Estimating the size of the UK grey seal population between 1984 and 2013, 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 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 the EDDSNM model used in previous briefing papers, and used the same priors on demographic parameters that have been used since 2005. We used the model to predict past the last data point (2012) to give estimates of population size in 2013. Estimated adult population size in 2013 was 106,300 (95% CI 86,100-131,300).

In addition, we fitted the model using a set of revised priors on demographic parameters that were introduced in a 2012 briefing paper, but with a new prior on adult sex ratio that assumes the ratio of adult males to females is 90% certain to be between 0.68:1 and 0.73:1. Using these revised priors, estimated adult population size in 2013 was 98,800 (95% CI 81,400-122,000).

Introduction

This paper presents estimates of British grey seal population size and related demographic parameters, using identical models and fitting methods to Thomas (2013, and previous years), but including pup production estimates for 2012 and projecting forward one more year to estimate population size in 2013. 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.

Some 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, 2013) to assess what difference these make to the population estimates and this study is repeated here. We also investigate the consequences of using a newly-derived prior on sex ratio, rather than assuming a fixed sex ratio, as in previous analyses. Thomas (2013) investigated the use of 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; we do not repeat this work in the current paper.

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) provided a prior for this multiplier, and this was further discussed by Thompson (2014). We therefore also obtained results using a prior based on Thompson (2014), as detailed below under Additional investigations.

Data, observation models, and priors

One source of input data was the pup production estimates for 1984-2010 and 2012 from Duck (2014), aggregated into regions. Note that the North Sea totals included the Inch Keith colony, which had not been included in previous models – this made the North Sea totals approximately 3% greater than previously (e.g., 252 pups added to 8062 in 2012).

The pup production 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). We followed previous papers (e.g., Thomas 2011) in undertaking an initial run of the model with the CV as a parameter to be estimated, and then fixing the value at the posterior mean in subsequent runs. The prior distribution used was gamma(shape=2.1, scale=66.67) on $1/CV^2$, which implies a prior mean CV of 10.4%, with prior 2.5th and 97.5th quantiles of 5.1% and 23.3%, respectively.

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 βs. 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) and subsequent papers; the only differences are that there is an additional year of pup production data (from 2012), the Inch Keith colony was included in the North Sea region and the observation error parameter has been re-estimated.

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). (The rejection control threshold used was w_c=1000, which is rather higher than that used in previous years. Initial investigations found that this had little effect on the Monte Carlo error in results, while greatly reducing the size of the posterior sample and hence making the outputs easier to work with on the computer.)

Additional investigations

Revised priors

We re-fitted the model using the revised priors suggested by Lonergan (2012; see Table 1). Here, 2,000 replicate runs of 1,000,000 samples were used.

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 by developing a prior based on the discussion by Thompson (2014) such that 90% of the prior mass was between 1.68 and 1.73 – the distribution (denoted ω in Table 1) had a prior mean of 1.70 and standard deviation of 0.020. (In practice, including the prior in the analysis involved re-weighting the outputs from the previous revised priors analysis, so no additional model runs were required.) Note that this prior is narrow, with a 90% prior interval of 0.05, and also close to the previous fixed value of 1.73 – hence we do not expect a large change in results from using this prior rather than the fixed value.

Results

Observation CV

The posterior mean estimate of $1/CV^2$ was 91.1 (SD 19.1), which corresponds with a CV of 10.5%. This value was used in all subsequent analyses. Note that this is very close to the value of 9.8% estimated by Thomas (2011) and used in Thomas (2012) and Thomas (2013), which was based on the 1984-2010 pup production data (i.e., without the 2012 data point).

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 213.4 (Table 2), and after inclusion of the independent population estimate was 21.2. ESSs this small 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. However, more runs of the model used for final inference may be prudent.

Parameter and population estimates

Model fits to the pup production estimates are shown in Figure 1. In all four regions (except perhaps Orkney), the estimated pup production fails to fit the most recent pup production – this pup production is significantly higher than any previous recorded value, and in Inner and Outer Hebrides is very different from the recent trajectory . The model in general provides a poor fit to some of the observed historical pup productions: in North Sea, it fails to capture the rapid acceleration in pup production from 2008 onwards and hence over-predicts pup production from 2001-2008, while under-predicting the most recent value; in Inner Hebrides, the most recent high pup production estimate has pulled the estimated trajectory upwards, so that all of the previous 13 pup production estimates are below the fitted line; in Outer Hebrides the fitted line misses the very rapid increase in pup production in the early 1990s and sudden levelling off around 1994; in Orkney the fitted line under-predicts pup production from 1994-2004 and then over-predicts all subsequent years until 2012. At least some of this lack of fit can be attributed to the most recent pup production estimates, which "pull" the estimated trajectory away from the data points from previous years (cf. the lines in Figure 1 with those in Figure 1 of Thomas 2013, which did not include the 2012 pup production estimate).

Estimated pup production is very similar with or without the addition of the independent population size estimate (cf. blue and red lines in Figure 1).

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 0.96), maximum juvenile survival to decrease (to 0.42), and fecundity to increase slightly (to 0.97) but stay very close to the prior distribution. Comparing the parameter estimates to those obtained without the 2012 pup production estimate (Table 1 and Figure 2 of Thomas 2013), we see that estimates of survival and fecundity are very similar, but that the estimates of carrying capacity in each region are higher, particularly for the North Sea region.

Adult population size estimates are shown in Figure 3; the values for 2013 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 (130,300, with 95% CI 101,700-162,500), although the credible/confidence intervals just overlap. When the independent estimate is included in the population dynamics model fitting, the estimate for 2008 from this model decreases by 22% to 101,600 (95%CI 85,800-121,700). Estimates for all years from the model fit to both pup production data and the independent estimate are given in Appendix 1. The estimates for recent years are approximately 5% greater than those for the same years given in Thomas (2013), i.e., those without the most recent pup production estimates.

Additional investigations

Revised priors

As might be expected (and as was shown in previous briefing papers), 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 0.99) and maximum pup survival to decrease further (to an also unlikely 0.27), while fecundity was also slightly higher.

Estimates of total population size are slightly lower without the independent population estimate (cf. blue lines on Figure 3 and 5; see also Table 4), which is unsurprising given the revised prior (and posterior) on fecundity is lower; the credible interval is also wider. The addition of the independent population size estimate again lowers the total population size estimate, and the result is somewhat lower than with the old priors (cf. red lines on Figures 3 and 5).

Prior on sex ratio

As expected, the prior on sex ratio does not change the posterior distributions on model parameters greatly, even with the addition of the 2008 independent population estimate (cf. Figures 6 and 4; Table 1). This is because the prior on sex ratio is highly informative relative to the information in the data (i.e., the independent population estimate) on sex ratio.

The resulting estimate of total population size was similar to that with the fixed prior on sex ratio – slightly lower because the prior mean on sex ratio was slightly lower than the fixed value (cf. Figures 7 and 5; Table 4). Estimates for all years from the model fit to both pup production data and the independent estimate are given in Appendix 2.

Discussion

Main analysis

The 2012 pup production estimate is 14% higher than the 2010 estimate – an increase of approximately 7% a year. This is greater than the median increase in estimated pup production of approximately 4% per year. This estimate caused the estimated total population size in recent years to be approximately 5% larger than estimates made previously without the 2010 data (e.g., Thomas, 2013). The new pup production estimate also caused the estimated population growth rate to increase slightly: the estimate from Thomas (2013) for the years 2011-2012 was 0.2%; the new estimate for the same pair of years is 0.9%.

The fitted model does not capture all the features of the pup production data – there are clear runs of positive or negative residuals (Figure 1), and in no region except Orkney does the model fit the last data point (from 2012) well. It may be useful to investigate potential causes of inter-annual variation in fecundity – an initial analysis could be made of the residuals verses potential explanatory variables.

Additional investigations

Thomas (2013) made an initial investigation of the sensitivity of the total population size estimate to changes in priors on demographic parameters. He found that changing priors on adult or pup survival had little effect on estimated total population size because of a strong inverse correlation between the two parameters; by contrast, changing the prior on fecundity had a strong effect since it was highly informative (in the sense that the posterior was almost identical to the prior) and not correlated with the other parameters. Hence it seems likely that the changes in population size observed with use of the revised priors is caused by the revised prior on fecundity.

Thomas (2013) also investigated the effect of allowing sex ratio to be a parameter, rather than assuming it to be fixed, but he used a very different prior on sex ratio from the one used here. Thomas (2013) used a prior with a mean of 1.2 and standard deviation of 0.63, based on the suggestion of Longeran (2012). This produced parameter estimates much closer to those obtained without the independent estimate, and a population size estimate also closer to that from the population model alone, although more precise. It is clear that the prior on sex ratio has a very strong effect on the final estimated population size. While the prior suggested by Lonergan (2012) is thought to include implausibly low values (Thompson 2014), we find that using the narrower, higher prior reported here leads to estimates of adult and maximum pup survival that are implausibly high and low, respectively. Clearly, more work is required to refine the prior distributions for population parameters.

Despite this ongoing uncertainty, our current estimates of adult population size in 2013 are not very different using old priors (106,300 with 95%CI 86,100-131,300) and new priors including the prior on sex ratio (98,800 with 95%CI 81,400-122,000).

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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 and 2012 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)	0.96 (0.015)	0.8+0.2*Be(1.6,1.2)	0.91 (0.05)	0.99 (0.01)	same as previous		0.99 (0.01)
pup survival ϕ_j	Be(14.53,6.23)	0.70 (0.10)	0.42 (0.09)	Be(2.87,1.78)	0.62 (0.20)	0.28 (0.05)	same as previous		0.28 (0.06)
fecundity $\alpha_{\max}$	Be(22.05,1.15)	0.95 (0.04)	0.97 (0.03)	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.91 (0.06)	same as previous		0.90 (0.06)
dens. dep. ρ	Ga(4,2.5)	10 (5)	3.77 (1.36)	same as previous		6.02 (2.38)	same as previous		5.96 (2.36)
NS carrying cap. χ_1	Ga(4,2500)	10000 (5000)	13100 (3390)	same as previous		14500 (5430)	same as previous		14400 (5260)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3680 (496)	same as previous		3770 (468)	same as previous		3760 (463)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	12500 (791)	same as previous		13100 (1580)	same as previous		13100 (1540)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	22300 (2800)	same as previous		23300 (3650)	same as previous		23300 (3660)
observation CV ψ	Fixed	0.098 (0)	-	Fixed	0.89 (0)	-	same as previous		-
sex ratio ω	Fixed	1.73 (0)	-	same as previous		-	1.6+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 estimate (ESS_{u2}).***

Model	K ($\times10^7$)	K^* ($\times10^6$)	U ($\times10^4$)	ESS_{u1}	ESS_{u2}
EDDSNM Old priors	1000	1.41	10.6	213.4	21.2
EDDSNM New priors	2000	3.93	7.17	702.7	121.9
EDDSNM New priors, estimated sex ratio	n/a				138.3

Table 3. **Estimated size, in thousands, of the British grey seal population at the start of the 2013 breeding season, derived from models fit to pup production data from 1984-2012 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	31.3 (21.9 41.1)	24.3 (18.1 32)
Inner Hebrides	9.7 (7.7 12.2)	7.8 (6 9.4)
Outer Hebrides	34.1 (27.5 41.4)	27 (22.1 32.4)
Orkney	63 (46.9 86.7)	47.2 (40 57.4)
Total	138.1 (104.1 181.5)	106.3 (86.1 131.3)

Table 4. **Estimated size, in thousands, of the British grey seal population at the start of the 2013 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	138.1 (104.1 181.5)	106.3 (86.1 131.3)
Revised priors	135.1 (91.1 192.8)	100.2 (82.2 124.8)
Revised priors with estimated sex ratio	133.1 (89.6 190.2)	98.8 (81.4 122)

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 1984-2012 (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.

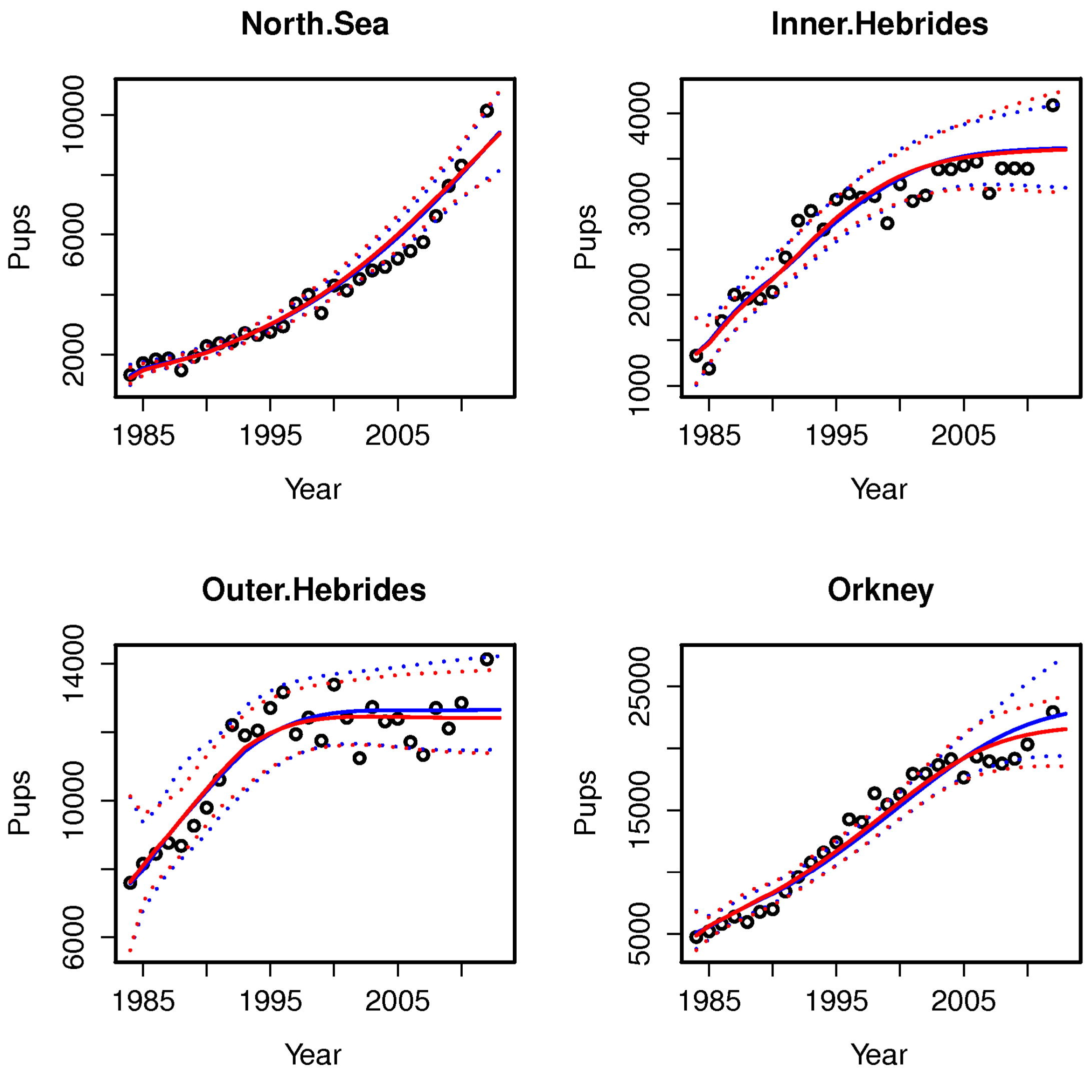
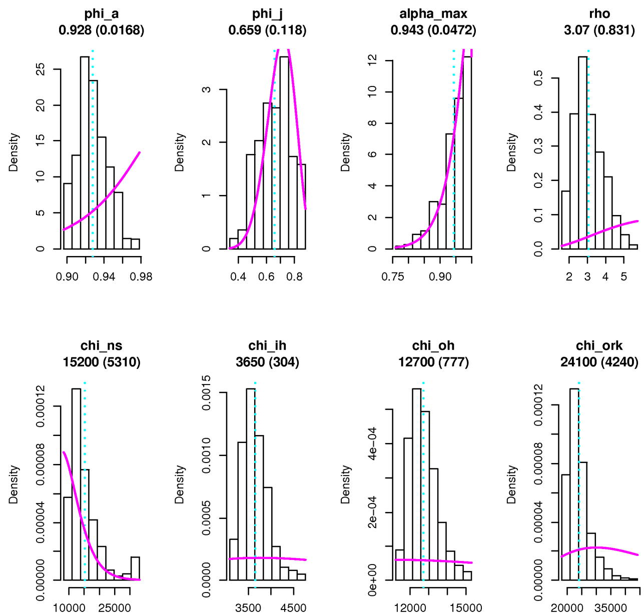


Figure 2. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008, using the old parameter priors. The vertical line shows the posterior mean; its value 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

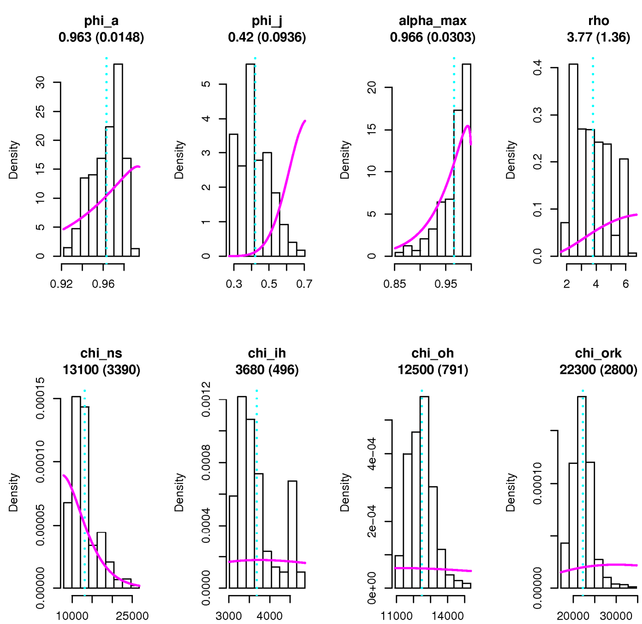


Figure 3. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2013 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2012 and a total population estimate from 2008 (circle, with horizontal lines indicating 95% confidence interval on the estimate), 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.

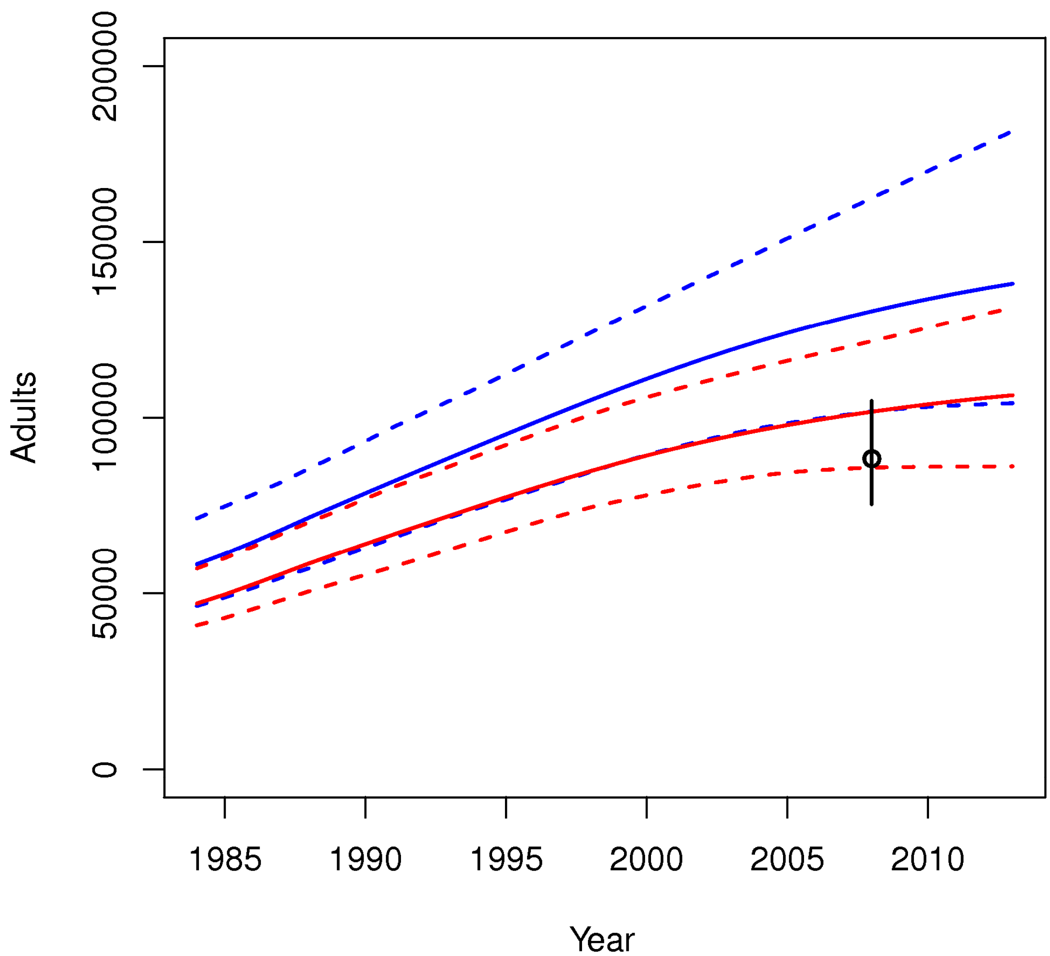
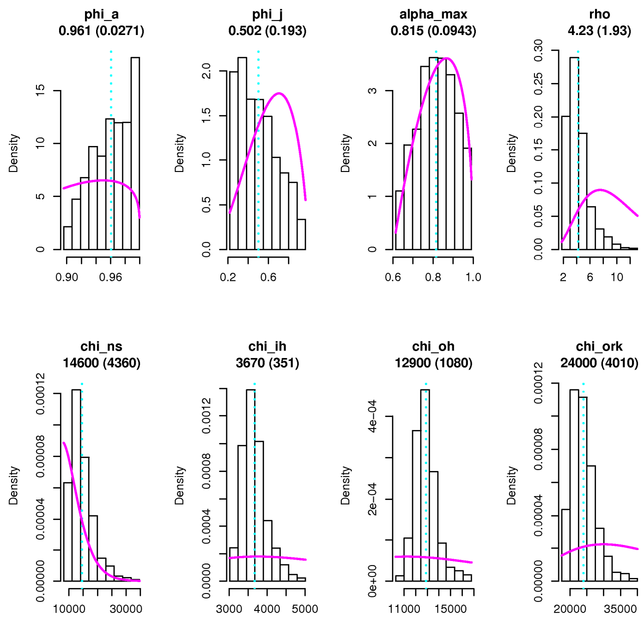


Figure 4. Prior (histograms) and posterior (solid lines) parameter estimates obtained using the revised priors. See Figure 2 legend for further explanation of the plots.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

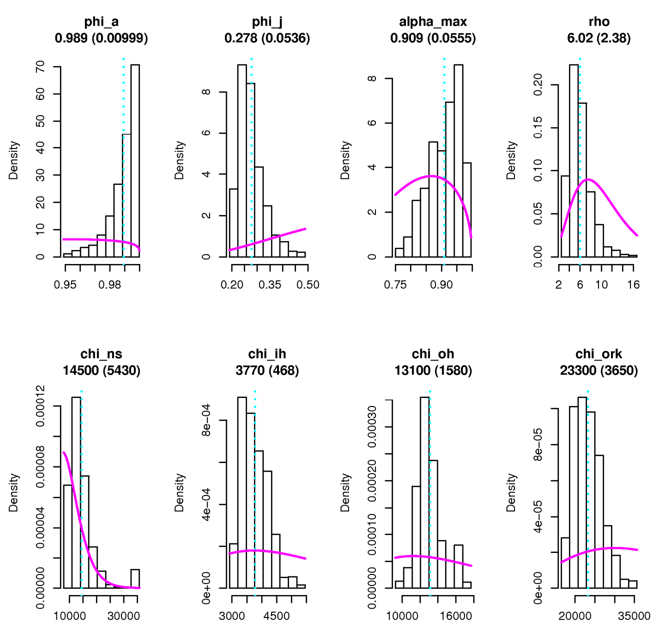


Figure 5. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size obtained using revised priors. See figure 3 legend for further explanation of the plot.

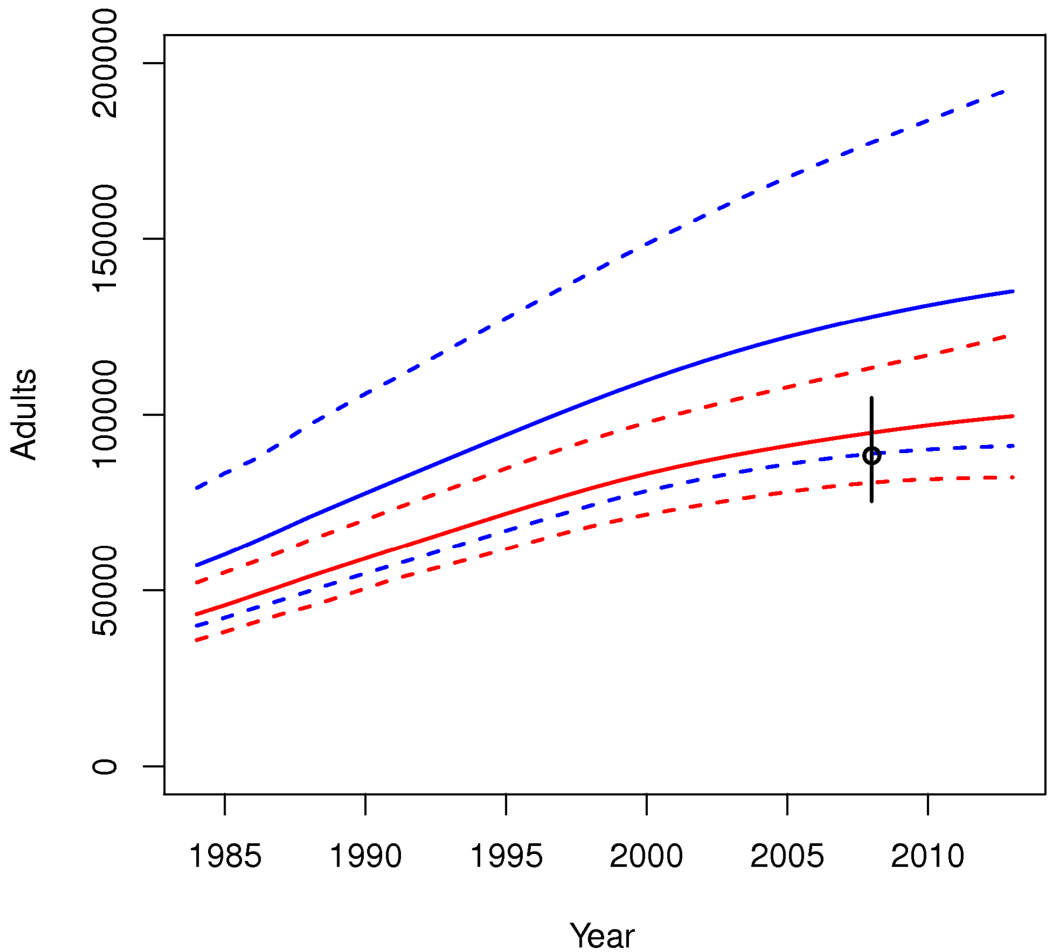
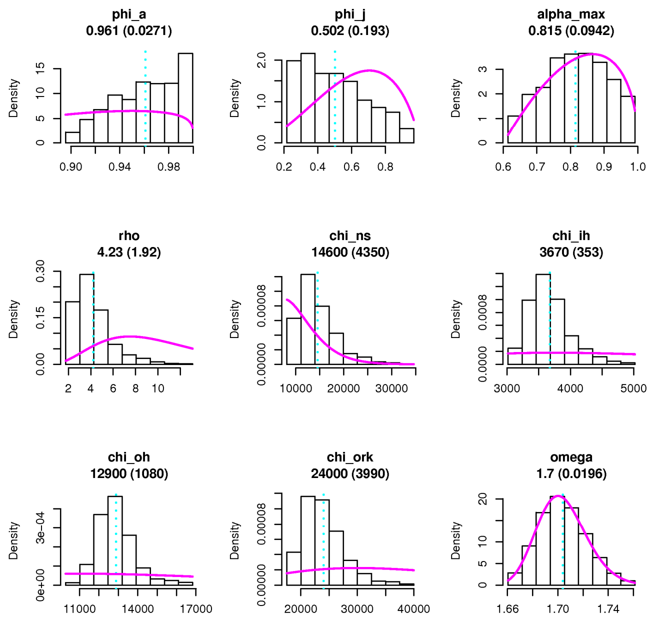


Figure 6. Prior (histograms) and posterior (solid lines) parameter estimates obtained using the revised priors, including a prior on sex ratio. See Figure 2 legend for further explanation of the plots.

(a) Pup production data alone



(b) Pup production data and 2008 population estimate

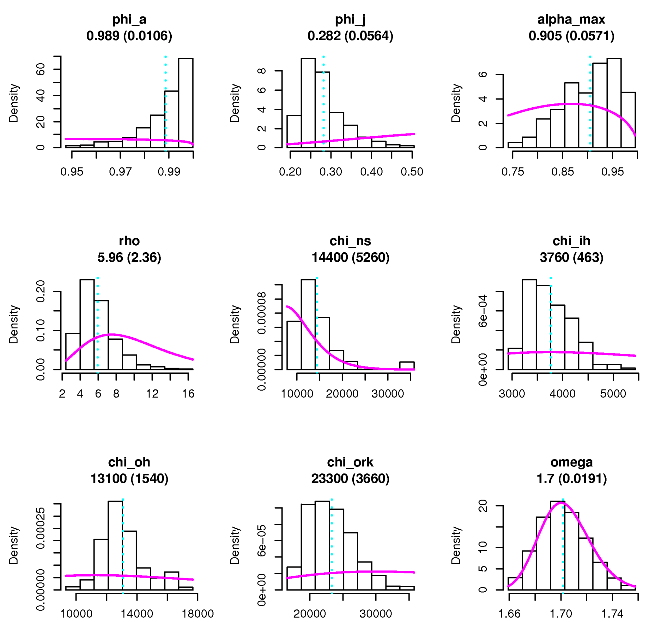
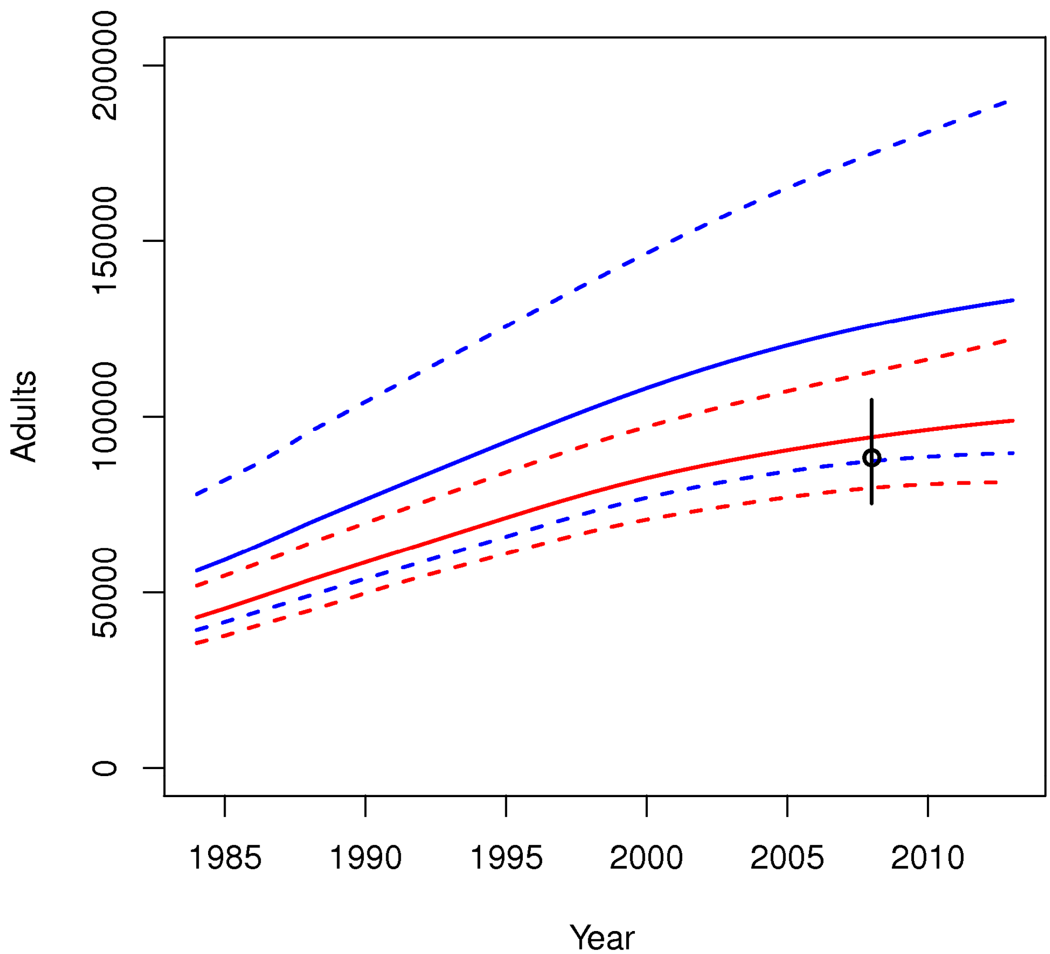


Figure 7. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size obtained using revised priors including a prior on sex ratio. See figure 3 legend for further explanation of the plot.



Appendix 1

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	4.2 (3.7 5)	4.5 (3.9 5.5)	21.5 (18.8 26.1)	16.9 (14.5 20.4)	47.1 (40.9 57)
1985	4.5 (4 5.3)	4.7 (4.1 5.8)	22.4 (19.4 27.3)	18 (15.5 21.6)	49.6 (43 60)
1986	4.8 (4.3 5.8)	5 (4.4 6.1)	23.4 (20.2 28.5)	19.3 (16.6 22.9)	52.5 (45.5 63.3)
1987	5.2 (4.6 6.2)	5.3 (4.6 6.5)	24.2 (21 29.6)	20.7 (17.8 24.6)	55.5 (48 66.8)
1988	5.6 (4.9 6.7)	5.6 (5 6.8)	25 (21.5 30.5)	22.2 (19.2 26.3)	58.5 (50.5 70.3)
1989	6.1 (5.3 7.2)	5.9 (5.2 7.1)	25.6 (21.9 30.9)	23.7 (20.6 28.2)	61.3 (52.9 73.4)
1990	6.5 (5.7 7.7)	6.2 (5.4 7.5)	26 (22.1 31.5)	25.3 (22.1 30.2)	64 (55.2 76.9)
1991	7 (6.1 8.3)	6.4 (5.6 7.8)	26.3 (22.3 32.1)	27 (23.6 32.1)	66.8 (57.6 80.3)
1992	7.5 (6.5 8.9)	6.6 (5.8 8.1)	26.6 (22.4 32.3)	28.7 (25.3 33.9)	69.5 (60 83.2)
1993	8.1 (7 9.6)	6.9 (5.9 8.3)	26.8 (22.5 32.4)	30.4 (27 35.9)	72.1 (62.5 86.2)
1994	8.7 (7.5 10.3)	7 (6 8.5)	26.9 (22.6 32.5)	32.2 (28.9 37.9)	74.8 (65 89.2)
1995	9.3 (8 11)	7.2 (6.1 8.7)	27 (22.7 32.5)	33.9 (30.7 40)	77.4 (67.5 92.2)
1996	10 (8.6 11.8)	7.3 (6.1 8.9)	27 (22.7 32.4)	35.6 (32.6 42)	79.9 (70 95.1)
1997	10.7 (9.2 12.7)	7.4 (6.1 9)	27 (22.7 32.3)	37.3 (34.3 43.9)	82.4 (72.3 98)
1998	11.4 (9.9 13.6)	7.5 (6.2 9.1)	27 (22.7 32.3)	38.8 (35.8 45.8)	84.8 (74.5 100.8)
1999	12.2 (10.6 14.5)	7.6 (6.2 9.2)	27 (22.6 32.3)	40.3 (36.9 47.5)	87.1 (76.2 103.4)
2000	13 (11.3 15.5)	7.6 (6.1 9.2)	27 (22.6 32.2)	41.5 (37.8 48.9)	89.2 (77.9 105.8)
2001	13.9 (12.2 16.5)	7.7 (6.1 9.2)	27 (22.6 32.2)	42.7 (38.7 50.1)	91.2 (79.5 108)
2002	14.7 (13 17.5)	7.7 (6.1 9.3)	27 (22.5 32.2)	43.6 (39.4 51.2)	93.1 (81 110.1)
2003	15.7 (13.9 18.6)	7.7 (6.1 9.3)	27 (22.5 32.2)	44.4 (39.8 52.1)	94.8 (82.3 112.2)
2004	16.6 (14.8 19.8)	7.7 (6.1 9.3)	27 (22.4 32.2)	45.1 (40.2 53)	96.4 (83.5 114.2)
2005	17.5 (15.5 21)	7.8 (6.1 9.3)	27 (22.3 32.2)	45.6 (40.5 53.7)	97.8 (84.4 116.2)
2006	18.4 (16.1 22.3)	7.8 (6 9.3)	26.9 (22.3 32.2)	46 (40.6 54.2)	99.2 (85 118)
2007	19.4 (16.6 23.6)	7.8 (6 9.3)	26.9 (22.2 32.2)	46.4 (40.6 54.7)	100.5 (85.4 119.8)
2008	20.3 (16.9 25)	7.8 (6 9.3)	26.9 (22.2 32.3)	46.6 (40.7 55.1)	101.6 (85.8 121.7)
2009	21.2 (17.2 26.5)	7.8 (6 9.3)	27 (22.2 32.3)	46.8 (40.5 55.6)	102.7 (85.9 123.6)
2010	22 (17.5 27.8)	7.8 (6 9.3)	27 (22.1 32.3)	46.9 (40.4 56.1)	103.8 (86 125.6)
2011	22.8 (17.7 29.3)	7.8 (6 9.4)	27 (22.1 32.4)	47 (40.2 56.6)	104.7 (86 127.6)
2012	23.6 (17.9 30.7)	7.8 (6 9.4)	27 (22.1 32.4)	47.1 (40.1 57)	105.6 (86.1 129.5)
2013	24.3 (18.1 32)	7.8 (6 9.4)	27 (22.1 32.4)	47.2 (40 57.4)	106.3 (86.1 131.3)

Appendix 2

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 new priors, including a prior on sex ratio. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	3.9 (3.3 4.7)	4.1 (3.5 5)	19.5 (15.9 23.7)	15.3 (12.9 18.5)	42.9 (35.6 51.9)
1985	4.2 (3.5 5)	4.4 (3.7 5.3)	20.5 (16.5 25)	16.3 (13.9 19.5)	45.4 (37.6 54.8)
1986	4.5 (3.8 5.3)	4.7 (4 5.6)	21.5 (17.6 26)	17.4 (14.9 20.8)	48 (40.2 57.7)
1987	4.8 (4 5.7)	5 (4.2 5.9)	22.4 (18.2 27)	18.6 (16 22.2)	50.7 (42.5 60.7)
1988	5.1 (4.4 6.1)	5.2 (4.5 6.2)	23.1 (18.8 27.9)	20 (17.1 23.7)	53.5 (44.8 64)
1989	5.5 (4.7 6.6)	5.5 (4.7 6.5)	23.6 (19.4 28.4)	21.4 (18.4 25.4)	56 (47.2 66.8)
1990	5.9 (5.1 7)	5.8 (5 6.8)	24.1 (20 28.8)	22.9 (19.7 27.1)	58.6 (49.7 69.7)
1991	6.3 (5.5 7.5)	6 (5.2 7.1)	24.4 (20.5 29.1)	24.4 (21.1 28.9)	61.1 (52.2 72.6)
1992	6.8 (5.9 8.1)	6.2 (5.3 7.4)	24.6 (20.8 29.3)	26 (22.5 30.8)	63.7 (54.5 75.5)
1993	7.3 (6.3 8.6)	6.4 (5.5 7.6)	24.8 (21 29.5)	27.7 (24 32.7)	66.2 (56.7 78.4)
1994	7.8 (6.7 9.3)	6.6 (5.6 7.8)	24.9 (21.1 29.6)	29.5 (25.4 34.6)	68.7 (58.9 81.3)
1995	8.4 (7.2 9.9)	6.7 (5.7 8)	25 (21.2 29.7)	31.2 (26.9 36.5)	71.2 (61.1 84.2)
1996	9 (7.7 10.6)	6.8 (5.8 8.1)	25.1 (21.3 29.8)	32.9 (28.4 38.4)	73.7 (63.2 86.9)
1997	9.6 (8.3 11.4)	6.8 (5.8 8.2)	25.1 (21.3 29.8)	34.6 (29.9 40.3)	76.1 (65.4 89.6)
1998	10.3 (8.9 12.2)	6.9 (5.9 8.3)	25.2 (21.4 29.8)	36.1 (31.2 42)	78.4 (67.3 92.3)
1999	11 (9.5 13.1)	6.9 (5.9 8.3)	25.2 (21.5 29.8)	37.4 (32.3 43.5)	80.5 (69.2 94.8)
2000	11.8 (10.2 14)	7 (6 8.3)	25.2 (21.5 29.9)	38.6 (33.1 44.9)	82.5 (70.8 97.1)
2001	12.6 (10.9 14.9)	7 (6 8.4)	25.2 (21.5 29.9)	39.6 (33.8 46.1)	84.4 (72.2 99.3)
2002	13.4 (11.6 15.9)	7 (6 8.4)	25.2 (21.6 29.9)	40.4 (34.4 47.2)	86 (73.5 101.4)
2003	14.3 (12.3 17)	7 (6 8.4)	25.2 (21.6 29.9)	41 (34.8 48.1)	87.6 (74.8 103.4)
2004	15.2 (13.1 18)	7.1 (6 8.4)	25.3 (21.6 29.9)	41.6 (35.2 48.9)	89.1 (76 105.3)
2005	16.1 (13.9 19.2)	7.1 (6 8.5)	25.3 (21.6 29.9)	42 (35.6 49.6)	90.4 (77.1 107.2)
2006	17 (14.6 20.4)	7.1 (6 8.5)	25.3 (21.6 30)	42.3 (35.8 50.2)	91.7 (78.1 109)
2007	18 (15.2 21.6)	7.1 (6.1 8.5)	25.3 (21.7 30)	42.6 (36.1 50.7)	93 (79 110.8)
2008	18.9 (15.8 22.8)	7.1 (6.1 8.5)	25.3 (21.7 30)	42.8 (36.2 51.2)	94.1 (79.7 112.6)
2009	19.8 (16.3 24.1)	7.1 (6.1 8.6)	25.3 (21.7 30)	43 (36.4 51.7)	95.2 (80.4 114.4)
2010	20.6 (16.6 25.4)	7.1 (6.1 8.6)	25.3 (21.7 30.1)	43.2 (36.5 52.1)	96.2 (80.8 116.2)
2011	21.4 (16.8 26.8)	7.1 (6.1 8.6)	25.4 (21.7 30.1)	43.3 (36.6 52.6)	97.2 (81.1 118.1)
2012	22.1 (17 28.3)	7.2 (6.1 8.6)	25.4 (21.7 30.1)	43.4 (36.6 53)	98 (81.3 120)
2013	22.7 (17.1 29.9)	7.2 (6.1 8.6)	25.4 (21.7 30.2)	43.5 (36.6 53.3)	98.8 (81.4 122)