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Estimating the size of the UK grey seal population between 1984 and 2007.

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Summary

We fitted and compared six Bayesian state-space models of British grey seal dynamics, based on regional estimates of pup production from 1984 to 2007. One model (DDS) assumed that pup survival follows a Beverton-Holt density dependent function, and that females recruiting to the breeding population show fitness dependent movement between regions. A companion model (DDF) assumed that density dependence occurs instead in fecundity. Two models (EDDS and EDDF) allowed more flexible forms of density dependence in pup survival or fecundity. The last two models (EDDSNM and EDDFNM) also allowed the more flexible forms of density dependence, but assumed no movement of females. The models were fit using a particle filtering algorithm similar to that used in previous briefing papers, but with improvements designed to give less bias in estimates of model parameters and population numbers. The DDS and DDF models did not fit the pup production data well; all of the other models provided an adequate fit, although there was still some evidence of systematic differences between model predictions and data. Using a model selection criterion based on parsimony, we found that the EDDSNM and EDDFNM models were preferred over the other models, with the former having slightly more support. The estimated adult population size in 2007 for these two models was 117,600 and 239,700 respectively. We calculated a combined 95% posterior credibility interval that accounts for the uncertainty about which model is correct – this gave the interval 84,500-304,500 adult seals.

Introduction

In this paper, we present estimates of population size and related demographic parameters, derived from state-space models of the grey seal population fit to regional estimates of pup production from 1984-2007. The state-space modelling framework is described in detail in a series of recent papers (Buckland *et al.* 2004, Thomas *et al.* 2005, Newman *et al.* 2006,

Buckland *et al.* 2007) and the models used here are variations of those first introduced by Thomas and Harwood (2003). Similar models have also been applied to the Northwest Atlantic grey seal population (Thomas *et al.* 2007)

We fit and compare six population models, the first four of which are the same as those used by Thomas and Harwood (2005, 2006, 2007). Two models 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 (see Thomas and Harwood 2005). We refer to these as extended density dependent pup survival (EDDS) extended density dependent fecundity (EDDF). Based on results of initial runs, we also fit two more models that allow extended density dependence but assume no movement between regions (EDDSNM and EDDFNM). The models are formulated within the Bayesian statistical framework, and 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.

As in previous reports, the models are fit using a computer-intensive algorithm called a Monte Carlo particle filter (Liu 2001). Improvements to the algorithm have been made, designed to increase the reliability of the results.

Materials and Methods

Models

The biological system is represented using a state-space model: a stochastic time-series model that includes a “state process” for the evolution of the true but unknown state of the

population through time, and an “observation process” that describes the measurements taken on the population.

In constructing the state processes, we divide the seal population in each region into 7 age classes: pups (age 0), age 1 – age 5 adult females (pre-breeding), and age 6 and older females. Note that our models do not include adult males.

The time step for the process models is 1 year, beginning just after the breeding season. The models are made up of four sub-processes: survival, age incrementation, movement of recruiting females and breeding.

Survival is modelled as a binomial random process. For the DDS model, we assume that pup survival follows a Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p \max}}{1 + \beta_r n_{0,r,t-1}}$$

where $n_{0,r,t-1}$ is the number of pups born in region r in year $t-1$, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p \max}$ is maximum pup survival rate, and $1/\beta_r$ is proportional to the carrying capacity of the region. The EDDS and EDDSNM models includes an extra parameter, ρ , that can alter the shape of the relationship between pup survival and pup numbers:

$$\phi_{p,r,t} = \frac{\phi_{p \max}}{1 + (\beta_r n_{0,r,t-1})^\rho}$$

For the DDF, EDDF and EDDFNM models, we assume pup survival is constant across regions and times, i.e., $\phi_{p,r,t} = \phi_p$.

Since half of the pups born will be male, the expected number of female pups surviving in both models will be $0.5 \phi_{p,r,t} n_{0,r,t-1}$. For all models, we assume that adult female survival rate, ϕ_a is constant across regions and time.

Age incrementation is deterministic – all seals age by one year (although those in the age 6+ category remain there).

To model movement in the DDS, EDDS, DDF and EDDF models, we assume that only females breeding for the first time may move from their natal region. Once a female has started breeding she remains faithful to that region. We assume

that movement is fitness dependent (Ruxton and Rohani 1998), such that females will only move if the value of the density dependent parameter (pup survival or fecundity) is higher elsewhere, and the probability of movement is proportional to the difference in the density dependent parameter between regions. In addition, we assume that females are more likely to move among regions that are close together, and that females show some degree of site fidelity – that is, they may not move even if conditions for their offspring will be better elsewhere. We model movement from each region as a multinomial random variable where probability of movement from region r to region i at time t is:

$$\rho_{r \rightarrow i,t} = \begin{cases} \frac{\theta_{r \rightarrow i,t}}{\sum_{j=1}^4 \theta_{j \rightarrow i,t}} & : \sum_{j=1}^4 \theta_{j \rightarrow i,t} > 0 \\ I_{i=r} & : \sum_{j=1}^4 \theta_{j \rightarrow i,t} = 0 \end{cases}$$

where $I_{i=r}$ is an indicator that is 1 when $i=r$ and 0 otherwise, and

$$\theta_{r \rightarrow i,t} = \begin{cases} \gamma_{sf} & : i = r \\ \frac{\gamma_{dd} \max(\Delta_{i,r,t}, 0)}{\exp(\gamma_{dist} d_{r,i})} & : i \neq r \end{cases}$$

where γ_{sf} , γ_{dd} , and γ_{dist} are three movement parameters that index the strength of the site fidelity, density dependence and distance effects respectively, $\Delta_{i,r,t}$ is the difference in the density dependent parameter between regions i and r (see below), and $d_{r,i}$ is the 20% trimmed mean of the distances between colonies in regions r and those in region i (standardized so that the largest distance is 1.0). For the DDS and EDDS models,

$$\Delta_{i,r,t} = \phi_{p,i,t} - \phi_{p,r,t}$$

while for the DDF and EDDF models,

$$\Delta_{i,r,t} = \alpha_{i,t} - \alpha_{r,t}$$

where $\alpha_{r,t}$ is the fecundity rate in region r at time t , as defined below. We assume no movement between regions in the EDDSNM and EDDFNM models.

We model breeding by assuming that the number of pups produced is a binomial random variable, with rate $\alpha_{r,t}$. For the DDS, EDDS and EDDSNM models, we assume this value is constant across regions and times, i.e., $\alpha_{r,t} = \alpha$. For the DDF model, we assume this value follows a Beverton-Holt function of the form:

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1 + \beta_r n_{6+,r,t}}$$

The EDDF and EDDFNM models are similar, with

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1 + (\beta_r n_{6+,r,t})^\rho}$$

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV), the value of which is governed by a model parameter, ψ , where $CV = 1/\sqrt{\psi}$ (i.e., ψ is a precision parameter). We estimated the value of ψ in an initial model run, and applied this estimate to other runs – see *Model outputs and comparison*, below.

In summary, the DDS and DDF models have 11 parameters. They share 9: adult survival ϕ_a , one carrying capacity parameter-related parameter for each region $\beta_1 - \beta_4$, three movement parameters γ_{sf} , γ_{dd} , and γ_{dist} , and the observation precision parameter ψ . They differ in two parameters: the DDS model has maximum pup survival $\phi_{p\max}$ and constant fecundity α , while the DDF model has constant pup survival ϕ_p and maximum fecundity α_{\max} . The EDDS and EDDF models have one additional parameter, ρ , for the shape of the density-dependent response. The EDDSNM and EDDFNM models have no movement parameters, and hence have 9 parameters each.

Data and Priors

Our input data were the pup production estimates for 1984-2007 from Duck and Mackey (2008), aggregated into regions.

Prior distributions for each parameter are given in Table 1, and are shown on Figure 1(b). We followed Thomas and Harwood (2005) in using a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region, denoted χ_r for region r , rather than directly on the β s.

Prior distributions for the states in the DDS, EDDS and EDDSNM model were generated using the priors for the parameters in conjunction with the 1984 data, as described by Thomas *et*

al. (2005). Prior states for the DDF, EDDF and EDDFNM model were generated in a similar manner, as described by Thomas and Harwood (2005). The prior distribution on ψ implies a prior mean on observation CV of 0.10 and prior standard deviation of 0.05.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}, \phi_p$	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, α_{\max}	Be(22.05,1.15)	0.95	0.04
ψ	Ga(2.1, 66.67)	140	96.61

Fitting Method

We used the particle filtering algorithm of Thomas and Harwood (2007), with two small, but significant, improvements. The first (tempering the resampling probabilities) was designed to decrease the Monte-Carlo variation between samples. This allowed implementation of the second improvement (increasing the kernel smoothing discount), which reduced the bias in estimates of parameters and states at a cost of increased Monte-Carlo variation. Overall, the estimates should be a better representation of the fit of the model to the data, compared with previous reports. An outline of the main features of the algorithm is given below, for completeness – it is not necessary to read the rest of this sub-section to understand the results that follow. The algorithm was coded in ANSI standard C and is freely available on request.

A particle filter is an algorithm that produces a set of weighted samples (particles) taken from the prior distributions on the parameters and states and projected forward stochastically through the time series. The weights relate to the manner in which the particles were sampled, how they were projected forward and the likelihood of the observed pup production given the simulated pup numbers. An introduction to

particle filtering algorithms in the context of wildlife studies is given by Newman *et al.* (2006), and a more detailed description of the algorithm used here, applied to a similar model of seals, is given by Newman *et al.* (in press).

Integrating out the observation error parameter. We have found that it is not practical to estimate both the observation precision parameter ψ simultaneously with the states and other model parameters (because of the strong influence of ψ on the likelihood and hence particle weights for a given set of state values). Instead, we integrate ψ out of the model, and estimate the marginal posterior of this parameter conditional on estimates of the states and other model parameters (Newman *et al.* in press). Given a gamma prior on ψ and a normal observation model, ψ has a gamma posterior distribution. The resulting likelihood weights in the integrated model are then based on the t -distribution.

Initial rejection control. The aim of this procedure is to weed out at an early stage sets of parameter and state combinations that are simulated from the prior but clearly have very low density in the posterior, so that computer time can be focussed on areas of parameter and state space that have higher posterior density. We simulated sets of 1,000,000 particles from the prior distributions, projected them forwards from 1984 to 1985 and calculated likelihood weights based on the 1985 data. We then applied rejection control, an algorithm that probabilistically removes particles with low weight (Liu 2001), using the mean of the particles weights as the rejection control criterion. This resulted in about a quarter to a tenth of the particles being retained (depending on the model and assumptions about observation error). We repeated this process until we had at least 1,000,000 particles surviving the initial rejection control stage.

Auxiliary particle filter (Liu and West 2001). With this procedure, we projected forward one time step at a time, starting in 1985, initially deterministically. We then resampled the particles using the deterministic weights – i.e., according to the expected pup production in the next time period – thereby producing a set of “promising” particles. The improvement to the algorithm of Thomas and Harwood (2007) came at this stage: instead of resampling with

probability proportional to the weights, we instead used probability proportional to the weights to the power of 0.25. This “tempered resampling” means that the particles become less focussed on the current and past data, and retain more diversity to better cope with future data points that may not match the current parameter values. This helps in the current dataset because later data points are much more strongly indicative of low carrying capacity values (relative to the prior) than the early data points.

Resampled copies of the same ancestor particle will have the same parameter values, so to maintain parameter diversity we used kernel smoothing to jitter the parameter values (see Liu and West 2001 for details). This can cause bias (Newman *et al.* in press), so we kept the amount of kernel smoothing to a minimum, using a discount value of 0.99997 (a value of 1.0 results in no jittering at all). Note that this is considerably less than the value used in previous reports (and in Newman *et al.* in press) of 0.997. After kernel smoothing, particles were then projected forward stochastically to the next time period, and weights were adjusted to take account of the initial resampling.

Final rejection control. At the last time period, rejection control was used to reduce the number of particles that must be stored. The rejection control criterion was the mean of the particle weights. This reduced the number of particles stored per run from 1,000,000 to around 700,000.

Multiple runs. The above procedures generated samples based on 1,000,000 particles (although fewer were stored after the final rejection control). However, even this many samples gave a very imprecise estimate of the posterior distributions of interest for all models. Hence, many multiple runs (up to 225) were used to reduce Monte Carlo error to acceptable levels. To reduce the resulting outputs down to a manageable level for post-processing (i.e., calculating posterior distributions on quantities of interest), it was necessary to apply further rejection control, this time using a rejection control criterion of the 99.999th percentile of the particle weights from all of the multiple runs for a particular model.

Model outputs and comparison

One metric of the degree of Monte Carlo error in the results is the number of unique ancestral

particles in our final sample. Thomas and Harwood (2007) set a target of 1,000 or more unique particles for reliable estimation of parameter and state means. However, this does not account for some of these particles having low weight and some high weight. We therefore also calculated the effective sample size (Liu 2001) of unique particles, computed as:

$$ESS_u = \frac{U}{1 + [CV(w_u)]^2}$$

where U is the number of unique particles and CV(w_u) is the coefficient of variation of the sum for each unique particle of the weights of particles with that ancestor.

To compare the models, we calculated the mean posterior Akaike Information Criterion, including the small sample correction, (AIC_c) using the same method as Thomas and Harwood (2006, 2007).

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 measurement error parameter by fitting the data to the DDS model alone (this being the model with most data support in previous briefing papers). We then took the estimated posterior mean and fit both models using this fixed value. We present model selection statistics for these two models using the fixed observation error value.

For all models, we also present posterior estimates of the model parameters and estimated pup production from 1984-2007. The models additionally estimate adult female numbers, but do not include adult males. 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 AIC_c weights (Burnham and Anderson 2001). We comment on the utility of this procedure in the Discussion. Note that this implicitly assumes that *a priori* all models have equal weight.

Results

Unique ancestral particle numbers

Using the revised algorithm we achieved a considerably higher retention of ancestral particles than that of Thomas and Harwood (2007), well over their target of 1,000 (Table 2). Effective sample sizes of unique particles was between 60 and 600; further runs are required to determine what level of Monte-Carlo variation this represents but we anticipate it will be low. One indicator of this is that the histograms of posterior parameter estimates that follow show little evidence of the multi-modality (“roughness”) associated with low sample size in past reports.

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
<i>ψ</i> estimated				
DDS	170	9.6	55.2	410.7
<i>ψ</i> fixed				
DDS	150	7.6	18.5	339.6
DDF	150	10.6	29.6	574.8
EDDS	150	11.4	9.0	114.7
EDDF	150	6.9	4.5	59.0
EDDSNM	225	24.4	33.5	445.0
EDDFNM	225	19.1	12.0	203.9

Estimate of observation precision parameter

Posterior estimates of both states and parameters from the DDS model run where *ψ* is estimated are shown in Figure 1. The estimates of pup production (Figure 1a) show clear, systematic lack of fit in all regions, particularly the Inner and Outer Hebrides where they 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, while the rapid growth in North Sea pup production is under-estimated.

Histograms of marginal parameter estimates (Figure 1b) indicate that the posterior estimates are almost identical to the priors for $\phi_{p,max}$ and α , indicating that essentially nothing has been learnt from the data about these parameters. In contrast, posteriors for the other parameters are somewhat modified relative to the priors. The estimated posterior mean of *ψ* is 89.5, and we

used this value in the two model runs reported in the next sub-section.

As an aside, posterior mean observation CV can easily be estimated, as the weighted average of the CV for each particle:

$$CV\hat{V} = \frac{\sum_{k=1}^{K^*} w^{[k]} \left(1/\sqrt{\psi^{[k]}}\right)}{\sum_{k=1}^{K^*} w^{[k]}}$$

where $w^{[k]}$ is the weight associated with particle k , $\psi^{[k]}$ is the observation precision parameter for that particle, and K^* is the total number of particles. Using this method, the computed estimate of CV is 0.11 (corresponding 95% credibility interval 0.08 - 0.13).

Comparison of models for density dependence and movement

Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the six models, run with ψ fixed at 89.5, are shown in Figure 2.

Unsurprisingly, the DDS model estimates (Figure 2a) are almost identical to those from the analysis where ψ was estimated (Figure 1a). The DDF model estimates (Figure 2b) are also similar, although the estimates for Outer Hebrides show some discontinuity for the period for 1984-1989 – likely a result of an estimated non-stable starting age structure.

Estimates of pup production from the EDSS and EDDF models (Figures 2c and 2d) show clear improvements to the fit, better reflecting the strong recent increases in the North Sea and the levelling off in counts in the Inner and Outer Hebrides. The recent levelling off in the Orkney is, however, not reflected in the fits. Qualitatively, the EDSS model appears to be a slightly closer fit to the data, especially in the initial time periods in the Outer Hebrides. Parameter estimates for fecundity are again nearly identical to the prior in both models (Figures 3c and 3d), as is pup survival for the EDDF model. Estimated adult survival is low in both models (0.92 and 0.91). The posterior mean estimate of the extended density dependence parameter, ρ , is higher for the EDSS model than the EDDF model (6.4 vs 3.7), although both have high variance; carrying capacities are estimated to be slightly higher under the EDSS model.

Estimates from the no movement models (EDDSNM and EDDFNM; Figures 2e and 2f) are similar to the extended density dependence models with movement for North Sea and Orkney, but for Inner and Outer Hebrides (particularly the latter), pup production is estimated to have declined slightly in recent years. Parameter estimates (Figures 3e and 3f) are similar to those from the EDSS and EDDF models.

According to the AIC_c statistics (Table 3), the models with no movement are strongly favoured over those with movement. Note that the mean posterior negative log-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.

Table 3. Mean posterior negative log-likelihood, AIC_c and Akaike weights for models with fixed observation precision of 89.5 fit to data from 1984-2007.

Model	-LnL	AIC _c	ΔAIC _c	Akaike (AIC _c) weight
DDS	750.37	1525.88	20.98	0.00
DDF	747.57	1520.29	15.39	0.00
EDDS	746.71	1521.18	16.29	0.00
EDDF	749.39	1526.54	21.65	0.00
EDDSNM	742.40	1504.90	0.00	0.65
EDDFNM	743.02	1506.13	1.23	0.35

Estimates of total population size

Estimated size of the 2007 adult population under each model are shown in Table 4; estimates for all other years are given in the Appendix.

Estimates from the DDS model are approximately 2.5 times less than those from the DDF model, and there is no overlap between the 94% posterior credibility intervals. Estimates from the EDSS model are higher than the DDS; those from the EDDF model are lower than the DDF model, making the results from the two extended density dependent models rather closer. The EDSSNM model estimates are closer to those of the DDS model – they are lower than the EDSS model because adult numbers are estimated to have declined in the Inner and Outer Hebrides since the 1990s (Appendix). The EDDFNM model estimates are between those of the DDF and EDDF models. Estimates from the

EDDSNM model are about half those from the EDDFNM model, and there is no overlap between posterior 95% credibility intervals. These two models have nearly all the posterior AICc weight (Table 3), and since the support for them is not too different, the posterior distribution of population size averaging across models is distinctly bimodal (Figure 4).

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. In previous reports, we used the *ad hoc* target of 1000 unique ancestral particles; with our adjusted fitting algorithm we far exceeded this target and on that basis expect the Monte Carlo variation to be low. Nevertheless, the effective sample size of unique particles (ESS_u) is low for some models, particularly the EDDF model, so we cannot be sure that statistics such as posterior AICc, which we have found to be particularly sensitive to small sample sizes of particles, are accurate. Further investigation of this is needed (e.g., by repeat runs as performed by Newman *et al.* (in press)).

A second aspect of reliability is bias induced by the fitting algorithm. The kernel smoothing of parameters that is employed within the auxiliary particle filter preserves the first two moments of the parameter distributions, but does not preserve the relationship between parameters and states. Using simulated data and comparisons with Markov chain Monte Carlo estimates, Newman *et al.* (in press) found that using a discount parameter of 0.997, led to negligible bias in the marginal posterior parameter and state estimates. However, a preliminary study using the 1984-2007 data and comparing state estimates for the DDS model with and without kernel smoothing (Thomas, unpublished) showed some bias in state estimates, particularly in the early part of the time series, resulting in non-negligible bias in model selection criterion estimates. In this report we used a considerably more conservative discount parameter of 0.99997. We anticipate that any remaining bias is very small, but this again requires further investigation.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2007 breeding season, derived from models fit to data from 1984-2007. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	DDF
North Sea	14.1 (11.2 19.0)	32.4 (23.1 46.2)
Inner Hebrides	9.2 (7.6 11.6)	25.5 (16.7 39.1)
Outer Hebrides	32.9 (25.9 42.3)	100.2 (62.4 160.2)
Orkney	57.4 (45.3 76.2)	123.4 (88.9 172.8)
Total	113.6 (90.0 149.1)	281.6 (191.2 418.3)
	EDDS	EDDF
North Sea	17.7 (10.7 26.5)	25.1 (19.8 32.5)
Inner Hebrides	9.5 (6.6 13.5)	16.6 (12.5 21.6)
Outer Hebrides	36.3 (24.7 50.5)	61.8 (45.8 80.0)
Orkney	73.1 (43.4 98.6)	92.5 (73.5 117.5)
Total	136.6 (85.4 189.1)	196.0 (151.6 251.6)
	EDDSNM	EDDFNM
North Sea	17.1 (10.6 25.9)	27.2 (20.7 38.2)
Inner Hebrides	8.3 (6.5 10.5)	21.4 (16.5 32.1)
Outer Hebrides	31.3 (24.0 39.1)	88.1 (67.0 143.0)
Orkney	60.9 (40.9 93.5)	103.0 (79.5 142.9)
Total	117.6 (89.1 168.9)	239.7 (188.8 356.2)
	Model averaged	
North Sea	20.5 (11.1 33.6)	
Inner Hebrides	12.9 (6.5 27.2)	
Outer Hebrides	51.2 (23.8 11.5)	
Orkney	75.4 (40.4 130.0)	
Total	160.1 (84.5 304.5)	

Comparison with previous estimates

The estimates of total population size are somewhat different from those from last year, comparing the same years and models. For

example, the 2006 estimate from Thomas and Harwood (2007) under the DDS model was 115,700 (95%CI 90,400-154,400), compared with the estimate for 2006 in the current report (Appendix) of 111,000 (88,300-144,700). The previous 2006 estimate for the DDF model was 248,000 (190,100-377,700), compared with new estimate of 270,400 (191,200-418,300). The change may be partially caused by the small increase in estimated observation error, or by the additional year of pup production estimates, but is almost certainly largely caused by the decreased bias due to less kernel smoothing being used in the fitting algorithm this year.

The DDS and DDF models were those best supported in last year's analysis; a no-movement model had been previously tried (Thomas and Harwood 2003) and found to be poorly supported by the data. Our new algorithm should lead to more accurate model selection, and it shows considerable support for models that do not include movement of recruiting females between regions. Estimates of total population size from the EDDSNM model are very similar to those from the DDS model reported last year (e.g., the 2006 estimates from EDDSNM are 116,300 with 95% CI 82,100-168,900); those from the EDDFNM model are a small amount lower than from the DDF estimates (2006 estimates from EDDFNM are 231,100 with 95%CI 177,700-342,100). Hence changing from reporting total population size estimates based on DDS and DDF to those based on EDDSNM and EDDFNM will not have a great effect on the reported "headline" values.

Multi-model inference

Incorporating model uncertainty is often recommended when there are multiple competing models that are biologically reasonable but give different results (e.g., Burnham and Anderson 2001). In this case, the multi-model confidence intervals usefully reflects our uncertainty about whether the EDDSNM or EDDFNM models are more accurate descriptions of the species' biology. However, the model averaged posterior mean estimates seem less useful: being between the EDDSNM and EDDFNM estimates, they are all in regions of low posterior density (Figure 4) and so have less support than any of the single model estimates. One potential course of action for summarizing the estimates in advice to non-specialists would be to report the posterior mean EDDSNM and EDDFNM estimates, together

with their AICc weights (which could be referred to as "model weights"), and the joint confidence interval.

Future work

Work aimed at further testing and improving the fitting algorithm is ongoing, as is work, in collaboration with others at SMRU, to improve the prior distributions on model parameters based on intensive mark-recapture studies of seals at the Isle of May and North Rhona. Even though the models used in this report fit the data much better than those employed in previous years, there are still some systematic departures of the estimated pup production, and alternative biological models will be investigated in an attempt to obtain better fits. One avenue of research will be to allow random variation in demographic parameters between years. In addition, we will investigate the use of pup production estimates from the period before 1984 to generate prior distributions for the initial population states. Although the EDDSNM and EDDFNM models provide much better fits to recent pup production estimates for most regions, they do not capture the recent changes in pup production in Orkney. This may be because of the large number of individual colonies in Orkney, many of which have very different growth trajectories. We will therefore investigate the development of a separate, spatially-structured model for this region.

Nevertheless, by far the biggest source of uncertainty comes from which is the appropriate demographic parameter to model density dependence in. We have previously demonstrated that a single additional estimate of total population size could resolve much of this uncertainty (Thomas and Harwood 2005, Matthiopoulos *et al.* 2006), and we hope to obtain such an estimate in the foreseeable future.

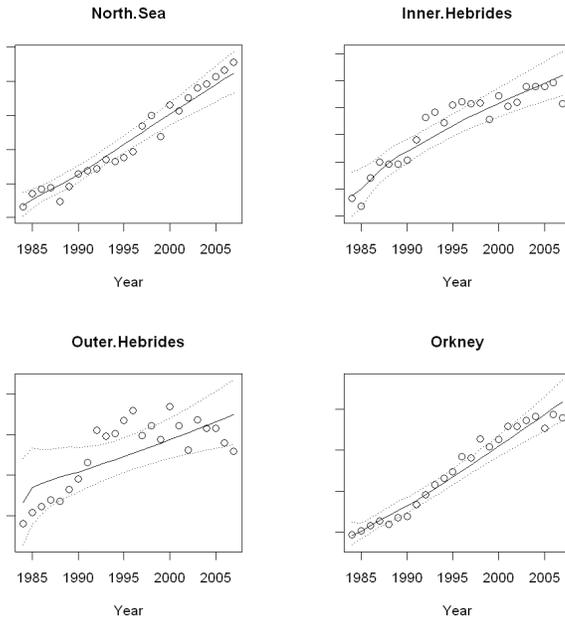
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Figure 1. Posterior estimates from a DDS model of grey seal population dynamics where the observation precision parameter ψ is estimated, fit to pup production estimates from 1984-2007.

(a) Estimates of true pup production (solid lines), together with 95% credibility interval (dotted lines) and observed pup production (circles).



(b) Parameter estimates (histograms) and priors (solid lines). 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.

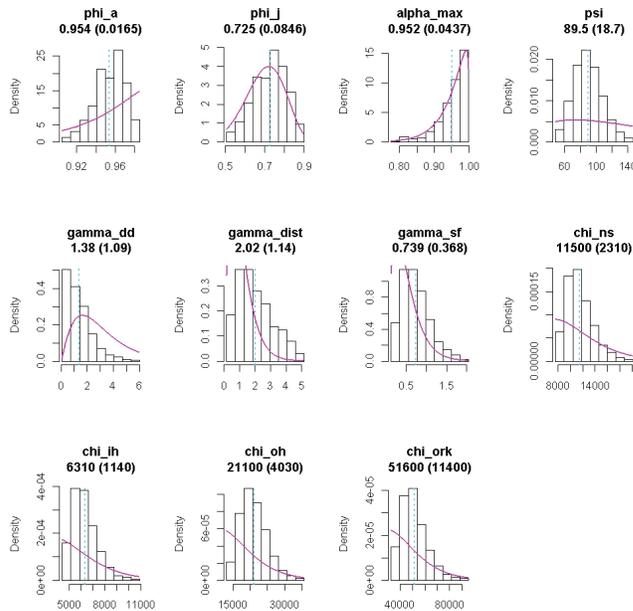
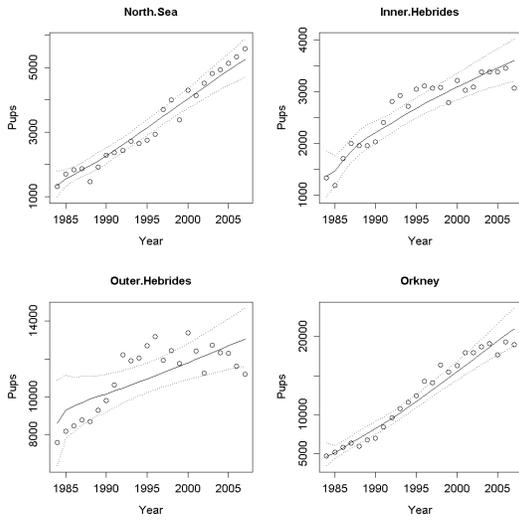
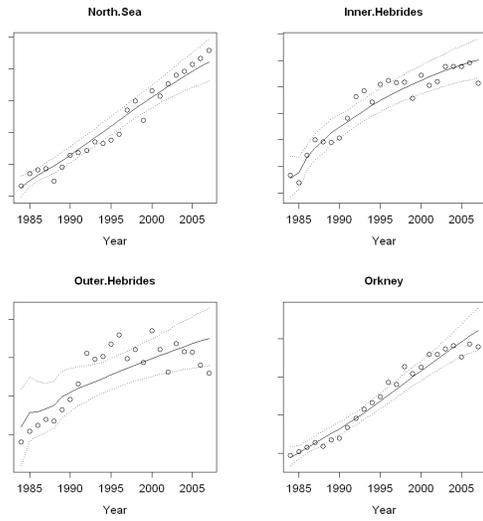


Figure 2. Estimates of true pup production from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

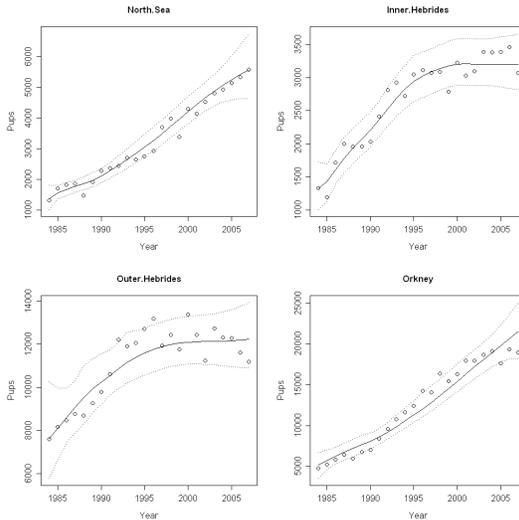
(a) Density dependent survival (DDS)



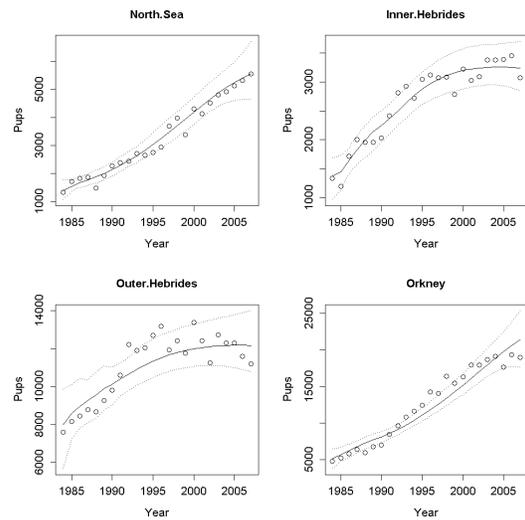
(b) Density dependent fecundity (DDF)



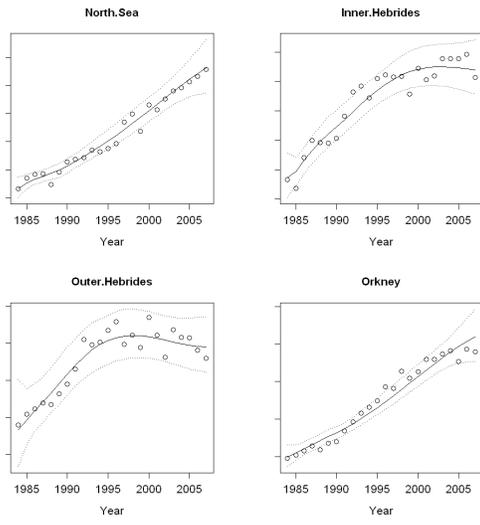
(c) Extended density dependent survival (EDDS)



(d) Extended density dependent fecundity (EDDF)



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



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

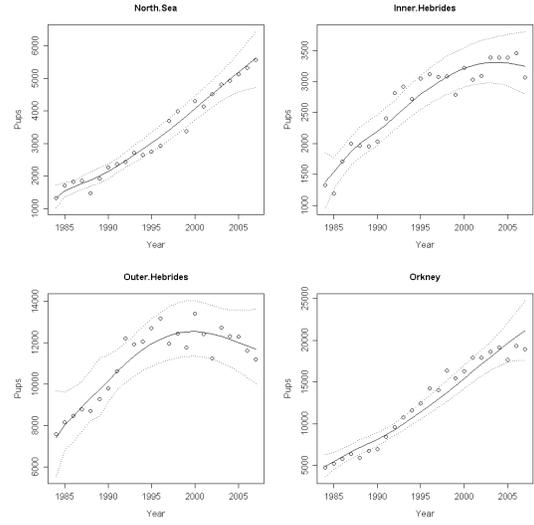
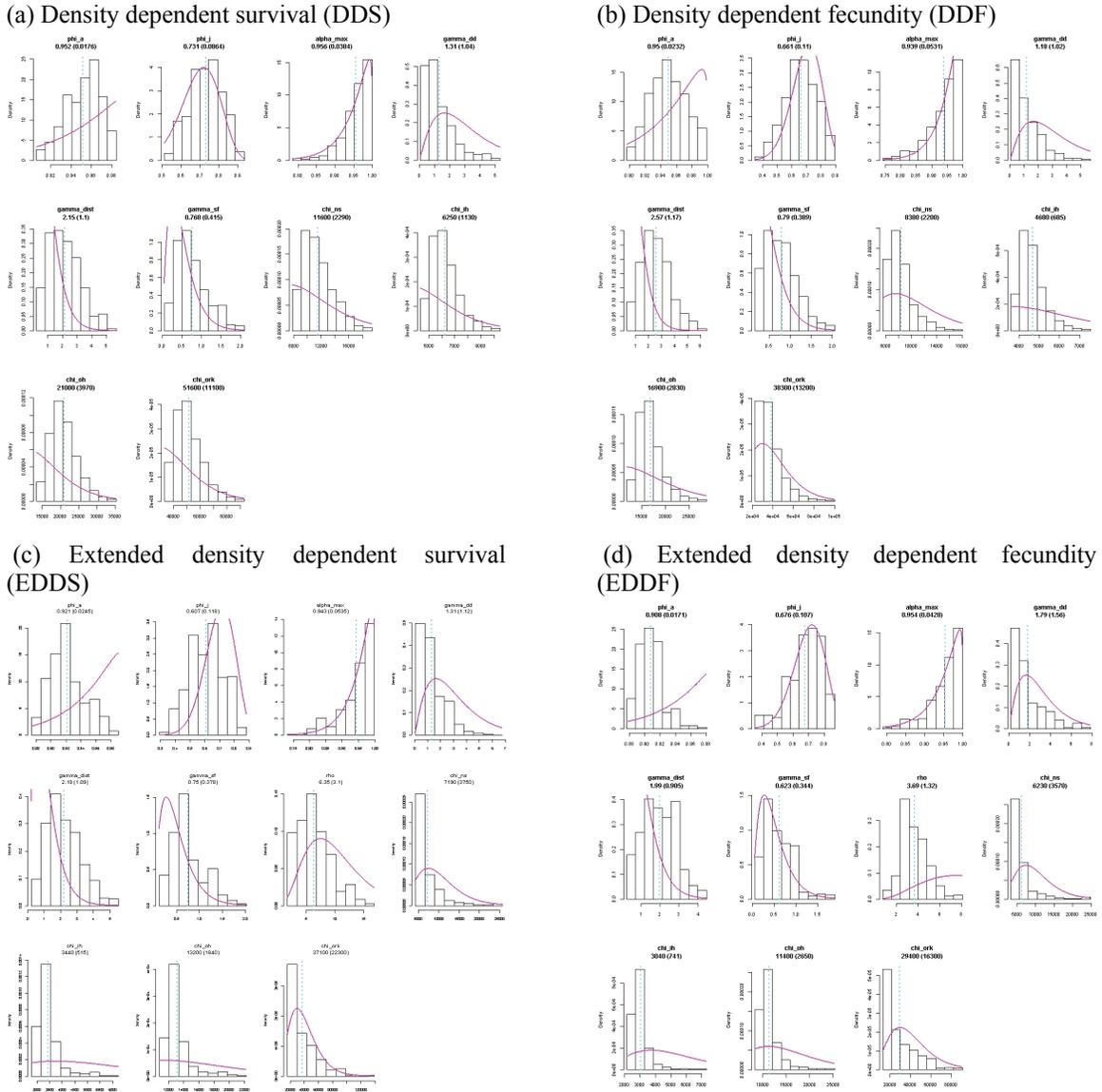
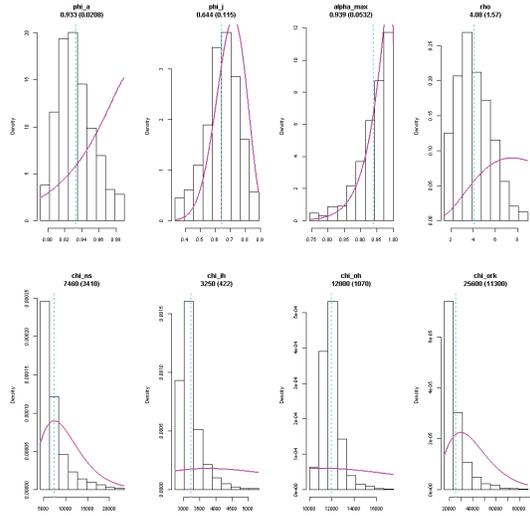


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from six models of grey seal population dynamics where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. The vertical line shows the posterior mean, its value is given in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



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



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

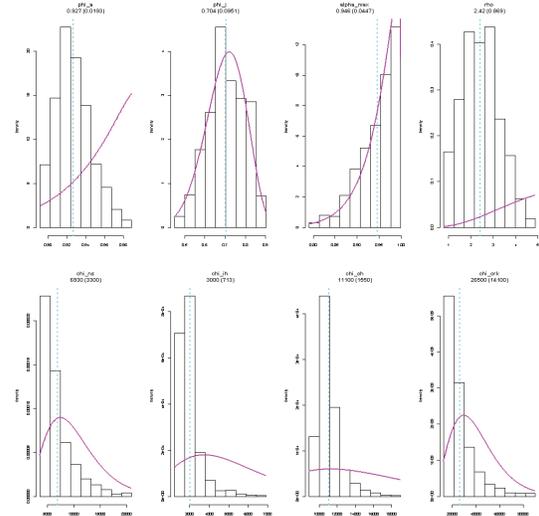
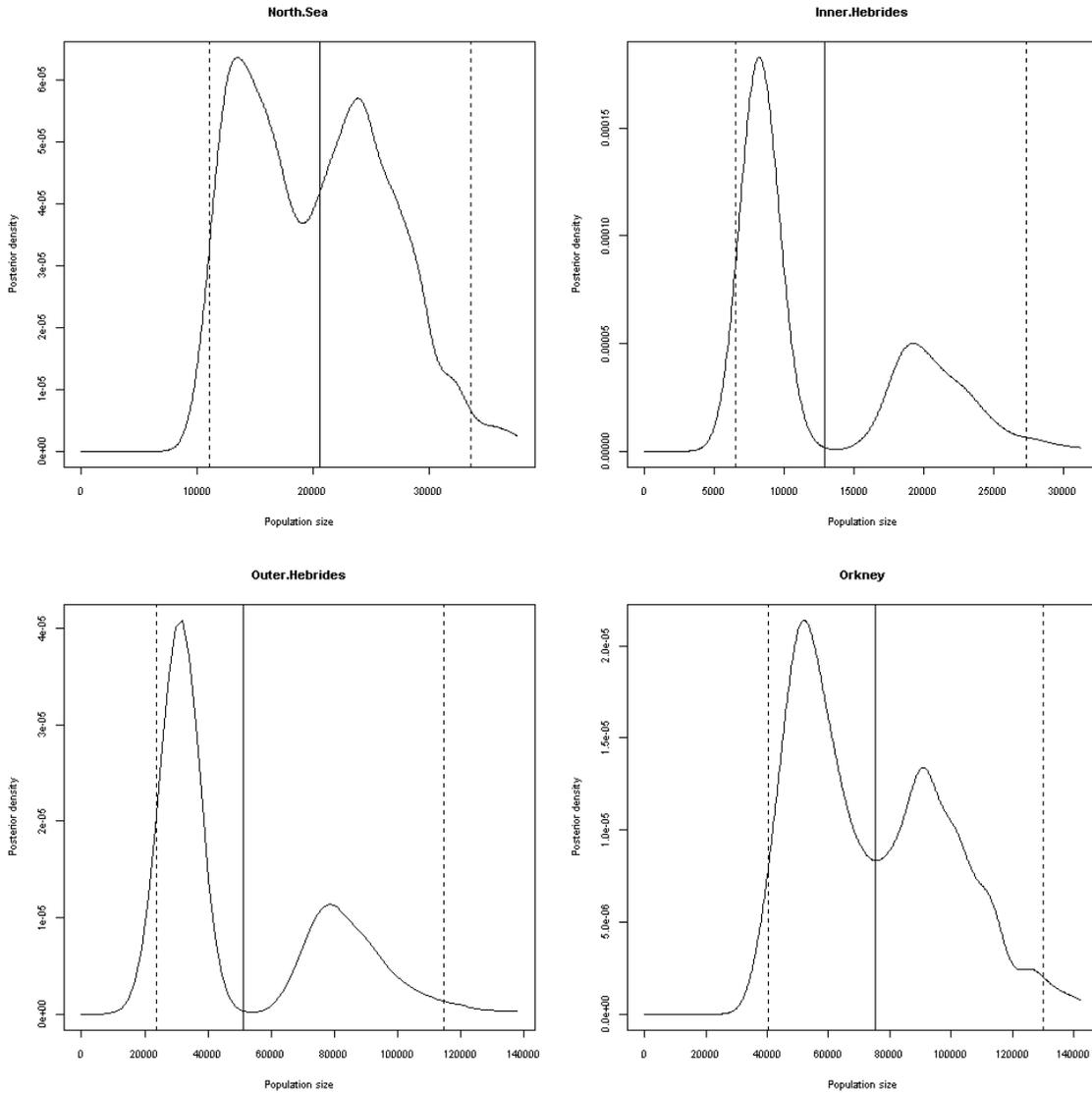


Figure 4. Posterior density of total population size at the beginning of the 2007 breeding season, combining the models. The two peaks in each plot represent the posterior modes of the EDDSNM and EDDFNM models (right and left peaks, respectively); the other models had almost zero support. Solid vertical 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	Orkneys	Total
1984	4.5 (3.6 5.6)	4.5 (3.5 5.9)	25.4 (19.9 34)	16.6 (13.4 20.8)	51.1 (40.4 66.3)
1985	4.9 (4 6)	4.8 (3.8 6.2)	25.5 (20.1 33.4)	18 (14.8 22.2)	53.3 (42.8 67.9)
1986	5.3 (4.4 6.6)	5.1 (4.1 6.5)	25.7 (20.4 33.3)	19.6 (16.2 23.8)	55.8 (45.2 70.3)
1987	5.8 (4.8 7.1)	5.4 (4.4 6.8)	25.9 (20.8 33.3)	21.2 (17.8 26.1)	58.4 (47.8 73.3)
1988	6.2 (5.2 7.6)	5.7 (4.6 7.1)	26.2 (21.1 33.4)	22.9 (19.2 28.1)	61 (50.2 76.3)
1989	6.6 (5.6 8.1)	6 (4.8 7.5)	26.5 (21.4 33.8)	24.6 (20.7 30.1)	63.7 (52.5 79.4)
1990	7.1 (5.9 8.6)	6.2 (5 7.8)	26.8 (21.8 34.1)	26.3 (22.2 32.3)	66.4 (54.9 82.8)
1991	7.5 (6.3 9.2)	6.4 (5.2 8.1)	27.1 (22.1 34.4)	28.1 (23.7 34.5)	69.1 (57.3 86.2)
1992	7.9 (6.6 9.7)	6.6 (5.4 8.4)	27.4 (22.4 34.8)	29.9 (25.2 36.8)	71.9 (59.6 89.7)
1993	8.4 (7 10.3)	6.8 (5.6 8.6)	27.8 (22.7 35.2)	31.7 (26.7 39.1)	74.7 (61.9 93.2)
1994	8.8 (7.3 10.8)	7 (5.8 8.9)	28.1 (22.9 35.7)	33.5 (28.2 41.5)	77.5 (64.2 96.9)
1995	9.2 (7.7 11.4)	7.2 (5.9 9.1)	28.5 (23.2 36)	35.4 (29.6 43.9)	80.3 (66.4 100.4)
1996	9.7 (8 12)	7.4 (6.1 9.3)	28.8 (23.4 36.3)	37.3 (31 46.4)	83.2 (68.6 104.1)
1997	10.1 (8.3 12.6)	7.6 (6.2 9.6)	29.2 (23.7 36.7)	39.1 (32.5 48.9)	86 (70.7 107.9)
1998	10.5 (8.6 13.3)	7.8 (6.4 9.8)	29.6 (23.9 37.3)	41 (33.9 51.4)	88.9 (72.8 111.8)
1999	10.9 (9 13.9)	8 (6.5 10)	29.9 (24.2 37.9)	42.9 (35.2 54)	91.7 (74.9 115.8)
2000	11.3 (9.3 14.6)	8.1 (6.7 10.2)	30.3 (24.4 38.5)	44.7 (36.6 56.6)	94.5 (76.9 119.8)
2001	11.8 (9.6 15.2)	8.3 (6.8 10.4)	30.7 (24.7 39.1)	46.6 (37.9 59.2)	97.3 (78.9 123.9)
2002	12.2 (9.8 15.9)	8.5 (7 10.6)	31.1 (24.9 39.7)	48.4 (39.2 61.8)	100.1 (80.9 128)
2003	12.6 (10.1 16.5)	8.6 (7.1 10.8)	31.4 (25.1 40.2)	50.3 (40.5 64.5)	102.9 (82.8 132)
2004	12.9 (10.4 17.2)	8.8 (7.2 11)	31.8 (25.3 40.7)	52.1 (41.8 67.3)	105.6 (84.7 136.2)
2005	13.3 (10.7 17.8)	8.9 (7.3 11.2)	32.2 (25.5 41.2)	53.9 (43 70.2)	108.3 (86.5 140.4)
2006	13.7 (10.9 18.4)	9.1 (7.5 11.4)	32.6 (25.7 41.8)	55.7 (44.2 73.2)	111 (88.3 144.7)
2007	14.1 (11.2 19)	9.2 (7.6 11.6)	32.9 (25.9 42.3)	57.4 (45.3 76.2)	113.6 (90 149.1)

Density dependent fecundity (DDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.4 7.2)	6.3 (4.3 8.5)	53.4 (35.8 104)	19.5 (15 24.9)	84.8 (59.5 144.6)
1985	6.2 (5 7.8)	7.1 (5.3 9.1)	54.5 (37.3 105.5)	21.5 (17 26.9)	89.4 (64.7 149.3)
1986	6.9 (5.6 8.6)	7.9 (6.1 9.9)	56.1 (38.9 106.9)	23.8 (19.2 29.4)	94.7 (69.9 154.9)
1987	7.7 (6.3 9.5)	8.8 (6.9 11)	57.6 (40.3 108.8)	26.3 (21.3 32.4)	100.4 (74.8 161.7)
1988	8.5 (6.9 10.5)	9.7 (7.6 12.2)	59.2 (41.6 110.5)	29.1 (23.6 35.5)	106.6 (79.8 168.8)
1989	9.4 (7.6 11.7)	10.5 (8.3 13.3)	61 (42.8 111.8)	32.1 (25.9 39.4)	113 (84.7 176.2)
1990	10.3 (8.2 12.9)	11.4 (9 14.7)	62.8 (44.1 112.3)	35.4 (28.4 43.8)	120 (89.7 183.6)
1991	11.3 (8.9 14.2)	12.3 (9.6 15.9)	64.8 (45.2 112.2)	38.9 (31.1 48.6)	127.2 (94.8 190.9)
1992	12.3 (9.7 15.7)	13.2 (10.1 17.2)	66.8 (46.4 114.6)	42.6 (33.8 53.7)	134.8 (99.9 201.1)
1993	13.4 (10.4 17.3)	14.1 (10.7 18.3)	68.8 (47.4 115)	46.5 (36.6 58.9)	142.7 (105.1 209.6)
1994	14.5 (11.1 19)	14.9 (11.3 19.5)	70.8 (48.5 115.7)	50.7 (39.6 64.8)	150.9 (110.5 219)
1995	15.7 (12 20.7)	15.8 (11.8 20.8)	72.9 (49.6 118.6)	55.1 (42.7 71.1)	159.4 (116 231.2)
1996	16.9 (12.8 22.6)	16.6 (12.3 22.2)	75 (50.7 122.1)	59.7 (45.8 77.9)	168.3 (121.6 244.6)
1997	18.1 (13.6 24.5)	17.5 (12.7 23.6)	77.2 (51.7 125.8)	64.6 (49.2 85.1)	177.4 (127.3 259)
1998	19.4 (14.5 26.4)	18.3 (13.2 25)	79.4 (52.8 129.8)	69.7 (52.6 92.4)	186.9 (133.1 273.6)
1999	20.8 (15.4 28.5)	19.1 (13.6 26.5)	81.6 (53.8 132.5)	75 (56.2 100.5)	196.6 (139.1 287.9)
2000	22.2 (16.4 30.5)	20 (14 28)	83.9 (54.8 135)	80.5 (59.9 109)	206.5 (145.1 302.5)
2001	23.6 (17.3 32.6)	20.8 (14.4 29.5)	86.2 (55.8 138)	86.2 (63.6 117.5)	216.7 (151.2 317.8)
2002	25 (18.2 34.9)	21.6 (14.8 31.1)	88.5 (56.9 140.1)	92.1 (67.6 126.3)	227.1 (157.5 332.3)
2003	26.4 (19.2 37.1)	22.4 (15.2 32.6)	90.8 (57.9 142.1)	98.1 (71.6 135.1)	237.7 (164 347)
2004	27.9 (20.2 39.4)	23.2 (15.6 34.2)	93.1 (59 145.2)	104.2 (75.7 144)	248.5 (170.6 362.9)
2005	29.4 (21.2 41.6)	24 (16 35.8)	95.5 (60.2 149.7)	110.5 (80 153.2)	259.4 (177.4 380.4)
2006	30.9 (22.1 43.9)	24.8 (16.4 37.5)	97.9 (61.3 155.1)	116.9 (84.4 162.8)	270.4 (184.2 399.3)
2007	32.4 (23.1 46.2)	25.5 (16.7 39.1)	100.2 (62.4 160.2)	123.4 (88.9 172.8)	281.6 (191.2 418.3)

Extended density dependent survival (EDDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.3 (3.7 6.8)	5.3 (4.2 7)	29.2 (20.6 38.9)	21 (13.4 29.3)	60.9 (42 82.1)
1985	5.6 (4.1 6.9)	5.7 (4.5 7.4)	30.2 (21.7 40)	22.1 (14.3 30)	63.6 (44.6 84.3)
1986	6 (4.5 7.3)	6 (4.8 7.7)	31.3 (22.5 40.8)	23.4 (15.6 30.9)	66.7 (47.3 86.7)
1987	6.5 (4.9 7.8)	6.4 (5.1 8.2)	32.4 (22.9 41.4)	24.8 (17 32)	70 (49.8 89.4)
1988	6.9 (5.4 8.2)	6.8 (5.3 8.6)	33.4 (23.3 42.2)	26.4 (18.5 33.7)	73.6 (52.5 92.8)
1989	7.4 (5.9 8.7)	7.3 (5.5 9)	34.2 (23.4 42.7)	28.1 (20.1 35.5)	77 (55 95.9)
1990	7.9 (6.3 9.2)	7.8 (5.7 9.6)	34.8 (23.4 43.2)	29.9 (21.8 37.8)	80.3 (57.2 99.8)
1991	8.4 (6.7 9.8)	8.2 (5.8 10.2)	35.2 (23.4 43.7)	31.8 (23.6 39.7)	83.7 (59.4 103.4)
1992	8.9 (7.2 10.5)	8.6 (5.9 10.7)	35.6 (23.5 44.3)	33.8 (25.3 41.4)	87 (61.8 107)
1993	9.6 (7.6 11.3)	9 (5.9 11.3)	35.8 (23.5 44.9)	35.9 (27.1 43.3)	90.3 (64.1 110.7)
1994	10.2 (7.9 12.2)	9.3 (6 11.8)	36 (23.6 45.3)	38.2 (28.8 45.4)	93.6 (66.4 114.7)
1995	10.9 (8.3 13)	9.4 (6.1 12.1)	36 (23.6 45.8)	40.6 (30.6 47.8)	96.9 (68.6 118.7)
1996	11.6 (8.6 13.9)	9.5 (6.2 12.1)	36.1 (23.7 46.2)	43.1 (32.4 50.5)	100.2 (70.9 122.6)
1997	12.3 (8.9 14.8)	9.5 (6.3 12.1)	36 (23.9 46.5)	45.6 (34 53.7)	103.4 (73 127.1)
1998	13 (9.2 15.8)	9.5 (6.3 12.3)	35.9 (24 46.8)	48.3 (35.6 57.2)	106.7 (75.1 132.1)
1999	13.7 (9.5 16.8)	9.5 (6.4 12.5)	35.8 (24 47.2)	51 (37.1 60.8)	110 (77 137.3)
2000	14.4 (9.7 17.9)	9.4 (6.4 12.6)	35.7 (24.1 47.7)	53.8 (38.5 64.6)	113.3 (78.7 142.8)
2001	15 (9.9 19)	9.4 (6.5 12.8)	35.7 (24.2 48.1)	56.5 (39.8 68.7)	116.6 (80.4 148.5)
2002	15.6 (10.1 20)	9.3 (6.5 12.9)	35.7 (24.3 48.4)	59.3 (41 73)	120 (81.8 154.4)
2003	16.2 (10.2 21.1)	9.3 (6.5 13)	35.8 (24.4 48.9)	62.1 (42 77.7)	123.3 (83.1 160.7)
2004	16.6 (10.4 22.4)	9.4 (6.6 13.2)	35.9 (24.4 49.3)	64.8 (42.9 82.6)	126.7 (84.2 167.5)
2005	17 (10.5 23.7)	9.4 (6.6 13.3)	36 (24.5 49.7)	67.6 (43.4 87.5)	130 (85 174.2)
2006	17.4 (10.6 25.1)	9.4 (6.6 13.4)	36.2 (24.6 50.1)	70.3 (43.7 93)	133.3 (85.5 181.6)
2007	17.7 (10.7 26.5)	9.5 (6.6 13.5)	36.3 (24.7 50.5)	73.1 (43.4 98.6)	136.6 (85.4 189.1)

Extended density dependent fecundity (EDDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.4 6.8)	5.9 (4.1 7.7)	34.1 (26.3 51.9)	22.2 (16.8 27.6)	67.9 (51.7 94)
1985	5.9 (4.6 7)	6.3 (4.8 7.9)	35.4 (27.8 48.9)	23.3 (18.3 28.5)	70.9 (55.5 92.4)
1986	6.4 (5 7.6)	6.7 (5.3 8.1)	36.8 (29.3 48.2)	24.6 (19.8 29.4)	74.4 (59.5 93.4)
1987	6.8 (5.4 8.2)	7.2 (5.8 8.7)	38.3 (31.2 49.2)	26.1 (21 31.1)	78.3 (63.4 97.2)
1988	7.3 (5.7 8.9)	7.7 (6.3 9.2)	39.7 (32.5 49.5)	27.8 (22.7 32.7)	82.5 (67.2 100.3)
1989	7.8 (6.2 9.5)	8.3 (6.8 9.9)	41.2 (33.3 50.5)	29.6 (24.3 34.4)	87 (70.6 104.4)
1990	8.4 (6.6 10.3)	8.9 (7.2 10.7)	42.7 (34.2 51.2)	31.6 (26 36.8)	91.6 (74.1 109)
1991	9 (7 11.1)	9.6 (7.7 11.3)	44.1 (34.8 52.1)	33.7 (27.7 39.5)	96.4 (77.2 114)
1992	9.7 (7.5 11.9)	10.2 (8.2 11.9)	45.5 (35.8 54.2)	35.9 (29.3 42.1)	101.3 (80.8 120.2)
1993	10.4 (8.1 12.8)	10.8 (8.7 12.7)	46.9 (36.7 57.2)	38.3 (31.1 44.9)	106.4 (84.5 127.6)
1994	11.1 (8.6 13.8)	11.4 (9.1 13.4)	48.3 (37.5 59.3)	40.9 (33.3 47.9)	111.8 (88.6 134.5)
1995	12 (9.2 14.9)	12 (9.5 14.2)	49.7 (38.3 61.3)	43.6 (35.7 51.6)	117.3 (92.8 142.1)
1996	12.9 (9.9 16.1)	12.6 (9.8 15)	51 (39.1 63)	46.6 (38 55.4)	123.1 (96.9 149.5)
1997	13.8 (10.6 17.4)	13.2 (10.2 15.8)	52.2 (39.8 64.7)	49.8 (40.5 59.3)	129 (101.2 157.3)
1998	14.9 (11.4 18.7)	13.7 (10.5 16.7)	53.4 (40.5 66.7)	53.2 (43.1 63.9)	135.2 (105.5 166)
1999	15.9 (12.2 20)	14.1 (10.8 17.4)	54.6 (41.1 68.5)	56.9 (45.8 68.6)	141.5 (109.8 174.5)
2000	17 (13 21.3)	14.5 (11 18.1)	55.6 (41.8 70.5)	60.7 (48.7 74.1)	147.9 (114.6 183.9)
2001	18.2 (13.9 22.8)	14.9 (11.3 18.7)	56.6 (42.6 72.3)	64.8 (51.7 80.5)	154.6 (119.5 194.2)
2002	19.4 (14.9 24.4)	15.2 (11.5 19.3)	57.6 (43.3 73.8)	69.1 (54.9 87.2)	161.3 (124.6 204.7)
2003	20.5 (15.8 26.1)	15.6 (11.7 19.8)	58.5 (44 75.3)	73.6 (58.2 93.9)	168.2 (129.8 215)
2004	21.7 (16.8 27.9)	15.8 (11.9 20.2)	59.4 (44.5 76.6)	78.2 (61.8 100.2)	175.1 (135 224.9)
2005	22.9 (17.8 29.6)	16.1 (12.1 20.7)	60.2 (45 77.7)	82.9 (65.5 106.2)	182.1 (140.4 234.2)
2006	24 (18.8 31)	16.3 (12.3 21.1)	61 (45.4 78.9)	87.7 (69.5 111.9)	189 (146 243)
2007	25.1 (19.8 32.5)	16.6 (12.5 21.6)	61.8 (45.8 80)	92.5 (73.5 117.5)	196 (151.6 251.6)

Extended density dependent survival with no movement (EDDSNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.3 (4.1 6.7)	5.6 (4.3 7.1)	26 (20 32.5)	20.3 (14.9 26.8)	57.2 (43.3 73.1)
1985	5.6 (4.5 7.1)	5.9 (4.6 7.4)	27.4 (21.3 34)	21.6 (16.2 27.6)	60.5 (46.6 76.1)
1986	6.1 (4.9 7.6)	6.2 (4.9 7.7)	28.7 (22.1 35.3)	23.1 (17.7 28.9)	64 (49.5 79.5)
1987	6.5 (5.2 8.1)	6.5 (5.1 8.1)	29.9 (22.8 36.9)	24.7 (19.3 30.5)	67.7 (52.5 83.6)
1988	7 (5.7 8.6)	6.9 (5.4 8.5)	30.9 (23.3 38.6)	26.5 (20.9 32.4)	71.4 (55.3 88.2)
1989	7.5 (6.1 9.2)	7.2 (5.6 9)	31.7 (23.6 39.5)	28.4 (22.5 34.6)	74.8 (57.8 92.3)
1990	8 (6.5 9.8)	7.5 (5.7 9.3)	32.2 (23.9 40.5)	30.4 (24.1 36.8)	78.2 (60.2 96.5)
1991	8.5 (6.9 10.5)	7.8 (5.9 9.7)	32.6 (24.1 41.2)	32.5 (25.8 39.2)	81.4 (62.7 100.7)
1992	9.1 (7.3 11.2)	8 (6.1 10)	32.8 (24.2 41.7)	34.6 (27.4 41.6)	84.5 (65 104.6)
1993	9.6 (7.8 11.9)	8.2 (6.2 10.3)	32.9 (24.3 41.9)	36.7 (29.2 44.2)	87.5 (67.4 108.3)
1994	10.2 (8.2 12.6)	8.4 (6.3 10.5)	32.8 (24.4 41.8)	39 (30.8 47)	90.4 (69.7 111.9)
1995	10.8 (8.6 13.3)	8.5 (6.3 10.6)	32.7 (24.4 41.5)	41.2 (32.4 49.9)	93.2 (71.8 115.3)
1996	11.4 (9 14.1)	8.6 (6.4 10.8)	32.4 (24.4 41.1)	43.5 (33.9 53)	95.9 (73.6 118.9)
1997	12.1 (9.3 14.9)	8.6 (6.5 10.8)	32.2 (24.3 40.6)	45.7 (35.3 56)	98.5 (75.4 122.3)
1998	12.7 (9.5 15.7)	8.6 (6.5 10.8)	31.9 (24.3 40.1)	47.9 (36.7 59.1)	101 (77 125.7)
1999	13.3 (9.8 16.6)	8.6 (6.5 10.7)	31.6 (24.2 39.7)	49.9 (37.8 62.5)	103.4 (78.3 129.4)
2000	13.8 (10 17.5)	8.5 (6.5 10.6)	31.4 (24.1 39.3)	51.9 (38.9 65.8)	105.7 (79.6 133.2)
2001	14.4 (10.2 18.4)	8.5 (6.6 10.6)	31.2 (24.1 39.1)	53.7 (39.7 69)	107.8 (80.5 137)
2002	14.9 (10.4 19.4)	8.4 (6.6 10.5)	31.1 (24 38.9)	55.3 (40.3 72.2)	109.7 (81.3 141)
2003	15.4 (10.5 20.5)	8.4 (6.5 10.5)	31.1 (24 38.8)	56.7 (40.7 75.3)	111.6 (81.8 145.1)
2004	15.9 (10.6 21.7)	8.3 (6.5 10.5)	31.1 (24 38.7)	58 (40.9 79.4)	113.3 (82 150.4)
2005	16.3 (10.6 23.1)	8.3 (6.5 10.5)	31.1 (24 38.8)	59.1 (41 83.9)	114.8 (82.1 156.2)
2006	16.7 (10.6 24.5)	8.3 (6.5 10.5)	31.2 (24 38.9)	60 (41 88.6)	116.3 (82.1 162.4)
2007	17.1 (10.6 25.9)	8.3 (6.5 10.5)	31.3 (24 39.1)	60.9 (40.9 93.5)	117.6 (81.9 168.9)

Extended density dependent fecundity with no movement (EDDFNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.6 6.9)	6.4 (5.1 8.6)	35.6 (23.7 93.8)	21.5 (17.1 26.3)	69.1 (50.5 135.6)
1985	6 (5 7.4)	6.8 (5.4 9.1)	37.5 (26.1 95.1)	22.9 (18.5 27.1)	73.2 (54.9 138.7)
1986	6.5 (5.4 8)	7.2 (5.8 9.7)	39.8 (27.9 94.2)	24.5 (19.9 29.2)	78 (59 141.1)
1987	7 (5.9 8.7)	7.7 (6.3 10.4)	42.1 (29.7 92.2)	26.4 (21.7 31.7)	83.3 (63.5 143)
1988	7.6 (6.3 9.4)	8.3 (6.7 11)	44.5 (31.6 90.5)	28.5 (23.4 34.1)	88.9 (68 145)
1989	8.2 (6.8 10.3)	8.9 (7.2 11.8)	47 (33.5 89)	30.8 (25.3 37)	95 (72.9 148.1)
1990	8.8 (7.3 11.2)	9.5 (7.7 12.6)	49.6 (35.7 89)	33.3 (27.2 40.5)	101.2 (77.9 153.4)
1991	9.5 (7.8 12.3)	10.2 (8.2 13.5)	52.3 (38 91.7)	35.8 (29.1 44.3)	107.7 (83.1 161.8)
1992	10.2 (8.3 13.4)	10.9 (8.7 14.3)	55 (40.4 94.7)	38.5 (31.2 47.3)	114.5 (88.6 169.7)
1993	10.9 (8.9 14.6)	11.5 (9.2 15.2)	57.8 (42.6 97.2)	41.4 (33.5 51.6)	121.7 (94.3 178.7)
1994	11.8 (9.5 15.9)	12.3 (9.7 16.3)	60.6 (45 100.1)	44.5 (35.9 56.6)	129.1 (100.1 188.8)
1995	12.6 (10.1 17.3)	13 (10.3 17.4)	63.4 (47.4 103)	47.8 (38.4 61.7)	136.8 (106.2 199.4)
1996	13.6 (10.7 18.8)	13.8 (10.9 18.5)	66.2 (49.8 106.5)	51.3 (41.1 67.1)	144.8 (112.5 210.9)
1997	14.5 (11.4 20.2)	14.5 (11.4 19.6)	68.9 (52.2 110)	55.1 (44 73.1)	153 (119 222.8)
1998	15.6 (12.1 21.8)	15.3 (12 20.7)	71.5 (54.5 113.1)	59 (46.9 79.2)	161.4 (125.6 234.8)
1999	16.7 (12.9 23.5)	16.1 (12.6 21.9)	74 (56.8 115.9)	63.2 (50.1 85.7)	169.9 (132.4 246.9)
2000	17.8 (13.7 25.3)	16.8 (13.2 23.1)	76.4 (58.9 118.8)	67.5 (53.3 92.5)	178.6 (139 259.7)
2001	19 (14.6 27.1)	17.6 (13.8 24.3)	78.6 (60.7 122.5)	72.1 (56.6 99.4)	187.3 (145.6 273.3)
2002	20.3 (15.5 28.9)	18.3 (14.3 25.6)	80.7 (62.4 126.1)	76.9 (60.1 106.2)	196.1 (152.3 286.8)
2003	21.6 (16.4 30.7)	19 (14.9 26.9)	82.5 (63.7 129.9)	81.8 (63.8 113.2)	204.9 (158.7 300.7)
2004	22.9 (17.4 32.6)	19.7 (15.3 28.2)	84.2 (64.8 132.9)	86.9 (67.5 120.3)	213.7 (165.1 313.9)
2005	24.3 (18.5 34.4)	20.3 (15.8 29.5)	85.7 (65.7 136.6)	92.2 (71.4 127.5)	222.5 (171.4 328)
2006	25.7 (19.6 36.3)	20.8 (16.2 30.8)	87 (66.4 139.9)	97.6 (75.5 135)	231.1 (177.7 342.1)
2007	27.2 (20.7 38.2)	21.4 (16.5 32.1)	88.1 (67 143)	103 (79.5 142.9)	239.7 (183.8 356.2)