Estimating the size of the UK grey seal population between 1984 and 2020.

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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 1984-2016, 2018 (North Sea region only) and 2019, and (2) independent estimates assumed to be of total population size just before the breeding season in 2008, 2014 and 2017. 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 and prior distributions are identical to those used to provide last year's advice; the data include the new 2019 pup production estimates and 2017 estimate of total population size, as well as slightly revised total population estimates from 2008 and 2014.

Estimated population size in regularly monitored colonies in 2020 was 140,700 (95% CI 129,300-153,500). The population overall is estimated to be increasing at a rate of 1.7% per year.

In a supplementary run, we used an alternative set of pup production estimates derived by making a different assumption about the probability of correctly classifying moulted pups from aerial digital images. The estimate of total population size was almost identical. However, a previous analyses has shown that assumptions made in the pup production model can affect estimates of total population size, so the result obtained here should not be generalized.

Historically one constraint on our ability to investigate and extend the model has been the time taken to fit it using the particle filtering algorithm developed by Thomas and colleagues in 2005. We have recently developed new algorithms that are significantly faster and are undertaking a simulation-based evaluation of the model as well as model extensions. We expect to report our findings at next year's meeting.

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 and are described in detail in Thomas et al. (2019); the prior distributions on model parameters are the same as those used for the last two years (see Russell et al. (2021) for justification). The data are a time series of regional pup production estimates (1984-2016; 2018 North Sea region only; 2019) of which the 2019 estimates are new for this briefing paper, and independent estimates of total population size (2008, 2014 and 2017) of which the 2017 estimates are new.

We present estimates of population size at the start of the 2020 breeding system (i.e., projected forward one year from the last pup production estimates). Note that all estimates of population size relate to seals associated with the regularly monitored colonies. A multiplier is required to account for the 6-8% of seals that breed outside these colonies.

The pup production estimation method is currently undergoing a revision, and one aspect of estimation that is being examined is the probability of correctly classifying a moulted pup from the film and digital aerial survey images ("PMoult"[1]). In the main run, the pup production estimates are based on a PMoult of 0.5 for film and 0.9 for digital images. The change to 0.9 was based on the increased quality of the digital images, compared to the film; this is the value used in previous briefing papers. However, work presented at the SCOS meeting in 2019 suggested that the improvement in correct classification with digital images is substantially less, and so a value less than 0.9 was warranted. To provide a sensitivity analysis, as with the 2020 briefing paper, we present results from a supplementary run of the population model using pup production estimates of 0.5 for both film and digital images.

Methods

Main run

Full details of the population dynamics model, data and fitting methods are given in Thomas et al. (2019). 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 $\chi_1 - \chi_4$ 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 $\omega - 1$). 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 justified in Russell et al. (2021) and summarised in Table 1 (detailed justification for prior distributions is given in Supporting Information of Thomas et al. 2019).

Input data were pup production estimates for 1984-2016, the North Sea region estimate for 2018, and for all regions in 2019 (Russell et al. 2021). The estimates for 1984-2016 are identical to those used in last year's briefing paper (Thomas 2020); the estimate for the North Sea region in 2018 is almost identical (18,845 vs the previous 16,778). The other source of data is the independent estimates of total population size from 2008, 2014 and, for the first time, 2017 (Russell et al. 2021). The estimates for 2008 and 2014 are approximately 5% lower than those used in previous briefing papers because an updated scaling factor has been used in converting from hauled-out seals counted to population estimate (Russell and Carter 2021). Note that the total population size estimates are assumed independent of one another, when in reality they are based on the same scaling factor. We return to this in the Discussion.

Model fitting, as in previous reports, used a stochastic simulation-based procedure called a particle filter (Thomas et al. 2019). Reliability of reported results depends on the number of simulations. Here, 4.6 billion simulations were used, which gave results accurate to 2-3 significant figures.

Supplementary run

As described earlier, one important parameter in pup production estimation is the probability of correctly classifying moulted pups from the images, PMoult (Russell et al. 2019). This probability has been set at 0.9 for the digital images collected since 2012. As part of an ongoing review of pup

[1] To be precise, this parameter is the probability of correctly classifying a light-coated pup as a moulted pup; the pup production model contains an assumption about the proportion of moulted pups that are dark-coated.

production estimation, it was desired to assess the effect of setting PMoult for digital images to 0.5. This results in lower pup production estimates for the digital survey years (post 2010), except in the North Sea region where the majority of pup production estimates are derived from ground counts. A supplementary run of the population model was performed (using 2.2 billion simulations) with these alternative pup production estimates.

Results

Main run

Estimated pup production by region from the model matches the observed values reasonably well although it is clear that the pup production estimates for Inner and Outer Hebrides and Orkney are substantially higher after the advent of digital surveys in 2012 and that this affects the fit: residuals for several years before this are all negative and after are all positive, except for Orkney in 2019 (Figure 1). In the case of Inner and Outer Hebrides, the post-2012 estimates are considerably higher than predicted. A similar tendency is seen in North Sea, but to a much lesser extent. Overall, pup production is estimated to be increasing strongly in North Sea, have stabilized in the decade after 1995 in Inner and Outer Hebrides, and be stabilizing in Orkney (Figure 1).

Total population size estimated using pup production data alone (Figure 2, blue lines) is somewhat larger but considerably less precise than that when the three independent estimates are added (Figure 2, red lines). In both cases, population size is estimated to have grown steadily, although at a slightly decreasing rate. When pup production data and independent estimates are both used (red lines in Figure 2), population size is estimated to have been larger than the independent estimate from 2008 and smaller than that from 2014 and 2017. Posterior mean population size in regularly monitored colonies in 2020 was 140,700 with 95% credible interval (CI) 129,300-153,500. Estimates by region are given in Table 2 and estimates for all years 1984-2020 are given in Appendix 1 (Table A1). The estimated growth in population size between 2019 and 2020 is 1.7%.

Posterior parameter distributions are shown in Figure 3, with numerical summaries in Table 1. The estimates are a little different from those reported by Thomas (2020), likely because of the additional independent estimate. Adult survival is estimated to be slightly higher and pup survival lower (the two are strongly negatively correlated, Thomas et al. 2019); the density dependent shape parameter is somewhat lower and carrying capacity higher. Three regions (Inner Hebrides, Outer Hebrides and Orkney) are estimated to be close to carrying capacity (i.e., posterior mean on carrying capacity parameter close to the pup production), while North Sea is at approximately 60% of carrying capacity (although that estimate is quite imprecise with SE/mean=0.3). Estimated sex ratio is, as previously, unchanged from the prior.

Supplementary run

Despite lower pup production estimates in Inner and Outer Hebrides and Orkney going into the model, the resulting estimates of total population size were very slightly (about 1%) larger (Table 2, last column). The difference is largely caused by a higher population estimate in North Sea, where pup production was least decreased; it is perhaps caused by the slightly lower fecundity estimate (Table 1), although the difference in population estimate is too small to deserve an in-depth examination.

Discussion

Estimated population size in the main run is approximately 3% higher than that reported in last year's briefing paper (Thomas 2020) for comparable years – for example the total population size estimate in 2019 from Thomas (2019) was 133,900 (95% CI 115,300-156,500) while here the estimate for the same year 138,300 (95% CI 127,700-150,500). There have been several updates to the input dataset, but likely the biggest contributor to the change is the introduction of the 2017 independent estimate of total population size, which was larger than the value predicted by the model and hence likely drew the estimates upward. It should be noted that (a) such small changes happen commonly as the data is updated – for example, minor changes to the data used in the 2020 briefing paper produced estimates that were approximately 4% lower than those produced the year before (see Thomas 2020), and (b) all of these changes are well within the estimated credible intervals on total population size.

In this analysis, the three independent estimates of total population size, from 2008, 2014 and 2017, are assumed to be statistically independent of one another. Although they are based on separate aerial surveys of hauled-out seals, in scaling up from counts of seals hauled out to total population size both rely on the same estimate of the proportion of seals hauled out (Russell and Carter 2021). This year, we investigated an approach to deal with this using an observation model that allows each annual haul-out count to follow a binomial distribution with the underlying haul-out probability assumed common across all three counts and following a beta distribution (Appendix 2). However, this model prooved to be too restrictive, strongly penalizing population trajectories that do not closely follow the ~6% per-year population growth implied by the values of the three haul-out counts. This growth rate is not supported by the population model fitted to pup production estimates. The new observation model assumes seals haul out independently and that haul-out probability is constant between years – we believe one or more of these assumptions needs to be relaxed before this model will be of use in the population modelling process. Hence, for this briefing paper, we have elected to stick with the assumption used in previous years that the total population estimates come from independent shifted gamma distributions.

Thomas et al. (2019) 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.

In our supplementary analysis, we found very little (1%) change to population size estimates from alternative assumption on pup production estimation. However, we also note that additional analyses undertaken by Thomas (2019) showed that small changes in pup production estimates did influence the total population estimates, so we caution our result here should not be generalized. As noted above, the independent estimates of population size may have been overly dominant in this analysis, and that will change in the future.

One constraint on making inferences from this model has been the time taken to fit it using the particle filtering algorithm used, which was first developed by Thomas et al. (2005) and Newman et al. (2006). The main run presented here was based on runs of 4.6 billion simulations, which took approximately 40 hours computer time, running on 40 processors in parallel. Such run times make it prohibitive to investigate aspects of model performance via simulation and to extend the model to include biologically-relevant factors such as time-varying fecundity. Over the past three years, PhD student Fanny Empacher has been researching alternative more efficient algorithms, and she has been joined in the past year by PhD student Cal Fagard-Jenkin who is working on highly parallel algorithms using Graphics Processing Units (GPUs). Both have made considerable progress and we anticipate over the next year we will be able to undertake some simulation studies of the model, and also switch estimation to the new algorithms.

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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). Analysis uses 1984-2016 and 2018 (North Sea only) pup production estimates, and the 2008 and 2014 total population estimates. Posterior estimates are shown for two runs: a main run, assuming probability of correct classification of moulted pups from digital aerial images is 0.9, and a supplementary run when where this probability is assumed to be 0.5.

Parameter	Prior distribution	Prior mean (SD)	Posterior mean (SD)	
			Main run	Suppl. run
adult survival ϕ_a	0.8+0.17*Be(1.79,1.53)	0.90 (0.04)	0.97 (0.01)	0.96 (0.01)
pup survival ϕ_{pmax}	Be(2.87,1.78)	0.62 (0.20)	0.42 (0.07)	0.49 (0.08)
Fecundity α	0.6+0.4*Be(2,1.5)	0.83 (0.09)	0.91 (0.05)	0.90 (0.06)
dens. dep. ρ	Ga(4,2.5)	10 (5)	3.3 (0.78)	3.81 (1.24)
NS carrying cap. χ_1	Ga(4,5000)	20000 (10000)	33200 (9700)	32100 (10300)
IH carrying cap. χ_2	Ga(4,1250)	5000 (2500)	4110 (457)	3670 (347)
OH carrying cap. χ_3	Ga(4,3750)	15000 (7500)	14000 (1180)	13000 (794)
Ork carrying cap. χ_4	Ga(4,10000)	40000 (20000)	23700 (4290)	20600 (2350)
observation prec. ψ	Ga(2.1,66.67)	140 (96.6)	67.4 (20.7)	74 (20.4)
sex ratio ω	1.6+Ga(28.08, 3.70E-3)	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 2020 breeding season, derived from a model fit to pup production data from 1984-2016, 2018 (North Sea only) and 2019, and the additional total population estimates from 2008, 2014 and 2017. Estimates from two runs are shown: a main run, assuming probability of correct classification of moulted pups from digital aerial images is 0.9, and a supplementary run when where this probability is assumed to be 0.5. Values in the table are posterior means with 95% credible intervals in brackets.

	Estimated population size in thousands (95% CI)	
	Main run	Supplementary run
North Sea	49.3 (38.1 62.7)	54.0 (41.1 68.9)
Inner Hebrides	9.1 (7.7 11)	8.7 (7.3 10.4)
Outer Hebrides	31 (27.1 35.7)	31 (27 34.7)
Orkney	51.3 (43.9 62.6)	48.7 (41.8 57.3
Total	140.7 (129.3 153.5)	142.5 (129 156.5)

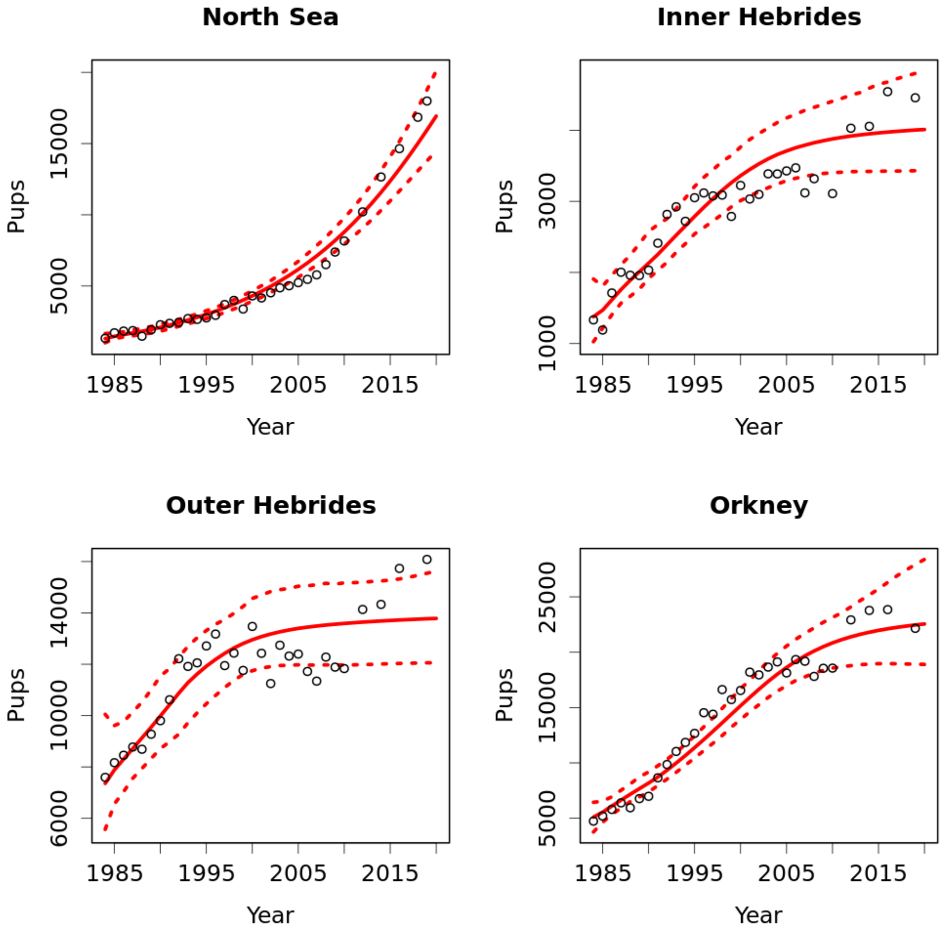

Figure 1. Posterior mean estimates of pup production (solid lines) and 95%CI (dashed lines) from the model of grey seal population dynamics, fitted to pup production estimates from 1984-2016, 2018 (North Sea only) and 2019 (circles) and the total population estimates from 2008, 2014 and 2017.

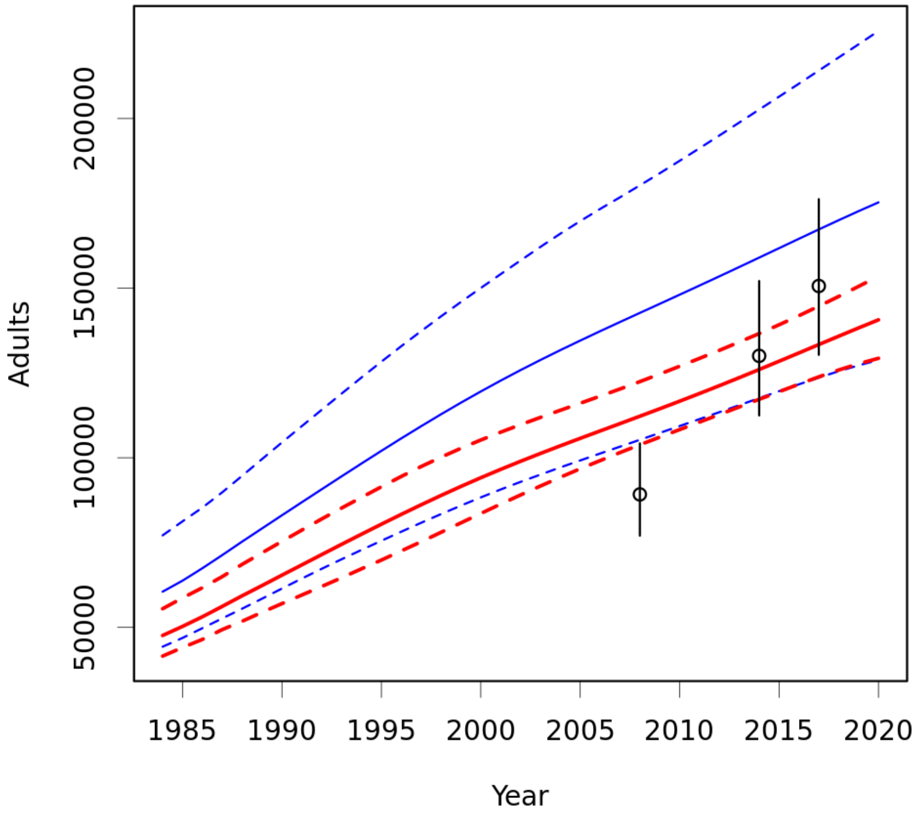

Figure 2. Posterior mean estimates (solid lines) and 95%CI (dashed lines) of total population size in 1984-2019 from the model of grey seal population dynamics, fit to pup production estimates from 1984-2016, 2018 (North Sea only) and 2019, and total population estimates from 2008, 2014 and 2017 (circles, with vertical lines indicating 95% confidence interval on the estimates). Blue lines show fit to pup production data alone, red lines show fit to pup production data and independent estimates.

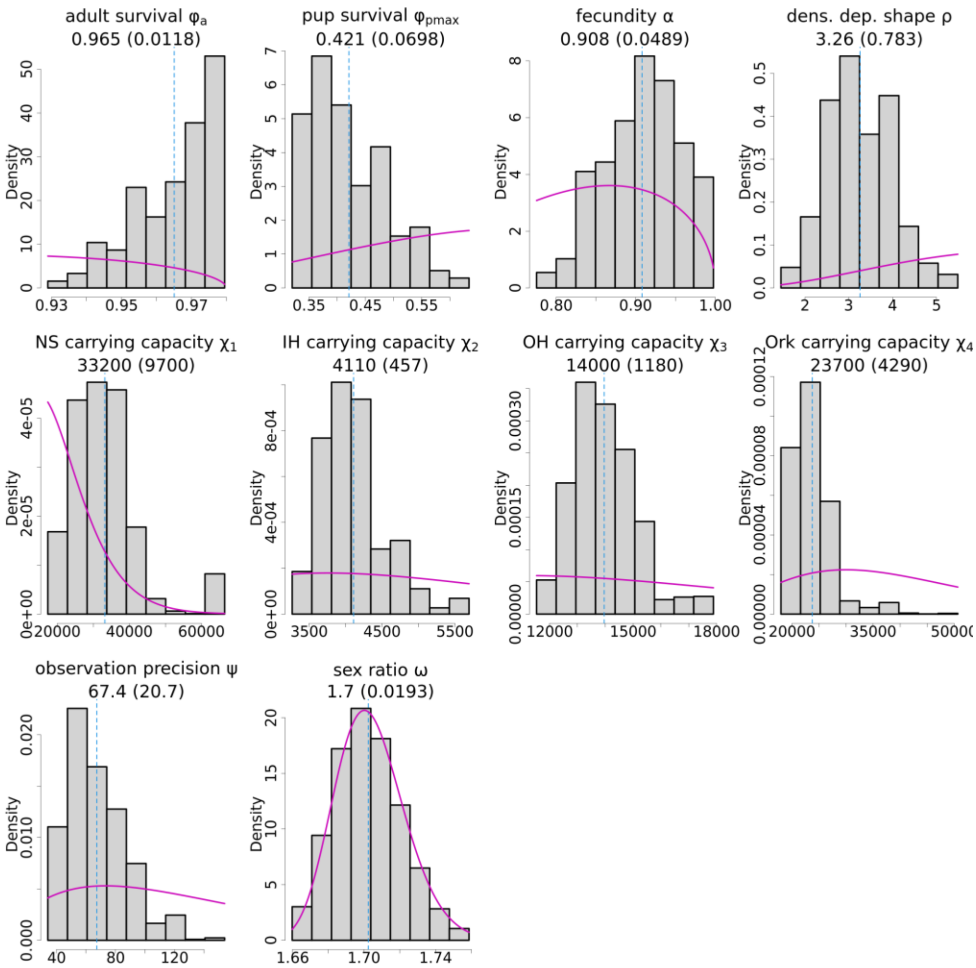

Figure 3. Posterior parameter distributions (histograms) and priors (solid lines) for the model of grey seal population dynamics, fit to pup production estimates from 1984-2016, 2018 (North Sea only) and 2019, and total populations estimate from 2008, 2014 and 2017. The vertical dashed line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

Appendix 1

Table A1. Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2020, made using the model of British grey seal population dynamics fit to pup production estimates from 1984-2016, 2018 (North Sea only) and 2019, and total population estimates from 2008, 2014 and 2017. Numbers are posterior means followed by 95% credible intervals in brackets.

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.4 (3.7 5.1)	4.5 (3.9 5.5)	21.5 (17.9 26)	17.2 (14.5 20.4)	47.6 (41.5 55.5)
1985	4.7 (4 5.4)	4.8 (4.1 5.8)	22.4 (18.7 27.3)	18.4 (15.7 21.7)	50.3 (44.1 58.7)
1986	5.1 (4.4 5.8)	5.1 (4.3 6.1)	23.4 (19.5 28.4)	19.6 (16.9 23)	53.1 (46.5 61.7)
1987	5.4 (4.8 6.2)	5.4 (4.6 6.4)	24.4 (20.4 29.4)	21 (18.1 24.5)	56.2 (49.4 65)
1988	5.8 (5.2 6.7)	5.7 (4.9 6.8)	25.4 (21.2 30.5)	22.4 (19.3 26.3)	59.3 (51.8 68.6)
1989	6.3 (5.6 7.2)	6 (5.1 7.1)	26.1 (22.1 31.3)	24 (20.5 28)	62.3 (54.4 72)
1990	6.8 (6 7.7)	6.3 (5.3 7.5)	26.8 (22.8 32)	25.6 (21.8 29.8)	65.4 (57 75.4)
1991	7.3 (6.4 8.3)	6.6 (5.5 7.8)	27.4 (23.4 32.5)	27.2 (23.1 31.7)	68.4 (59.5 78.7)
1992	7.8 (6.9 8.9)	6.8 (5.7 8.1)	27.9 (23.9 32.9)	28.9 (24.5 33.6)	71.5 (62.1 82)
1993	8.4 (7.4 9.6)	7.1 (5.9 8.4)	28.4 (24.4 33.2)	30.6 (26 35.6)	74.5 (64.6 85.2)
1994	9 (8 10.3)	7.3 (6 8.7)	28.8 (24.9 33.5)	32.3 (27.4 37.5)	77.5 (67.3 88.3)
1995	9.7 (8.5 11)	7.6 (6.2 9)	29.1 (25.3 33.7)	34.1 (28.9 39.6)	80.4 (69.8 91.4)
1996	10.4 (9.1 11.8)	7.8 (6.3 9.3)	29.4 (25.6 33.9)	35.8 (30.4 41.6)	83.3 (72.6 94.5)
1997	11.2 (9.8 12.7)	7.9 (6.5 9.5)	29.6 (25.9 34.1)	37.4 (31.9 43.5)	86.1 (75.2 97.4)
1998	12 (10.5 13.7)	8.1 (6.6 9.7)	29.8 (26.1 34.2)	39 (33.5 45.2)	88.9 (78 100.2)
1999	12.9 (11.2 14.7)	8.2 (6.7 9.9)	30 (26.3 34.3)	40.5 (35 46.7)	91.6 (80.8 102.8)
2000	13.9 (12 15.8)	8.3 (6.9 10)	30.1 (26.5 34.4)	41.8 (36.5 48.1)	94.1 (83.6 105.2)
2001	14.9 (12.9 17)	8.4 (7 10.1)	30.2 (26.7 34.5)	43.1 (37.9 49.3)	96.6 (86.3 107.6)
2002	16 (13.8 18.3)	8.5 (7.1 10.2)	30.3 (26.7 34.5)	44.2 (39.1 50.4)	99 (89 109.8)
2003	17.1 (14.8 19.7)	8.6 (7.2 10.3)	30.4 (26.8 34.6)	45.2 (40 51.4)	101.3 (91.7 111.9)
2004	18.4 (15.8 21.2)	8.7 (7.3 10.4)	30.4 (26.8 34.6)	46 (40.8 52.2)	103.5 (94.3 114)
2005	19.7 (16.9 22.7)	8.7 (7.3 10.4)	30.5 (26.9 34.7)	46.8 (41.4 53)	105.7 (96.8 116.1)
2006	21.2 (18 24.4)	8.8 (7.4 10.4)	30.6 (26.9 34.7)	47.4 (41.9 53.7)	107.9 (99.2 118.2)
2007	22.7 (19.2 26.3)	8.8 (7.5 10.5)	30.6 (26.9 34.8)	48 (42.3 54.3)	110.1 (101.5 120.3)
2008	24.3 (20.5 28.2)	8.8 (7.5 10.5)	30.7 (26.9 34.8)	48.5 (42.6 55)	112.2 (103.8 122.4)
2009	26 (21.9 30.3)	8.9 (7.5 10.6)	30.7 (27 34.9)	48.9 (42.9 55.6)	114.4 (106.1 124.7)
2010	27.8 (23.2 32.6)	8.9 (7.6 10.6)	30.7 (27 35)	49.2 (43.2 56.2)	116.7 (108.3 127)
2011	29.7 (24.7 35)	8.9 (7.6 10.6)	30.8 (27 35)	49.6 (43.4 56.7)	118.9 (110.5 129.3)
2012	31.7 (26.1 37.7)	8.9 (7.6 10.7)	30.8 (27.1 35.1)	49.8 (43.5 57.3)	121.3 (112.7 131.7)
2013	33.7 (27.6 40.4)	9 (7.7 10.7)	30.9 (27.1 35.1)	50.1 (43.6 57.9)	123.6 (115 134.1)
2014	35.8 (29.2 43.2)	9 (7.7 10.8)	30.9 (27.1 35.2)	50.3 (43.7 58.7)	126 (117.2 136.6)
2015	38 (30.7 46.3)	9 (7.7 10.8)	30.9 (27.1 35.3)	50.5 (43.8 59.4)	128.5 (119.5 139.2)
2016	40.3 (32.3 49.4)	9 (7.7 10.8)	30.9 (27.1 35.3)	50.7 (43.9 60)	130.9 (121.7 141.9)
2017	42.5 (33.9 52.7)	9 (7.7 10.9)	31 (27.1 35.4)	50.8 (43.9 60.7)	133.4 (123.9 144.7)
2018	44.8 (35.4 56.1)	9 (7.7 10.9)	31 (27.1 35.5)	51 (43.9 61.3)	135.8 (125.9 147.6)
2019	47.1 (36.8 59.4)	9 (7.7 10.9)	31 (27.1 35.6)	51.1 (43.9 61.9)	138.3 (127.7 150.5)
2020	49.3 (38.1 62.7)	9.1 (7.7 11)	31 (27.1 35.7)	51.3 (43.9 62.6)	140.7 (129.3 153.5)

Appendix 2. Alternative observation model for independent estimates.

Let y_t be the count of hauled-out adult (i.e., non-pup) grey seals in year t, where $t = 1,2,3$ corresponds to the three years 2008, 2014 and 2016. Let n_t be the total population size of adult grey seals from regularly-monitored colonies in year t. We assume seals haul out independently of one another, and that the probability a seal hauls out, p, is constant between years. Hence, the number hauled out is a binomial random variable

$$y_t \sim \mathrm{Bin}(n_t, p)$$

The haul out probability is not known, and we assume uncertainty in p is described by a beta distribution with parameters a and b. We estimate these parameters by fitting a beta distribution to a non-parametric bootstrap sample of haul-out probabilities derived from the analysis of Russell and Carter (2021). The likelihood for observed haul-out counts $\mathbf{y} = \{y_1, y_2, y_3\}'$ given a, b and $\mathbf{n} = \{n_1, n_2, n_3\}'$ is obtained by integrating over the unknown p:

$$\mathcal{L}(\mathbf{y}|\mathbf{n}; a, b) = \int_{p=0}^{1} \left(\prod_{t=1}^{3} f_y\,(y_t|n_t, p) \right) f_p(p|a, b) dp$$

where $f_y()$ denotes the binomial probability mass function and $f_p()$ the beta probability density function.