Len Thomas and John Harwood

Estimating the size of the UK grey seal population between 1984 and 2008.

NERC Sea Mammal Research Unit and Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 8LB

Summary

We fitted six Bayesian state-space models of British grey seal population dynamics to regional estimates of pup production from 1984 to 2008. The models and fitting methods were the same as those used by Thomas and Harwood (2008), updated to include the 2008 data. We compared models by calculating Bayesian posterior model probabilities, firstly giving equal prior weight to each model and secondly assigning prior weights that penalized models with more parameters. Results for both sets of priors were similar. As with last year's briefing paper, models that allow for flexible forms of density dependence, but no movement of recruiting seals among regions, were strongly favoured over those with simpler density dependence or with movement between regions. However, unlike last year, the model with density dependent pup survival (EDDSNM) had significantly more support than that with density dependent female fecundity (EDDFNM; posterior model probabilities 0.95 and 0.05 respectively with the weighted prior). The estimated adult population size in 2008 using these two models was 118,700 (95% CI 85,900-168,100) and 255,900 (95% CI 196,500-439,600) respectively. A combined model, containing populations in proportion to their posterior model probability, yielded an estimate of 126,200 (95% CI 89,200-244,800). The estimated model probabilities should be treated with caution because, in theory, it should be hard to distinguish the two models from pup count data alone.

Introduction

This paper presents updated estimates of population size and related demographic parameters, based on the models and fitting methods described in Thomas and Harwood (2008). Six models are fit to regional estimates of pup production from 1984-2008, using a Bayesian state space modelling framework, with fitting performed using a computer-intensive algorithm called a Monte Carlo particle filter. Models are compared using methods similar to those of Thomas and Harwood (2008), updated slightly to bring them into line with mainstream practice.

The six models are as follows. Two allow for density dependent pup survival (DDS) and density dependent fecundity (DDF). In both cases, the density dependent relationship follows a Beverton-Holt function. Also, female seals are assumed to show fitness-dependent dispersal among regions in the year before they recruit into the breeding population. Two further models extend the density dependent function by adding an extra parameter that allows the effect of density dependence to be lessened until the population is close to carrying capacity. We refer to these as extended density dependent pup survival (EDDS) extended density dependent fecundity (EDDF). The final two models allow extended density dependence but assume no movement between regions (EDDSNM and EDDFNM). All models include an observation model that assumes pup production estimates are normally distributed about the true pup production with no bias and constant coefficient of variation. Informative priors are specified on the model parameters and initial states (the 1984 population numbers). In addition to comparing the models, we also make joint inference from them.

Materials and Methods

Models

The models are described fully in Thomas and Harwood (2008) and papers cited therein. In summary, they track seal population numbers in 7 age groups (pups, age 1-5 females and age 6+ females) in each of four regions (North Sea, Inner Hebrides, Outer Hebrides and Orkney). There are four population sub-processes: survival, ageing and pup sexing, movement of recruiting females, and breeding. The six models make different assumptions about these sub-processes. Models have up to 11 parameters. All share 5: adult survival ϕ_a, one carrying capacity parameter-related parameter for each region β_1 - β_4 and the observation precision parameter ψ. Models with density dependent survival (DDS, EDDS, EDDSNM) have a parameter for maximum pup survival $\phi_{p\max}$ and another for constant fecundity α, while models with density dependent fecundity (DDF, EDDF, EDDFNM) have a parameter for maximum fecundity $\alpha_{\max}$ and constant pup survival ϕ_p. Models with extended density dependence (all those starting "E") have an additional parameter, ρ, for the shape of the density-dependent response. DDS, DDF, EDDS and EDDF models have three additional movement parameters, controlling the relative importance of site faithfulness (γ_{sf}) density dependence (γ_{dd}), and distance between regions (γ_{dist}) in affecting movement.

Data and Priors

Our input data were the pup production estimates for 1984-2007 from Duck (2009), aggregated into regions.

Prior distributions for each parameter were the same as those of Thomas and Harwood (2008) and are given in Table 1. We followed previous briefing papers in using a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region, denoted χ_r for region *r*, rather than directly on the β s.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}$, ϕ_p	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5
γ_{dd}	Ga(2.25,1.33)	3	2
γ_{dist}	Ga(2.25,0.49)	1.10	0.70
γ_{sf}	Ga(2.25,0.22)	0.5	0.33
α , $\alpha_{\max}$	Be(22.05,1.15)	0.95	0.04
ψ	Ga(2.1, 66.67)	140	96.61

Prior distributions for the states were generated using the 1984 data, as described by Thomas and Harwood (2008). The prior distribution on ψ implies a prior mean on observation CV of 0.10 and prior standard deviation of 0.05.

Fitting Method

We used the particle filtering algorithm of Thomas and Harwood (2008). This involves simulating samples from the prior distributions, projecting them forward in time according to the population model, and then resampling and/or reweighting them according to their likelihood given the data. The final output is a weighted sample from the posterior distribution. Many samples are required for accurate estimation of the posterior, and we generated between 121 and 250 runs of 1,000,000 samples, depending on the model (Table 2). 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). As an additional check, we ran the simulations for the two best supported models twice, to check the inferences were sufficiently accurate..

Model comparison and model outputs

In previous briefing papers we have compared models using the mean posterior Akaike Information Criterion (AIC). While this has a good justification in likelihood-based inference, it is not a commonly used measure in Bayesian statistics, so we instead calculated the more standard posterior model probability (e.g., Hoeting et al. 1999) – this is the posterior probability that each model is the correct model, given that one of them is.

To calculate posterior model probability, one must specify a prior probability for each model. We did this in two ways. First, we assumed an equal prior probability for each of the six models, as is standard practice. Second, to more closely mimic the previous use of mean posterior AIC, we assumed that each additional parameter in a model halved the prior probability for that model relative to the other models. For example, the prior probabilities for two models, one with 9 parameter and one with 11 would be 0.8 and 0.2 respectively. This effectively places a prior penalty on parameter-rich models relative to simple models.

As explained by Thomas and Harwood (2007), it is not useful to compare models where the observation error parameter has been estimated independently for each model. Hence, we first estimated the observation precision parameter ψ by fitting the data to the DDS model alone (this being the model with most data support in historical briefing papers). We then took the estimated posterior mean ψ from this run and used this as a fixed value when fitting all six models. We present model selection statistics for all models using the fixed observation error value.

For all models, we also present posterior estimates of the model parameters and estimated pup production from 1984-2008. The models additionally estimate adult female numbers, but do not include adult males. As with previous briefing papers, we therefore calculated total pre-breeding population sizes by assuming that the number of adult males is 73% of the number of adult females (Hiby and Duck, unpublished).

We also present model averaged estimates of population size, combining the models according to their posterior model probabilities.

Results

Unique ancestral particle numbers

The number of particles retained and effective sample sizes (Table 2) were similar to those of Thomas and Harwood (2008).

Table 2. Number of particles simulated (K), number saved after final rejection control step (K), number of unique ancestral particles (U) and effective sample size of unique particles (ESS_u).*

Model	*K* ($x10^7$)	*K** ($x10^7$)	*U* ($x10^4$)	ESS_u
ψ estimated				
DDS	121	4.7	14.0	48.6
ψ fixed				
DDS	150	15.9	17.3	235.8
DDF	150	14.3	24.0	267.7
EDDS	150	14.2	8.2	126.6
EDDF	150	9.8	4.2	62.4
EDDSNM	250	34.2	28.8	421.8
EDDFNM	250	24.8	11.0	218.9

Estimate of observation precision parameter

The DDS model run where ψ is estimated produced a posterior mean estimate of 87.9 with 95% posterior credibility interval (CI) of 56.8 to 123.6. This value corresponds to an estimated CV of 0.11 (95%CI 0.09 – 0.13). The value of ψ =87.9 was then used in all model runs reported in subsequent sections.

Comparison of models for density dependence and movement

Smoothed posterior mean estimates of pup production for the six models, run with ψ fixed at 87.9, are shown in Figure 1, while smoothed posterior means and 95% credible intervals are shown in Figure 2. Posterior parameter estimates are shown in Figure 3.

The pup production estimates from the DDS and DDF models show clear, systematic lack of fit in all regions, except perhaps North Sea. For Inner and Outer Hebrides the estimates fail to reflect the observed rapid growth and then levelling-off in pup production since the mid 1990s. The recent slowing in growth in Orkney is also not reflected in the estimates. The DDF model estimates for Outer Hebrides also show some minor discontinuity for the period 1984-1989. This is probably a result of irregularities in the estimated starting age structure. Parameter estimates are quite similar between these models. The posterior distributions of pup survival and fecundity are both very similar to their priors; adult survival has a similar mean to the prior but a smaller variance; the movement parameters are somewhat different from their priors – in particular γ_{dd} is rather smaller, indicating less movement than though a priori; the carrying capacity parameter estimates are somewhat higher than their priors, although more so for the DDS than DDF model.

Estimates of pup production from the EDDS and EDDF models show clear improvements to the fit, better reflecting the levelling off in counts in the Inner and Outer Hebrides. The recent levelling off in the Orkney is, however, again not reflected in the fits. The most recent high estimate from North Sea is well fit, at the expense of a series of negative residuals in previous years. Parameter estimates for pup survival and fecundity are again nearly identical to the prior in both models. Estimated adult survival is low in both models (0.91). The posterior mean estimate of the extended density dependence parameter, ρ, is higher for the EDDS model than the EDDF model (5.5 vs 3.5), although both have high variance. The carrying capacities of pups are estimated to be lower than their prior means and quite similar between the models.

Estimates from the no movement models (EDDSNM and EDDFNM) are similar to the extended density dependence models with movement for North Sea and Orkney, but for Inner and Outer Hebrides the fit does a somewhat better job of capturing the rapid increase in the 1980s, and pup production is estimated to have declined slightly in recent years. Parameter estimates are similar to those from the EDDS and EDDF models, although the estimated ρ is lower for EDDSNM than EDDS.

According to the model selection statistics (Table 3), the models with no movement are strongly favoured over those with movement. Note that the negative log integrated likelihood is actually smaller for these models than those with movement, indicating that they are a better fit to the data even without taking into account the 3 parameters saved by excluding the movement model. Further, and in contrast to the results reported in Thomas and Harwood (2008), the EDDSNM model is strongly favoured over the EDDFNM model. The choice of priors for the models (equal vs. weighted to penalize parameter-rich models) makes little difference to the posterior model probabilities.

Table 3. Number of parameters, negative log integrated likelihood (-LnIL) and posterior model probabilities (p(M)) for models with fixed observation precision of 88.3 fit to data from 1984-2008. The first posterior model probability assumes equal prior weight to each model while the second penalizes models with more parameters (see text for details).

Model	# params	-LnIL	p(M) equal prior	p(M) wtd prior
DDS	10	774.66	0.00	0.00
DDF	10	771.72	0.00	0.00
EDDS	11	769.83	0.01	0.00
EDDF	11	771.10	0.00	0.00
EDDSNM	8	765.22	0.93	0.95
EDDFNM	8	768.12	0.05	0.05

Estimates of total population size

Estimated sizes of the 2008 adult population under each model are shown in Table 4; estimates for all other years are given in the Appendix.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2008 breeding season, derived from models fit to data from 1984-2008. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	DDF
North Sea	15.0 (12.0 19.5)	33.4 (25.0 47.6)
Inner Hebrides	9.4 (7.6 11.8)	25.1 (17.4 38.3)
Outer Hebrides	33.7 (26.3 43.1)	96.4 (64.7 155.6)
Orkney	58.2 (46.0 76.8)	123.2 (92.4 172.3)
Total	116.3 (91.9 151.1)	278.3 (199.4 414.0)
	EDDS	EDDF
North Sea	20.2 (12.3 29.4)	27.9 (21.2 37.2)
Inner Hebrides	10.1 (7.6 13.2)	17.0 (12.0 23.7)
Outer Hebrides	38.7 (29.1 50.6)	63.9 (48.0 85.4)
Orkney	74.3 (44.2 103.1)	95.5 (75.9 120.4)
Total	143.3 (93.2 196.3)	204.3 (157.2 266.7)
	EDDSNM	EDDFNM
North Sea	18.8 (12.1 26.9)	29.8 (22.9 46.2)
Inner Hebrides	8.7 (6.9 10.8)	22.6 (17.5 37.6)
Outer Hebrides	32.3 (25.4 39.2)	94.4 (70.4 181.3)
Orkney	58.9 (41.4 91.2)	109.0 (85.6 174.1)
Total	118.7 (85.9 168.1)	255.9 (196.5 439.6)
	Model averaged (wtd prior)	
North Sea	19.4 (12.2 29.6)	
Inner Hebrides	9.5 (6.9 21.8)	
Outer Hebrides	35.7 (25.5 87.7)	
Orkney	61.6 (41.6 107.0)	
Total	126.2 (89.2 244.8)	

Estimates from the DDS model are approximately 2.4 times less than those from the DDF model, and there is no overlap between the 95% posterior credibility intervals. Estimates from the EDDS model are higher than the DDS model, whereas those from the EDDF model are lower than the DDF model, making the results from the two extended density dependent models rather closer. The EDDSNM model estimates are closer to those of the DDS model, and indeed the total adult population estimate is nearly identical. These estimates are lower than those from the EDDS model because adult numbers are estimated to have declined in the Inner and Outer Hebrides since the 1990s (Appendix). The EDDFNM model estimates are intermediate between those of the DDF and EDDF models. Estimates from the EDDSNM model are about 2.2 times smaller than those from the EDDFNM model, and there is no overlap between posterior 95% credibility intervals. These two models have virtually all the posterior model probability (Table 3) but, because much of this is due to the EDDSNM model, the resulting model averaged posterior means are similar to the EDDSNM values (Table 3 and Figure 4). The confidence intervals, however, are much wider, reflecting the estimated small chance that EDDFNM could be the correct model.

Second run of EDDSNM and EDDFNM models
A duplicate run of both these models produced very similar results to the first. The negative log integrated likelihoods were the same to 3 significant figures. Estimates of states and parameter estimates were also identical to 2 or 3 significant figures, apart from the estimate of carrying capacity of pups in Orkney, which differed in both cases by a digit in the second significant figure (i.e., by 1000).

Discussion

Reliability of results
One aspect of reliability is Monte Carlo variation – i.e., variability in results that would be obtained by repeatedly running the fitting algorithm on the same data. By repeating the estimation procedure for the two favoured models, we have shown that Monte Carlo variation is tolerably low.

A second aspect of reliability is bias induced by the fitting algorithm. As discussed in previous reports, we expect this to be negligible given the current implementation of the algorithm, but further investigation is justified.

A third aspect is the stability of results. The model selection results are rather different from those obtained by Thomas and Harwood (2008), who used an almost identical dataset (just 2008 missing), and almost identical methods (slight change in model comparison methods). Previous work has shown that models with density dependent pup survival and fecundity should be nearly indistinguishable based on pup count data, so it is surprising that the current results indicate one model favoured over the other. Until this result is better understood, the conclusion that the EDDSNM model is greatly preferred over EDDFNM based on pup count data should be treated with caution.

Comparison with previous estimates
The estimates of total population size are similar those from last year, comparing the same years and models. The largest difference is the EDDS model, from which Thomas and Harwood (2008) obtained an estimate of adult population size in 2007 of 136, 600 (95%CI 85,400-189,100) and which in this paper is estimated as 140,500 (95%CI 94,100-188,500). Since the algorithm and models are the same, these differences must be caused by the additional year of data adjusting historical estimates.

Estimates of total population size from the EDDSNM model are very similar to those from the DDS model, which is the one traditionally used to report population estimates. Since the DDS model is clearly fitting the data very poorly, there seems ample justification to switch to the EDDSNM model, even if multi-model inference is not used in reporting the "headline" numbers.

Future work
At the 2008 SCOS meeting, the committee asked us to develop and fit a model combining density dependent survival and fecundity. This has proved more difficult than expected, and work on this is ongoing. We have also been working to improve the prior distribution on model parameters, based on new analyses of intensive mark-recapture studies of seals at the Isle of May and North Rhona. These studies provide strong support for fecundity values higher than those obtained in the current density dependent fecundity models.

As detailed by Duck (2009), the aerial survey methods were slightly different in 2008 (the plane flew lower to obtain better quality images). This led to different assumptions about the mis-classification rate for moulted pups being made in the models that produce the pup production estimates, which in turn led to slightly higher estimates of pup production (around 5% higher). Although these estimates are believed to be reliable, it is of interest to know how much the change in assumed mis-classification has affected the resulting estimate of adult population size. We are currently undertaking model runs to determine this, and will report results at the meeting.

Even though the models used in this report fit the data reasonably well, there are still some systematic departures of the estimated pup production from the observed values. We have begun investigating alternative biological models, focussing initially on a model that allows random annual variation in fecundity. We have also been investigating the use of pup production estimates from before 1984, as well as different methods to initialize the population model to avoid artefacts, such as those observed in the early DDF pup production estimates.

As stated earlier, the finding that the EDDSNM model has greater posterior model probability than EDDFNM should be treated with caution because, in theory, the pup production trajectories produced by these two models should be very similar. Further investigation of this finding is a priority.

References

Duck, C.D. 2009. Grey seal pup production in Britain in 2008. *SCOS Briefing Paper 09/1*.

Hiby, L. and C.D. Duck. Unpublished. Estimates of the size of the British grey seal *Halichoerus grypus* population and levels of uncertainty.

Hoeting, J.A., D. Madigan, A.E. Raftery and C.T. Volinsky. Bayesian Model Averaging: A Tutorial. *Statistical Science* 14: 382-417.

Thomas, L. and J. Harwood. 2007. Estimating the size of the UK grey seal population between 1984 and 2006. *SCOS Briefing Paper 07/3*

Thomas, L. and J. Harwood. 2008. Estimating the size of the UK grey seal population between 1984 and 2007. *SCOS Briefing Paper 08/3*

Figure 1. Posterior mean estimates of true pup production (lines) from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 88.3, fit to pup production estimates from 1984-2008 (circles).

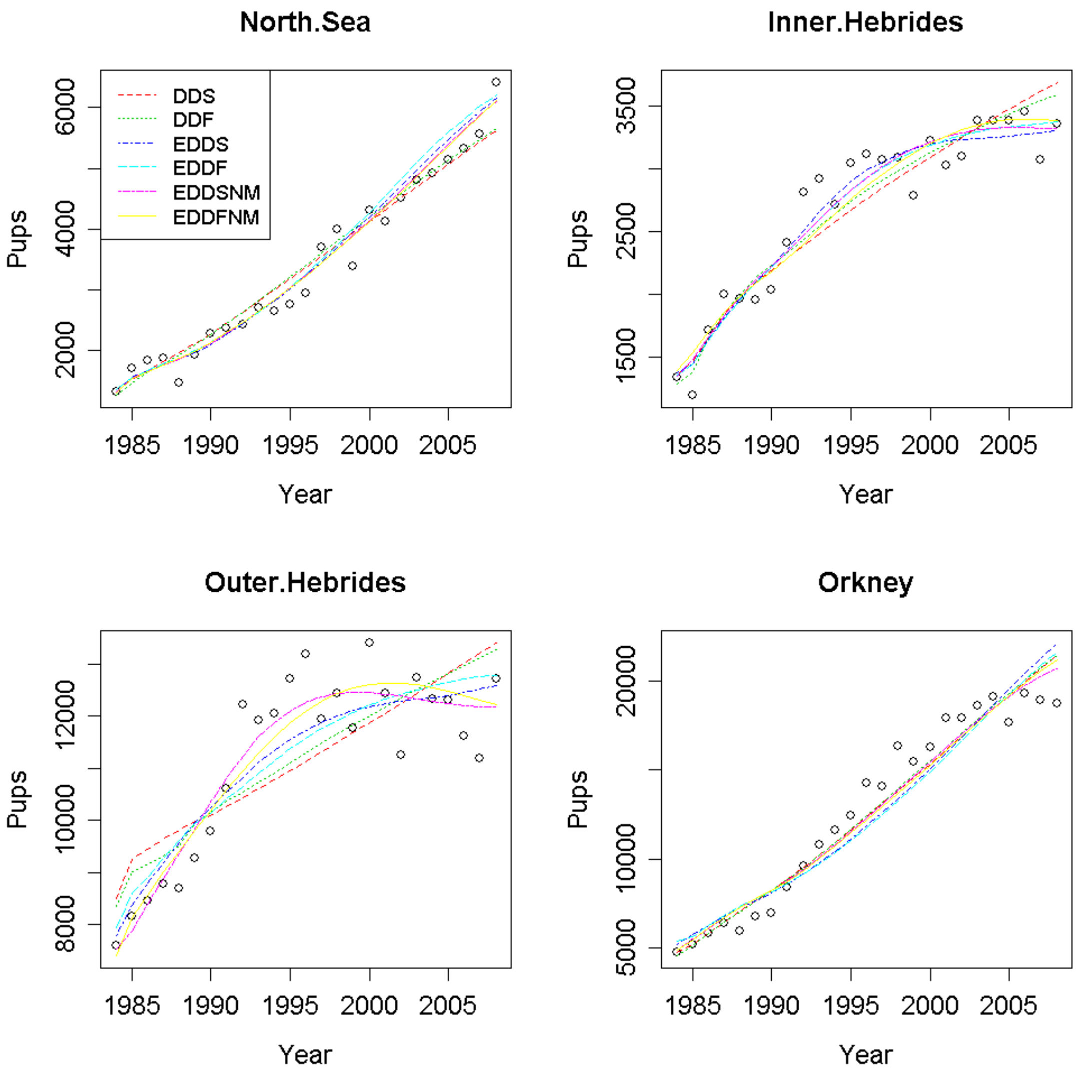
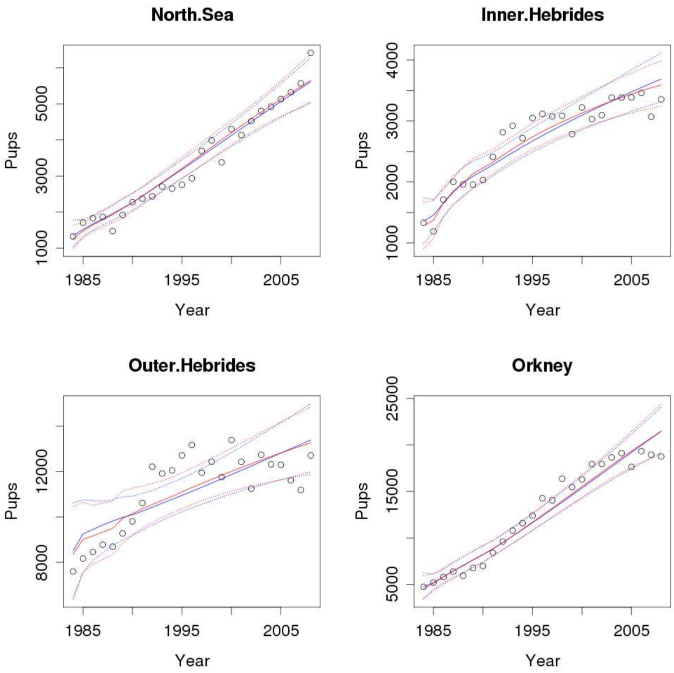
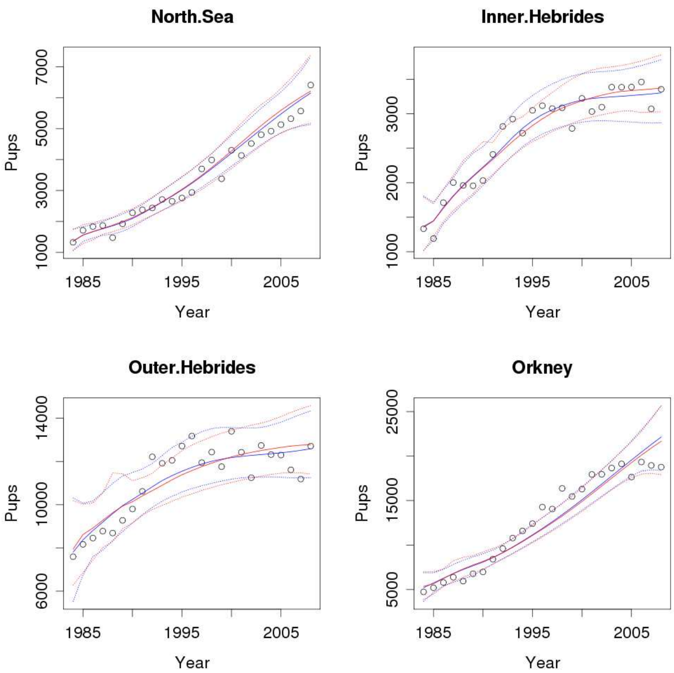


Figure 2. Estimates of true pup production from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 87.9, fit to pup production estimates from 1984-2008. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility intervals. For ease of comparison, estimates from two models are shown on each plot.

(a) Density dependent survival (DDS, blue); density dependent fecundity (DDF, red)



(b) Extended density dependent survival (EDDS, blue); extended density dependent fecundity (EDDF, red)



(c) Extended density dependent survival with no movement (EDDSNM, blue), extended density dependent fecundity with no movement (EDDFNM, red)

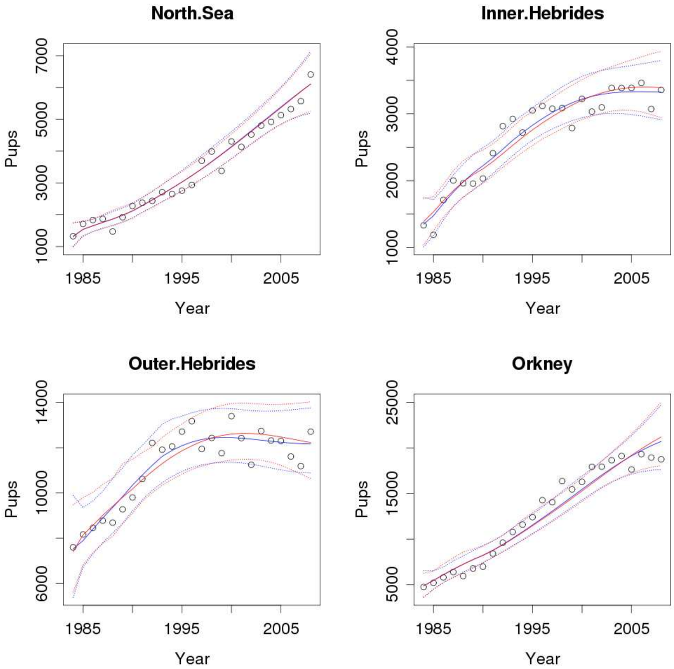
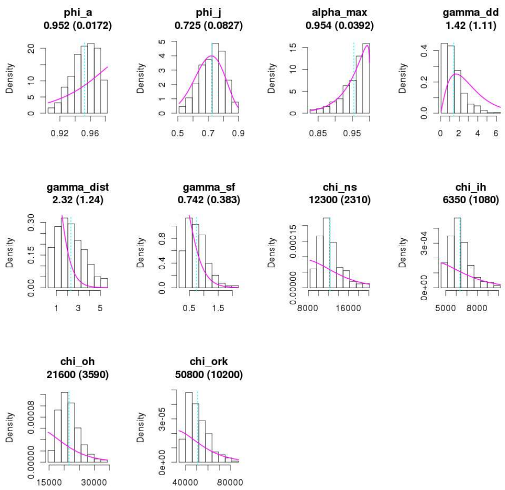
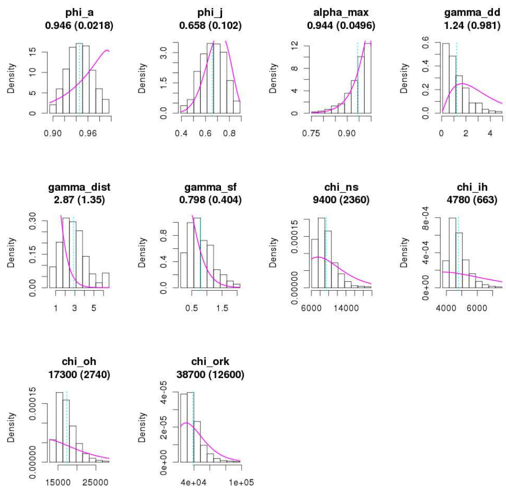


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from six models of grey seal population dynamics where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

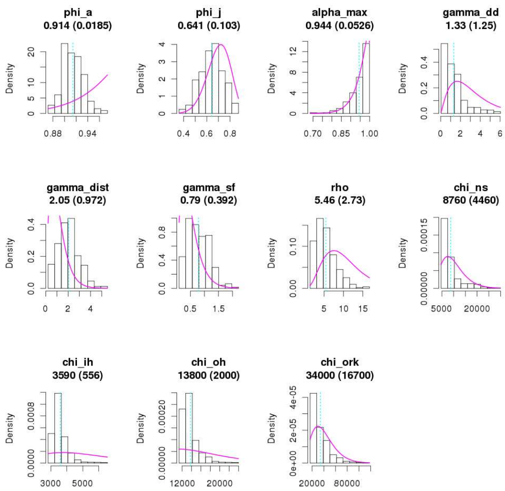
(a) Density dependent survival (DDS)



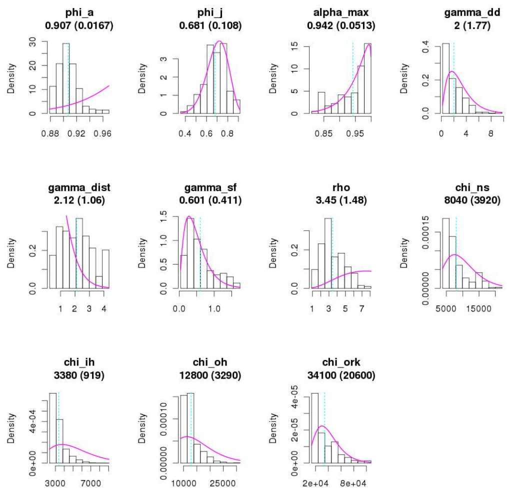
(b) Density dependent fecundity (DDF)



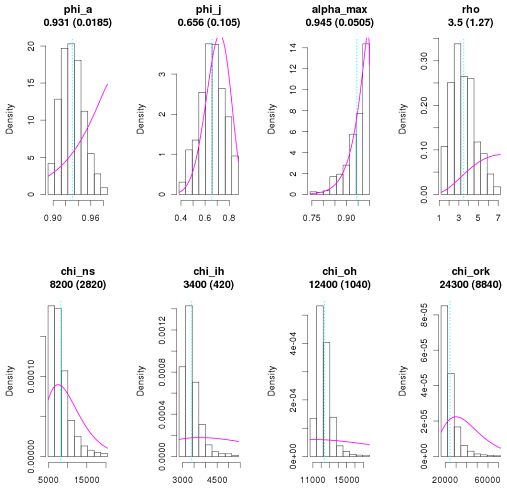
(c) Extended density dependent survival (EDDS)



(d) Extended density dependent fecundity (EDDF)



(e) Extended density dependent survival with no movement (EDDSNM)



(f) Extended density dependent fecundity with no movement (EDDFNM)

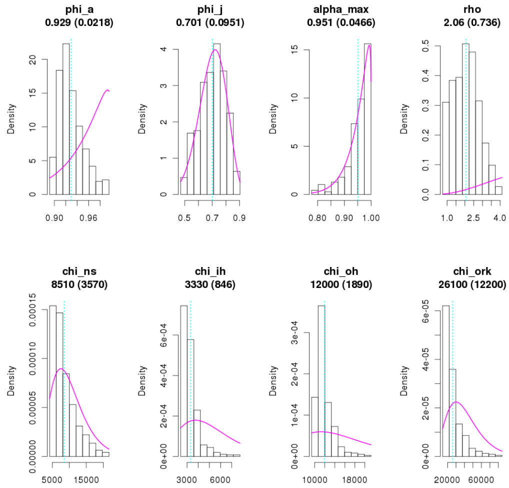
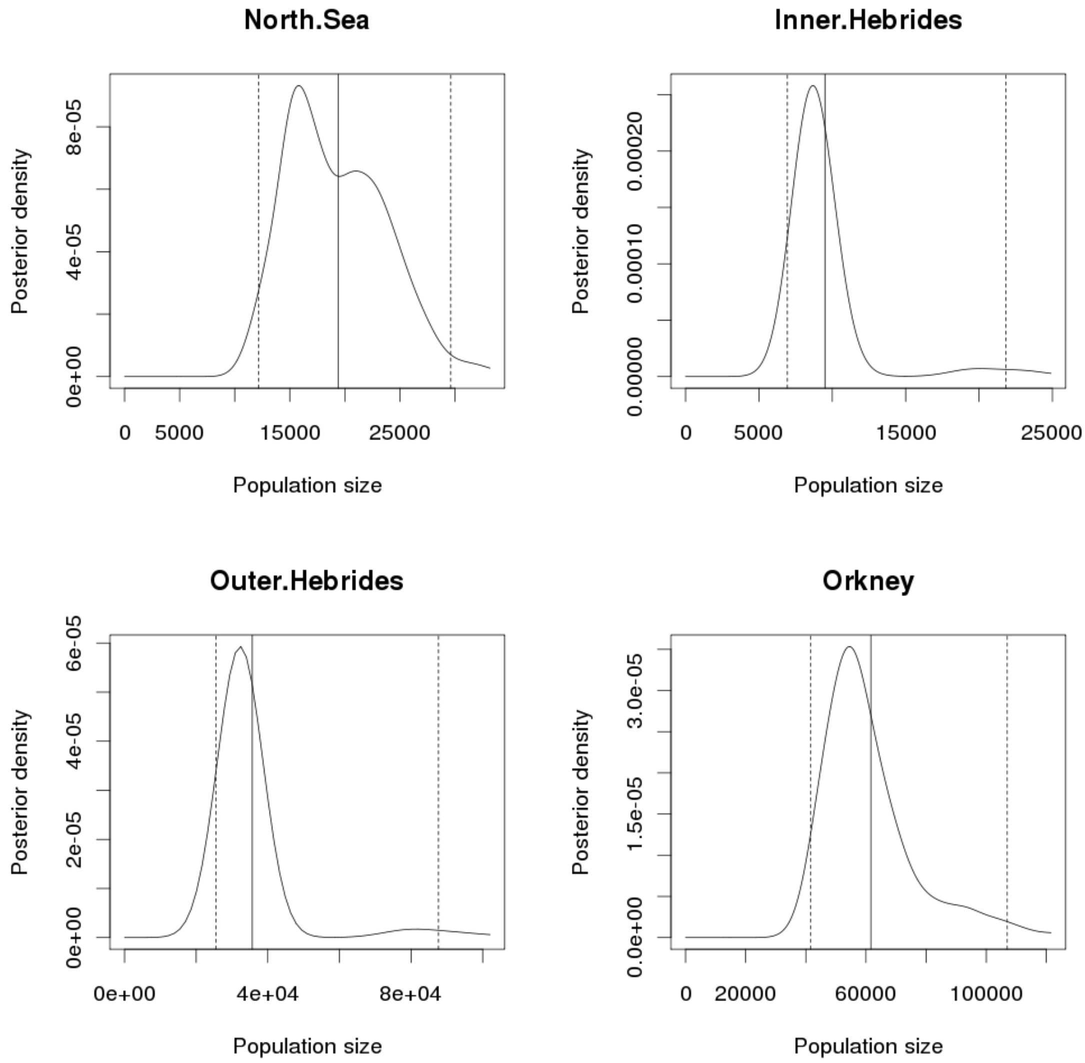


Figure 4. Posterior density of total population size at the beginning of the 2008 breeding season, combining the models and using prior model probabilities that penalize models with more parameters (see text). Only the EDDSNM and EDDFNM models have non-negligible posterior model probabilities, and these are responsible for the (large) left and (small) right peaks in the plots. Solid vertical lines are the mean posterior estimates; dashed lines indicate posterior 95% credibility intervals.



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2007, made using six models of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival (DDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	4.5 (3.6 5.6)	4.5 (3.5 5.7)	25.2 (20.2 32.3)	16.7 (13.4 21.2)	50.8 (40.8 64.8)
1985	4.9 (4 6)	4.8 (3.9 6)	25.3 (20.5 31.8)	18.1 (14.8 22.8)	53 (43.2 66.5)
1986	5.3 (4.4 6.4)	5.1 (4.1 6.3)	25.5 (20.9 31.6)	19.6 (16.2 24.3)	55.4 (45.6 68.6)
1987	5.8 (4.8 6.9)	5.4 (4.4 6.7)	25.7 (21.3 31.7)	21.1 (17.6 25.9)	58 (48.1 71.1)
1988	6.2 (5.2 7.4)	5.6 (4.7 7.1)	26.1 (21.6 32.2)	22.8 (19 27.7)	60.7 (50.4 74.3)
1989	6.7 (5.6 7.9)	5.9 (4.9 7.4)	26.4 (21.8 32.6)	24.4 (20.4 29.6)	63.4 (52.7 77.5)
1990	7.1 (6 8.5)	6.1 (5.1 7.7)	26.7 (22 32.9)	26.2 (21.9 31.5)	66.2 (55 80.7)
1991	7.6 (6.4 9)	6.4 (5.3 8)	27.1 (22.2 33.3)	27.9 (23.4 33.6)	68.9 (57.3 83.9)
1992	8 (6.8 9.6)	6.6 (5.5 8.2)	27.4 (22.5 33.7)	29.6 (24.8 35.7)	71.7 (59.6 87.2)
1993	8.5 (7.2 10.2)	6.8 (5.6 8.5)	27.8 (22.8 34.1)	31.4 (26.3 37.9)	74.5 (61.9 90.8)
1994	8.9 (7.5 10.8)	7 (5.8 8.8)	28.2 (23 34.7)	33.2 (27.8 40.2)	77.3 (64.1 94.4)
1995	9.4 (7.9 11.4)	7.2 (6 9)	28.5 (23.3 35.2)	35 (29.2 42.6)	80.2 (66.3 98.2)
1996	9.8 (8.3 12)	7.4 (6.1 9.2)	28.9 (23.5 35.7)	36.9 (30.6 44.9)	83.1 (68.5 101.9)
1997	10.3 (8.6 12.6)	7.6 (6.3 9.5)	29.3 (23.7 36.3)	38.7 (32.1 47.3)	85.9 (70.7 105.6)
1998	10.8 (9 13.2)	7.8 (6.4 9.7)	29.7 (24 36.9)	40.5 (33.5 49.7)	88.8 (72.9 109.5)
1999	11.2 (9.3 13.8)	8 (6.6 9.9)	30.1 (24.2 37.4)	42.3 (34.9 52.3)	91.6 (74.9 113.4)
2000	11.7 (9.6 14.4)	8.1 (6.7 10.1)	30.5 (24.4 38)	44.2 (36.2 54.8)	94.5 (77 117.4)
2001	12.1 (9.9 15)	8.3 (6.8 10.4)	30.9 (24.6 38.6)	46 (37.6 57.4)	97.3 (79 121.4)
2002	12.5 (10.3 15.7)	8.5 (6.9 10.6)	31.3 (24.9 39.2)	47.8 (38.8 60)	100.1 (80.9 125.5)
2003	13 (10.6 16.3)	8.6 (7.1 10.8)	31.7 (25.2 39.9)	49.6 (40.1 62.8)	102.9 (82.9 129.7)
2004	13.4 (10.9 17)	8.8 (7.2 11)	32.1 (25.4 40.5)	51.3 (41.3 65.5)	105.6 (84.7 134)
2005	13.8 (11.1 17.6)	9 (7.3 11.2)	32.5 (25.6 41.1)	53.1 (42.5 68.3)	108.4 (86.6 138.3)
2006	14.2 (11.4 18.2)	9.1 (7.4 11.4)	32.9 (25.9 41.8)	54.8 (43.7 71.1)	111.1 (88.4 142.5)
2007	14.6 (11.7 18.9)	9.3 (7.5 11.6)	33.4 (26.1 42.4)	56.5 (44.8 73.9)	113.7 (90.1 146.8)
2008	15 (12 19.5)	9.4 (7.6 11.8)	33.7 (26.3 43.1)	58.2 (46 76.8)	116.3 (91.9 151.1)

Density dependent fecundity (DDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.5 (4.2 7)	6.2 (4.5 8.4)	49.4 (35.1 71.8)	20 (15.2 25.3)	81 (59 112.5)
1985	6 (4.7 7.6)	7 (5.3 9.1)	50.5 (36.6 73.7)	21.9 (16.9 27.1)	85.4 (63.6 117.5)
1986	6.7 (5.3 8.3)	7.8 (6.1 9.9)	51.9 (38.4 74.9)	24 (18.8 29.4)	90.4 (68.6 122.6)
1987	7.4 (5.9 9.3)	8.6 (6.9 10.7)	53.4 (39.8 76.6)	26.5 (20.9 32.4)	95.9 (73.6 128.9)
1988	8.2 (6.6 10.3)	9.4 (7.6 11.9)	55 (40.9 78.1)	29.2 (23.1 35.7)	101.8 (78.2 135.9)
1989	9 (7.2 11.3)	10.3 (8.3 12.9)	56.7 (42.1 79.5)	32 (25.4 39.3)	108 (83 143.1)
1990	9.9 (7.8 12.6)	11.1 (8.9 14.1)	58.5 (43.4 81.7)	35.1 (27.9 43.3)	114.6 (88 151.7)
1991	10.8 (8.5 13.9)	12 (9.5 15.3)	60.4 (44.6 84.1)	38.4 (30.3 47.6)	121.5 (92.9 160.9)
1992	11.8 (9.2 15.3)	12.8 (10.1 16.5)	62.3 (45.8 86.1)	41.8 (32.8 52.3)	128.7 (98 170.2)
1993	12.8 (10 16.8)	13.6 (10.7 17.7)	64.3 (47.1 89.7)	45.5 (35.7 57.5)	136.2 (103.5 181.6)
1994	13.9 (10.8 18.4)	14.4 (11.2 18.9)	66.2 (48.3 93.2)	49.4 (38.8 63)	144 (109.1 193.5)
1995	15 (11.6 20.1)	15.2 (11.8 20.2)	68.2 (49.5 96.5)	53.5 (41.7 68.9)	152 (114.7 205.6)
1996	16.2 (12.5 21.8)	16 (12.3 21.5)	70.3 (50.8 100.1)	57.9 (44.8 75.1)	160.4 (120.4 218.6)
1997	17.5 (13.4 23.7)	16.8 (12.8 22.8)	72.3 (52 103.7)	62.4 (48.1 81.9)	169.1 (126.3 232.2)
1998	18.8 (14.4 25.6)	17.6 (13.3 24.2)	74.4 (53.1 108)	67.2 (51.5 89.3)	178 (132.3 247.1)
1999	20.1 (15.3 27.5)	18.4 (13.7 25.5)	76.6 (54.3 111.6)	72.1 (55.1 96.8)	187.2 (138.5 261.5)
2000	21.5 (16.4 29.6)	19.2 (14.2 27)	78.7 (55.5 116.5)	77.2 (58.9 104.7)	196.6 (144.9 277.7)
2001	22.9 (17.4 31.7)	19.9 (14.6 28.4)	80.9 (56.7 121.7)	82.5 (62.8 112.7)	206.2 (151.5 294.5)
2002	24.3 (18.4 33.9)	20.7 (15 29.8)	83.1 (57.8 127.1)	87.9 (66.8 120.8)	216 (158.1 311.6)
2003	25.8 (19.5 36.1)	21.4 (15.4 31.2)	85.3 (58.9 132.3)	93.5 (70.9 129.2)	226 (164.8 328.8)
2004	27.3 (20.6 38.3)	22.2 (15.8 32.6)	87.5 (60.1 137.5)	99.3 (75 137.7)	236.2 (171.5 346)
2005	28.8 (21.7 40.6)	22.9 (16.2 34)	89.7 (61.3 141.9)	105.1 (79.2 146.3)	246.6 (178.3 362.8)
2006	30.3 (22.8 42.9)	23.7 (16.6 35.4)	91.9 (62.4 145.8)	111.1 (83.5 155.1)	257 (185.2 379.3)
2007	31.9 (23.9 45.3)	24.4 (17 36.9)	94.2 (63.5 150.8)	117.2 (87.8 163.8)	267.6 (192.2 396.8)
2008	33.4 (25 47.6)	25.1 (17.4 38.3)	96.4 (64.7 155.6)	123.3 (92.4 172.3)	278.3 (199.4 414)

Extended density dependent survival (EDDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.4 (4.2 6.8)	5.6 (4.2 7.4)	30.1 (22.3 38.3)	21.7 (15.3 27.5)	62.8 (46 80)
1985	5.7 (4.5 7.2)	5.9 (4.6 7.6)	31.1 (23.4 39.4)	22.8 (16.9 28.7)	65.5 (49.5 82.9)
1986	6.1 (4.9 7.4)	6.3 (4.9 7.8)	32.2 (24.6 40.7)	24 (18.5 30.4)	68.6 (53 86.3)
1987	6.6 (5.4 7.9)	6.7 (5.3 8.2)	33.3 (24.9 41.5)	25.5 (20.2 31.9)	72 (55.7 89.4)
1988	7 (5.8 8.4)	7.1 (5.6 8.5)	34.4 (26.1 42.9)	27.1 (21.7 33.7)	75.6 (59.1 93.5)
1989	7.5 (6.1 8.9)	7.6 (5.9 9.2)	35.2 (27.1 44.1)	28.8 (23.2 35.8)	79.1 (62.3 98)
1990	8 (6.5 9.5)	8.1 (6.3 9.9)	35.9 (28.1 44.8)	30.7 (25 37.8)	82.6 (65.9 102)
1991	8.5 (7 10.1)	8.5 (6.6 10.5)	36.5 (28.4 45.4)	32.6 (26.8 40.2)	86.1 (68.8 106.1)
1992	9.1 (7.5 10.7)	8.9 (7 11)	36.9 (28.5 46)	34.6 (28.5 42.3)	89.6 (71.4 110)
1993	9.8 (8 11.5)	9.3 (7.2 11.5)	37.3 (28.6 46.7)	36.8 (30.3 44.6)	93.1 (74.1 114.3)
1994	10.5 (8.5 12.3)	9.5 (7.3 11.9)	37.6 (28.7 47.3)	39.1 (32 47.3)	96.7 (76.6 118.8)
1995	11.2 (9 13.1)	9.7 (7.4 12.4)	37.8 (28.8 47.7)	41.5 (34.1 50.3)	100.2 (79.3 123.4)
1996	11.9 (9.5 14)	9.9 (7.5 12.5)	37.9 (28.7 47.9)	44 (36.1 53.4)	103.7 (81.8 127.8)
1997	12.7 (10.1 15)	9.9 (7.6 12.6)	37.9 (28.6 48)	46.6 (38.1 56.6)	107.2 (84.5 132.2)
1998	13.5 (10.8 16)	9.9 (7.6 12.6)	38 (28.6 48.1)	49.3 (40.1 60)	110.7 (87.1 136.7)
1999	14.3 (11.5 17.1)	9.9 (7.6 12.6)	37.9 (28.6 48.2)	52 (42.1 63.4)	114.2 (89.8 141.4)
2000	15.1 (12.1 18.2)	9.9 (7.5 12.6)	37.9 (28.7 48.3)	54.7 (44.1 66.9)	117.7 (92.4 146.1)
2001	15.9 (12.6 19.4)	9.9 (7.5 12.7)	37.9 (28.7 48.5)	57.4 (45.5 70.5)	121.2 (94.2 151)
2002	16.7 (12.8 20.6)	9.9 (7.5 12.7)	38 (28.7 48.8)	60.1 (46.4 74.3)	124.6 (95.4 156.4)
2003	17.4 (12.8 21.9)	9.9 (7.5 12.8)	38 (28.8 49.2)	62.6 (46.8 78.4)	128 (95.8 162.2)
2004	18 (12.6 23.2)	9.9 (7.4 12.9)	38.1 (28.8 49.4)	65.1 (46.8 82.6)	131.3 (95.7 168.1)
2005	18.7 (12.5 24.6)	10 (7.5 12.9)	38.3 (28.9 49.6)	67.5 (46.7 87.1)	134.4 (95.6 174.2)
2006	19.2 (12.4 26.1)	10 (7.5 13)	38.4 (29 49.9)	69.9 (46.1 92.1)	137.5 (95 181.1)
2007	19.7 (12.4 27.7)	10 (7.5 13.1)	38.6 (29 50.3)	72.1 (45.1 97.4)	140.5 (94.1 188.5)
2008	20.2 (12.3 29.4)	10.1 (7.6 13.2)	38.7 (29.1 50.6)	74.3 (44.2 103.1)	143.3 (93.2 196.3)

Extended density dependent fecundity (EDDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.7 (4.5 6.7)	5.8 (4.6 7.4)	35.2 (26.3 49.2)	22.8 (17.8 27.8)	69.5 (53.3 91.1)
1985	6 (4.8 7)	6.2 (5 7.8)	36.2 (27.4 50.9)	24 (19 28.9)	72.4 (56.2 94.5)
1986	6.4 (5.2 7.5)	6.6 (5.5 8.1)	37.5 (29 52.2)	25.2 (20.5 30.1)	75.8 (60.2 97.9)
1987	6.9 (5.6 8.1)	7.1 (5.9 8.7)	38.8 (30.7 52.4)	26.7 (22 31.5)	79.5 (64.3 100.7)
1988	7.4 (6.1 8.6)	7.7 (6.3 9.3)	40.2 (32.2 53.1)	28.4 (23.5 33.2)	83.7 (68.1 104.3)
1989	7.9 (6.6 9.3)	8.3 (6.9 10.1)	41.7 (33.2 53)	30.2 (24.7 35.8)	88.1 (71.3 108.1)
1990	8.5 (7.1 10.1)	8.9 (7.3 11.1)	43.1 (34.3 54.4)	32.3 (26.4 38.9)	92.8 (75 114.4)
1991	9.1 (7.5 10.9)	9.6 (7.8 11.9)	44.5 (35.5 56.1)	34.4 (28.1 42.4)	97.5 (78.9 121.3)
1992	9.8 (7.9 11.8)	10.2 (8.3 12.7)	45.8 (36.8 57.6)	36.6 (29.7 45.6)	102.4 (82.7 127.7)
1993	10.5 (8.3 12.8)	10.8 (8.8 13.4)	47.2 (37.8 59.2)	39 (31.4 49.1)	107.4 (86.4 134.5)
1994	11.3 (8.9 13.9)	11.4 (9.3 14.3)	48.6 (39 61.3)	41.5 (33.4 52.6)	112.7 (90.5 142.1)
1995	12.1 (9.5 15)	12 (9.6 15)	49.9 (39.8 63.6)	44.2 (35.5 56.3)	118.2 (94.5 149.9)
1996	13 (10.1 16.2)	12.5 (10 15.8)	51.2 (40.8 65.6)	47.2 (37.8 60.4)	123.9 (98.6 158)
1997	14 (10.8 17.4)	13.1 (10.3 16.5)	52.5 (41.5 67.2)	50.3 (40.3 64.8)	129.9 (103 165.9)
1998	15.1 (11.6 18.7)	13.6 (10.5 17.2)	53.8 (42.5 69)	53.6 (43 69.3)	136 (107.6 174.2)
1999	16.2 (12.4 20.1)	14 (10.8 17.9)	55 (43.1 70.9)	57.1 (46 74)	142.3 (112.3 182.9)
2000	17.4 (13.2 21.6)	14.4 (11 18.6)	56.1 (43.7 72.7)	60.8 (49.1 78.7)	148.7 (117 191.7)
2001	18.7 (14.1 23.1)	14.8 (11.2 19.3)	57.2 (44.3 74.6)	64.6 (52 83.6)	155.3 (121.6 200.6)
2002	20 (15 24.9)	15.2 (11.3 20)	58.2 (44.9 76.3)	68.7 (55 88.4)	162.1 (126.3 209.7)
2003	21.3 (16 26.8)	15.5 (11.5 20.7)	59.3 (45.4 78.1)	72.9 (58.2 93.3)	169 (131.1 218.9)
2004	22.6 (17 28.7)	15.8 (11.6 21.3)	60.2 (46 79.8)	77.3 (61.4 98.5)	176 (135.9 228.2)
2005	24 (18 30.8)	16.1 (11.7 21.8)	61.2 (46.5 81.4)	81.8 (64.7 103.6)	183.1 (140.9 237.7)
2006	25.3 (19.1 32.9)	16.4 (11.8 22.4)	62.2 (47 83)	86.3 (68.1 109)	190.2 (146.1 247.3)
2007	26.6 (20.2 35.1)	16.7 (11.9 23)	63.1 (47.6 84.3)	90.9 (71.9 115.3)	197.3 (151.5 257.7)
2008	27.9 (21.2 37.2)	17 (12 23.7)	63.9 (48 85.4)	95.5 (75.9 120.4)	204.3 (157.2 266.7)

Extended density dependent survival with no movement (EDDSNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.3 (4 6.5)	5.6 (4.3 6.9)	26 (20.2 32.7)	20.6 (15.3 26.3)	57.4 (43.8 72.3)
1985	5.6 (4.3 6.9)	5.9 (4.7 7.2)	27.3 (21.2 33.9)	21.8 (16.7 27.1)	60.6 (46.9 75.1)
1986	6 (4.7 7.4)	6.2 (4.9 7.4)	28.6 (22 35.4)	23.2 (18.2 28.5)	64 (49.8 78.7)
1987	6.5 (5.2 7.9)	6.5 (5.2 7.8)	29.7 (22.7 36.4)	24.8 (19.6 30.4)	67.6 (52.6 82.5)
1988	7 (5.6 8.4)	6.9 (5.4 8.3)	30.7 (23.4 37.8)	26.7 (21.2 32.3)	71.3 (55.6 86.8)
1989	7.5 (6.1 9)	7.2 (5.6 8.7)	31.5 (23.9 38.8)	28.5 (22.8 34.7)	74.7 (58.4 91.1)
1990	8 (6.5 9.6)	7.5 (5.8 9.1)	32 (24.3 39.5)	30.5 (24.5 37.1)	78 (61.1 95.3)
1991	8.5 (6.9 10.2)	7.7 (6 9.4)	32.4 (24.7 40.2)	32.5 (26.2 39.6)	81.2 (63.8 99.4)
1992	9.1 (7.4 10.8)	8 (6.2 9.8)	32.7 (24.8 40.6)	34.5 (27.8 42)	84.3 (66.2 103.2)
1993	9.7 (7.8 11.5)	8.2 (6.3 10.1)	32.9 (25 40.7)	36.6 (29.4 44.4)	87.4 (68.6 106.7)
1994	10.3 (8.3 12.2)	8.4 (6.4 10.3)	33 (25.2 40.7)	38.7 (31.1 46.9)	90.4 (71 110.1)
1995	10.9 (8.7 13)	8.5 (6.5 10.6)	33 (25.2 40.5)	40.8 (32.7 49.3)	93.3 (73.1 113.4)
1996	11.6 (9.2 13.8)	8.6 (6.6 10.7)	32.9 (25.2 40.3)	43 (34.3 51.8)	96.1 (75.3 116.6)
1997	12.3 (9.6 14.6)	8.7 (6.7 10.8)	32.8 (25.3 40.1)	45 (35.7 54.3)	98.8 (77.4 119.8)
1998	12.9 (10.1 15.5)	8.8 (6.8 10.9)	32.6 (25.3 39.9)	47 (36.9 57)	101.3 (79 123.2)
1999	13.6 (10.4 16.4)	8.8 (6.8 10.9)	32.5 (25.3 39.6)	48.9 (38 59.6)	103.8 (80.5 126.5)
2000	14.3 (10.7 17.3)	8.8 (6.9 10.9)	32.4 (25.4 39.4)	50.6 (38.9 62.4)	106.1 (81.8 129.9)
2001	14.9 (11 18.2)	8.8 (6.9 10.9)	32.3 (25.4 39.2)	52.2 (39.8 65.5)	108.2 (83 133.8)
2002	15.6 (11.2 19.3)	8.8 (6.9 10.8)	32.2 (25.4 39.1)	53.6 (40.4 68.6)	110.2 (83.9 137.8)
2003	16.2 (11.4 20.4)	8.8 (6.9 10.8)	32.1 (25.4 39.1)	54.9 (40.9 71.9)	112 (84.6 142.1)
2004	16.8 (11.6 21.5)	8.8 (6.9 10.8)	32.1 (25.4 39)	56 (41.3 75.4)	113.6 (85.2 146.8)
2005	17.3 (11.8 22.8)	8.8 (6.9 10.8)	32.1 (25.4 39)	56.9 (41.5 79.1)	115.1 (85.6 151.7)
2006	17.9 (11.9 24.1)	8.7 (6.9 10.8)	32.2 (25.4 39)	57.7 (41.6 83)	116.4 (85.8 156.9)
2007	18.4 (12 25.5)	8.7 (6.9 10.8)	32.2 (25.4 39.1)	58.3 (41.6 87)	117.6 (85.9 162.4)
2008	18.8 (12.1 26.9)	8.7 (6.9 10.8)	32.3 (25.4 39.2)	58.9 (41.4 91.2)	118.7 (85.9 168.1)

Extended density dependent fecundity with no movement (EDDFNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.5 (4.4 6.8)	6.5 (5.1 9.5)	38.5 (24.9 88.7)	21.8 (17 26.8)	72.4 (51.4 131.8)
1985	5.9 (4.9 7.3)	6.9 (5.3 9.9)	40.5 (26.7 92.7)	23.2 (18.4 27.9)	76.5 (55.3 137.8)
1986	6.4 (5.3 7.9)	7.4 (5.7 10.5)	42.8 (28.7 97)	24.8 (20.2 30)	81.4 (59.9 145.4)
1987	7 (5.7 8.5)	7.9 (6.1 11.1)	45.2 (30.9 100.4)	26.8 (21.9 32.8)	86.8 (64.6 152.9)
1988	7.6 (6.2 9.3)	8.5 (6.6 11.7)	47.7 (33.2 102.2)	28.9 (23.7 35.6)	92.6 (69.7 158.9)
1989	8.2 (6.7 10.1)	9.1 (7.1 12.4)	50.2 (35.3 103.3)	31.3 (25.6 39.5)	98.7 (74.6 165.4)
1990	8.8 (7.2 11.1)	9.7 (7.6 13.4)	52.8 (37.5 107.4)	33.8 (27.6 43.2)	105.1 (79.8 175)
1991	9.5 (7.7 12.3)	10.4 (8.1 14.4)	55.5 (39.7 111.4)	36.4 (29.7 46.5)	111.7 (85.2 184.5)
1992	10.2 (8.3 13.5)	11 (8.7 15.4)	58.3 (42 115.6)	39.1 (31.9 50)	118.6 (90.8 194.4)
1993	11 (8.9 14.7)	11.7 (9.2 16.4)	61 (44.4 119.6)	42.1 (34.3 54.1)	125.8 (96.7 204.8)
1994	11.8 (9.5 16.2)	12.5 (9.8 17.6)	63.9 (46.7 123.7)	45.2 (36.7 59.8)	133.4 (102.7 217.2)
1995	12.7 (10.2 17.5)	13.2 (10.4 18.6)	66.6 (49.2 128.3)	48.6 (39.2 66)	141.2 (108.9 230.4)
1996	13.7 (10.9 19.2)	14 (11 19.8)	69.4 (51.6 132.2)	52.2 (41.9 72.5)	149.3 (115.3 243.6)
1997	14.7 (11.6 21)	14.8 (11.6 21.1)	72.1 (54 137.5)	56 (44.7 79.3)	157.5 (121.9 258.8)
1998	15.8 (12.4 22.9)	15.5 (12.2 22.4)	74.8 (56.2 141.8)	59.9 (47.8 86.6)	166 (128.6 273.6)
1999	16.9 (13.2 24.9)	16.3 (12.8 23.8)	77.3 (58.4 141.1)	64.1 (50.9 94.2)	174.7 (135.4 283.9)
2000	18.1 (14.1 27)	17.1 (13.5 25.3)	79.8 (60.5 143.6)	68.5 (54.2 102)	183.5 (142.3 297.9)
2001	19.4 (15.1 29.1)	17.9 (14.1 26.7)	82.1 (62.3 147.4)	73.1 (57.6 110.2)	192.4 (149.1 313.5)
2002	20.7 (16 31.4)	18.6 (14.6 28.2)	84.3 (64.1 152.5)	77.8 (61.2 118.7)	201.4 (156 330.7)
2003	22.1 (17.1 33.7)	19.4 (15.2 29.7)	86.4 (65.6 155.5)	82.7 (65 127.4)	210.5 (162.9 346.3)
2004	23.5 (18.1 36.1)	20.1 (15.8 31.2)	88.3 (67 159.7)	87.8 (68.9 136.3)	219.7 (169.8 363.2)
2005	25 (19.3 38.5)	20.8 (16.3 32.8)	90.1 (68.1 164.4)	92.9 (72.9 145.4)	228.8 (176.6 381.1)
2006	26.6 (20.4 41)	21.4 (16.7 34.4)	91.7 (69.1 169.5)	98.2 (77 154.8)	237.9 (183.3 399.7)
2007	28.2 (21.7 43.5)	22 (17.1 36)	93.1 (69.9 175.5)	103.6 (81.3 164.4)	246.9 (190 419.4)
2008	29.8 (22.9 46.2)	22.6 (17.5 37.6)	94.4 (70.4 181.6)	109 (85.6 174.1)	255.9 (196.5 439.6)