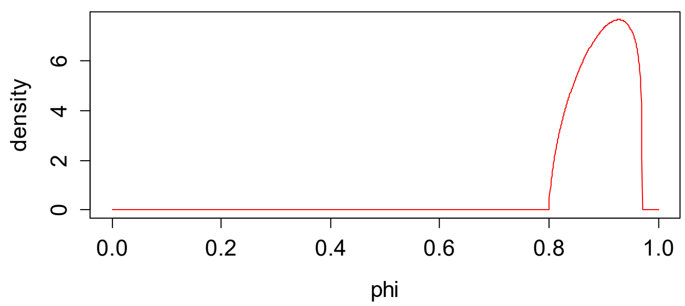


Figure 2. Posterior mean estimates of pup production (solid lines) and 95%CI (dashed lines) from the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 (circles) and a total population estimate from 2008. Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

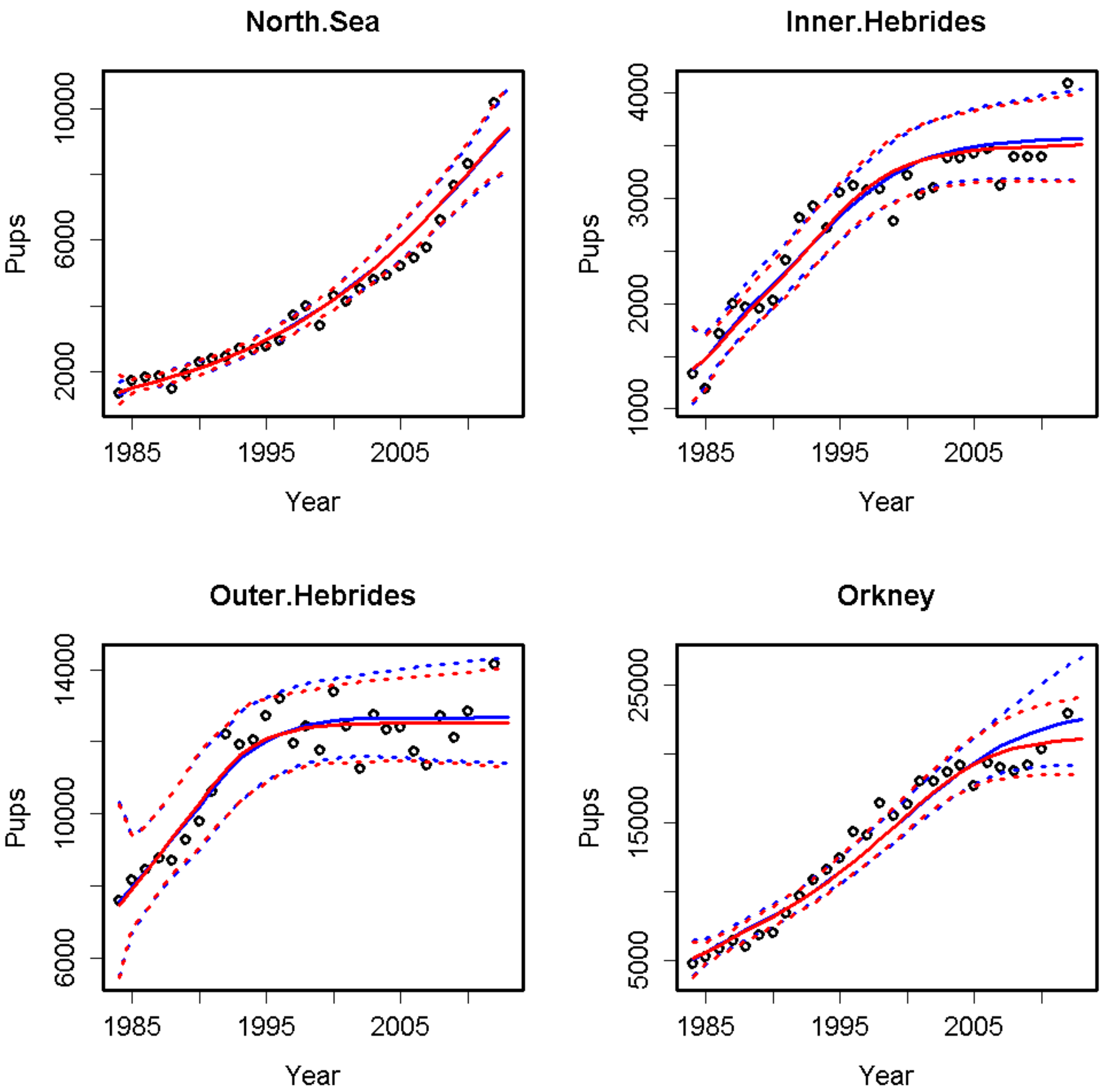


Figure 3. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2014 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate). Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

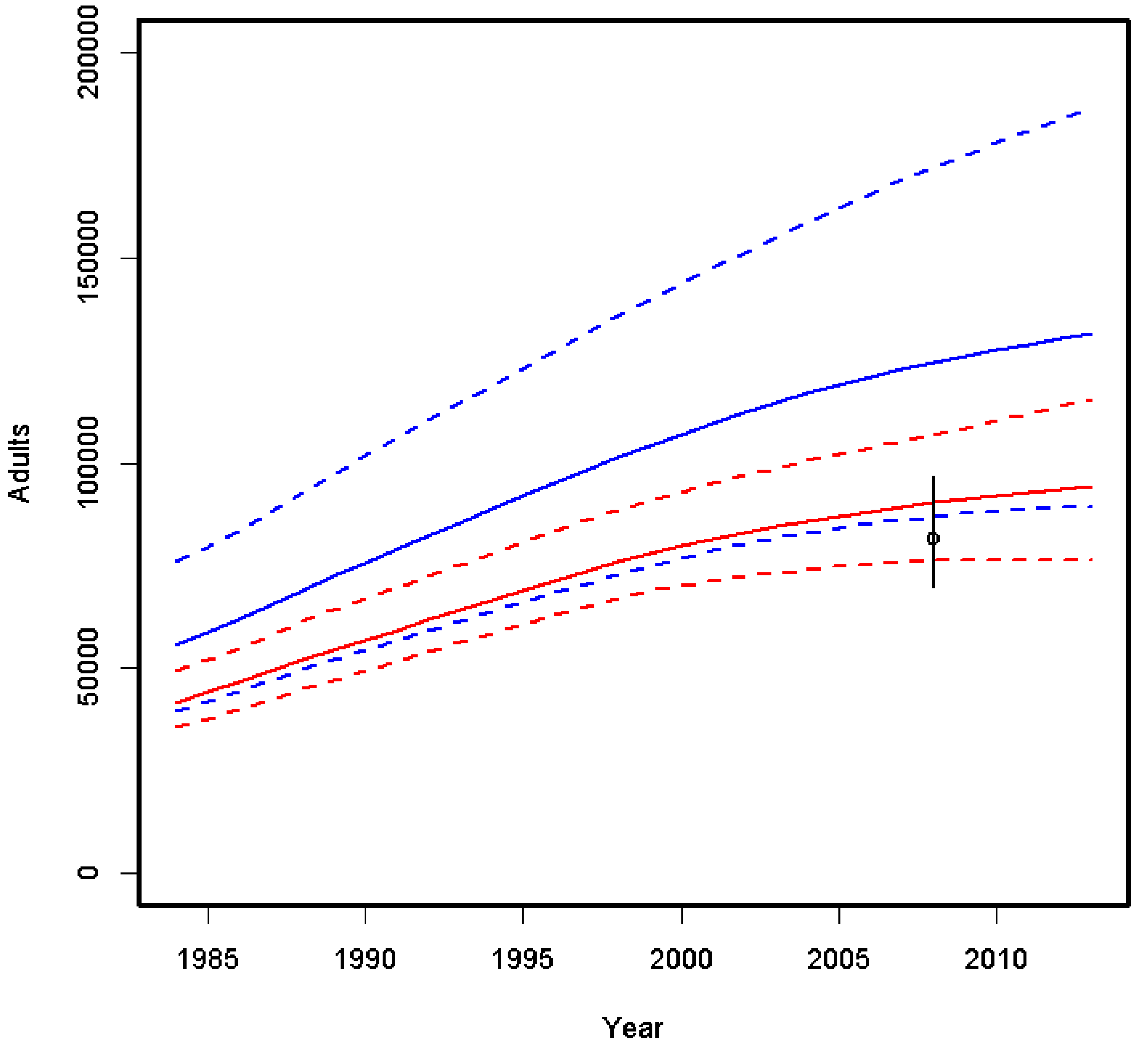
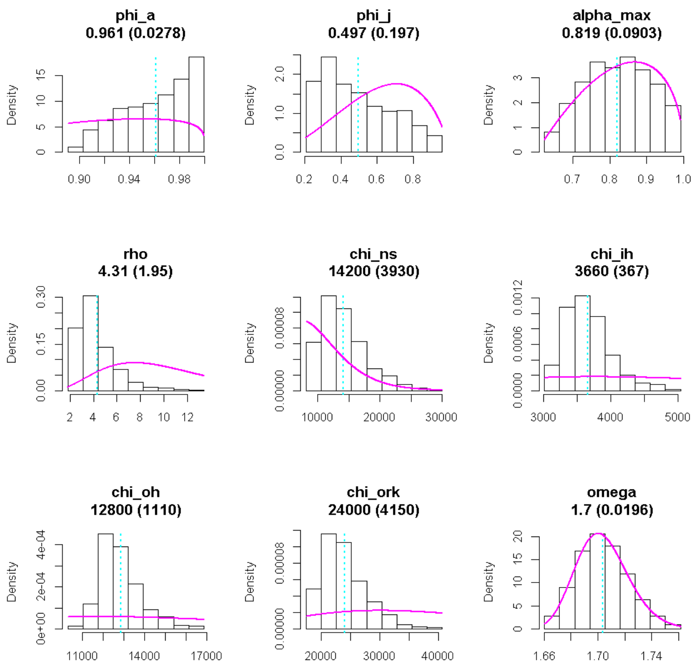


Figure 4. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008. The vertical line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

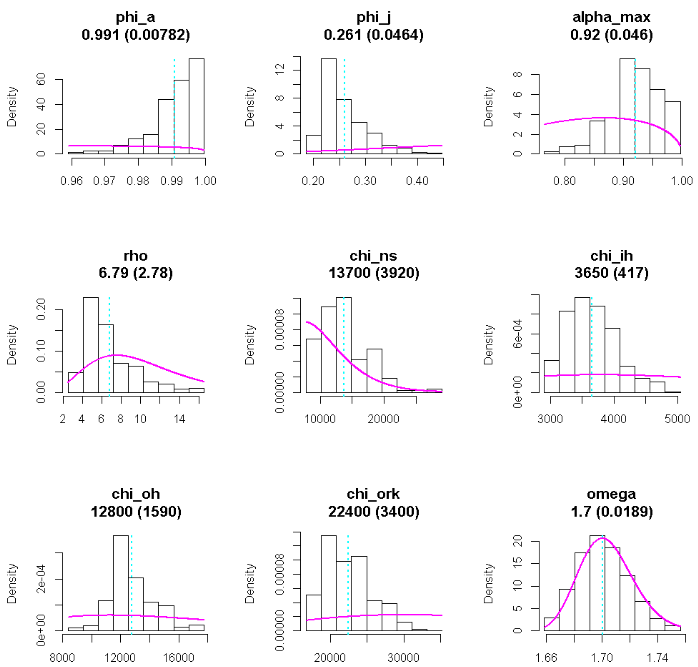


Figure 5. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2014 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate), and using a prior on adult survival constrained to have a maximum of 0.97. Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

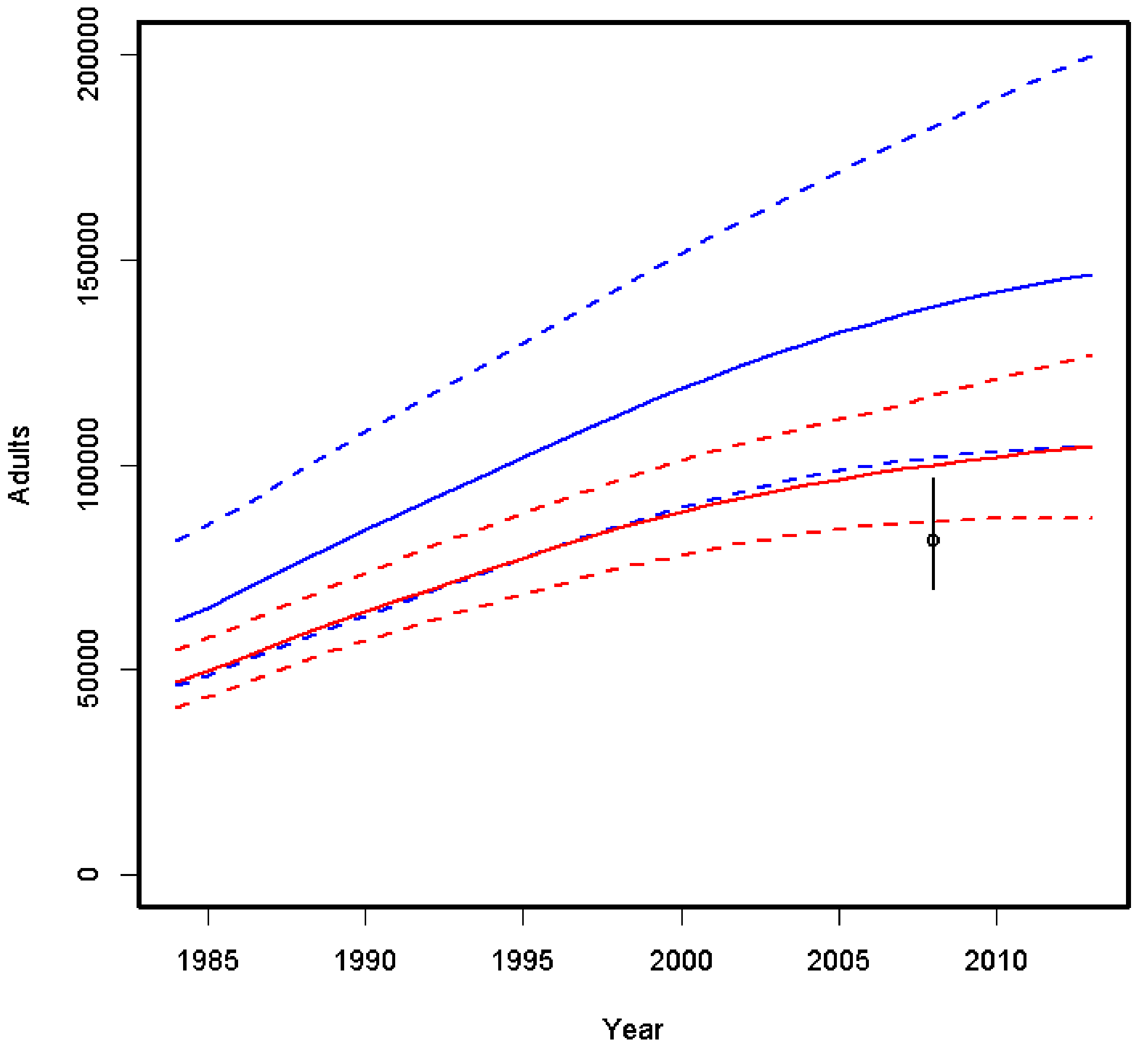
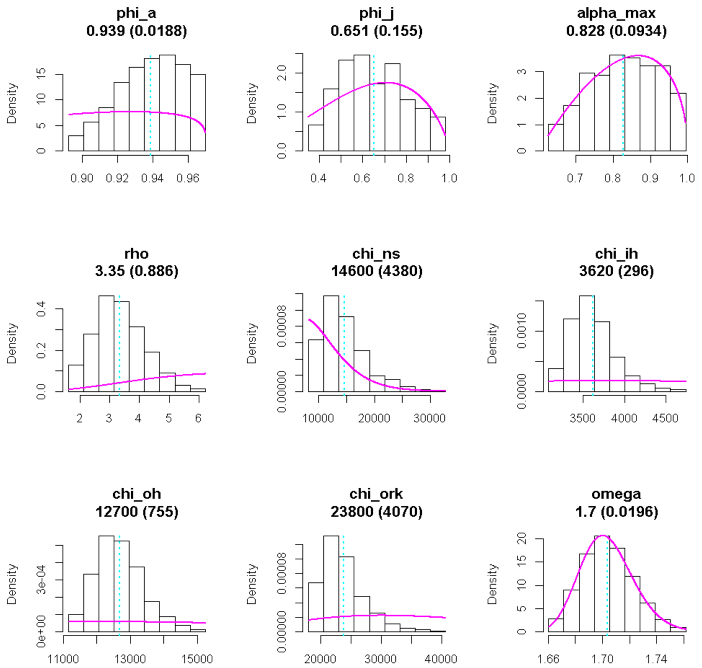


Figure 6. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008, and using a prior on adult survival constrained to have a maximum of 0.97. The vertical 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

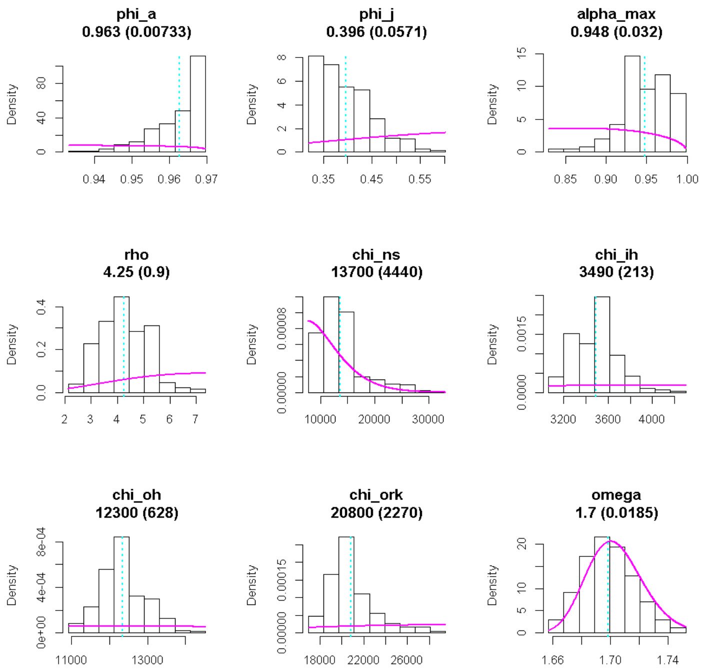


Figure 7. Age specific survival function used to investigate senescence, assuming baseline survival rate of 1.0.

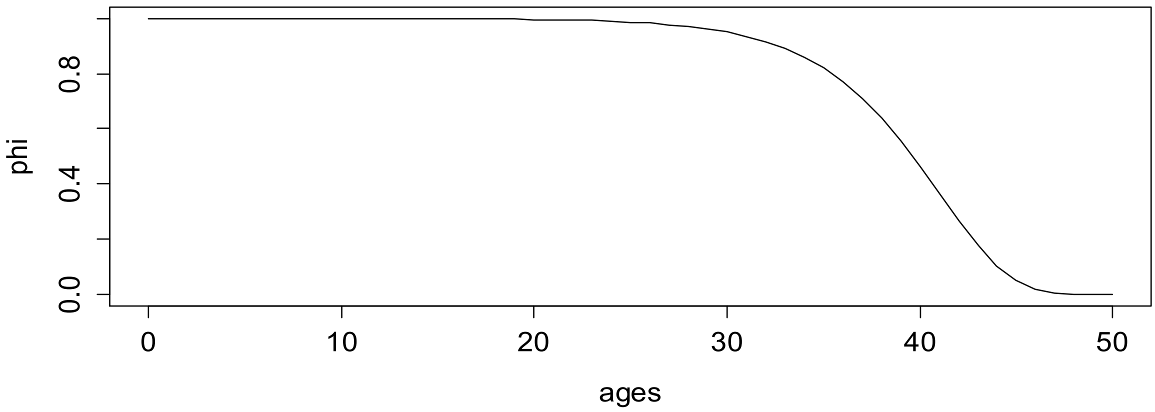


Figure 8. Life tables, showing the number of adults in at each age, relative to those aged 1 using the age-specific survival function in Figure 7, but assuming baseline adult survival rates of 0.97, 0.95 and 0.90.

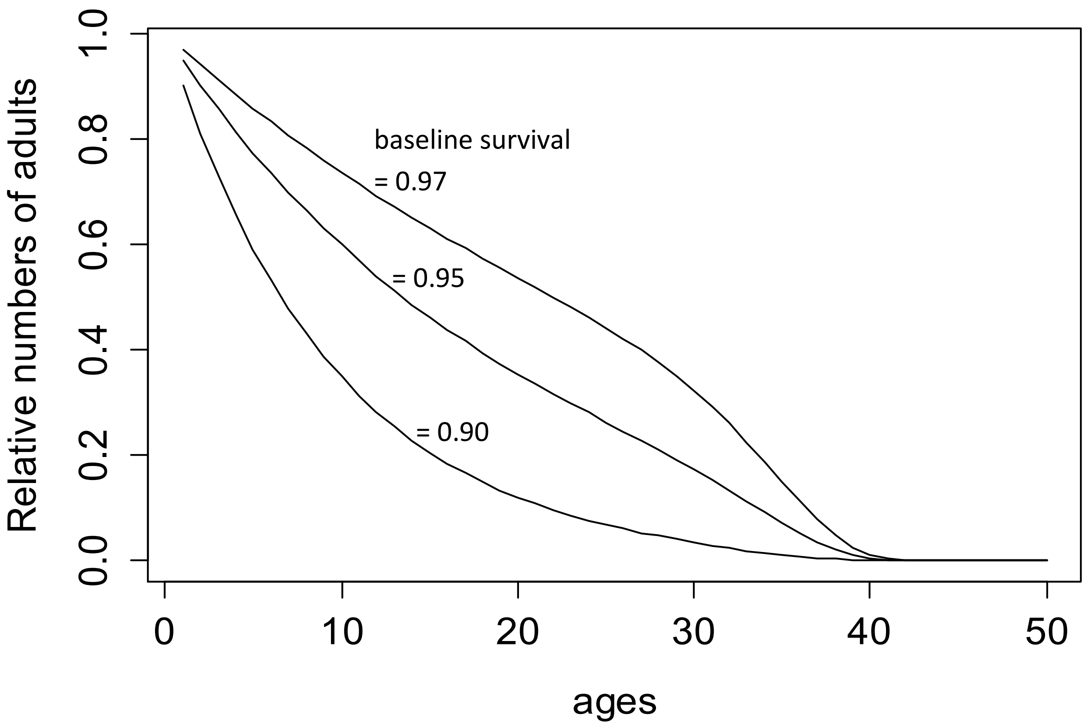


Figure 9. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2014 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate), and using a prior on adult survival constrained to have a maximum of 0.97 and a less informative prior on sex ratio. Blue lines show the fit to pop production estimates alone; red lines show the fit to pup production estimates plus the total population estimate.

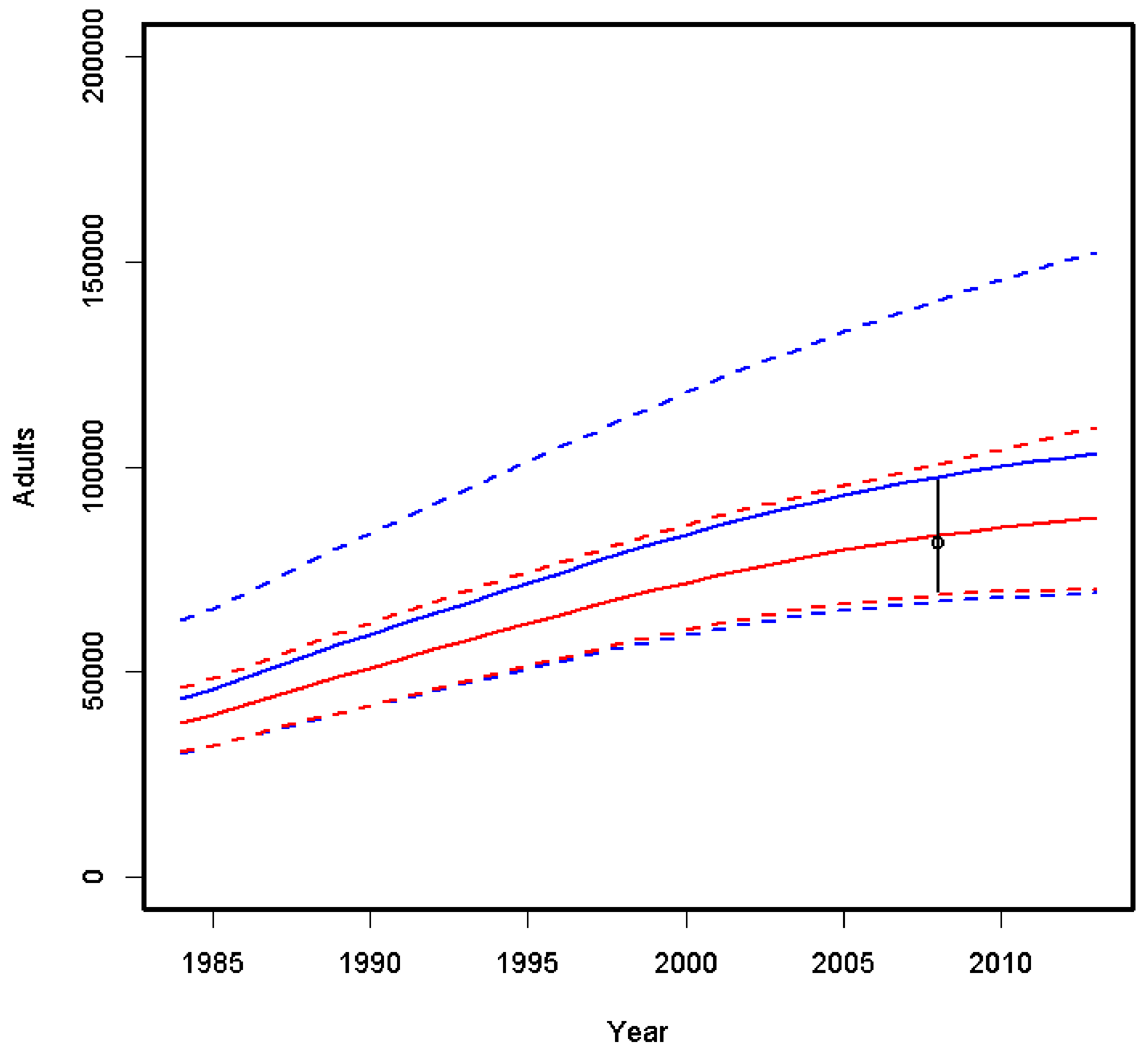
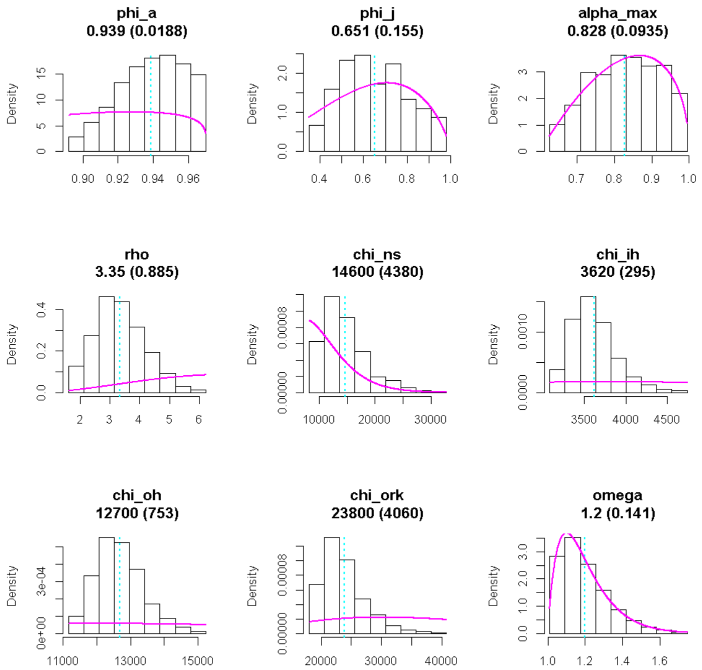
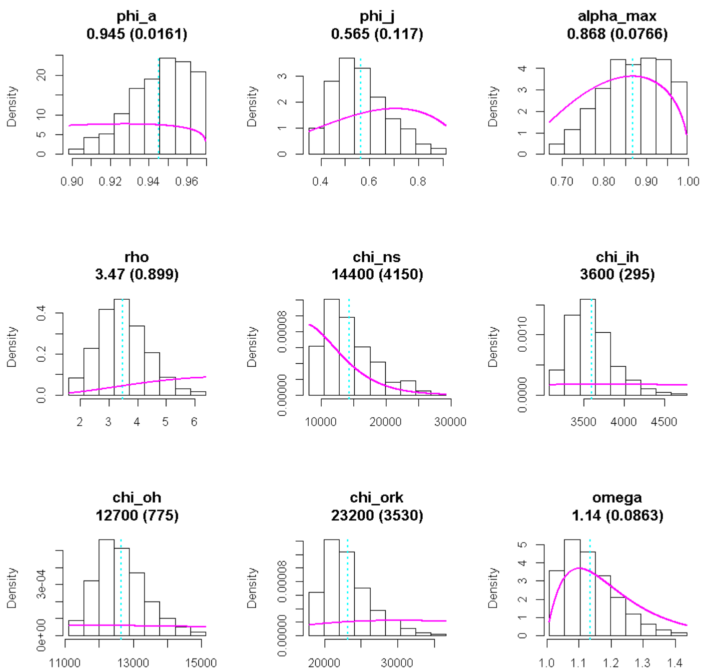


Figure 10. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008, and using a prior on adult survival constrained to have a maximum of 0.97. The vertical 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



Appendix 1

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2014, made using the 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% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	3.8 (3.3 4.5)	3.9 (3.4 4.7)	19.1 (16.1 22.8)	14.8 (12.7 17.4)	41.7 (35.6 49.4)
1985	4.1 (3.6 4.8)	4.2 (3.6 5)	20 (16.9 23.9)	15.8 (13.6 18.5)	44.1 (37.7 52.2)
1986	4.4 (3.9 5.1)	4.5 (3.9 5.3)	20.9 (17.8 24.8)	16.9 (14.5 19.8)	46.7 (40 55)
1987	4.7 (4.2 5.5)	4.7 (4.1 5.6)	21.8 (18.6 25.7)	18.1 (15.6 21.2)	49.3 (42.5 58)
1988	5 (4.5 5.9)	5 (4.4 5.9)	22.6 (19.3 26.8)	19.3 (16.7 22.7)	52 (44.8 61.3)
1989	5.4 (4.8 6.3)	5.3 (4.6 6.2)	23.1 (19.8 27.3)	20.7 (17.9 24.3)	54.5 (47.1 64.1)
1990	5.8 (5.1 6.8)	5.6 (4.9 6.6)	23.4 (20.2 27.6)	22.1 (19.2 26)	56.9 (49.4 66.9)
1991	6.2 (5.5 7.3)	5.8 (5.1 6.9)	23.7 (20.5 27.9)	23.6 (20.5 27.7)	59.3 (51.7 69.7)
1992	6.6 (5.9 7.8)	6 (5.3 7.1)	23.9 (20.8 28.2)	25.2 (22 29.5)	61.7 (53.9 72.5)
1993	7.1 (6.3 8.3)	6.2 (5.4 7.3)	24 (21 28.3)	26.8 (23.5 31.3)	64.1 (56.2 75.3)
1994	7.6 (6.7 8.9)	6.3 (5.6 7.5)	24.1 (21.1 28.4)	28.5 (25.1 33.2)	66.6 (58.5 78)
1995	8.1 (7.2 9.6)	6.4 (5.7 7.6)	24.2 (21.2 28.4)	30.2 (26.7 35.1)	69 (60.7 80.7)
1996	8.7 (7.7 10.2)	6.5 (5.7 7.7)	24.2 (21.3 28.4)	31.9 (28.3 37)	71.3 (63 83.4)
1997	9.3 (8.2 11)	6.6 (5.8 7.8)	24.3 (21.4 28.5)	33.5 (29.8 38.8)	73.6 (65.2 86.1)
1998	10 (8.8 11.7)	6.6 (5.8 7.9)	24.3 (21.4 28.5)	35 (31.1 40.4)	75.8 (67.1 88.5)
1999	10.6 (9.4 12.5)	6.7 (5.8 7.9)	24.3 (21.4 28.6)	36.3 (32.2 41.8)	77.9 (68.9 90.8)
2000	11.4 (10 13.4)	6.7 (5.8 8)	24.3 (21.4 28.6)	37.4 (33 43)	79.8 (70.3 93)
2001	12.2 (10.7 14.3)	6.7 (5.8 8)	24.3 (21.4 28.6)	38.3 (33.4 44.1)	81.5 (71.4 95.1)
2002	13 (11.4 15.3)	6.8 (5.8 8)	24.3 (21.4 28.7)	39 (33.7 45)	83 (72.4 97)
2003	13.8 (12.2 16.3)	6.8 (5.8 8)	24.3 (21.4 28.7)	39.5 (33.8 45.8)	84.4 (73.2 98.8)
2004	14.7 (12.9 17.3)	6.8 (5.8 8)	24.3 (21.4 28.7)	39.9 (33.9 46.5)	85.7 (74 100.6)
2005	15.6 (13.7 18.3)	6.8 (5.8 8)	24.3 (21.3 28.7)	40.3 (33.9 47.1)	87 (74.7 102.2)
2006	16.5 (14.4 19.4)	6.8 (5.8 8)	24.3 (21.3 28.8)	40.5 (33.9 47.6)	88.1 (75.4 103.8)
2007	17.4 (15.1 20.5)	6.8 (5.8 8.1)	24.3 (21.3 28.8)	40.7 (33.9 48.1)	89.2 (76 105.4)
2008	18.2 (15.5 21.6)	6.8 (5.8 8.1)	24.3 (21.2 28.8)	40.9 (33.9 48.6)	90.3 (76.4 107.1)
2009	19.1 (15.7 22.7)	6.8 (5.8 8.1)	24.3 (21.2 28.8)	41 (33.8 49)	91.3 (76.5 108.7)
2010	19.9 (15.9 23.9)	6.8 (5.8 8.1)	24.3 (21.1 28.9)	41.1 (33.8 49.4)	92.2 (76.6 110.3)
2011	20.6 (15.9 25.3)	6.8 (5.8 8.1)	24.3 (21.1 28.9)	41.2 (33.8 49.8)	93 (76.6 112.1)
2012	21.3 (16 26.8)	6.8 (5.7 8.1)	24.4 (21 28.9)	41.3 (33.8 50.1)	93.8 (76.5 113.9)
2013	22 (16 28.2)	6.8 (5.7 8.1)	24.4 (21 28.9)	41.4 (33.8 50.4)	94.5 (76.5 115.7)
2014	22.5 (16 29.7)	6.9 (5.7 8.1)	24.4 (20.9 29)	41.4 (33.8 50.7)	95.2 (76.4 117.5)

Appendix 2

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2014, made using the model of British grey seal population dynamics fit to pup production estimates and a total population estimate from 2008*)*, and using a prior on adult survival constrained to have a maximum of 0.97. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.3 (3.7 4.9)	4.4 (3.8 5.2)	21.3 (18.7 25.1)	16.8 (14.6 19.5)	46.9 (40.8 54.7)
1985	4.6 (4 5.2)	4.7 (4 5.5)	22.4 (19.6 26.3)	18 (15.8 20.8)	49.6 (43.4 57.8)
1986	4.9 (4.3 5.6)	5 (4.3 5.7)	23.5 (20.7 27.6)	19.2 (16.9 21.9)	52.5 (46.3 60.9)
1987	5.3 (4.7 6)	5.3 (4.6 6.1)	24.5 (21.8 28.6)	20.5 (18.1 23.3)	55.5 (49.2 64.1)
1988	5.7 (5.1 6.4)	5.6 (4.9 6.4)	25.4 (22.7 29.7)	21.9 (19.4 24.9)	58.6 (52 67.5)
1989	6.1 (5.4 6.9)	5.9 (5.2 6.8)	26 (23.3 30.3)	23.4 (20.8 26.6)	61.3 (54.7 70.6)
1990	6.5 (5.8 7.4)	6.1 (5.4 7.1)	26.5 (23.7 30.8)	25 (22.2 28.4)	64.1 (57.1 73.7)
1991	7 (6.2 7.9)	6.4 (5.6 7.4)	26.9 (24 31.2)	26.6 (23.6 30.3)	66.8 (59.4 76.7)
1992	7.4 (6.7 8.5)	6.6 (5.8 7.7)	27.1 (24.2 31.4)	28.3 (25.1 32.1)	69.5 (61.8 79.7)
1993	7.9 (7.2 9.1)	6.9 (6 7.9)	27.3 (24.3 31.5)	30 (26.6 34)	72.1 (64.1 82.6)
1994	8.5 (7.7 9.8)	7.1 (6.2 8.2)	27.4 (24.4 31.5)	31.8 (28.1 36)	74.7 (66.3 85.4)
1995	9.1 (8.2 10.4)	7.2 (6.3 8.4)	27.4 (24.5 31.5)	33.5 (29.6 37.9)	77.3 (68.6 88.2)
1996	9.7 (8.8 11.2)	7.4 (6.4 8.5)	27.4 (24.5 31.5)	35.2 (31 39.8)	79.7 (70.7 91)
1997	10.4 (9.4 12)	7.5 (6.5 8.6)	27.4 (24.5 31.4)	36.9 (32.4 41.7)	82.1 (72.7 93.7)
1998	11.1 (10 12.8)	7.5 (6.6 8.7)	27.3 (24.4 31.3)	38.4 (33.6 43.5)	84.4 (74.6 96.3)
1999	11.9 (10.7 13.6)	7.6 (6.6 8.8)	27.2 (24.4 31.2)	39.9 (34.8 45.1)	86.6 (76.5 98.7)
2000	12.7 (11.4 14.6)	7.6 (6.6 8.8)	27.1 (24.3 31.1)	41.1 (35.8 46.6)	88.6 (78.1 101.1)
2001	13.5 (12.1 15.5)	7.6 (6.6 8.8)	27.1 (24.3 31)	42.2 (36.6 47.9)	90.5 (79.7 103.3)
2002	14.4 (12.9 16.6)	7.7 (6.7 8.8)	27 (24.2 31)	43.1 (37.3 49)	92.2 (81.1 105.3)
2003	15.3 (13.7 17.6)	7.7 (6.7 8.8)	26.9 (24.1 30.9)	43.8 (37.9 49.9)	93.8 (82.4 107.3)
2004	16.3 (14.5 18.8)	7.7 (6.6 8.8)	26.9 (24 30.9)	44.4 (38.3 50.7)	95.2 (83.5 109.2)
2005	17.3 (15.3 20)	7.6 (6.6 8.8)	26.8 (24 30.8)	44.8 (38.4 51.4)	96.5 (84.4 111.1)
2006	18.3 (16 21.3)	7.6 (6.6 8.8)	26.8 (23.9 30.8)	45.1 (38.6 52.1)	97.8 (85.2 113)
2007	19.3 (16.6 22.6)	7.6 (6.6 8.8)	26.8 (23.9 30.8)	45.2 (38.7 52.7)	98.9 (85.8 114.9)
2008	20.3 (17.2 24.1)	7.6 (6.6 8.8)	26.8 (23.9 30.8)	45.3 (38.6 53.2)	100 (86.3 116.9)
2009	21.2 (17.6 25.6)	7.6 (6.6 8.8)	26.7 (23.9 30.8)	45.4 (38.6 53.8)	101 (86.6 119)
2010	22.2 (17.9 27.2)	7.6 (6.6 8.8)	26.7 (23.9 30.8)	45.4 (38.5 54.2)	101.9 (86.9 121.1)
2011	23.1 (18.2 28.8)	7.6 (6.6 8.8)	26.7 (23.9 30.8)	45.4 (38.3 54.7)	102.8 (87 123.1)
2012	24 (18.4 30.4)	7.6 (6.6 8.9)	26.7 (23.9 30.8)	45.3 (38.1 55)	103.7 (87 125.1)
2013	24.9 (18.5 32)	7.6 (6.6 8.9)	26.7 (23.9 30.8)	45.3 (38 55.4)	104.5 (87 127)
2014	25.6 (18.6 33.5)	7.6 (6.6 8.9)	26.8 (23.9 30.8)	45.2 (37.9 55.7)	105.2 (87 128.8)