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Estimating the size of the UK grey seal population between 1984 and 2010.

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Summary

We fitted a Bayesian state-space model of British grey seal population dynamics to two sources of data: (1) regional estimates of pup production from 1984 to 2010, and (2) an independent estimate assumed to be of total population size just before the 2008 breeding season. The model (denoted EDDSNM) allowed for density dependence in pup survival, with a flexible form of density dependence, but allowed no movement of recruiting females between regions. If we assumed the coefficient of variation (CV) on pup production estimates was known, and was 10.64% (a value used in previous briefing papers), the estimated adult population size in 2010 was 124,000 (95% CI 92,600-164,200) using just the pup production estimates, and 99,300 (95% CI 80,200-122,900) using both pop production and independent total population estimates. A second model was run where the pup production CV was estimated based on realistic priors. This gave an estimated CV of 9.8% and population size estimates that were very similar to those given above.

Introduction

This paper presents updated estimates of population size and related demographic parameters, based on the models and fitting methods of Thomas (2010)[1]. Models are specified using a Bayesian state space framework, and fitted using a Monte Carlo particle filter. Only the best model from previous years' briefing papers is used (denoted EDDSNM in those papers): it assumes that density dependence occurs in pup survival, via an extended form of the Beverton-Holt function, that adult survival and fecundity are constant, and that recruiting females do not move between regions.

Materials and Methods

The models used and fitting methods are identical to those used in previous years, and so are not repeated here. In summary, the model used is a Bayesian state-space model, with the process model component (i.e., the population dynamics model) tracking the population numbers in 7 age categories (pups, age 1-5 females and age 6+ females), and the observation model linking data on estimated pup production to the pup numbers in the process model. Priors on model parameters are given in Table 1 of Thomas (2010). We followed Thomas (2010) in basing our main inferences on a model that assumed the pup production estimates are normally distributed about the actual pup production, with a fixed coefficient of variation (CV) of 10.64%. However, this value can be estimated rather than being fixed in the model – the reason for basing inference on a model with a fixed CV in previous briefing papers was to facilitate comparison among multiple population models. Here we only use one population model, so we also tried a second state-space model where the CV was estimated, with the prior distribution on this parameter being that used in past briefing papers (Table 1 of Thomas 2010).

We used the independent estimate of total population size in 2008 given by Lonergan *et al.* (2010; updated after the 2010 SCOS meeting) of 88,300 with 95% CI 75,400-105,700, which we approximated with a shifted gamma distribution as described by Thomas (2010).

As with previous briefing papers, estimates of adult female numbers from the state-space model were converted to estimates of total female numbers by multiplying by 1.73.

Model fitting used a particle filtering algorithm identical to that of Thomas (2010). In essence

[1] Note that an update was made to the briefing paper presented at the 2010 SCOS meeting, based on an updated independent estimate of total population size in 2008 (Lonergan 2010). This revised version is dated 18th March 2011, and is a supplement to the briefing papers presented to this year's SCOS.

this involves simulating seal populations according to the prior distribution of model parameters and weighting the simulations according to the data likelihood. Each simulation is called a "particle" and they are "filtered" according to the likelihood. Further details are given in Thomas and Harwood (2008). In this briefing paper, results were generated from 1,000 runs of 1,000,000 samples for the fixed CV model and 500 runs of 1,000,000 samples for the estimated CV model.

Results

Monte Carlo accuracy

The effective sample size (ESS) of particles is a useful measure of the accuracy of the simulation. For the fixed CV model, the ESS based on pup count data alone was 767.2 (Table 1), although this was reduced substantially (to 108.4) with inclusion of the independent population estimate. This reduction is not surprising given that the estimate was some distance from that implied by the pup count data and priors alone (see later in *Results*). ESSs in this region have been shown in previous briefing papers to produce population and parameter estimates accurate to around 3 significant figures. The ESS for the models where CV is estimated are about half the size – nor surprising given that time limitations meant that only half the number of particles were simulated. Results from this model might be considered more tenuous, except that as we shall see they are very similar to those from the fixed CV model.

Table 1. 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}).The first model assumed the CV on pup production was fixed (i.e., known); the second model estimated this quantity.*

CV	K ($\times 10^7$)	K^* ($\times 10^7$)	U ($\times 10^4$)	ESS_{u1}	ESS_{u2}
Fixed	1000	41.5	49.0	767.2	108.4
Estimated	500	21.0	23.1	224.8	41.4

Model fit – CV assumed fixed

Here, we show results for the fixed CV model; those for the estimated CV model were very similar. The estimated posterior pup population trajectory (Figure 1) and demographic parameters (Figure 2) are largely very similar to those from last year's briefing paper (Thomas 2010), as one would expect when just one more year of data is added to a 26-year dataset. The model broadly provides a reasonable fit to the pup production data, but there are some clear deficiencies: it does not adequately capture the rapid rise and sudden levelling off in pup production in the Hebrides during the early 1990s, nor levelling off in Orkney in the late 1990s; it over-estimates pup production in the North Sea in the late 1990s and early 2000s, and does not track the strong increases in pup production there in the past 3 years. Addition of the 2008 independent estimate does not change the fit to pup production data greatly, although there are some changes to the model parameter estimates (Figure 2).

Table 2. Estimated size, in thousands, of the British grey seal population at the start of the 2010 breeding season, derived from the EDDSNM model fit to pup production data from 1984-2010 and the additional total population estimate from 2008. Numbers are posterior means with 95% credibility intervals in brackets.

CV assumed fixed		
	Pup production data only	Pup production and total population estimate
North Sea	24.6 (16.6 32.5)	19.1 (14.0 26.5)
Inner Hebrides	8.9 (7.1 10.9)	7.5 (6.2 9.0)
Outer Hebrides	33.0 (26.3 39.5)	27.6 (23.4 32.8)
Orkney	57.5 (42.6 81.3)	45.1 (36.5 54.7)
Total	124.0 (92.6 164.2)	99.3 (80.2 122.9)
CV estimated		
	Pup production data only	Pup production and total population estimate
North Sea	25.2 (17.1 33.0)	19.4 (14.1 28.3)
Inner Hebrides	8.8 (7.1 10.7)	7.5 (6.5 9.0)
Outer Hebrides	32.8 (26.3 39.8)	27.5 (22.9 32.9)
Orkney	57.9 (42.6 82.8)	45.2 (37.4 55.5)
Total	124.7 (93.1 166.3)	99.6 (80.9 125.7)

Estimates of total population size with and without the total population estimate – CV assumed fixed

The estimated trajectories of adult population size both with and without the 2008 independent estimate are shown in Figure 3 and the Appendix, and estimated adult population sizes in 2010 are given in Table 2. Note that the independent estimate of total population size for 2008 (of 88,300 with 95% CI 75,400-105,700) is substantially lower than the estimate for that year based on pup production data alone (122,100 with 95%CI 92,900-157,700), and so combining the two sources of data results in a population estimate that is a compromise between the two values (for 2008 it is 98,500 with 95%CI 80,600-119,600).

Results with CV estimated

The posterior mean CV was 9.8% both for the pup production data alone and with the addition of the independent estimate. This was slightly higher than the prior (prior mean 8.4%), and similar to the assumed value used in the fixed CV model (of 10.64%). It is therefore not surprising that the estimates for the other parameters (not shown), and for the population sizes (Table 2 and Appendix) were almost identical.

Discussion

Addition of the 2008 independent estimate reduced the estimated adult population size based on pup production data by around 20% (e.g., the 2010 estimates drop from 124,000 to 99,300). One factor that determines how much the 2008 independent population size estimate influences the results is the relative precision of the independent estimate compared with the precision of the pup production estimates. Variance of the independent estimate (CV 8.49%) comes from Lonergan (2010), and can be regarded as the best estimate available. On the other hand, the variance of the pup production estimates in the fixed CV run (CV 10.64%) comes from an estimate made by Thomas and Harwood (2009), obtained by fitting a simpler density dependent survival model to the pup count data from 1984-2008, with the observation error parameter assumed unknown rather than fixed. Pup production estimate variance is traditionally assumed fixed in SCOS analyses because this facilitates comparison between different population dynamics models (there has previously be an interest in models with density dependent fecundity); however in the current case it could be estimated if no other population models will be considered. Surprisingly, when this was done, the estimated CV was very similar to that obtained previously from the fit to a simpler model – we were anticipating that a more complex model would produce a smaller estimated CV, since the fit to the data is better. Because the estimated CV is similar to the assumed fixed CV, the two models produce very similar estimates of population size. Hence at present, we conclude that the estimates are not sensitive to (reasonable) assumptions about the CV of the pup production estimates.

We here assumed the multiplier that converts adult female population size to total population size is 1.73, equivalent to an adult sex ratio of 57% female, and is known with certainty. One potential use of the 2008 independent population size estimate, instead of using it to produce a compromise population trajectory, is to use it to estimate the adult sex ratio. This was done by Thomas (2010), who assumed a uniform prior $U(0.5,1.0)$ on sex ratio, and obtained a posterior mean ratio of 79% female (95%CI 0.59-0.98). Such analyses could be repeated this year, but would likely give similar results. This points to either some deficiency in our assumptions about sex ratio, or an inadequacy of the independent population size estimate. The conclusion of Thomas (2010) was that if uncertainty in the sex ratio was to be accounted for, it would be important to think carefully about what prior is appropriate on this parameter. We would welcome some guidance on this matter.

Other models for population dynamics are possible, and in previous years we have also run models that allow for density dependent fecundity, and models that allow movement of recruiting females between regions. Thomas and Harwood (2009) showed that there was little support from the data for the movement models, and Thomas (2010) showed the same for the fecundity model, particularly when the additional population size estimate was included. Longeran et al. (2011) have found evidence for variation in adult survival between regions, and that bears further investigation within this framework. We also anticipate that allowing annual variability in fecundity within regions (via a random effect on the fecundity parameter) would significantly improve model fit – although this may make little difference to estimated adult population size.

New estimates of other population parameters are becoming available – for example of fecundity at two intensively-monitored colonies (Smout et al. 2010). These could potentially be incorporated by revising the priors, or as observation data – the latter being more appropriate for parameters that vary through time such as through density dependence.

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Figure 1. Posterior mean estimates of true pup production from the EDDSM model of grey seal population dynamics, fit to pup production estimates from 1984-2010 (circles) and a total population estimate from 2008, assuming the CV of the pup production estimates is10.64% . Lines show the posterior mean bracketed by the 95% credibility intervals for analyses fitted to the pup production data alone (blue lines) and to both pup production data and the 2008 total population estimate (red lines).

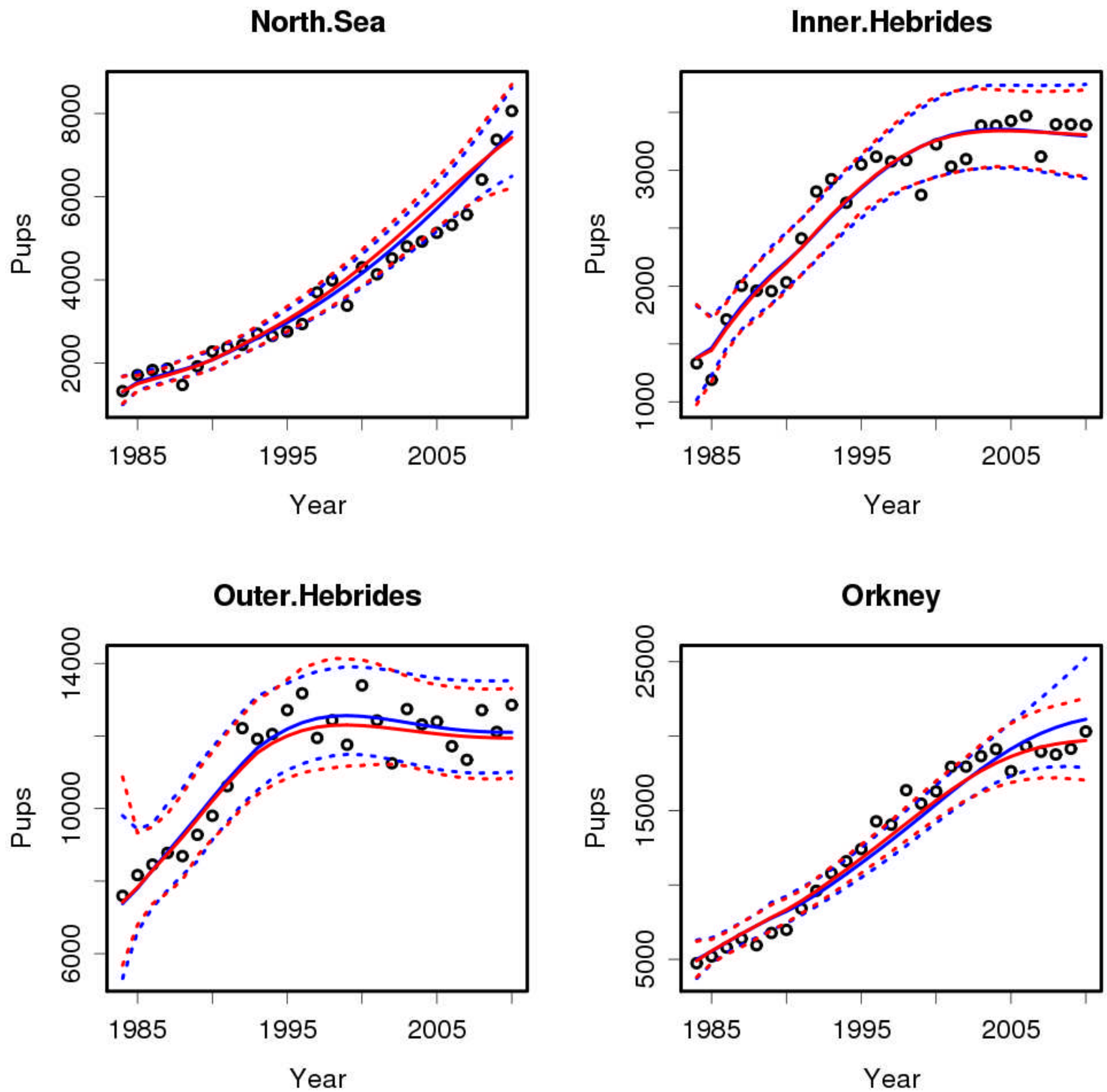
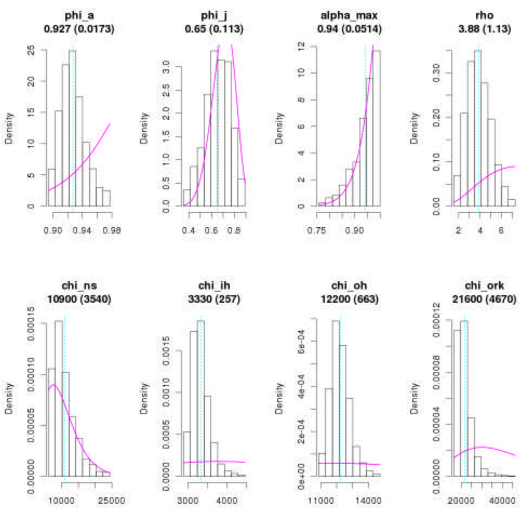


Figure 2. Posterior parameter estimates (histograms) and priors (solid lines) from the EDSSNM model of grey seal population dynamics, fit to pup production estimates from 1984-2010 (circles) and a total population estimate from 2008, assuming the CV of the pup production estimates is10.64%. The vertical 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 only



(b) Pup production data and 2008 population estimate

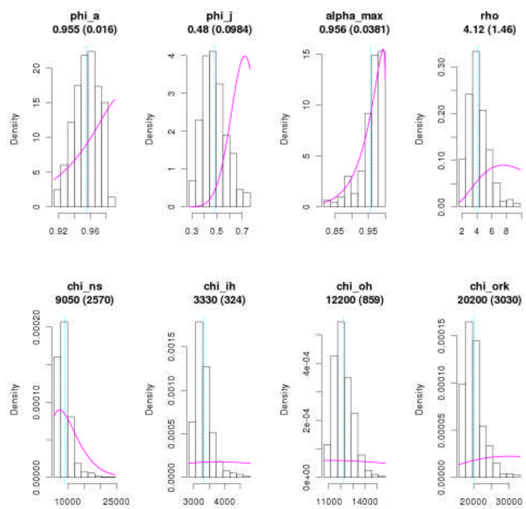
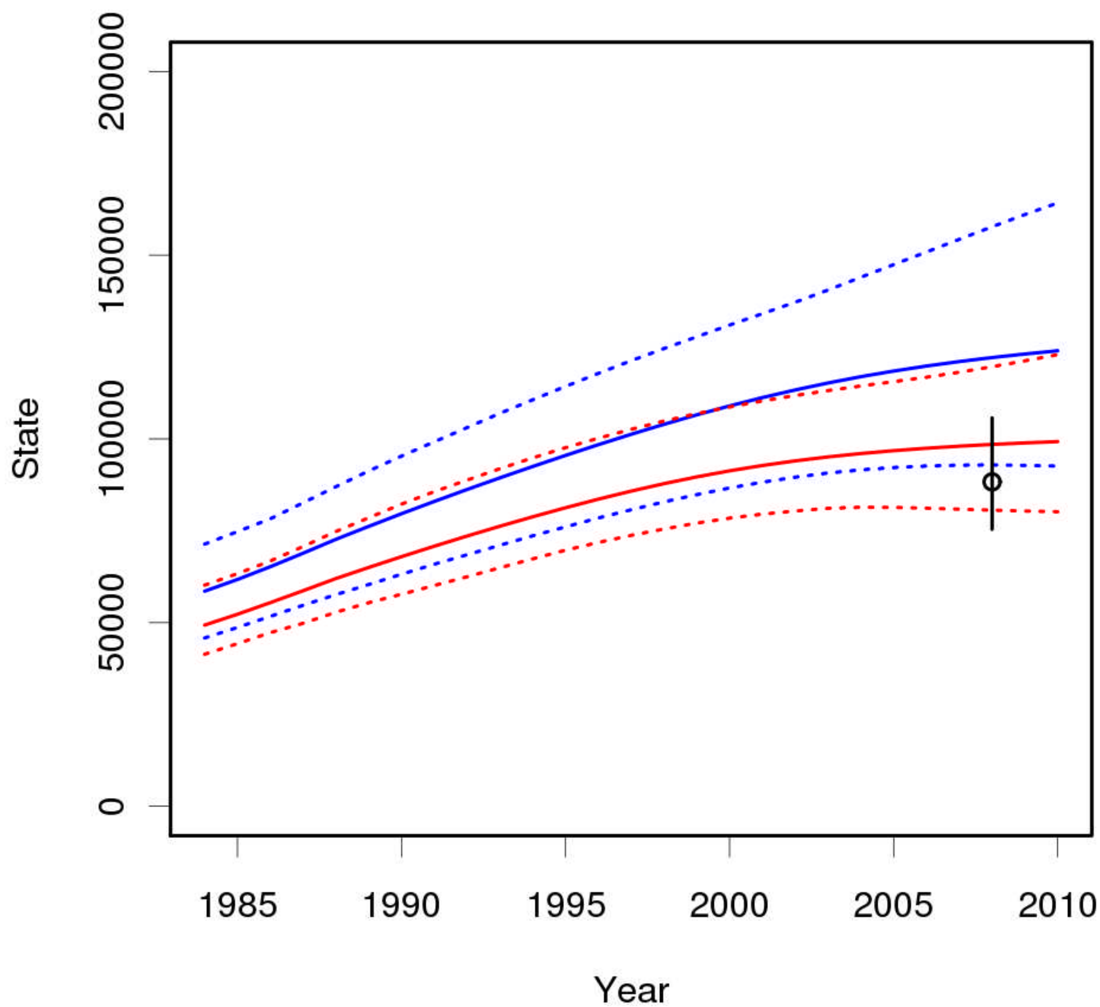


Figure 3. Posterior mean estimates of total population size from the EDDSNM model of grey seal population dynamics, fit to pup production estimates from 1984-2010 only (blue lines), and pup production estimates plus a total population estimate from 2008 (red lines), assuming the CV of the pup production estimates is10.64%. Lines show the posterior mean bracketed by the 95% credibility intervals The independent estimate is shown by a circle, with horizontal lines indicating 95% confidence interval on the estimate.



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2010, made using the EDDSNM (extended density dependent survival with no movement) 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% credibility intervals in brackets.

Table A1: Pup production data only, fixed CV

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.3 (4 6.5)	5.7 (4.4 6.9)	26.5 (20.9 32.2)	21.1 (16.4 25.7)	58.5 (45.8 71.4)
1985	5.6 (4.3 6.9)	6 (4.7 7.2)	27.9 (22.1 33.8)	22.3 (17.5 26.9)	61.7 (48.7 74.8)
1986	6.1 (4.8 7.4)	6.3 (5 7.5)	29.2 (23.2 35.1)	23.7 (18.7 28.2)	65.2 (51.7 78.2)
1987	6.5 (5.1 7.9)	6.6 (5.3 7.9)	30.4 (24.3 36.7)	25.3 (20 30.2)	68.9 (54.7 82.6)
1988	7 (5.6 8.4)	7 (5.6 8.3)	31.6 (25 38.1)	27.1 (21.5 32.2)	72.7 (57.6 87)
1989	7.5 (6 9)	7.3 (5.8 8.8)	32.3 (25.5 39.1)	29 (23.1 34.5)	76.2 (60.4 91.3)
1990	8 (6.4 9.6)	7.7 (6.1 9.1)	33 (25.9 40)	31 (24.8 36.7)	79.6 (63.2 95.3)
1991	8.6 (6.9 10.2)	8 (6.3 9.5)	33.5 (26.2 40.5)	33 (26.5 39)	83 (65.9 99.2)
1992	9.2 (7.4 10.9)	8.2 (6.5 9.9)	33.8 (26.4 40.8)	35 (28.2 41.4)	86.2 (68.5 103.1)
1993	9.8 (8 11.6)	8.5 (6.7 10.2)	34 (26.5 41.1)	37.2 (29.9 44)	89.4 (71 107)
1994	10.5 (8.5 12.4)	8.7 (6.8 10.5)	34 (26.6 41.1)	39.3 (31.7 46.6)	92.5 (73.6 110.6)
1995	11.2 (9.1 13.2)	8.8 (6.9 10.8)	33.9 (26.6 41)	41.5 (33.4 49.3)	95.5 (76.1 114.3)
1996	12 (9.7 14.1)	9 (7 10.9)	33.8 (26.7 40.8)	43.7 (35.1 52)	98.4 (78.5 117.8)
1997	12.8 (10.3 15)	9 (7 11)	33.6 (26.6 40.5)	45.8 (36.7 54.7)	101.3 (80.7 121.3)
1998	13.6 (11 16)	9.1 (7.1 11.1)	33.4 (26.6 40.2)	47.9 (38.2 57.3)	104 (82.9 124.6)
1999	14.5 (11.7 17)	9.1 (7.1 11.1)	33.2 (26.5 39.9)	49.8 (39.5 59.8)	106.5 (84.8 127.8)
2000	15.3 (12.4 18.1)	9.1 (7.2 11.1)	33.1 (26.4 39.6)	51.5 (40.7 62.2)	109 (86.6 131)
2001	16.3 (13.1 19.2)	9.1 (7.2 11)	32.9 (26.4 39.4)	53 (41.6 64.4)	111.2 (88.2 134.1)
2002	17.2 (13.7 20.4)	9 (7.2 11)	32.8 (26.4 39.3)	54.3 (42.3 66.5)	113.3 (89.6 137.2)
2003	18.2 (14.4 21.7)	9 (7.2 11)	32.7 (26.3 39.2)	55.3 (42.8 68.7)	115.2 (90.7 140.5)
2004	19.2 (14.9 23)	9 (7.2 11)	32.7 (26.3 39.2)	56.1 (43.2 70.9)	116.9 (91.6 144)
2005	20.1 (15.4 24.4)	8.9 (7.1 10.9)	32.7 (26.3 39.2)	56.7 (43.4 73)	118.5 (92.2 147.4)
2006	21.1 (15.8 25.8)	8.9 (7.1 10.9)	32.7 (26.3 39.2)	57.1 (43.4 75)	119.8 (92.6 150.9)
2007	22 (16.1 27.4)	8.9 (7.1 10.9)	32.8 (26.3 39.2)	57.4 (43.4 76.8)	121 (92.8 154.3)
2008	22.9 (16.3 29)	8.9 (7.1 10.9)	32.8 (26.3 39.3)	57.5 (43.2 78.5)	122.1 (92.9 157.7)
2009	23.8 (16.5 30.7)	8.9 (7.1 10.9)	32.9 (26.3 39.4)	57.5 (42.9 80)	123.1 (92.8 161.1)
2010	24.6 (16.6 32.5)	8.9 (7.1 10.9	33 (26.3 39.5)	57.5 (42.6 81.3)	124 (92.6 164.2)

Table A2: Pup production data and 2008 total population estimate, fixed CV

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.4 (3.7 5.4)	4.7 (4 5.8)	22.6 (18.7 27.5)	17.6 (15 21.5)	49.3 (41.4 60.2)
1985	4.7 (4.1 5.7)	5 (4.2 6.1)	23.8 (19.9 28.7)	18.8 (16 22.7)	52.3 (44.3 63.3)
1986	5.1 (4.4 6.2)	5.3 (4.5 6.4)	24.9 (20.9 30.1)	20.1 (17.4 24.1)	55.4 (47.3 66.8)
1987	5.5 (4.8 6.6)	5.6 (4.8 6.8)	25.9 (21.5 31.5)	21.6 (18.7 25.9)	58.7 (49.8 70.7)
1988	6 (5.1 7.1)	5.9 (5.1 7.2)	26.9 (22.4 32.8)	23.2 (20.2 27.7)	62 (52.8 74.8)
1989	6.4 (5.5 7.7)	6.2 (5.3 7.6)	27.5 (23 33.6)	24.8 (21.6 29.7)	65 (55.4 78.5)
1990	6.9 (5.9 8.2)	6.5 (5.5 7.9)	28 (23.3 34.4)	26.6 (23 31.7)	67.9 (57.7 82.2)
1991	7.4 (6.3 8.8)	6.8 (5.6 8.3)	28.3 (23.6 34.7)	28.3 (24.6 33.9)	70.8 (60.1 85.6)
1992	7.9 (6.7 9.4)	7 (5.8 8.5)	28.5 (23.7 35)	30.1 (26.2 35.9)	73.6 (62.5 88.8)
1993	8.5 (7.2 10.1)	7.2 (6 8.8)	28.6 (23.9 35)	31.9 (27.8 38)	76.2 (64.9 91.9)
1994	9.1 (7.7 10.8)	7.3 (6.1 9)	28.6 (24.1 34.9)	33.8 (29.5 40.1)	78.8 (67.3 94.8)
1995	9.7 (8.3 11.5)	7.4 (6.2 9.2)	28.5 (24.2 34.7)	35.5 (31 42.2)	81.3 (69.7 97.6)
1996	10.4 (8.9 12.3)	7.5 (6.2 9.3)	28.4 (24.2 34.4)	37.3 (32.5 44.2)	83.6 (71.8 100.2)
1997	11.1 (9.5 13.1)	7.6 (6.3 9.3)	28.3 (24.2 34)	38.9 (33.8 46.2)	85.8 (73.7 102.6)
1998	11.8 (10.1 13.9)	7.6 (6.3 9.3)	28.1 (24.1 33.6)	40.3 (34.9 48)	87.8 (75.5 104.9)
1999	12.5 (10.7 14.8)	7.6 (6.4 9.3)	28 (24.1 33.3)	41.6 (35.9 49.6)	89.7 (77.1 106.9)
2000	13.2 (11.3 15.6)	7.6 (6.4 9.2)	27.9 (23.9 33)	42.6 (36.8 50.9)	91.3 (78.4 108.7)
2001	13.9 (11.8 16.5)	7.6 (6.4 9.2)	27.7 (23.8 32.8)	43.5 (37.5 51.9)	92.8 (79.5 110.3)
2002	14.7 (12.2 17.5)	7.6 (6.4 9.1)	27.7 (23.7 32.6)	44.1 (38 52.6)	94 (80.4 111.8)
2003	15.4 (12.6 18.5)	7.5 (6.4 9.1)	27.6 (23.7 32.5)	44.6 (38.4 53.2)	95.1 (81.1 113.1)
2004	16 (13 19.5)	7.5 (6.4 9)	27.5 (23.6 32.4)	44.9 (38.4 53.5)	96 (81.4 114.4)
2005	16.7 (13.3 20.5)	7.5 (6.3 9)	27.5 (23.5 32.4)	45.1 (38.2 53.7)	96.8 (81.4 115.6)
2006	17.3 (13.5 21.6)	7.5 (6.3 9)	27.5 (23.5 32.4)	45.2 (37.9 53.8)	97.5 (81.1 116.8)
2007	17.8 (13.7 22.7)	7.5 (6.3 9)	27.5 (23.5 32.5)	45.2 (37.5 54)	98 (80.9 118.1)
2008	18.3 (13.8 23.9)	7.5 (6.2 9)	27.6 (23.4 32.6)	45.2 (37.1 54.2)	98.5 (80.6 119.6)
2009	18.7 (13.9 25.2)	7.5 (6.2 9)	27.6 (23.4 32.7)	45.1 (36.8 54.4)	98.9 (80.4 121.3)
2010	19.1 (14 26.5)	7.5 (6.2 9)	27.6 (23.4 32.8)	45.1 (36.5 54.7)	99.3 (80.2 122.9)

Table A3: Pup production data only, estimated CV

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.3 (4.1 6.4)	5.7 (4.5 7)	26.3 (20.8 32.4)	21 (16.4 27)	58.2 (45.8 72.8)
1985	5.6 (4.4 6.9)	5.9 (4.8 7.2)	27.7 (22 33.8)	22.2 (17.6 28.4)	61.4 (48.8 76.3)
1986	6 (4.8 7.4)	6.3 (5.1 7.4)	29 (23.2 35)	23.6 (18.9 29.5)	64.9 (52.1 79.3)
1987	6.5 (5.3 7.9)	6.6 (5.3 7.9)	30.3 (24.3 36.5)	25.2 (20.4 31.4)	68.6 (55.3 83.7)
1988	7 (5.7 8.4)	7 (5.6 8.4)	31.4 (25 38)	27 (21.9 33.6)	72.4 (58.3 88.4)
1989	7.5 (6.2 9)	7.3 (5.9 8.6)	32.2 (25.4 38.7)	28.9 (23.5 35.9)	75.9 (60.9 92.3)
1990	8 (6.6 9.6)	7.7 (6.1 9)	32.9 (25.7 39.5)	30.8 (25.1 38.4)	79.4 (63.5 96.5)
1991	8.6 (7.1 10.2)	8 (6.3 9.4)	33.3 (26 40.2)	32.9 (26.7 41)	82.7 (66.1 100.8)
1992	9.2 (7.6 10.9)	8.2 (6.5 9.7)	33.7 (26.3 40.7)	34.9 (28.5 43.3)	86 (68.8 104.5)
1993	9.8 (8.1 11.6)	8.5 (6.7 10.1)	33.8 (26.5 41.1)	37.1 (30.4 45.9)	89.2 (71.6 108.6)
1994	10.5 (8.7 12.3)	8.6 (6.8 10.4)	33.9 (26.6 41.4)	39.3 (32.2 48.5)	92.3 (74.4 112.6)
1995	11.2 (9.3 13.2)	8.8 (6.9 10.6)	33.8 (26.8 41.5)	41.5 (34 50.9)	95.3 (77 116.1)
1996	12 (9.9 14)	8.9 (7 10.8)	33.7 (26.8 41.2)	43.7 (35.7 53.4)	98.3 (79.4 119.5)
1997	12.8 (10.6 15)	9 (7 10.9)	33.5 (26.7 41.1)	45.9 (37.3 55.8)	101.1 (81.6 122.8)
1998	13.6 (11.2 15.9)	9 (7.1 11)	33.3 (26.7 40.9)	47.9 (38.6 58.1)	103.9 (83.6 125.8)
1999	14.5 (11.9 16.9)	9 (7.2 11)	33.1 (26.6 40.6)	49.8 (39.8 60.1)	106.5 (85.5 128.7)
2000	15.4 (12.6 18)	9 (7.2 10.9)	33 (26.5 40.4)	51.6 (40.8 62.1)	109 (87.1 131.4)
2001	16.3 (13.2 19.1)	9 (7.2 10.9)	32.8 (26.4 40.2)	53.1 (41.6 64)	111.3 (88.4 134.2)
2002	17.3 (13.9 20.2)	9 (7.2 10.8)	32.7 (26.3 40)	54.4 (42.2 66.4)	113.4 (89.5 137.4)
2003	18.3 (14.5 21.5)	8.9 (7.2 10.8)	32.6 (26.2 39.9)	55.5 (42.6 68.9)	115.4 (90.5 141)
2004	19.3 (15.1 22.8)	8.9 (7.2 10.8)	32.6 (26.2 39.8)	56.3 (42.9 71.5)	117.2 (91.4 144.8)
2005	20.3 (15.7 24.2)	8.9 (7.2 10.7)	32.6 (26.2 39.7)	57 (43.4 73.6)	118.8 (92.4 148.3)
2006	21.3 (16.2 25.8)	8.8 (7.1 10.7)	32.6 (26.2 39.7)	57.4 (43.6 75.7)	120.2 (93.2 151.8)
2007	22.3 (16.6 27.4)	8.8 (7.1 10.7)	32.7 (26.2 39.7)	57.7 (43.4 77.7)	121.5 (93.4 155.5)
2008	23.3 (16.8 29.2)	8.8 (7.1 10.7)	32.7 (26.2 39.7)	57.8 (43.2 79.4)	122.7 (93.4 159)
2009	24.3 (17 31.1)	8.8 (7.1 10.7)	32.8 (26.3 39.7)	57.9 (42.8 81.2)	123.8 (93.2 162.6)
2010	25.2 (17.1 33)	8.8 (7.1 10.7)	32.8 (26.3 39.8)	57.9 (42.6 82.8)	124.7 (93.1 166.3)

Table A4: Pup production data and 2008 total population estimate, estimated CV

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.4 (3.8 5.3)	4.8 (3.9 5.8)	22.3 (18.4 27.8)	17.9 (14.8 21.4)	49.4 (40.8 60.4)
1985	4.8 (4.1 5.7)	5 (4.2 6.1)	23.4 (18.8 29.2)	19.1 (16.2 22.6)	52.4 (43.3 63.5)
1986	5.2 (4.5 6.1)	5.3 (4.5 6.4)	24.5 (19.9 30.3)	20.5 (17.4 24.1)	55.5 (46.3 66.9)
1987	5.6 (4.9 6.6)	5.7 (4.8 6.8)	25.6 (21 31.6)	22 (18.8 25.6)	58.8 (49.5 70.6)
1988	6 (5.3 7.1)	6 (5.1 7.2)	26.5 (21.3 32.8)	23.6 (20.3 27.4)	62.1 (52.1 74.6)
1989	6.5 (5.7 7.7)	6.3 (5.3 7.5)	27.1 (21.5 33.5)	25.3 (21.9 29.3)	65.2 (54.4 78)
1990	7 (6.1 8.2)	6.5 (5.5 7.9)	27.6 (21.7 34.1)	27 (23.5 31.4)	68.1 (56.8 81.6)
1991	7.5 (6.5 8.8)	6.8 (5.6 8.2)	27.9 (21.9 34.6)	28.8 (25 33.5)	71 (59 85.1)
1992	8 (7 9.5)	7 (5.7 8.5)	28.1 (22 34.8)	30.6 (26.5 35.5)	73.7 (61.2 88.3)
1993	8.6 (7.4 10.1)	7.2 (5.8 8.8)	28.2 (22.1 34.9)	32.4 (28 37.7)	76.4 (63.4 91.5)
1994	9.2 (8 10.9)	7.4 (5.9 9)	28.3 (22.2 35)	34.2 (29.4 40)	79 (65.5 94.9)
1995	9.9 (8.5 11.7)	7.5 (6 9.2)	28.2 (22.3 34.8)	35.9 (30.8 42.2)	81.5 (67.6 97.9)
1996	10.6 (9.1 12.5)	7.6 (6 9.3)	28.1 (22.4 34.5)	37.6 (31.9 44.3)	83.8 (69.4 100.6)
1997	11.3 (9.7 13.3)	7.6 (6.1 9.4)	28 (22.5 34.2)	39.1 (33 46.2)	86 (71.3 103)
1998	12 (10.3 14.1)	7.7 (6.2 9.4)	27.9 (22.5 33.9)	40.5 (34.1 48)	88 (73.1 105.3)
1999	12.7 (11 15)	7.7 (6.2 9.3)	27.8 (22.6 33.6)	41.7 (35 49.6)	89.9 (74.8 107.6)
2000	13.5 (11.6 15.9)	7.7 (6.3 9.3)	27.6 (22.6 33.4)	42.7 (35.8 51)	91.5 (76.3 109.5)
2001	14.2 (12.2 16.9)	7.7 (6.3 9.2)	27.5 (22.7 33.2)	43.5 (36.5 52)	92.9 (77.7 111.2)
2002	15 (12.7 17.8)	7.6 (6.3 9.1)	27.5 (22.7 33)	44.1 (37.1 52.6)	94.2 (78.8 112.5)
2003	15.7 (13.1 18.8)	7.6 (6.4 9.1)	27.4 (22.7 32.8)	44.6 (37.6 53.1)	95.3 (79.8 113.8)
2004	16.4 (13.4 19.9)	7.6 (6.4 9.1)	27.4 (22.8 32.7)	44.9 (38.1 53.6)	96.2 (80.6 115.2)
2005	17 (13.7 21.1)	7.6 (6.4 9)	27.4 (22.8 32.6)	45.1 (38.3 54)	97 (81.2 116.7)
2006	17.6 (13.9 22.4)	7.6 (6.4 9)	27.4 (22.8 32.6)	45.2 (38.2 54.3)	97.7 (81.3 118.4)
2007	18.1 (14 23.8)	7.5 (6.4 9)	27.4 (22.9 32.7)	45.2 (38 54.6)	98.2 (81.3 120.1)
2008	18.6 (14.1 25.3)	7.5 (6.4 9)	27.4 (22.9 32.7)	45.2 (37.8 54.9)	98.7 (81.2 121.9)
2009	19 (14.1 26.8)	7.5 (6.5 9)	27.4 (22.9 32.8)	45.2 (37.6 55.2)	99.2 (81.1 123.8)
2010	19.4 (14.1 28.3)	7.5 (6.5 9)	27.5 (22.9 32.9)	45.2 (37.4 55.5)	99.6 (80.9 125.7)