Estimating the size of the UK grey seal population between 1984 and 2017.

Len Thomas.

Scottish Oceans Institute and Centre for Research into Ecological and Environmental Modelling, The University of St Andrews, The Observatory, St Andrews, Fife, KY16 9LZ

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, and (2) independent estimates assumed to be of total population size just before the 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 with the exception that one prior distribution (on carrying capacity in North Sea region) has been slightly altered.

The above model was fitted with three different inputs. For the main analysis, these were pup production estimates from 1984-2016, as given in briefing paper SCOS-BP 18/01, and independent estimates of population size from 2008 and 2014. In additional analysis 1, the same data were used, but only for the period 1984-2010. In additional analysis 2, data for the period 1984-2010 was also used, but with pup production data derived using a slightly different assumption (PCorrectClass parameter set to 0.5 for all years).

For the main analysis, estimated population size in regularly monitored colonies in 2017 was 135,700 (95% CI 118,500-155,200). The population overall is estimated to be increasing at a rate of 2% per year. For additional analysis 1, the estimated population size in 2010 was 10% lower than for the main analysis in the same year, and the estimated rate of population increase was closer to 1% per year. For additional analysis 2, estimated population size in 2010 was a further 3% lower.

We conclude that estimates of the current population size and trajectory are somewhat sensitive to the assumptions made when deriving pup production estimates, and on whether and how the post-2010 data are included.

Introduction

This paper presents estimates of British grey seal population size and related demographic parameters, obtained using a Bayesian state-space model of population dynamics fitted to pup production estimates (from aerial surveys of breeding colonies) and independent estimates of total population size (from haul-out counts). The model and fitting methods are the same as those employed in recent years (e.g., Thomas 2016) and are described in detail in SCOS-BP 18/05.

The main analysis uses pup production estimates for 1984-2016 (SCOS-BP 18/01), plus independent estimates of total population size from 2008 and 2014 (Russell et al. 2016). The survey and analysis methods for deriving pup production estimates have changed somewhat over the years, and it was of interest to compare estimates of population size derived using different pup production inputs. To facilitate this, two additional analyses were undertaken: first, only data up to 2010 was used; second, data up to 2010 was used but with a pup production estimation parameter changed (probability of correctly classifying moulted pups as moulted, PCorrectClass, set to 0.5). This latter set of pup production estimates were derived by Russell et al. (SCOS-BP 18/02), and the results using these data that are reported here are taken from Thomas et al. (SCOS-BP 18/05).

For the main analysis, we present estimates of population size at the start of the 2017 breeding system (i.e., projected forward one year from the last data point). For the two additional analyses, we present estimates for 2010, the last year of data in those analyses.

Note that all estimates of population size relate to seals associated with the regularly-monitored colonies. A multiplier is required to account for the ~10% of seals that breed outside these colonies.

Methods

Full details of the population dynamics model, data and fitting methods are given in SCOS-BP 18/05. In summary, an age-structured population dynamics model is specified for each of four regions (North Sea, Inner Hebrides, Outer Hebrides and Orkney), with 7 ages included in the model: pups, age 1-5 females (assumed not to reproduce) and age 6+ females (which may breed). The model assumes constant adult (age 1+) survival (indexed by a parameter ϕ_a), constant fecundity (probability that an age 6+ female will birth a pup, α) and density-dependent pup survival with separate carrying capacity in each region (carrying capacity parameters χ_1 χ_4 and common parameters for maximum pup survival $\phi_{p\max}$ and shape of the density dependence function ρ). The modelled pup production is linked to the data by assuming the data follow a normal distribution centred on true pup production and with precision parameter ψ. Adult males are not tracked explicitly in the population model, but instead, the total population size (of males and females) is derived by multiplying estimated adult females by a parameter ω that represents the ratio of total adults to adult females (sometimes called "sex ratio" as shorthand, although sex ratio is actually given by ω 1). The modelled total population size (age 1+ animals) is linked to the independent estimates using the empirically derived uncertainty on the independent estimates. Informative prior distributions are used on model parameters, as detailed in SCOS-BP 18/03 and SCOS-BP 18/05. These prior distributions were largely identical to those used in 2016 and 2017, with one minor change: expected carrying capacity in North Sea was doubled from 10,000 to 20,000 (with a prior coefficient of variation as before of 50%).

Three runs are reported here, using different input data:

- Main analysis. Pup production data from 1984-2016 (SCOS-BP 18/01), plus independent estimates of population size from size from 2008 and 2014 (Russell et al. 2016).
- Additional analysis 1. Pup production data from 1984-2010, as reported by Duck and Morris (SCOS-BP 18/01), plus an independent estimate of population size from 2008 (Russell et al. 2016).
- Additional analysis 2. Pup production data from 1984-2010, as reported by Russell et al. (submitted, i.e., with PCorrectClass set to 0.5), plus an independent estimates of population size from 2008 (Russell et al. 2016). (This is the dataset analyzed in SCOS-BP 18/05)

The pup production estimates for these last two analyses differ only in the years 2008, 2009 and 2010, with the latter being on average 8% lower in those years. Also, the pup production estimate for Inner Hebrides for 2009 is marked as missing in the latter dataset, where the value from 2008 is copied over to 2009 in the former.

Model fitting, as in previous reports, used a stochastic simulation-based procedure called a particle filter (SCOS-BP 18/05). Reliability of reported results depends on the number of simulations. For the main analysis, 2 billion simulations were used, which resulted in reported results accurate to 3 significant figures in most cases (2 for some parameters); for the additional analyses, 1 billion simulations were used for additional analysis 1, while 4 billion simulations were used for additional analysis 2. (The latter used a larger number of simulations for additional accuracy because it was used in a submitted paper.)

Results

Main analysis

Estimated pup productions from the model match the observed values reasonably well (Figure 1), although there is evidence for systematic lack of fit from the last three observations in each region (2012, 2014 and 2016), all of which are above the fitted trend. Pup production is estimated to be increasing strongly in North Sea, stable in Outer Hebrides, nearly so in Inner Hebrides and approaching stability in Orkney (Figure 1). Estimates of pup production based on just the pup production data are very similar to those based on pup production data and the independent estimates of population size (compare red and blue lines in Figure 1).

Total population size from the pup production data alone (blue line in Figure 2) is estimated to be higher than the independent estimates of population size. When the independent estimates are included in inference, the total population size estimate decreases to become larger than the independent estimate from 2008 and smaller than that from 2014 (red line in Figure 2). Posterior mean population size in regularly-monitored colonies in 2017 was 135,700 with 95% credible interval (CI) 118,500-155,200. Estimates by region are given in Table 2 and estimates for all years 1984-2017 are given in the Appendix.

Posterior parameter distributions are shown in Figure 3, with numerical summaries in Table 1. Adult survival is estimated to be rather higher than the prior distribution, with posterior mean 0.96 (SE 0.01) and most mass near the upper boundary of 0.97. Pup survival is estimated to be lower than the prior (mean 0.45 SE 0.07) and fecundity somewhat higher (mean 0.92 SE 0.48). Three regions (Inner Hebrides, Outer Hebrides and Orkney) are estimated to be close to or slightly over carrying capacity (i.e., posterior mean on carrying capacity parameter at or close to the pup production in 2016), while North Sea is at approximately half of carrying capacity (although that estimate is very imprecise with SE/mean=0.5 like the prior). Estimated sex ratio is unchanged from the prior.

Additional analysis 1: 1984-2010 data

The estimated pup production trajectories are significantly lower given 1984-2010 data (Figure 4, top 4 panels) than with the 1984-2016 data used in the main analysis (Figure 1). Pup production is estimated to have peaked in Outer Hebrides in the late 1990s, in Inner Hebrides in the early 2000s and be levelling off in Orkney in 2010 (when the time series stops). North Sea is estimated to still be increasing at a near-exponential rate, but with a somewhat lower trajectory than when the 2012-16 data are included. These differences are down to the pup production estimates and not the 2014 independent estimate of population size, because they are evident when just pup production data is used in the analysis (blue lines in both plots).

Posterior mean population size in 2010 is 107,100 (95% CI 93,700-127,400), approximately 10% lower than the estimate from 2010 obtained when 1984-2016 data are used (Table 3). The two population trajectories are compared in Figure 5.

Additional analysis 2: 1984-2010 data and PCorrectClass=05

Estimated pup projection trajectories are slightly lower than for additional analysis 1 (Figure 4, lower 4 panels). Posterior mean on total population size in 2010 is 104,000 (95% Ci 88.1-124.1), approximately 3% lower than for additional analysis 1 and 13% lower than the main analysis (see also Figure 5).

Discussion

Estimated population size from the main analysis is slightly higher than that reported in last year's briefing paper (Thomas 2017) for a comparable year – for example the estimate for this year for 2016 is 133,300 (95% CI 117,000-152,400), while that of Thomas (2017) was 128,200 (95% CI

106,200-154,400), a difference of 4%. The difference is due to the addition of the pup production estimate for 2016, which like that for 2012 and 2014 (since the advent of digital aerial photography for the surveys), is higher than expected based on previous counts. As additional analysis 1 has shown, together, the three most recent pup production estimates cause an increase of approximately 10% in the 2010 population estimate – this difference will be even more pronounced by the time of the 2017 population estimate because the estimated rate of growth in the population is rather less if only data up to 2010 are used (Figure 5). Additional analysis 2 has shown that a relatively small change in the pup production estimation procedure for the pre-digital surveys can produce a further change in estimated total population size, although only of a few percentage points. Overall, it seems clear that an investigation of the methods used to derive pup production is warranted.

Depending on the data used, it appears that pup production in Outer Hebrides, Inner Hebrides and Orkney has stabilized; there is even evidence that the trajectory first overshot carrying capacity before falling back. This pattern of damped oscillation can occur under delayed density dependence as here, where there is a 5-year lag between pup survival declining due to the onset of density dependent processes and the resulting cohort of pups recruiting into the breeding population. This (and other possible population dynamics models) is discussed in SCOS-BP 18/05.

Given the very different trajectory of North Sea compared with the other regions, it is of interest to compare the estimated pup survival rates. The population dynamics model used has a parameter for maximum pup survival rate, $\phi_{p\max}$, which occurs when pup production is far from carrying capacity. In the main analysis, the posterior mean on this parameter is 0.45. Thomas et al. (submitted) showed that at carrying capacity, pup survival is given by

$$\phi_{pcc} = \frac{1 \quad \phi_a}{0.5\alpha\phi_a^5}$$

(SCOS-BP 18/05, equation 4); plugging in the posterior mean estimates for the main analysis (Figure 1), gives $\widehat{\phi}_{pcc}$=0.11. Pup survival in the North Sea is estimated to be closer to 0.45, while that in the other regions is estimated to be close to or at 0.11. (Note that estimates of uncertainty on these quantities should be derived for proper interpretation.)

The posterior distribution on adult survival has a mode close to the upper bound 0.97. In addition, den Heyer & Bowen (2017) obtained mark-recpature-based estimates of adult female survival in Canada that was higher than this upper bound (0.976 SE 0.001). Hence, consideration should be given to raising the upper bound on the prior for this parameter.

Thomas et al. (SCOS-BP 18/05) discuss how sensitive the estimate of total population size may be to the parameter priors, and conclude that fecundity and adult:female ratio are two parameters that strongly affect total population size but for which the prior specification is particularly influential. Hence a renewed focus on priors for these parameters may be appropriate.

References

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Table 1. Prior parameter distributions and summary of posterior distributions. Be denotes beta distribution, Ga Gamma distribution (with parameters shape and scale, respectively). Main analysis uses both 1984-2016 pup production estimates, and the 2008 and 2014 total population estimates; additional analysis 1 uses 1984-2010 pup production estimates and the 2008 total population estimate; additional analysis 2 uses 1984-2010 pup production estimates derived with the PCorrectClass parameter set to 0.5 and the 2008 total population estimate.

Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)		
			Main analysis: 1984-2016 data	Additional analysis 1: 1984-2010 data	Additional analysis 2: 1984-2010 data with PCorrectClass=0.5
adult survival ϕ_a	0.8+0.17*Be(1.6,1.2)	0.90 (0.04)	0.96 (0.01)	0.96 (0.01)	0.95 (0.01)
pup survival ϕ_{pmax}	Be(2.87,1.78)	0.62 (0.20)	0.45 (0.07)	0.46 (0.07)	0.48 (0.09)
Fecundity α	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.92 (0.05)	0.92 (0.06)	0.90 (0.06)
dens. dep. ρ	Ga(4,2.5)	10 (5)	3.02 (0.66)	4.81 (1.43)	5.95 (.173)
NS carrying cap. χ_1	Ga(4,5000)	20000 (10000)	34200 (12500)	22500 (13500	15500 (822)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	3930 (354)	3260 (215)	3110 (173)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	13300 (914)	12100 (609)	11700 (535)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	24500 (3320)	19600 (2580)	17800 (1680)
observation CV ψ	Ga(2.1,66.67)	140 (96.6)	73 (16.3)	108 (30.7)	111 (34.5)
sex ratio ω	1.6+Ga(28.08, 3.70E-3)	1.7 (0.02)	1.7 (0.02)	1.7 (0.02)	1.7 (0.02)

Table 2. Estimated size, in thousands, of the British grey seal population at the start of the 2017 breeding season, derived from a model fit to pup production data from 1984-2016 and the additional total population estimates from 2008 and 2014. Numbers are posterior means with 95% credible intervals in brackets.

	Estimated population size in thousands (95% CI)
North Sea	41.8 (32.1 51.4)
Inner Hebrides	8.9 (7.4 10.9)
Outer Hebrides	30.5 (26.4 36.5)
Orkney	54.5 (45.1 67.4)
Total	135.7 (118.5 155.2)

Table 3. Estimated size, in thousands, of the British grey seal population at the start of the 2010 breeding season. Main analysis uses both 1984-2016 pup production estimates, and the 2008 and 2014 total population estimates; additional analysis 1 uses 1984-2010 pup production estimates and the 2008 total population estimate; additional analysis 2 uses 1984-2010 pup production estimates derived with the PCorrectClass parameter set to 0.5 and the 2008 total population estimate. Numbers are posterior means with 95% credible intervals in brackets.

	Estimated population size in thousands (95% CI)		
	Main analysis: 1984-2016 data	Additional analysis 1: 1984-2010 data	Additional analysis 2: 1984-2010 data with PCorrectClass=0.5
North Sea	27.7 (22.6 32.5)	25.5 (19 31.7)	24.8 (17.1 32.1)
Inner Hebrides	8.8 (7.4 10.7)	7.6 (6.4 9.3)	7.4 (6.2 9.1)
Outer Hebrides	30.3 (26.4 36.1)	28.1 (24.1 34.1)	28.5 (23.6 35.1)
Orkney	52.5 (44.8 62.1)	46 (37.3 58.3)	43.1 (34.6 54.4)
Total	119.2 (105.9 136.2)	107.1 (93.7 127.4)	104 (88.1 124.1)

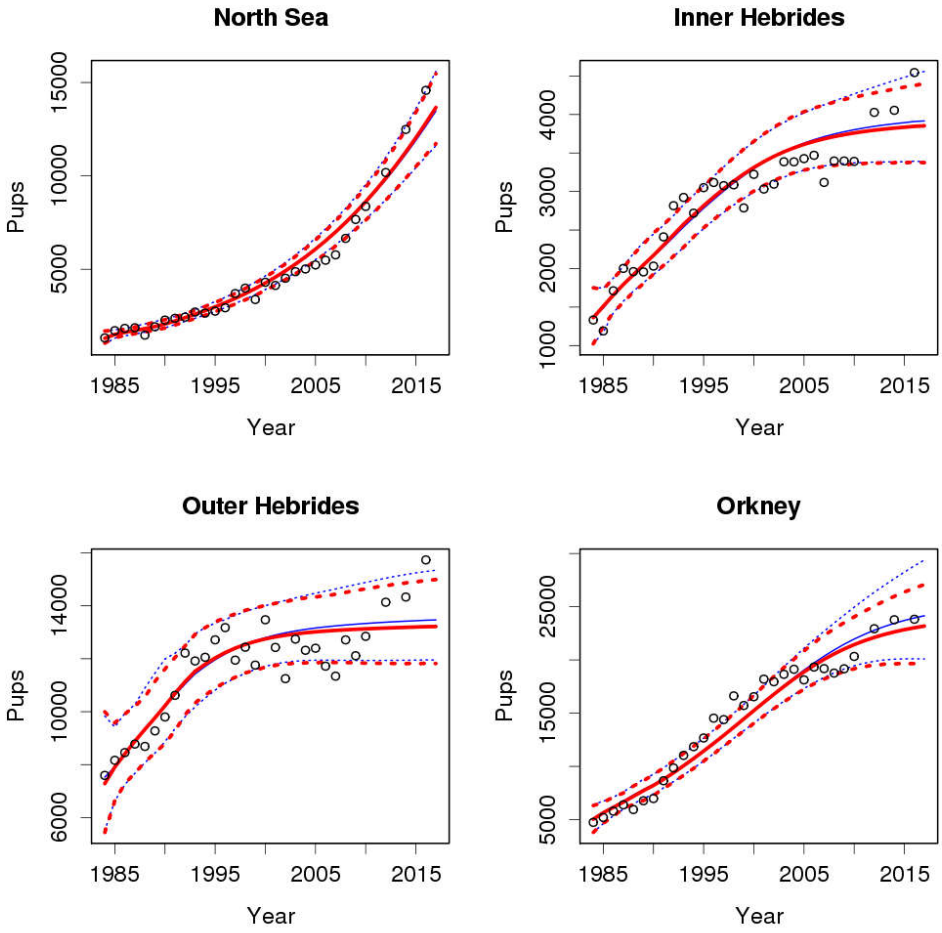

Figure 1. Posterior mean estimates of pup production (solid lines) and 95%CI (dashed lines) from the model of grey seal population dynamics, fitted to pup production estimates from 1984-2016 (circles) and the total population estimates from 2008 and 2014. Thinner blue lines (partly obscured) show the fit to pup production estimates alone; thicker red lines show the fit to pup production estimates plus the total population estimates.

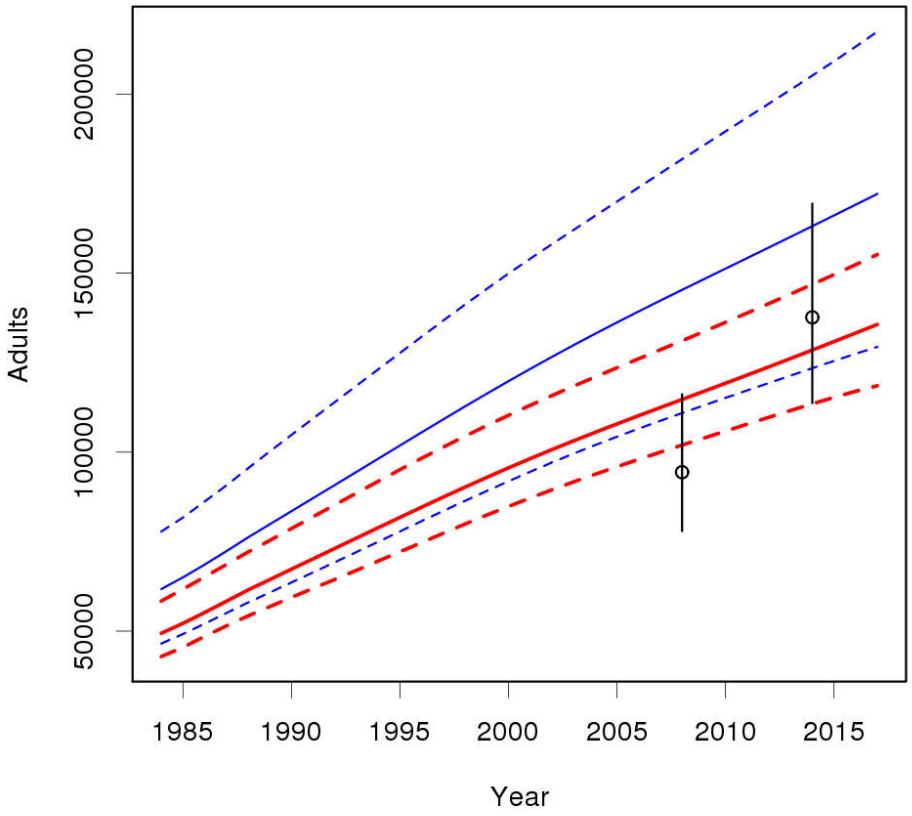

Figure 2. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2016 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2016 and total population estimates from 2008 and 2014 (circles, with vertical lines indicating 95% confidence interval on the estimates). Blue lines show the fit to pup production estimates alone; red lines show the fit to pup production estimates plus the total population estimates.

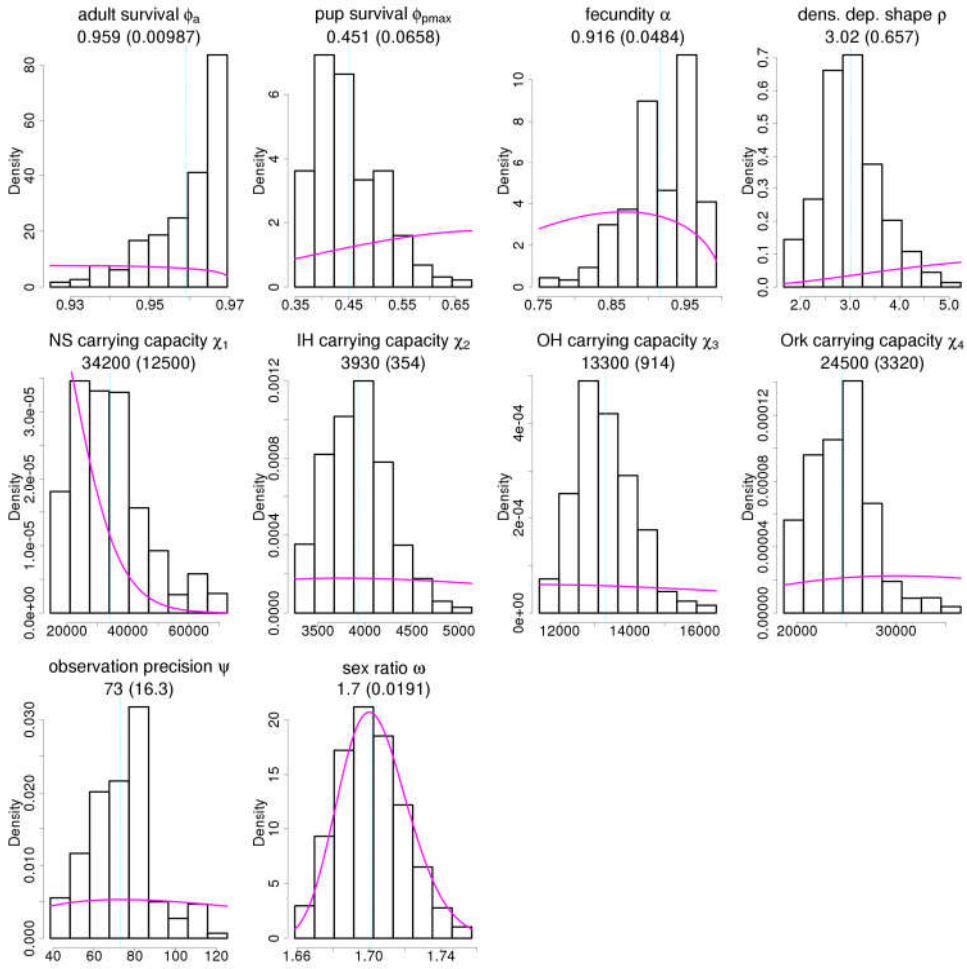

Figure 3. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2016 and total populations estimate from 2008 and 2014. The vertical dashed line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

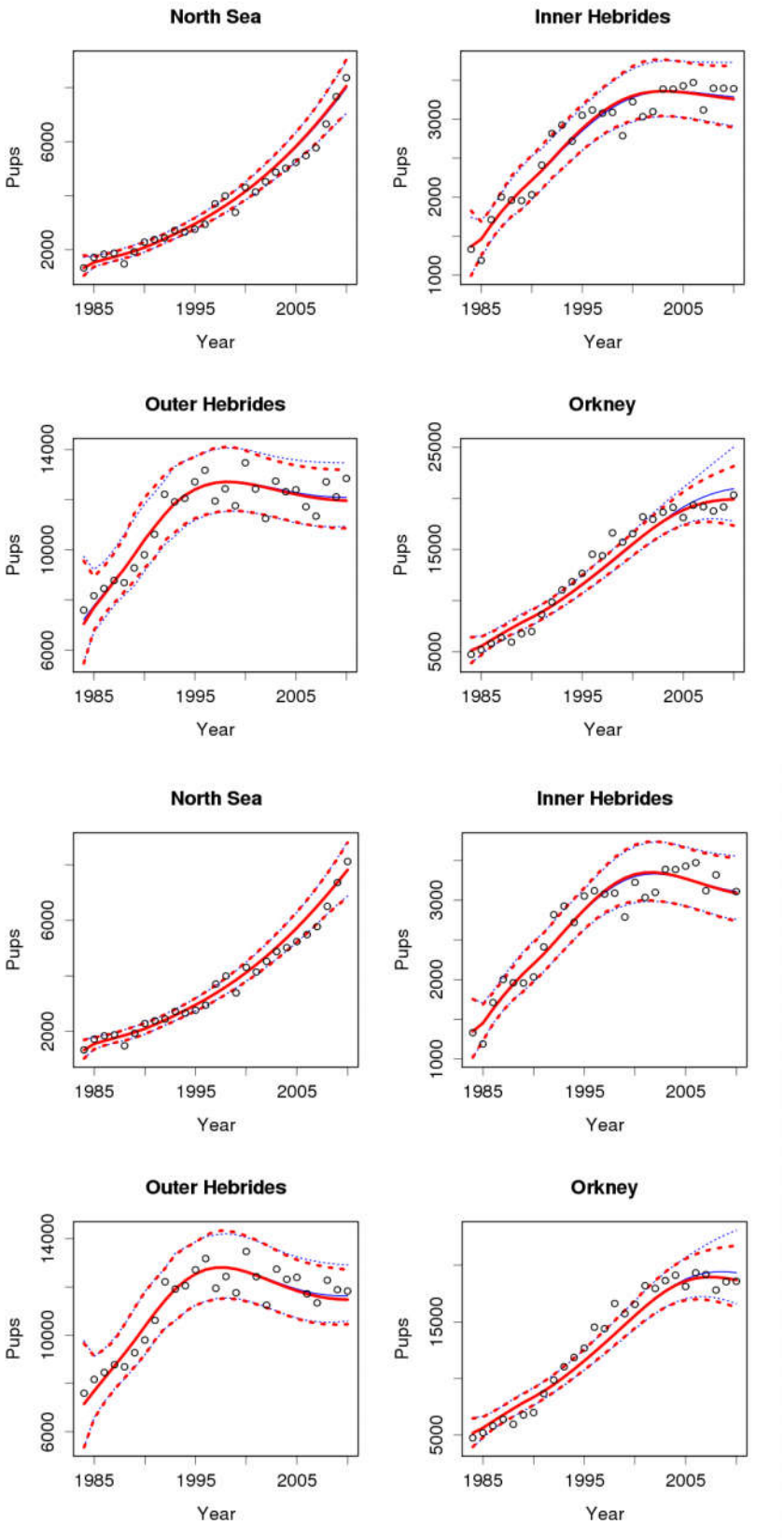

Figure 4. Posterior mean estimates of pup production for additional analysis 1 (top 4 plots) and 2 (bottom 4 plots). Note that the pup production data from 2008-2010 are different between the two analyses.

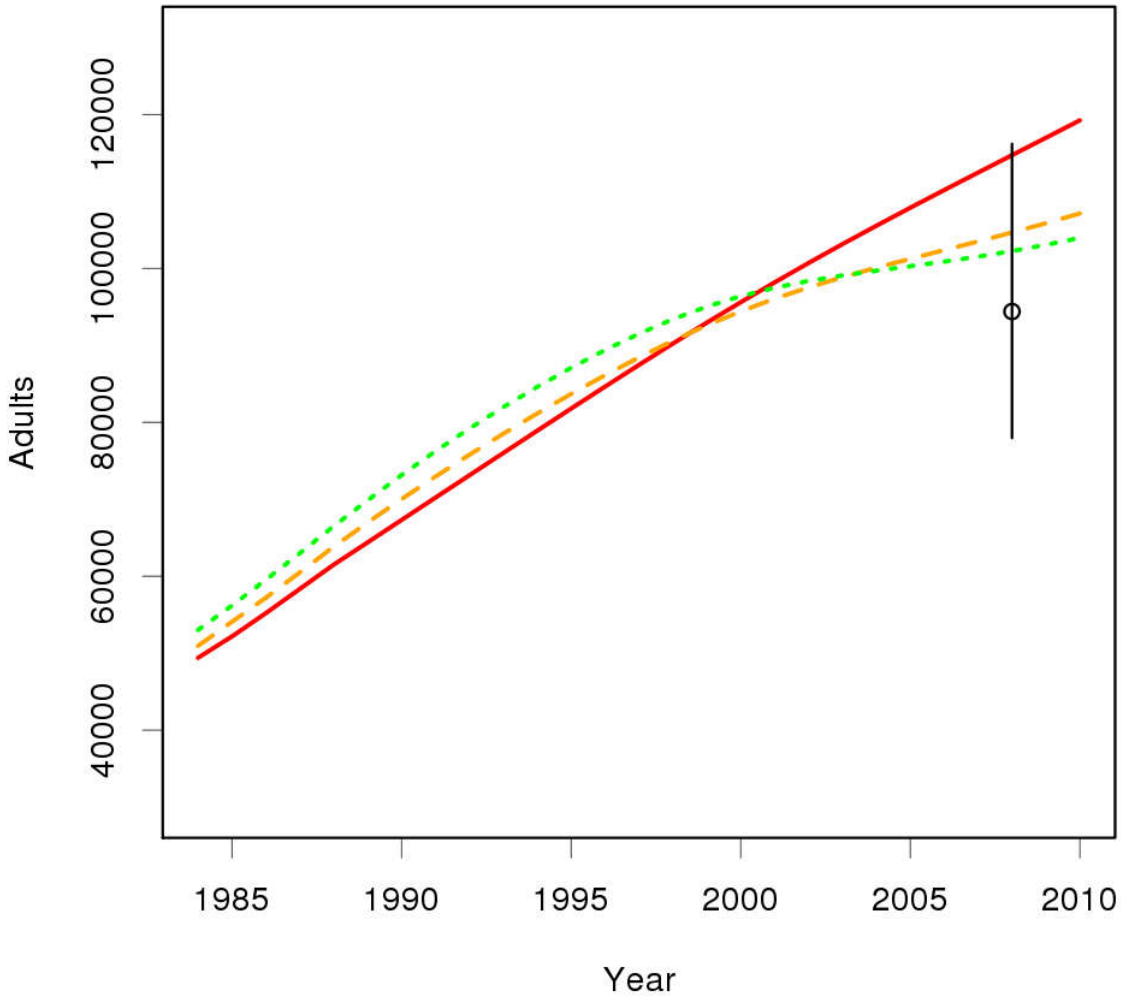

Figure 5. Posterior mean estimates of total population size in 1984-2010 from the model of grey seal population dynamics. Red solid line – main analysis; orange dashed line – additional analysis 1; green dotted line – additional analysis 2. Shown as a circle is the independent estimate from 2008 (horizontal lines indicate 95% confidence interval).

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Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2017, made using the model of British grey seal population dynamics fit to pup production estimates from 1984-2016 and total population estimates from 2008 and 2014. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.5 (3.7 5.3)	4.7 (4 5.7)	22.5 (19.4 27.2)	17.8 (14.5 21.8)	49.4 (42.9 58.4)
1985	4.8 (4 5.7)	5 (4.2 6)	23.5 (20.2 28.5)	18.9 (15.5 23)	52.2 (45.5 61.7)
1986	5.1 (4.4 6.1)	5.3 (4.5 6.2)	24.6 (21.3 29.5)	20.2 (16.9 24.4)	55.2 (48.5 65.2)
1987	5.5 (4.7 6.5)	5.6 (4.7 6.6)	25.6 (22.1 30.5)	21.6 (18.3 26)	58.3 (51.4 68.6)
1988	6 (5.1 7)	5.9 (5 7)	26.5 (22.9 31.7)	23.1 (19.7 27.7)	61.5 (54.2 72.1)
1989	6.4 (5.4 7.5)	6.2 (5.3 7.3)	27.1 (23.5 32.4)	24.7 (21.1 29.6)	64.4 (56.8 75.3)
1990	6.9 (5.8 8.1)	6.5 (5.5 7.7)	27.7 (24.1 33)	26.3 (22.5 31.4)	67.3 (59.5 78.6)
1991	7.4 (6.2 8.7)	6.7 (5.8 8)	28.1 (24.5 33.5)	28 (24.1 33.3)	70.2 (61.9 82)
1992	7.9 (6.7 9.3)	7 (6 8.3)	28.5 (24.9 33.8)	29.7 (25.7 35.2)	73.1 (64.4 85.3)
1993	8.5 (7.2 9.9)	7.2 (6.2 8.6)	28.8 (25.2 34.1)	31.5 (27.3 37.2)	76 (67 88.6)
1994	9.1 (7.7 10.7)	7.4 (6.4 8.9)	29.1 (25.5 34.3)	33.2 (29 39.2)	78.9 (69.6 91.9)
1995	9.8 (8.2 11.4)	7.6 (6.6 9.1)	29.3 (25.7 34.5)	35 (30.6 41.3)	81.8 (72.2 95.1)
1996	10.5 (8.8 12.3)	7.8 (6.7 9.3)	29.5 (25.9 34.6)	36.8 (32.3 43.3)	84.6 (74.7 98.3)
1997	11.3 (9.4 13.2)	8 (6.9 9.5)	29.6 (26 34.8)	38.6 (33.9 45.4)	87.4 (77.3 101.4)
1998	12.1 (10.1 14.1)	8.1 (7 9.7)	29.7 (26.1 34.9)	40.3 (35.4 47.3)	90.2 (79.9 104.4)
1999	13 (10.9 15.1)	8.2 (7.1 9.8)	29.8 (26.2 35)	41.9 (36.8 49.2)	92.9 (82.4 107.4)
2000	14 (11.6 16.2)	8.3 (7.1 10)	29.9 (26.2 35)	43.4 (38 50.9)	95.6 (84.8 110.3)
2001	15 (12.5 17.4)	8.4 (7.2 10.1)	30 (26.2 35.1)	44.8 (39.2 52.5)	98.2 (87.2 113.1)
2002	16.1 (13.4 18.7)	8.5 (7.2 10.2)	30 (26.3 35.2)	46.1 (40.2 53.9)	100.7 (89.5 115.8)
2003	17.2 (14.3 20.1)	8.5 (7.3 10.3)	30.1 (26.3 35.3)	47.3 (41.2 55.2)	103.1 (91.7 118.4)
2004	18.5 (15.3 21.5)	8.6 (7.3 10.4)	30.1 (26.3 35.4)	48.3 (42 56.4)	105.5 (93.8 121)
2005	19.8 (16.4 23.1)	8.6 (7.3 10.5)	30.2 (26.3 35.6)	49.3 (42.7 57.5)	107.9 (95.9 123.6)
2006	21.2 (17.5 24.8)	8.7 (7.3 10.5)	30.2 (26.3 35.7)	50.1 (43.3 58.5)	110.2 (98 126.1)
2007	22.7 (18.7 26.5)	8.7 (7.3 10.6)	30.2 (26.3 35.8)	50.8 (43.9 59.5)	112.4 (100 128.6)
2008	24.3 (19.9 28.4)	8.8 (7.4 10.6)	30.3 (26.3 35.9)	51.4 (44.3 60.4)	114.7 (102 131.1)
2009	25.9 (21.3 30.4)	8.8 (7.4 10.7)	30.3 (26.3 36)	52 (44.6 61.3)	117 (103.9 133.7)
2010	27.7 (22.6 32.5)	8.8 (7.4 10.7)	30.3 (26.4 36.1)	52.5 (44.8 62.1)	119.2 (105.9 136.2)
2011	29.5 (24 34.8)	8.8 (7.4 10.7)	30.3 (26.4 36.2)	52.9 (45 62.9)	121.5 (107.8 138.8)
2012	31.4 (25.5 37.2)	8.9 (7.4 10.8)	30.4 (26.4 36.2)	53.2 (45.1 63.7)	123.8 (109.7 141.5)
2013	33.4 (27 39.7)	8.9 (7.4 10.8)	30.4 (26.4 36.3)	53.5 (45.1 64.5)	126.1 (111.6 144.2)
2014	35.4 (28.5 42.4)	8.9 (7.4 10.8)	30.4 (26.4 36.3)	53.8 (45.2 65.3)	128.5 (113.5 146.8)
2015	37.5 (29.8 45.3)	8.9 (7.4 10.9)	30.4 (26.4 36.4)	54.1 (45.2 66.1)	130.9 (115.3 149.6)
2016	39.7 (31 48.3)	8.9 (7.4 10.9)	30.4 (26.4 36.4)	54.3 (45.1 66.8)	133.3 (117 152.4)
2017	41.8 (32.1 51.4)	8.9 (7.4 10.9)	30.5 (26.4 36.5)	54.5 (45.1 67.4)	135.7 (118.5 155.2)