Assessment of the East Greenland-Iceland fin whale population using a four-area model

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Abstract

The East Greenland-Iceland (EGI) fin whale population is modeled as four subpopulations with movement between the following areas: East Greenland (area 1), West Iceland (area 2), East Iceland (area 3) and the Far East (area 4). The model is sex- and age-structured, and is fitted to CPUE, sightings survey abundance, and mark-recapture data using both maximum likelihood and Bayesian approaches. Movement parameters are not differentiated by sex since the inclusion of sex-specific movement parameters did not improve the AIC. For the base case assessment scenario, best fits to the data were obtained when West Iceland and East Iceland are effectively fully mixed with a low level of interchange with East Greenland and little interchange with the Far East region. For the base case and all sensitivity tests, the overall recruited population is increasing and above 74% (base case 84%) of pre-exploitation abundance (*K*), and subpopulations in all areas are above 68% (base case 78%) of the individual *K* values. MSYR for the recruited population is 0.020 for the base case and 0.014 to 0.036 for the sensitivity tests. Projections for annual catches of 0, 100, and 200 whales taken from West Iceland indicate that only the last would result in abundance decreases compared to current levels. Under catch levels of 200 whales the probability of the total EGI population falling below 60% of pre-exploitation levels within the next 30 years was 5.7%, 7.3% and 11.5% for the 1+, recruited and mature components of the population, although there was a 51% probability of this occurring for the West Iceland mature component.

Introduction

The most recent assessments of the East Greenland-Iceland (EGI) population have assumed that the population is divided into subpopulations inhabiting different areas, with movement between the subpopulations. Subpopulation models are required to explain three sources of information: sharp declines in CPUE in 1901-1915, stable CPUE indices in 1962-1987 and relatively high current abundance estimates for the population as a whole.

Cunningham and Butterworth (2003) fitted a two-subpopulation model (with “inshore” and “offshore” regions) to CPUE and abundance estimates, and estimated that the maximum population growth rate was 0.04 per annum, annual inter-area movement proportions were around 0.02, and that the population was at 0.965 of pre-exploitation levels.

Gunnlaugsson (2003) additionally incorporated mark-recapture data, modeled four subpopulations, and estimated sex-specific movement proportions, showing that an annual catch of 200 whales over the next two decades from West Iceland would be sustainable.

The NAMMCO working group on minke and fin whales (NAMMCO 2003) requested that the modelling work be extended to models with four subpopulations, that catch, CPUE and mark-recapture data be split between the associated areas, and that the results be presented in 2005. The assessment model presented here therefore assumes that the East Greenland-Iceland population of fin whales comprises subpopulations inhabiting four areas: East Greenland (area 1), West Iceland (area 2), East Iceland (area 3) and the Far East (area 4) and that a fixed proportion of whales move out of each area annually into the adjacent area. Eastward movements are denoted by λ parameters and westward movements by μ parameters (Figure 1). The model is sex- and age-structured and is fitted to the CPUE, sightings survey estimates and mark-recapture data.

The model presented here is very similar to that presented to a NAMMCO meeting in October 2005 (Branch and Butterworth 2005). The key new features are:

1. A revised catch series is used, which includes catches in the East Greenland area. Previously catches were only taken from West Iceland and East Iceland. The additional catches required minor revisions to the model structure.
2. The “FprB90” series are now used for the two early CPUE series in 1901-1913.

3. Separate abundance estimates are now used for the individual area for 1988, and these are very slightly corrected from previous estimates.
4. The density-dependence parameter is adjusted so that the maximum sustainable yield (MSY) is obtained when the population is at 60% of pre-exploitation levels.
5. Estimates of the MSY rate (MSYR) are calculated.
6. As a result the model estimates somewhat greater uncertainty in the population, and a slightly higher probability of the population falling below 60% of pre-exploitation levels in the forward projections. However, the key findings do not differ from the previous model results.

Data available

Assumed biological parameter values

Natural mortality (*M*) has been taken to be independent of age and equal to 0.04 yr^{-1} as in previous analyses (e.g., Cunningham and Butterworth 2003). For simplicity, age at recruitment and age at first parturition are assumed to be knife-edge. The age at recruitment is set to 5 yr for males and 4 yr for females (as in Cunningham and Butterworth 2003), and the age at first parturition to 10 yr on the advice of Lockyer (pers. comm.). Ages are modelled to 15, after which numbers accumulate in a 15 yr plus group.

Catch data

The catch series used in previous analyses (Butterworth and Punt 1992, Cunningham and Butterworth 2003) has now been revised for the 1883-1939 period based on data provided by Gunnlaugsson (pers. comm.). Catch data are based on the analyses presented in Sigurjónsson and Gunnlaugsson (2006). The raw catch data are adjusted for struck and lost whales by the following multiplicative factors: 2.0 (1883-1886), 1.5 (1887-1903) and 1.15 (1904-1915). These adjustment factors correspond to those used in Butterworth and Punt (1992) and were based on the reasoning outlined in Gunnlaugsson *et al*. (1989). In the earlier period (1883-1915) not all whales caught were sexed, but of the 1871 catches that were, 970 (52%) were female, and therefore catches in the 1883-1915 period were assumed to be 52% female. The final catch series is given in Table 1 and plotted in Figure 2. Compared to the series used in Butterworth and Punt (1992), the number of fin whales caught in each year increased in some years (by up to 157 in 1932) and decreased in others (by up to 140 in 1930), but the overall total altered only marginally from 22,718 to 22,771 (Figure 3).

A sensitivity test was also conducted using the original catch data. These data were split between West and East Iceland using the proportions in the revised catch series (Table 2). Model results of this sensitivity test were nearly identical to the base case model.

CPUE data.

The late CPUE series 1-4 provide effective-catch-per-time-searching for four vessels over various portions of 1962-87 for West Iceland (Butterworth and Punt 1992). The early CPUE series (5-6) previously used was quite simplistic since it pooled all whale species together and assumed equal effort in each year (Gunnlaugsson *et al*. 1989, p. 271). Earlier CPUE series comprising annual-catch-per-boat (of all species) have now been separated for West Iceland (series 5, 1901-15) and East Iceland (series 6, 1904-13), and adjusted for time spent catching other whale species. The separated early CPUE series were taken from the "FprB90" column in Table 4 of Sigurjónsson and Gunnlaugsson (2006), and are reproduced in Table 3 of this paper.

The variances of the CPUE indices were estimated by quadratically detrending the log-transformed indices. For the late series, the variance-covariance matrix in Butterworth and Punt (1992) was used (Table 4). For the early series the same detrending method was used to obtain values of $\sigma_5 = 0.272$ and $\sigma_6 = 0.366$ (see Appendix for details).

The early CPUE series does not account for the number of days whaled by each vessel. An alternative series is also provided which accounts for total days in the fishery, the catch-per-boat-month series, and this was further adjusted for time spent catching other whale species. Data for this series were obtained from the "FpBM-o2" column in Table 8 of Sigurjónsson and Gunnlaugsson (2006). This alternative series has many missing data points for West Iceland but does provide a complete time series for East Iceland from 1904 to 1913 (Table 5). The data for 1903 are omitted because of a high proportion of humpback whales caught in that year (Gunnlaugsson, pers. comm.). As a sensitivity, the model is run with this alternate series replacing CPUE series 6, and a recalculated $\sigma_6 = 0.219$.

Estimates of abundance

Sightings surveys were re-estimated for the EGI population for various combinations of the four areas in 1988 (a combination of the 1987 and 1989 surveys), 1995 and 2001 (Pike and Gunnlaugsson 2006, recombined in NAMMCO 2006). These updated estimates differ slightly (no more than 6%) from previous total abundance estimates used for the EGI population (Pike *et al*. 2003, Cunningham and Butterworth 2003), and are listed in Table 6. The base case model was fit to areas 1, 2, and 3+4 for the 1988, 1995 and 2001 estimates.

Mark-recapture information

Fin whales were marked between 1965 and 1984 in the East Greenland/Iceland population (Sigurjónsson and Gunnlaugsson 1985, Gunnlaugsson and Sigurjónsson 1989). Marks were placed in East Greenland (99; 9 recaptured), West Iceland (185; 46 recaptured) and East Iceland (9; 0 recaptured). During the period of marking, whaling was conducted only in West Iceland, thus all recaptures were in this area. Small discrepancies in the original sources (Sigurjónsson and Gunnlaugsson 1985, Gunnlaugsson and Sigurjónsson 1989) were resolved by referring to the original data (Gunnlaugsson, pers. comm). Data from the 1989 season were provided by Gunnlaugsson (pers. comm.) and were also used in Gunnlaugsson (2003). Marks were not recorded as placed by sex (for obvious reasons), but recaptures were normally recorded by sex; where this was not the case, the recaptures were divided equally between the sexes. Mark-recapture data are outlined in Table 7 and Table 8.

Methods

The model is sex-structured and age-structured and includes movement between subpopulations in four areas. The detailed model structure is outlined in the Appendix. For the maximum likelihood estimates (MLEs), the estimable parameters of the model are the pre-exploitation recruited abundances (*K*) in each of the four areas, the maximum possible rate of increase (*r*), and the various movement parameters (λ and μ) between the areas. Parameter values are detailed in Table 9. Model minimization to obtain MLEs was conducted using AD Model Builder. Confidence intervals for the parameters were obtained by likelihood profiling, i.e., by finding the values of the parameter in question that result in a total negative log likelihood 1.92 units higher than the MLE.

MLE base case and sensitivity tests

The following cases were run for MLEs (summarized in Table 10):

1. Base case: estimated parameters are $K_1, K_2, K_3, K_4, \lambda_1, \lambda_3,$ and r , but λ_2 is fixed at 0.2, natural mortality at 0.04, the mark loss rate at zero and the mark detection proportion at one. Male and female movement parameters are assumed to be equal.
2. Estimate all movements: male and female movement parameters were estimated separately, and λ_2 is estimated instead of being fixed.
3. Low *M*: a low fixed value (0.02) was used for *M*.
4. High *M*: a high fixed value (0.07) was used for *M*.
5. High mark loss: the mark loss rate was fixed at 0.4 instead of 0.0.
6. Low mark detection: the mark detection proportion was fixed at 0.5 instead of 1.0.
7. Density dependence K_{total}: the density dependence term was proportional to pre-exploitation abundance of all areas combined instead of for each area separately.
8. Alternative CPUE 6: the catch-per-boat-month series replaced CPUE series 6.
9. Fit to total abundance: abundance estimates were not split into areas.
10. Exclude mark-recapture: all mark-recapture data were excluded from the model.

AIC (Akaike's Information Criterion) was used to decide whether estimating additional parameters in the model was warranted. For this criterion the model with the lowest AIC value is considered to best explain the data:

$$AIC = -2\ln L - 2n$$

where *n* is the number of parameters that are estimated.

Bayesian analysis

A Bayesian analysis was conducted assuming uniform priors (ranges in Table 9) for all estimated parameters, except for *M*. In addition to the parameters estimated in the base case MLE run, τ (mark loss proportion) and ξ (mark detection proportion) were also included as estimable parameters. Attempts to additionally include *M* as an estimable parameter resulted in posteriors including a range of values (>0.09) that were unrealistically high given the age distribution for this population, and therefore an informative prior was used for natural mortality: M ~ N(0.04, 0.01^2). When λ_2 was estimated, zero probability was assigned to estimates below the upper bound, so this parameter was kept fixed at the upper bound. The posterior distribution was obtained using a custom-written Markov Chain Monte Carlo (MCMC) algorithm in Visual Basic for Excel. During MCMC runs model evaluations were excluded if westward movement parameters exceeded 0.75 (μ_{max}) since this would have resulted in near-complete emigration from an area. An MCMC chain of 2.4 million (sampling every 2,000, discarding the first 20% of the chain) provided good convergence (autocorrelation < 0.04 for all estimated parameters).

The modeled population was projected 30 years into the future with annual catches of 0, 100 and 200 fin whales. All catches were assumed to be taken from West Iceland (area 2) and to comprise of 54.2% females (the sex ratio in the most recent ten years of catches, 1980-1989).

Results

MLE results

Parameter estimates are displayed in Table 11, estimates of recruited population size and depletion levels in Table 12 and 95% confidence intervals in Table 13. MSYR values reported here are for the recruited population.

Base case: the best estimate of r was 0.132, MSYR was 0.020, and λ_3 was estimated to be 0.0001 at its lower bound (i.e., no movement between East Iceland and Far East). The proportion moving between East Greenland and West Iceland was estimated to be 0.035 per annum. Current depletion levels (ratio of recruited abundance in 2004 to pre-exploitation recruited abundance) for each individual area were >0.78, and 0.84 for all areas combined. The Far East subpopulation was hardly affected by whaling, as follows from the very low proportions estimated to be moving between East Iceland and Far East. The model provided good fits to all of the CPUE series (Figure 4) and to the abundance estimates (Figure 5), but predicted lower number of recaptures than observed for marks placed in East Greenland and West Iceland (Figure 6). Predicted cumulative recaptures from East Iceland were less than one, compared to zero actual recaptures (Figure 6).

Estimate all movements: results differed little from the base case. The negative log likelihood (NLL) decreased by only 0.17 units despite estimating four additional parameters when assuming differential movement proportions by sex, thus the deterioration in the AIC statistic (253.5 vs. 251.9) did not support the estimation of these sex differentiated parameters in the model.

Low M (0.02) and High M (0.07): the total NLL was within five units of the base case NLL. However, r was estimated to be smaller (0.102, MSYR 0.016) in the Low M case, and higher (0.194, MSYR 0.028) in the High M case, and the total population was estimated to be slightly more depleted (0.82) under the High M case.

High mark loss and Low mark detection: these sensitivity cases provided a much worse fit (by 16-31 NLL units) to the mark-recapture data, but were otherwise similar to the base case model.

Density dependence K_{total}: similar to the base case results, although the depletion levels in the individual areas differ somewhat.

Alternative CPUE 6: the population was estimated to be further below K than for the base case (0.69 for both West Iceland and East Iceland) and for the total population (0.75), and r was estimated to be lower (0.089, MSYR 0.014).

Fit to total abundance: pre-exploitation abundance estimates differed greatly from the base case. The greatest population was estimated to be in the Far East (10,700 vs. 2,000 for the base case) and not in East Greenland (300 vs. 6900). Estimated movement proportions were also high (0.029 vs. 0.0001) between East Iceland and Far East and higher between East Greenland and West Iceland (0.058 vs. 0.035). The estimate of r was also much higher (0.24 vs. 0.13) corresponding to MSYR of 0.034. However, depletion levels were estimated to be very similar to those for the base case.

Exclude mark-recapture: movement proportions to East Greenland and the Far East were nearly zero but the estimated value for r doubled to 0.26 (MSYR 0.036) suggesting that a higher rate of increase is possible. Subpopulations and the total population were estimated to be very close (>0.88) to K.

Bayesian results

Credibility intervals (95% posterior intervals) for the estimated parameters were similar to the confidence intervals obtained from likelihood profiles (Table 13). Pre-exploitation recruited abundance was estimated to be greatest in East Greenland and smallest in the Far East, although the greatest uncertainty related to the Far East abundance (Figure 7).

The posterior for λ_1 indicates this to be well defined by the data. However, posterior distributions for several parameters indicated greatest support for values at one of their bounds: λ_3 at zero, the mark detection proportion at one and the mark loss rate at zero (Figure 8). The posterior distribution for *M* was only slightly shifted to the right compared to its informative prior.

West Iceland and East Iceland were estimated to be more depleted areas and the Far East the least depleted (Figure 9). The bulk of the posterior depletion level distributions for the total population were concentrated between 0.6 and 1.0 for the mature, recruited and 1+ components of the population (Figure 9). Population trajectories indicated little change (but considerable uncertainty in terms of absolute level) for the Far East population (Figure 10). However, the West Iceland and East Iceland populations had narrow posterior population trajectory distributions, which indicated that these were depleted severely in the late 1800s and early 1900s, followed by increases until about 1950, then gradual declines to the mid-1980s, and finally increases again after commercial whaling ceased to the present time (Figures 10).

Future projections indicated that the total EGI population would continue increasing under zero catches, increase very slowly under catches of 100 per year (remaining stable in West Iceland), and decline under catches of 200 per year (Figure 11). The probability of the total EGI population falling below 60% of pre-exploitation levels within the next 30 years was 5.7%, 7.3% and 11.5% for catches of 200 per year for the 1+, recruited and mature female components respectively. However, under catch levels of 200 there was a medium probability that the mature female component in area 2 (51%) and area 3 (31%) would fall below 60% of *K* (Table 14).

Discussion

The four area/subpopulation model provided good fits to the early and late CPUE series and the absolute abundance estimates, but predicted lower numbers of mark recaptures from marks originally placed in East Greenland and West Iceland and scarcely match the increasing trend in survey abundance estimates from East Greenland. Model fits were obtained by estimating effectively full mixing between West Iceland and East Iceland, a low level of movement between East Greenland and West Iceland, and essentially no movement between East Iceland and Far East. The Far East area seems needed in the model only to allow a better fit to the sightings estimates for the combined East Iceland and Far East areas.

Because there were more recaptures of marks originally placed in East Greenland and West Iceland than predicted by the model (because abundance estimates were higher than suggested by the mark-recapture data), there is little support for mark loss proportions greater than zero or for mark detection proportions smaller than one.

Under the base case MLE and Bayesian estimation approach, and for all sensitivity tests, the total East Greenland-Iceland population is estimated to be above 74% of pre-exploitation abundance. Populations in individual areas are all above 68% of pre-exploitation levels. The population is estimated to be increasing at present and is predicted to continue increasing under future annual catch levels up to at least 100 fin whales. There is an 11.5% probability that future catches of 200 whales will result in the mature component of the total EGI population falling below 60% of pre-exploitation levels in 30 years.

Appendix: Model equations and specifications

Symbols used

$N_{t,a}^{s,k}$ is the number of whales of sex *s* of age *a* in area *k* at the start of year *t*

$\tilde{N}_t^k$ is the number of age 1+ whales in area *k* at the start of year *t*

$\bar{N}_t^k$ is the sightings abundance estimate for area(s) *k* assumed to be at the start of year *t*

$C_t^{s,k}$ is the number of whales of sex *s* harvested from area *k* in year *t*

$F_t^{s,k}$ is the annual fishing mortality proportion of sex *s* in area *k* in year *t* of recruited whales

K^k is the pre-exploitation equilibrium size of the recruited (past age at recruitment) population in area *k*

D^k is a density dependent function of the recruited population in area *k* (in a sensitivity test this is taken to relate to the entire population)
α is the annual calf production per female at pre-exploitation equilibrium abundance levels
β is the degree of density-dependence in the model
r is a population growth rate parameter that effectively increases birth proportions at low population sizes.
$CPUE_t^{k,i}$ is the *i*th CPUE index for area *k* at the start of year *t*
a_r^s is the age at recruitment to the fishery for sex *s*, assuming knife-edge selectivity
a_m^f is the age at first parturition for females, assuming knife-edge selectivity
X_t^k is the total abundance of recruited individuals of both sexes in area *k* in year *t*
M is the instantaneous natural mortality rate, assumed constant for all ages
n is the age of the plus group, which is identical for both sexes in all areas
λ_1^s is the annual proportion of whales of sex *s* moving from area 1 to area 2
λ_2^s is the annual proportion of whales of sex *s* moving from area 2 to area 3
λ_3^s is the annual proportion of whales of sex *s* moving from area 3 to area 4
μ_1^s is the annual proportion of whales of sex *s* moving from area 2 to area 1
μ_2^s is the annual proportion of whales of sex *s* moving from area 3 to area 2
μ_3^s is the annual proportion of whales of sex *s* moving from area 4 to area 3
$p_t^{s,v}$ is the number of whales of sex *s* marked in area *v* during year *t*
$\underline{P}_t^{s,k,v}$ is the number of whales of sex *s* originally marked in area *v* that are currently in area *k* at the start of year *t* and were *not* marked in the current year
$r_t^{s,k,v}$ is the number of whales of sex *s* originally marked in area *v* that are recaptured in area *k* in year *t*, and that were at large for at least one year
$\tilde{r}_t^{s,v}$ is the number of whales of sex *s* originally marked in area *v* that were recaptured in year *t* in the same year that they were released
τ is a proportion of mark-induced mortality and loss of marks, assumed to be zero for the base case
ξ is the mark detection proportion, assumed to be one for the base case
-ln*L* is the negative log-likelihood component

Subscripts

s is the sex of the whale (either *m* or *f*)
a is the age of the whale (0, 1, …, *n* where *n* is the plus group)
k is the area (1, 2, 3, 4)
t is the year
v is the area in which a mark was originally placed (1, 2 or 3)
i is the CPUE index (1 to 6)

Population dynamics

Dynamic equations for population 1

(Note that the general area superscript *k* is kept for the first two lines that follow as these hold for all areas.)

$$N_{t+1,0}^{s,k} = 0.5\sum_{a=a_m^f}^{n} N_{t,a}^{f,k}\left[\alpha + rD^k(\underset{\sim}{N}_t)\right]$$

$$N_{t+1,a+1}^{s,k} = N_{t,a}^{s,k}e^{-M} \qquad 0 \le a \le a_r^s - 1$$

$$N_{t+1,a+1}^{s,1} = ([1-\lambda_1^s]N_{t,a}^{s,1} + \mu_1^s N_{t,a}^{s,2})e^{-M} \qquad a_r^s \le a \le n-2$$

$$N_{t+1,n}^{s,1} = (N_{t,n-1}^{s,1} + [1-\lambda_1^s]N_{t,n}^{s,1} + \mu_1^s N_{t,n}^{s,2})e^{-M}$$

where

$$D^k(\underset{\sim}{N}_t) = 1 - \left(\frac{\sum\limits_{s=m,f} \sum\limits_{a=a_r^s}^{n} N_{t,a}^{s,k}}{K^k} \right)^{\beta}$$

and β = 1.98 ensures that $MSYL$ = 0.6K (the conventional assumption) when r = 0.148. Note that the value of r was estimated at 0.148 prior to the modifications in this paper. These in turn resulted in a slightly lower estimate of r for the base case, but as MSYL is primarily determined by the value of β the MSYL is still 0.60.

This assumes that density-dependence only operates on the recruited population. Note that for $\underset{\sim}{N} = \underset{\sim}{K},\ D(\underset{\sim}{N}) = 0$. This occurs at pre-exploitation equilibrium (when immigration and emigration numbers each year balance). At this point the female births ($N_{0,0}^{f,k}$) will result in an equilibrium mature female abundance that will produce $N_{0,0}^{f,k}$ female births:

$$N_{0,0}^{f,k} = 0.5\alpha N_{0,0}^{f,k} \left(\frac{e^{-a_m^f M}}{1 - e^{-M}} \right)$$

and hence:

$$\alpha = \frac{2\left(1 - e^{-M}\right)}{e^{-a_m^f M}}$$

By definition the pre-exploitation recruited abundance is given by:

$$K^k = \sum_{s=m,f} \sum_{a=a_r^s}^{n} N_{0,a}^{s,k} = \sum_{s=m,f} \frac{N_{0,0}^{s,k} e^{-a_r^s M}}{1 - e^{-M}}$$

Assuming equal sex ratios at birth, the starting abundance of each age in year 0 is then given by:

$$N_{0,0}^{s,k} = \frac{K^k (1 - e^{-M})}{e^{-a_r^f M} + e^{-a_r^m M}}$$

$$N_{0,a+1}^{s,k} = N_{0,a}^{s,k} e^{-M} \qquad 0 \le a \le n-2$$

$$N_{0,n}^{s,k} = \frac{N_{0,n-1}^{s,k} e^{-M}}{1 - e^{-M}}$$

Movement equations for populations 1,2,3,4

Note that movement is assumed to occur only for recruited whales, and thus the equations for movement are as follows for each area (the equation for area 1 is repeated for comparison):

$$N^{s,1}_{t+1,a+1} = \left[(1-\lambda^s_1)N^{s,1}_{t,a} + \mu^s_1 N^{s,2}_{t,a}\right](1-F^{s,1}_t)e^{-M} \qquad a^s_r \le a \le n-2$$

$$N^{s,1}_{t+1,n} = \left[(1-\lambda^s_1)(N^{s,1}_{t,n-1} + N^{s,1}_{t,n}) + \mu^s_1(N^{s,2}_{t,n-1} + N^{s,2}_{t,n})\right](1-F^{s,1}_t)e^{-M}$$

$$N^{s,2}_{t+1,a+1} = \left[\lambda_1 N^{s,1}_{t,a} + (1-\mu^s_1-\lambda^s_2)N^{s,2}_{t,a} + \mu^s_2 N^{s,3}_{t,a}\right](1-F^{s,2}_t)e^{-M} \qquad a^s_r \le a \le n-2$$

$$N^{s,2}_{t+1,n} = \left[\lambda^s_1(N^{s,1}_{t,n-1} + N^{s,1}_{t,n}) + (1-\mu^s_1-\lambda^s_2)(N^{s,2}_{t,n-1} + N^{s,2}_{t,n}) + \mu^s_2(N^{s,3}_{t,n-1} + N^{s,3}_{t,n})\right](1-F^{s,2}_t)e^{-M}$$

$$N^{s,3}_{t+1,a+1} = \left[\lambda^s_2 N^{s,2}_{t,a} + (1-\mu^s_2-\lambda^s_3)N^{s,3}_{t,a} + \mu^s_3 N^{s,4}_{t,a}\right](1-F^{s,3}_t)e^{-M} \qquad a^s_r \le a \le n-2$$

$$N^{s,3}_{t+1,n} = \left[\lambda^s_2(N^{s,2}_{t,n-1} + N^{s,2}_{t,n}) + (1-\mu^s_2-\lambda^s_3)(N^{s,3}_{t,n-1} + N^{s,3}_{t,n}) + \mu^s_3(N^{s,4}_{t,n-1} + N^{s,4}_{t,n})\right](1-F^{s,3}_t)e^{-M}$$

$$N^{s,4}_{t+1,a+1} = \left[\lambda^s_3 N^{s,3}_{t,a} + (1-\mu^s_3)N^{s,4}_{t,a}\right]e^{-M} \qquad a^s_r \le a \le n-2$$

$$N^{s,4}_{t+1,n} = \left[\lambda^s_3(N^{s,3}_{t,n-1} + N^{s,3}_{t,n}) + (1-\mu^s_3)(N^{s,4}_{t,n-1} + N^{s,4}_{t,n})\right]e^{-M}$$

where:

$$F^{s,1}_t = \frac{C^{s,1}_t}{(1-\lambda^s_1)\sum_{a=a^s_r}^{n} N^{s,1}_{t,a} + \mu^s_1 \sum_{a=a^s_r}^{n} N^{s,2}_{t,a}}$$

$$F^{s,2}_t = \frac{C^{s,2}_t}{\lambda^s_1\sum_{a=a^s_r}^{n} N^{s,1}_{t,a} + (1-\mu^s_1-\lambda^s_2)\sum_{a=a^s_r}^{n} N^{s,2}_{t,a} + \mu^s_2 \sum_{a=a^s_r}^{n} N^{s,3}_{t,a}}$$

$$F^{s,3}_t = \frac{C^{s,3}_t}{\lambda^s_2\sum_{a=a^s_r}^{n} N^{s,2}_{t,a} + (1-\mu^s_2-\lambda^s_3)\sum_{a=a^s_r}^{n} N^{s,3}_{t,a} + \mu^s_3 \sum_{a=a^s_r}^{n} N^{s,4}_{t,a}}$$

Note that no catch was taken from area 4, and thus the fishing proportion term is omitted from the equations for that area. Note further that these equations assume that events occur in the following order each year: i) inter-area movement as a pulse, ii) harvesting as a pulse, and finally iii) natural mortality continuously.

The estimable parameters of the model above, given fixed values of M and n are input, are:

$$K^1, K^2, K^3, K^4, \text{ and } r$$
$$\lambda^s_1, \lambda^s_2, \lambda^s_3, \mu^s_1, \mu^s_2, \text{ and } \mu^s_3$$

Thus there are 17 parameters in total, or 11 parameters if male and female movement rates are assumed to be equal. However, the number of parameters can be reduced because immigration and emigration numbers must balance at pre-exploitation equilibrium, and hence:

$$\lambda^s_1 K^1 = \mu^s_1 K^2 \quad \Rightarrow \quad \mu^s_1 = \lambda^s_1 \frac{K^1}{K^2}$$

$$\lambda^s_2 K^2 = \mu^s_2 K^3 \quad \Rightarrow \quad \mu^s_2 = \lambda^s_2 \frac{K^2}{K^3}$$

$$\lambda^s_3 K^3 = \mu^s_3 K^4 \quad \Rightarrow \quad \mu^s_3 = \lambda^s_3 \frac{K^3}{K^4}$$

so that the number of estimable parameters reduces to 11 or 8 respectively. Note that under certain circumstances (namely when $K_k \gg K_{k+1}$), μ_k will be large resulting in a total emigration proportion exceeding 100%, clearly unrealistic. For this reason an upper bound of $\mu_{\max} = 0.75$ is placed on the westward movement proportions.

Marks and recaptures

Marks are placed in either area 1, 2 or 3 and tracked individually. Recaptures can occur only in area 2 since there was no whaling in the other areas during the mark-recapture period. Individual tracking of marks requires additional subscripts to reflect the area in which they were originally marked.

Assumptions:

1. Marking takes place before migration or harvesting each year.
2. Only recruited whales are marked.
3. Movement takes place before harvesting in each year.
4. Same year recaptures are not included in the likelihood because of inadequate opportunity to mix fully into the population in the area or in other areas.

Note: if data on recoveries further link to the year of marking, then the equations below still follow but with $\underline{P}$, *r*, and $\tilde{r}$ each having a further subscript t' which refers to the year of marking. However, this additional complexity has not yet been implemented in the model.

It is implicitly assumed that all same-season recaptures come from area 2 since that is where all the harvests took place. The model allows for movement before recapture thus it is possible for marks placed in area 1 to be recaptured in the same season in area 2.

The expected numbers of area 1 marks in each area at the start of year *t* that have been at large for at least one year are given by:

$$\underline{P}_{1965}^{s,k,1} = 0, \quad k = 1,2,3,4$$

$$\underline{P}_{t+1}^{s,1,1} = \left[(\underline{P}_t^{s,1,1} + p_t^{s,1} - \frac{\tilde{r}_t^{s,1}}{\xi})(1-\lambda_1^s) + \underline{P}_t^{s,2,1}\mu_1^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,2,1} = \left[(\underline{P}_t^{s,1,1} + p_t^{s,1} - \frac{\tilde{r}_t^{s,1}}{\xi})\lambda_1^s + \underline{P}_t^{s,2,1}(1-\mu_1^s-\lambda_2^s) + \underline{P}_t^{s,3,1}\mu_2^s \right] (1-F_t^{s,2}) e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,3,1} = \left[\underline{P}_t^{s,2,1}\lambda_2^s + \underline{P}_t^{s,3,1}(1-\mu_2^s-\lambda_3^s) + \underline{P}_t^{s,4,1}\mu_3^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,4,1} = \left[\underline{P}_t^{s,3,1}\lambda_3^s + \underline{P}_t^{s,4,1}(1-\mu_3^s) \right] e^{-\tilde{M}}$$

The expected numbers of area 2 marks in each area at the start of year *t* that have been at large for at least one year are given by:

$$\underline{P}_{1965}^{s,k,2} = 0, \quad k = 1,2,3,4$$

$$\underline{P}_{t+1}^{s,1,2} = \left[\underline{P}_t^{s,1,2}(1-\lambda_1^s) + (\underline{P}_t^{s,2,2} + p_t^{s,2} - \frac{\tilde{r}_t^{s,2}}{\xi})\mu_1^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,2,2} = \left[\underline{P}_t^{s,1,2}\lambda_1^s + (\underline{P}_t^{s,2,2} + p_t^{s,2} - \frac{\tilde{r}_t^{s,2}}{\xi})(1-\mu_1^s-\lambda_2^s) + \underline{P}_t^{s,3,2}\mu_2^s \right] (1-F_t^{s,2}) e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,3,2} = \left[(\underline{P}_t^{s,2,2} + p_t^{s,2} - \frac{\tilde{r}_t^{s,2}}{\xi})\lambda_2^s + \underline{P}_t^{s,3,2}(1-\mu_2^s-\lambda_3^s) + \underline{P}_t^{s,4,2}\mu_3^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,4,2} = \left[\underline{P}_t^{s,3,2}\lambda_3^s + \underline{P}_t^{s,4,2}(1-\mu_3^s) \right] e^{-\tilde{M}}$$

The expected numbers of area 3 marks in each area at the start of year *t* that have been at large for at least one year are given by:

$$\underline{P}_{1965}^{s,k,3} = 0, \; k = 1,2,3,4$$

$$\underline{P}_{t+1}^{s,1,3} = \left[\underline{P}_t^{s,1,3}(1-\lambda_1^s) + \underline{P}_t^{s,2,3}\mu_1^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,2,3} = \left[\underline{P}_t^{s,1,3}\lambda_1^s + \underline{P}_t^{s,2,3}(1-\mu_1^s-\lambda_2^s) + (\underline{P}_t^{s,3,3} + p_t^{s,3} - \frac{\tilde{r}_t^{s,3}}{\xi})\mu_2^s \right](1-F_t^{s,2})e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,3,3} = \left[\underline{P}_t^{s,2,3}\lambda_2^s + (\underline{P}_t^{s,3,3} + p_t^{s,3} - \frac{\tilde{r}_t^{s,3}}{\xi})(1-\mu_2^s-\lambda_3^s) + \underline{P}_t^{s,4,3}\mu_3^s \right] e^{-\tilde{M}}$$

$$\underline{P}_{t+1}^{s,4,3} = \left[(\underline{P}_t^{s,3,3} + p_t^{s,3} - \frac{\tilde{r}_t^{s,3}}{\xi})\lambda_3^s + \underline{P}_t^{s,4,3}(1-\mu_3^s) \right] e^{-\tilde{M}}$$

where

$$\tilde{M} = M + \tau$$

Notes:

1. A term for the fishing proportion F is added only for area 2 in each case, since whaling was conducted only in this area during the marking and recapture period.
2. Recaptures within the same year may occur for whales marked in areas 1, 2 or 3 (not only in area 2) since movement is assumed to take place after marking and before whaling. First-year recaptures are subtracted from the original area in which they were marked.

The sex-specific numbers marked are not known, only the total number of whales marked:

$$p_t^v = p_t^{m,v} + p_t^{f,v}$$

However, the assumption is made that marking by sex is proportional to the recruited numbers in the population:

$$p_t^{m,v} = \frac{p_t^v \sum_{a=a_r^m}^{n} N_{t,a}^{m,v}}{\sum_{a=a_r^m}^{n} N_{t,a}^{m,v} + \sum_{a=a_r^f}^{n} N_{t,a}^{f,v}}$$

$$p_t^{f,v} = p_t^v - p_t^{m,v}$$

This computation must be completed before updating the $\underline{P}$ for the year concerned.

Thus the expected number of marked animals at large for ≥ 1 year that were originally marked in either area 1 or 2 and recovered in area 2 in year t of sex s is:

$$\hat{r}_t^{s,2,1} = \xi \underline{P}_t^{s,2,1} F_t^{s,2}$$

$$\hat{r}_t^{s,2,2} = \xi \underline{P}_t^{s,2,2} F_t^{s,2}$$

$$\hat{r}_t^{s,2,3} = \xi \underline{P}_t^{s,2,3} F_t^{s,2}$$

If a Poisson error distribution is assumed, the negative log-likelihood is given by summing over combinations of sex, area and year for which $\hat{r}$ is non-zero:

$$-\ln L_1 = \sum_{s=m,f} \sum_{t=1965}^{1988} \sum_{v=1}^{3} \left[\hat{r}_t^{s,2,v} - r_t^{s,2,v} \ln \hat{r}_t^{s,2,v} + \ln(r_t^{s,2,v}!) \right]$$

The last term can be ignored during minimization as this remains constant as it is independent of the values of any of the estimable parameters.

CPUE indices

The assumption is made that the *i*th CPUE series is proportional to the recruited abundance in the corresponding area *k* and year *t*.

$$CPUE_t^{k,i} = q_i X_t^k$$

$$X_t^k = \sum_{s=m,f} \sum_{a=a_r^s}^{n} N_{t,a}^{s,k}$$

A closed form solution is used to provide the estimated maximum likelihood value for the proportionality constants q_i (nuisance parameters of the model):

$$\ln \hat{q}_i = \frac{\sum_t (\ln CPUE_t^{k,i} - \ln X_t^k)}{n^i}$$

where n^i is the number of data points for CPUE series *i*.

The negative log-likelihood for the later period CPUE series (*i* = 1 to 4) over 1966 to 1982 is given by:

$$-\ln L_2 = 0.5 \sum_t \boldsymbol{\eta}_t [\mathbf{V}^{-1}] \boldsymbol{\eta}_t^T$$

where $\mathbf{V}^{-1}$ is the inverse of the variance-covariance matrix $\mathbf{V}$ (Table 4) for the late series CPUE indices, and $\boldsymbol{\eta}_t$ is a vector comprised of four elements, the *i*th element of which is:

$$\boldsymbol{\eta}_t^i = \ln CPUE_t^i - \ln q_i X_t^2$$

This method applies to the years in which values from all four series are available (1966-1982). Where there are values available from only three (1962-1965 and 1983-1985) or two (1986-1987) of the series, the contributions to $-\ln L_2$ are similar but $\mathbf{V}$ and $\boldsymbol{\eta}_t$ are reduced by removing the row(s) and column(s) for which no values are available.

For the earlier period CPUE series (*i* = 5 or 6) the negative log-likelihoods are:

$$-\ln L_3 = \sum_{i=5}^{6} \left(\frac{\sum_t \left[\ln CPUE_t^{k,i} - \ln(q_i X_t^k) \right]^2}{2\sigma_i^2} \right)$$

where values of σ_5 and σ_6 were obtained by quadratic detrending of these data (as in Butterworth and Punt 1992), i.e. fitting a quadratic equation to the CPUE data to obtain predicted CPUE values, and then applying the following equation:

$$\sigma_5 = \sqrt{\frac{1}{n-3} \sum_{t=1901}^{1915} (y_t^2 - \hat{y}_t^2)^2}$$

$$\sigma_6 = \sqrt{\frac{1}{n-3} \sum_{t=1904}^{1913} (y_t^3 - \hat{y}_t^3)^2}$$

where y_t^k is the CPUE for area *k* and year *t*, $\hat{y}_t^k$ is the CPUE predicted by the quadratic fit, and *n* is the relevant number of CPUE data points, reduced since the quadratic fit estimates three parameters (and hence there is a loss of three degrees of freedom).

Abundance estimates

The abundance estimates in year t are assumed to apply to the 1+ population in the relevant area at the start of that year:

$$\tilde{N}_t^k = \sum_{s=m,f} \sum_{a=1}^{n} N_{t,a}^{s,k}$$

The abundance estimates are assumed to be lognormally distributed, thus the negative log likelihoods are given by:

$$\begin{aligned}
-\ln L_4 = &\frac{1}{2\sigma_1^2}\left[\ln \bar{N}_{1988}^1 - \ln \tilde{N}_{1988}^1\right]^2 + \frac{1}{2\sigma_2^2}\left[\ln \bar{N}_{1988}^2 - \ln \tilde{N}_{1988}^2\right]^2 + \frac{1}{2\sigma_3^2}\left[\ln \bar{N}_{1988}^{34} - \ln(\tilde{N}_{1988}^3 + \tilde{N}_{1988}^4)\right] \\
&+ \frac{1}{2\sigma_4^2}\left[\ln \bar{N}_{1995}^1 - \ln \tilde{N}_{1995}^1\right]^2 + \frac{1}{2\sigma_5^2}\left[\ln \bar{N}_{1995}^2 - \ln \tilde{N}_{1995}^2\right]^2 + \frac{1}{2\sigma_6^2}\left[\ln \bar{N}_{1995}^{34} - \ln(\tilde{N}_{1995}^3 + \tilde{N}_{1995}^4)\right]^2 \\
&+ \frac{1}{2\sigma_7^2}\left[\ln \bar{N}_{2001}^1 - \ln \tilde{N}_{2001}^1\right]^2 + \frac{1}{2\sigma_8^2}\left[\ln \bar{N}_{2001}^2 - \ln \tilde{N}_{2001}^2\right]^2 + \frac{1}{2\sigma_9^2}\left[\ln \bar{N}_{2001}^{34} - \ln(\tilde{N}_{2001}^3 + \tilde{N}_{2001}^4)\right]^2
\end{aligned}$$

where the σ values are the CVs associated with the abundance estimates, and the indices for the abundance estimates indicate to which area or combination of areas they apply.

Minimization

Maximum likelihood estimates for the parameters were obtained by minimizing the sum of the negative log likelihoods:

$$-\ln L = -\sum_{i=1}^{4} \ln L_i$$

Maximum sustainable yield calculations

Estimates of MSYR are obtained from a simplified version of the model with no sex distinction and only one area. The value used for β is fixed at 1.98, while r is varied. K is set arbitrarily to 1000. For a given r and catch proportion F, there is a unique solution for N_0 satisfying this equation:

$$N_0 = 0.5\left(\sum_{a=a_m}^{n} N_a\right)\left(\alpha + r - r\left[\frac{\sum_{a=a_r}^{n} N_a}{K}\right]^{\beta}\right) \qquad \text{(A)}$$

Note that the right hand side can be written in terms of known parameters and N_0 since:

$$\begin{aligned}
&N_1 = N_0 e^{-M} \\
&N_{a+1} = N_a e^{-M} \qquad 1 \le a < a_r \\
&N_{a+1} = N_a (1-F) e^{-M} \qquad a_r \le a < n-2 \\
&N_n = \left(N_n + N_{n-1}\right)(1-F)e^{-M} \\
&K = N_0 \frac{e^{-a_r M}}{1-e^{-M}} \\
&\alpha = \frac{2(1-e^{-M})}{e^{-a_m M}}
\end{aligned}$$

Solver in Excel is used to find the value of N_0 that solves equation (A) for a particular value of *F*. This process is repeated with a range of values of *F* to find F_{msy} that maximizes the catch:

$$C = F\sum_{a=a_r}^{n} N_a$$

The quantities of interest are then given by:

$$MSY = F_{msy}\sum_{a=a_r}^{n} N_a$$

$$MSYR(recruited) = F_{msy}$$

$$MSYR(1+) = \frac{MSY}{\sum_{a=1}^{n} N_a}, \quad MSYL = \frac{1}{K}\sum_{a=a_r}^{n} N_a$$

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Table 1. Revised catch series for East Greenland-Iceland population used in the base case model (Gunnlaugsson, pers. comm.).

	East Greenland		West Iceland		East Iceland	
Year	M	F	M	F	M	F
1883	0	0	0	0	0	0
1884	0	0	0	0	0	0
1885	0	0	6	6	0	0
1886	0	0	8	8	0	0
1887	0	0	14	15	0	0
1888	0	0	30	32	0	0
1889	0	0	55	60	0	0
1890	0	0	56	61	0	0
1891	0	0	66	72	0	0
1892	0	0	91	98	0	0
1893	0	0	205	222	0	0
1894	0	0	151	164	0	0
1895	0	0	206	223	0	0
1896	0	0	130	141	0	0
1897	0	0	215	232	0	0
1898	0	0	143	155	0	0
1899	0	0	213	231	0	0
1900	0	0	226	245	9	10
1901	0	0	282	306	25	27
1902	0	0	255	277	86	93
1903	0	0	162	176	189	204
1904	0	0	104	112	165	179
1905	0	0	83	89	185	201
1906	0	0	61	66	129	139
1907	0	0	54	58	256	277
1908	0	0	57	60	254	276
1909	0	0	107	115	314	341
1910	4	5	79	84	193	210
1911	6	7	59	64	156	169
1912	4	4	36	39	45	48
1913	2	2	19	21	33	35
1914	1	1	10	11	0	0
1915	6	7	18	19	0	0
1916	0	0	21	21	0	0
1917	0	0	0	0	0	0
1918	0	0	0	0	0	0
1919	0	0	0	0	0	0
1920	0	0	34	34	0	0
1921	0	0	22	22	0	0
1922	0	0	20	19	0	0
1923	0	0	24	24	0	0
1924	0	0	30	31	0	0
1925	0	0	29	28	0	0
1926	0	0	19	20	0	0
1927	0	0	23	20	0	0
1928	0	0	36	34	0	0
1929	0	0	53	56	0	0
1930	17	16	25	25	22	24
1931	0	0	4	4	0	0
1932	59	58	117	117	0	0
1933	26	25	145	155	0	0
1934	0	0	50	46	0	0
1935	0	0	12	13	0	0
1936	0	0	26	46	0	0
1937	0	0	134	101	11	7
Total	125	125	4025	4278	2072	2240

	West Iceland	
Year	M	F
1938	55	58
1939	66	43
1940	0	0
1941	0	0
1942	0	0
1943	0	0
1944	0	0
1945	0	0
1946	13	10
1947	27	22
1948	106	116
1949	123	156
1950	162	172
1951	143	200
1952	99	127
1953	107	111
1954	70	107
1955	120	120
1956	134	165
1957	190	235
1958	143	151
1959	97	81
1960	81	79
1961	65	77
1962	166	139
1963	152	134
1964	114	116
1965	161	136
1966	163	149
1967	111	128
1968	102	101
1969	117	134
1970	153	138
1971	97	111
1972	122	116
1973	135	132
1974	142	143
1975	127	118
1976	132	143
1977	64	80
1978	106	131
1979	127	133
1980	117	120
1981	121	133
1982	96	98
1983	70	74
1984	67	100
1985	73	88
1986	27	49
1987	38	42
1988	31	37
1989	23	45
Total	4755	5098

Table 2 Original catch series (from Butterworth and Punt 1992) split into West Iceland and East Iceland for 1883-1939. This series differs from the revised catch series in 1883-1915 and 1930-1939. In other years the catches have not been revised from the original.

	West Iceland		East Iceland	
Year	M	F	M	F
1883	3	3	0	0
1884	11	11	0	0
1885	13	15	0	0
1886	11	11	0	0
1887	15	16	0	0
1888	25	28	0	0
1889	55	60	0	0
1890	56	60	0	0
1891	66	72	0	0
1892	90	97	0	0
1893	214	231	0	0
1894	157	170	0	0
1895	208	226	0	0
1896	137	149	0	0
1897	223	241	0	0
1898	155	168	0	0
1899	234	253	0	0
1900	220	238	0	0
1901	249	269	11	12
1902	219	237	61	67
1903	187	202	201	218
1904	101	109	150	162
1905	89	96	189	205
1906	65	71	129	139
1907	57	61	257	279
1908	59	64	255	277
1909	111	120	311	337
1910	84	91	185	201
1911	60	65	143	155

	West Iceland		East Iceland	
Year	M	F	M	F
1912	34	36	38	41
1913	20	22	32	35
1914	24	26	0	0
1915	58	63	0	0
1916	21	21	0	0
1917	0	0	0	0
1918	0	0	0	0
1919	0	0	0	0
1920	34	34	0	0
1921	22	22	0	0
1922	20	19	0	0
1923	24	24	0	0
1924	30	31	0	0
1925	29	28	0	0
1926	19	20	0	0
1927	23	20	0	0
1928	36	34	0	0
1929	53	56	0	0
1930	157	112	0	0
1931	1	8	0	0
1932	98	96	0	0
1933	118	102	0	0
1934	59	56	0	0
1935	21	23	0	0
1936	37	56	0	0
1937	165	124	0	0
1938	82	77	0	0
1939	84	63	0	0

Table 3 CPUE time series for EGI fin whales. Later CPUE series were from Butterworth and Punt (1992), and the two early series are the "FprB90" series in Sigurjónsson and Gunnlaugsson (2006).

Later period					Early period		
Year	CPUE i=1	CPUE i=2	CPUE i=3	CPUE i=4	Year	CPUE i=5	CPUE i=6
1962	0.1398	0.1512	0.1048	–	1901	22.44	64.57
1963	0.1363	0.0841	0.0671	–	1902	21.09	32.27
1964	0.0770	0.0551	0.0492	–	1903	18.57	28.78
1965	0.1979	0.1519	0.1204	–	1904	19.91	22.85
1966	0.1150	0.1083	0.0863	0.1310	1905	23.44	28.18
1967	0.1040	0.1280	0.1798	0.1350	1906	16.16	15.86
1968	0.1548	0.0990	0.1314	0.1672	1907	14.27	31.39
1969	0.0541	0.0880	0.0691	0.0495	1908	14.74	23.33
1970	0.1040	0.1596	0.1466	0.1282	1909	21.79	30.12
1971	0.0824	0.0591	0.0523	0.0703	1910	16.48	16.52
1972	0.0836	0.0718	0.0648	0.0601	1911	15.23	13.71
1973	0.0785	0.0853	0.0708	0.0791	1912	9.31	6.31
1974	0.0810	0.1134	0.0861	0.1132	1913	5.59	7.73
1975	0.1115	0.0958	0.0779	0.1011	1914	7.06	–
1976	0.1067	0.0909	0.0993	0.0779	1915	11.25	–
1977	0.0296	0.0651	0.0443	0.0390			
1978	0.0507	0.0583	0.0732	0.0675			
1979	0.1817	0.1494	0.1389	0.1276			
1980	0.0891	0.0933	0.1317	0.1220			
1981	0.1572	0.1134	0.1333	0.1271			
1982	0.1677	0.1190	0.1094	0.0974			
1983	0.0804	–	0.0597	0.0837			
1984	0.1169	–	0.1233	0.1283			
1985	0.1170	–	0.0777	0.0857			
1986	–	–	0.0744	0.0856			
1987	–	–	0.1792	0.0990			

Table 4 Variance-covariance matrix for the late CPUE series obtained by quadratically detrending the log-transformed data (Butterworth and Punt 1992).

	1	2	3	4
1	0.171	0.089	0.102	0.118
2	0.089	0.103	0.105	0.076
3	0.102	0.105	0.156	0.104
4	0.118	0.076	0.104	0.127

Table 5 Alternative early CPUE series 6 using catch-per-boat-month instead of annual-catch-per-vessel (Gunnlaugsson, pers. comm.). This series accounts for differences in the number of days spent whaling by each vessel and was used in a sensitivity test.

Early period	
Year	CPUE i=6
1901	–
1902	–
1903	–
1904	6.4
1905	8.6
1906	5.1
1907	7.1
1908	6.0
1909	8.0
1910	4.8
1911	5.6
1912	3.4
1913	4.3
1914	–
1915	–

Table 6 Estimates of abundance corresponding to various combinations of the four areas in 1988 (combination of 1987 and 1989 survey), 1995 and 2001 (Pike and Gunnlaugsson 2005). The total abundance for all four areas in each year is given in the bottom three lines and compared with previously used estimates (as listed in Cunningham and Butterworth 2003).

		Pike and Gunnlaugsson (2005)		Previous	
Year	Area/s	Estimate	CV	Estimate	CV
1988	1	5,024	0.228		
1988	2	3,452	0.259		
1988	3+4	6,856	0.427		
1995	1	8,412	0.294		
1995	2	6,800	0.231		
1995	3+4	4,145	0.368		
2001	1	11,706	0.195		
2001	2	6,565	0.195		
2001	3+4	5,405	0.292		
1988	1+2+3+4	15,332	0.216	15,614	0.216
1995	1+2+3+4	19,357	0.220	18,932	0.160
2001	1+2+3+4	23,676	0.133	22,307	0.146

Table 7 Number of fin whales marked in each year in East Greenland (1), West Iceland (2) and East Iceland (3) and the number recaptured in the same season as they were marked.

Year	Area	Marks	SameSeason
1967	1	8	0
1968	1	14	1
1970	1	3	0
1973	1	3	0
1980	1	3	0
1981	1	29	0
1983	1	7	0
1984	1	32	0
1965	2	13	0
1968	2	3	0
1970	2	1	0
1972	2	3	1
1979	2	34	1
1980	2	9	1
1981	2	62	4
1982	2	52	3
1983	2	8	0
1982	3	2	0
1984	3	7	0

Table 8 Number of fin whales marked in East Greenland (1) and West Iceland (2) that were recaptured in each year (in West Iceland). There were no recaptures of whales marked in East Iceland. Individual entries represent males and females (M / F). Years with no recaptures are not included. Where sex of a recaptured whale was not recorded, 0.5 was added to males and to females.

Year	Area 1	Area 2
1966	0 / 0	3 / 0
1969	1 / 0	0 / 0
1972	0 / 0	1 / 0
1973	0 / 0	1 / 0
1977	0 / 1	0 / 0
1980	0 / 0	1 / 1
1981	0 / 0	0.5 / 0.5
1982	0 / 0	2 / 5
1983	0 / 1	3.5 / 1.5
1984	0 / 0	4.5 / 4.5
1985	0 / 0	3 / 1
1986	0 / 1	1 / 0
1988	2 / 1	0 / 0
1989	0 / 1	2 / 0

Table 9 Parameter values and bounds used in the (base case) model. For maximum likelihood estimation, the values were used for fixed parameters and the bounds for estimated parameters. For the Bayesian analyses, uniform priors were assumed to cover the ranges shown. Where both fixed values and bounds are listed, these parameters were fixed for maximum likelihood estimation and estimated in the Bayesian analyses. The reason for the bounds on the eastward movement parameters is to avoid possible technical computational difficulties levels outside this range. Although sometimes the estimate falls on the upper bound of 0.2, a higher value would make no practical difference as this value already reflects effectively complete mixing between the subpopulations concerned.

Parameter	Symbol	Value or bounds	Bayesian prior
Pre-exploitation abundance in area k	K^1, K^2, K^3, K^4	[100; 30,000]	U[100; 30,000]
Maximum increase in calf production when depleted	r	[0; 0.383][1]	U [0; 0.383][1]
Eastward movement for males	$\lambda_1^m, \lambda_2^m, \lambda_3^m$	[0.0001; 0.2]	U [0.0001; 0.2]
Eastward movement for females	$\lambda_1^f, \lambda_2^f, \lambda_3^f$	[0.0001; 0.2]	U [0.0001; 0.2]
Maximum westward movement	$\mu_{\max}$	0.75	
Initial year	–	1883	
Final year	–	2005	
Female age at maturity	a_m^f	10	
Male age at recruitment	a_r^m	5	
Female age at recruitment	a_r^f	4	
Plus group age	n	15	
Natural mortality	M	0.04	N(0.04, 0.01^2) and [0.0001; 0.2]
Density dependence parameter	β	1.98	
Detection proportion of recaptured marks	ξ	1.0 or [0.2; 1.0]	U[0.2; 1.0]
Mark mortality plus loss rate	τ	0.0 or [0.0; 0.8]	U[0.0; 0.8]

[1] The upper bound for *r* reflects the greatest biologically possible given demographic constraints (i.e., a pregnancy rate of 0.5, age at first parturition of 10 yr, and natural mortality of 0.04 yr^{-1})

Table 10 Summary of sensitivity tests. Cells with bold text indicate where each sensitivity tests differs from the base case. For CPUE series 6, FprB90 is fin whale catch per boat, while FpBM-o2 fin whale catch per boat month (adjusted for days worked per boat and for time taken to catch other species).

Parameter or dataset	Base case	Estimate all movements	Low M	High M	High mark loss	Low mark detection	Density dependence K_{total}	Alternative CPUE 6	Fit to total abundance	Exclude mark-recapture
K_1	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
K_2	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
K_3	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
K_4	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
r	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
λ_1^m (eastward male)	Estimated	**Estimated**	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
λ_2^m (eastward male)	0.2	**Estimated**	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
λ_3^m (eastward male)	Estimated	**Estimated**	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated
λ_1^f (eastward female)	=Male	**Estimated**	=Male	=Male	=Male	=Male	=Male	=Male	=Male	=Male
λ_2^f (eastward female)	=Male	**Estimated**	=Male	=Male	=Male	=Male	=Male	=Male	=Male	=Male
λ_3^f (eastward female)	=Male	**Estimated**	=Male	=Male	=Male	=Male	=Male	=Male	=Male	=Male
Natural mortality (M)	0.04	0.04	**0.02**	**0.07**	0.04	0.04	0.04	0.04	0.04	0.04
Mark loss rate (τ)	0.0	0.0	0.0	0.0	**0.4**	0.0	0.0	0.0	0.0	0.0
Mark detection propn (ξ)	1.0	1.0	1.0	1.0	1.0	**0.5**	1.0	1.0	1.0	1.0
Density-dependence	K_k	K_k	K_k	K_k	K_k	K_k	$\boldsymbol{\sum K_k}$	K_k	K_k	K_k
CPUE 6	FprB90	FprB90	FprB90	FprB90	FprB90	FprB90	FprB90	**FpBM-o2**	FprB90	FprB90
Abundance estimates	By area	By area	By area	By area	By area	By area	By area	By area	**EGI total**	By area
Mark-recapture data	Included	Included	Included	Included	Included	Included	Included	Included	Included	**Excluded**

Table 11 Maximum likelihood estimates, negative log likelihoods (NLLs) and AIC values for the base case and the sensitivity tests. Note that cells with bold font denote cases where the data or likelihood was altered; in these cases NLL and AIC values are not directly comparable to other cases. Estimates of male and female movement rates are distinguished only in the "estimate all movements" sensitivity test. K values are in terms of the recruited component of the population. The MSYR values are calculated by finding the maximum yield (taken from the recruited portion of the population) as a proportion of the recruited population and the 1+ population; in these calculations β is held constant at 1.98 while r is varied.

Parameter / NLL	Base case	Estimate all movements	Low M	High M	High mark loss	Low mark detection	Density dependence K_{total}	Alternative CPUE 6	Fit to total abundance	Exclude mark-recapture
K_1	7994	8199	8422	7381	8116	8021	7367	9059	293	7160
K_2	6090	6017	6318	5739	6331	6486	6574	7242	3308	5886
K_3	3606	3590	3560	3671	3479	3438	3744	4143	4895	3614
K_4	2033	2005	2315	1640	2440	2443	1678	2022	10860	1670
r	0.132	0.126	0.102	0.194	0.119	0.123	0.114	0.089	0.243	0.264
MSYR (recruited)	0.020	0.020	0.016	0.028	0.019	0.019	0.018	0.014	0.034	0.036
MSYR (1+)	0.017	0.016	0.014	0.023	0.016	0.016	0.015	0.012	0.027	0.029
λ_1 (male / female)	0.0350	0.0244	0.0330	0.0376	0.0310	0.0282	0.0333	0.0401	0.0578	0.0001
λ_2 (male / female)	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000
λ_3 (male / female)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0107	0.0001	0.0288	0.0001
NLL mark-recapture	47.93	47.54	47.93	48.03	78.64	62.29	48.10	48.59	43.11	**0.00**
NLL CPUE early	13.49	13.77	13.57	13.42	13.43	13.29	13.73	**14.48**	10.62	11.61
NLL CPUE late	45.96	45.95	45.97	45.96	46.10	46.11	45.96	46.10	45.62	45.97
NLL sightings estimate	11.55	11.49	11.65	11.40	13.56	12.73	12.24	11.35	**1.70**	11.26
Total NLL	118.93	118.76	121.12	123.31	151.74	134.42	120.04	**120.52**	**101.05**	**68.83**
Estimated parameters	7	8	7	7	7	7	7	7	7	7
AIC	251.86	253.51	256.24	260.61	317.47	282.84	254.08	**255.05**	**216.10**	**151.67**

Table 12 Maximum likelihood estimates for the recruited abundance of fin whales in each area (and all combined) in 2004, and the ratio of these values to pre-exploitation recruited abundance.

Parameter / NLL	Base case	Estimate all movements	Low M	High M	High mark loss	Low mark detection	Density dependence K_{total}	Alternative CPUE 6	Fit to total abundance	Exclude mark-recapture
$N^{1}_{rec,2004}$	6898	6940	7411	6201	6668	6745	6761	6876	267	7159
$N^{2}_{rec,2004}$	4841	4802	5142	4420	4514	4664	4932	5023	2991	5178
$N^{3}_{rec,2004}$	2842	2849	2876	2799	2450	2444	2793	2845	4461	3180
$N^{4}_{rec,2004}$	2031	2003	2314	1638	2437	2440	1960	2018	10661	1669
$N^{total}_{rec,2004}$	16611	16594	17742	15058	16070	16294	16447	16762	18381	17185
$N^{1}_{rec,2004} / K^{1}_{rec}$	0.863	0.847	0.880	0.840	0.822	0.841	0.918	0.759	0.912	1.000
$N^{2}_{rec,2004} / K^{2}_{rec}$	0.795	0.798	0.814	0.770	0.713	0.719	0.750	0.694	0.904	0.880
$N^{3}_{rec,2004} / K^{3}_{rec}$	0.788	0.794	0.808	0.763	0.704	0.711	0.746	0.687	0.911	0.880
$N^{4}_{rec,2004} / K^{4}_{rec}$	0.999	0.999	0.999	0.999	0.999	0.999	1.168	0.998	0.982	1.000
$N^{tot}_{rec,2004} / K^{tot}_{rec}$	0.842	0.838	0.861	0.817	0.789	0.799	0.849	0.746	0.950	0.938

Table 13 Maximum likelihood estimates (MLEs) and 95% confidence intervals (obtained from likelihood profiles) compared with Bayesian median and 95% credibility intervals for the estimated parameters for the base case. Bold numbers indicate instances where MLEs fell on parameter bounds; Bayesian posteriors for these parameters were very skewed with highest probability density near the bounds. MLE confidence intervals were not estimated for *M*, which was fixed on input.

		Likelihood profiles		Bayesian intervals		
Parameter	MLE	Lower 95%	Upper 95%	Median	Lower 95%	Upper 95%
K_1	7,994	6,360	10,540	7,884	6,251	10,514
K_2	6,090	4,660	>7,780*	5,859	4,442	7,815
K_3	3,606	2,470	4,750	3,261	2,221	4,519
K_4	2,033	380	3,940	2,415	677	4,638
r	0.132	0.076	0.224	0.114	0.058	0.225
λ_1	0.035	0.020	0.074	0.036	0.016	0.082
λ_2	**0.2**	0.085	**0.2**	**0.2**	**0.2**	**0.2**
λ_3	**0.0001**	**0.0001**	0.066	0.033	0.002	0.160
M	0.04	–	–	0.041	0.022	0.062
Mark loss rate (τ)	**0**	**0**	0.036	0.013	0.001	0.057
Mark detection proportion (ξ)	**1**	0.881	**1**	0.961	0.841	0.998

*Poorly behaved, did not converge for values greater than this.

Table 14. Posterior probability that the abundance in 2035 will be below 60% of the corresponding pre-exploitation equilibrium abundance for the mature female, recruited and 1+ components in each area and for all areas combined, under future catches of 0, 100 and 200 fin whales per year. Values were obtained from posterior distributions obtained from Bayesian analyses. Zero probability is indicated by a "–".

Mature female	Area 1	Area 2	Area 3	Area 4	All areas
0	0.003	0.004	0.004	0.001	0.002
100	0.017	0.068	0.054	0.007	0.020
200	0.044	0.511	0.311	0.033	0.115

Recruited	Area 1	Area 2	Area 3	Area 4	All areas
0	0.002	0.001	0.001	–	0.001
100	0.010	0.035	0.027	0.004	0.012
200	0.025	0.246	0.167	0.017	0.073

1+	Area 1	Area 2	Area 3	Area 4	All areas
0	0.001	0.001	0.001	–	0.001
100	0.009	0.028	0.024	0.003	0.011
200	0.020	0.192	0.144	0.014	0.057

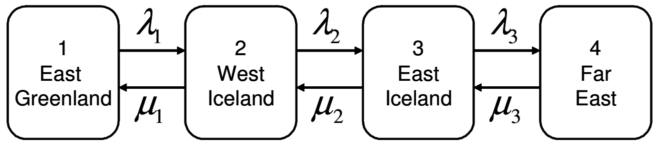

Figure 1. Model of whale movement. A fixed proportion of whales move out of each area each year and into the adjacent area.

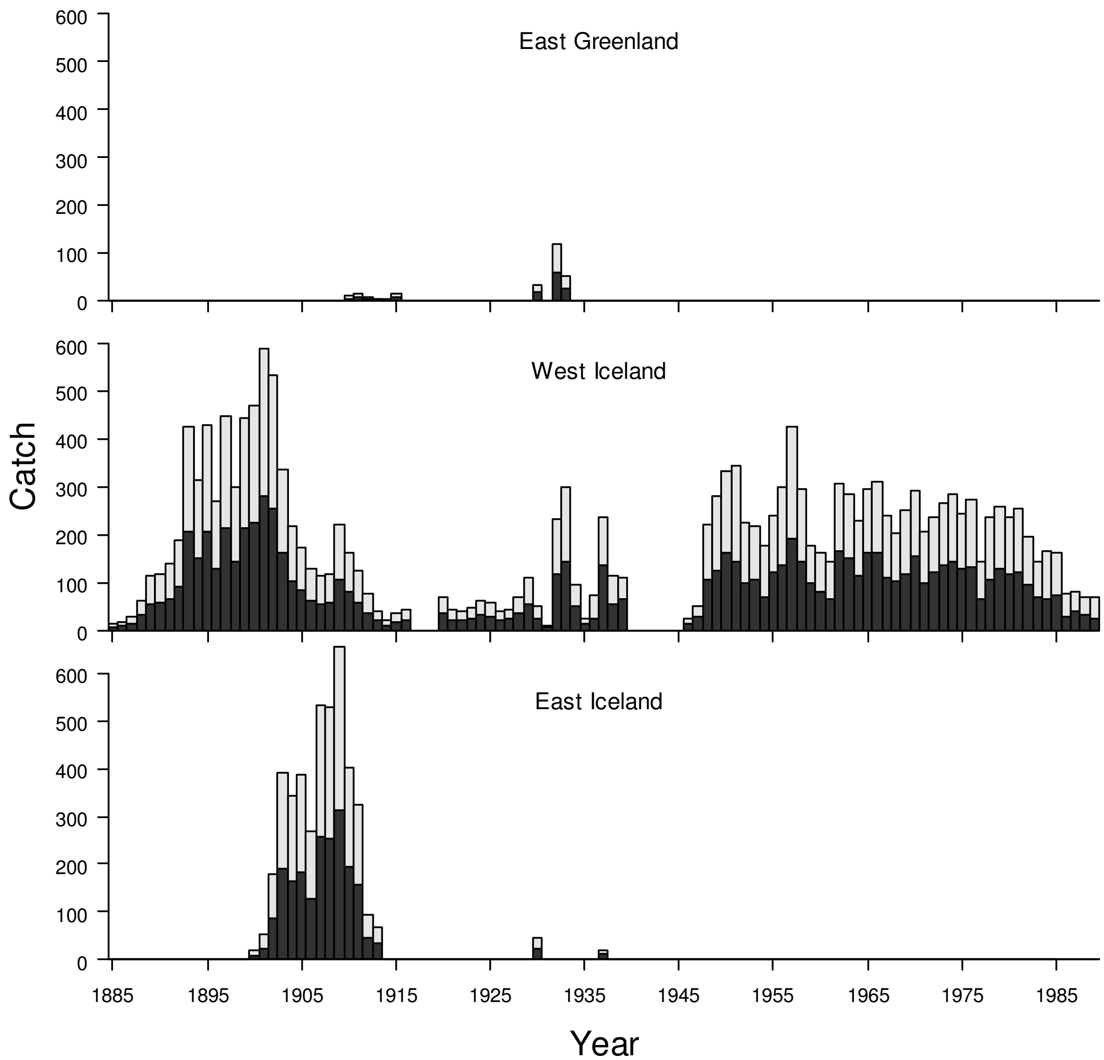

Figure 2. Catch series used in the model for area 1 (East Greenland), area 2 (West Iceland) and area 3 (East Iceland) (Gunnlaugsson, pers. comm.). The dark bars represent males and the lighter bars females.

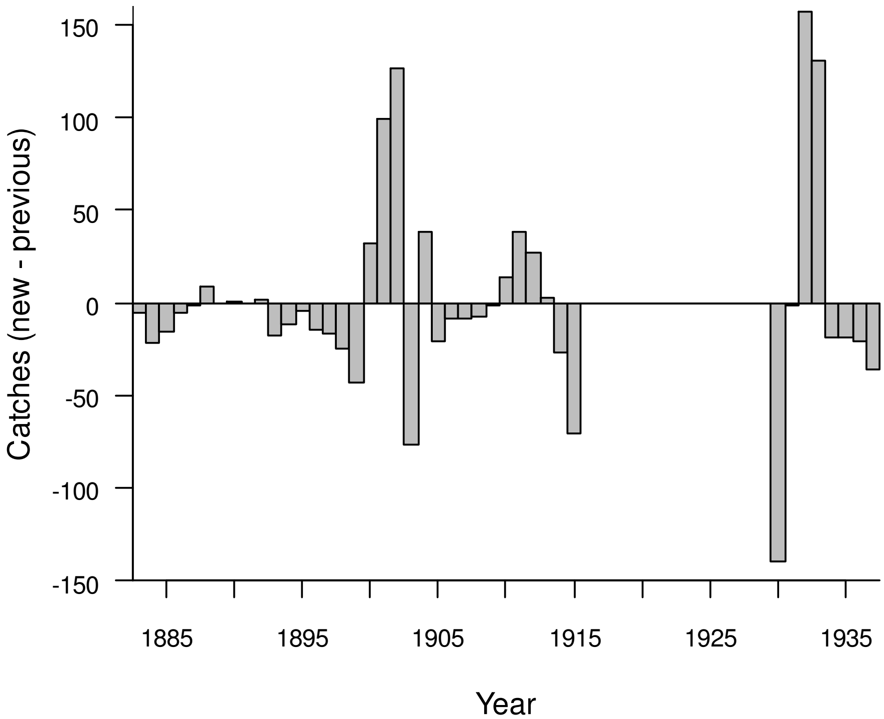

Figure 3. Differences in catches in the early years between the new catch series (summed over areas and sex) used in this paper (Gunnlaugsson, pers. comm.) and the previous catch series (Butterworth and Punt 1992, Cunningham and Butterworth 2003).

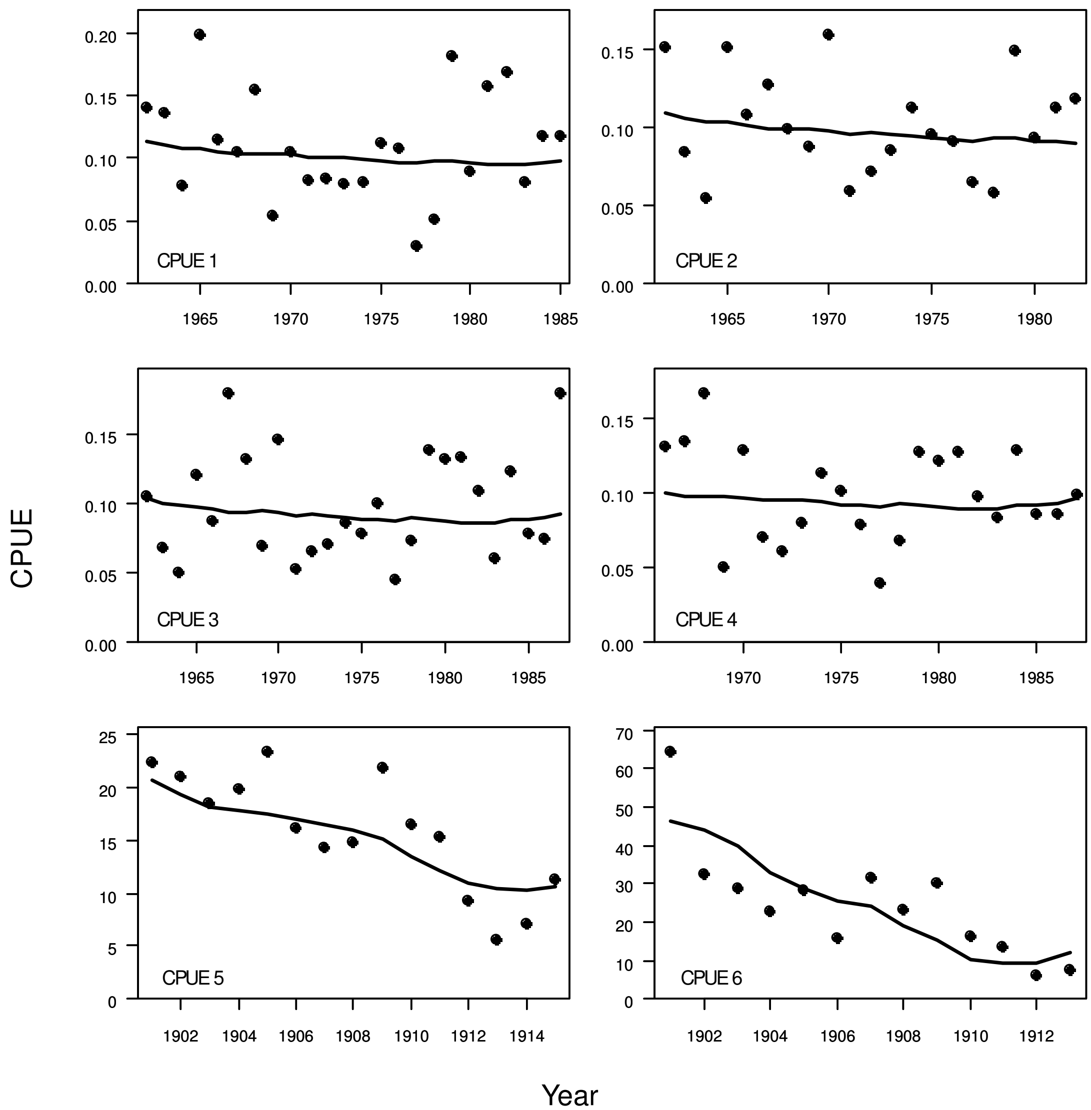

Figure 4. Base case maximum likelihood fits (lines) to each of the six CPUE series (points).

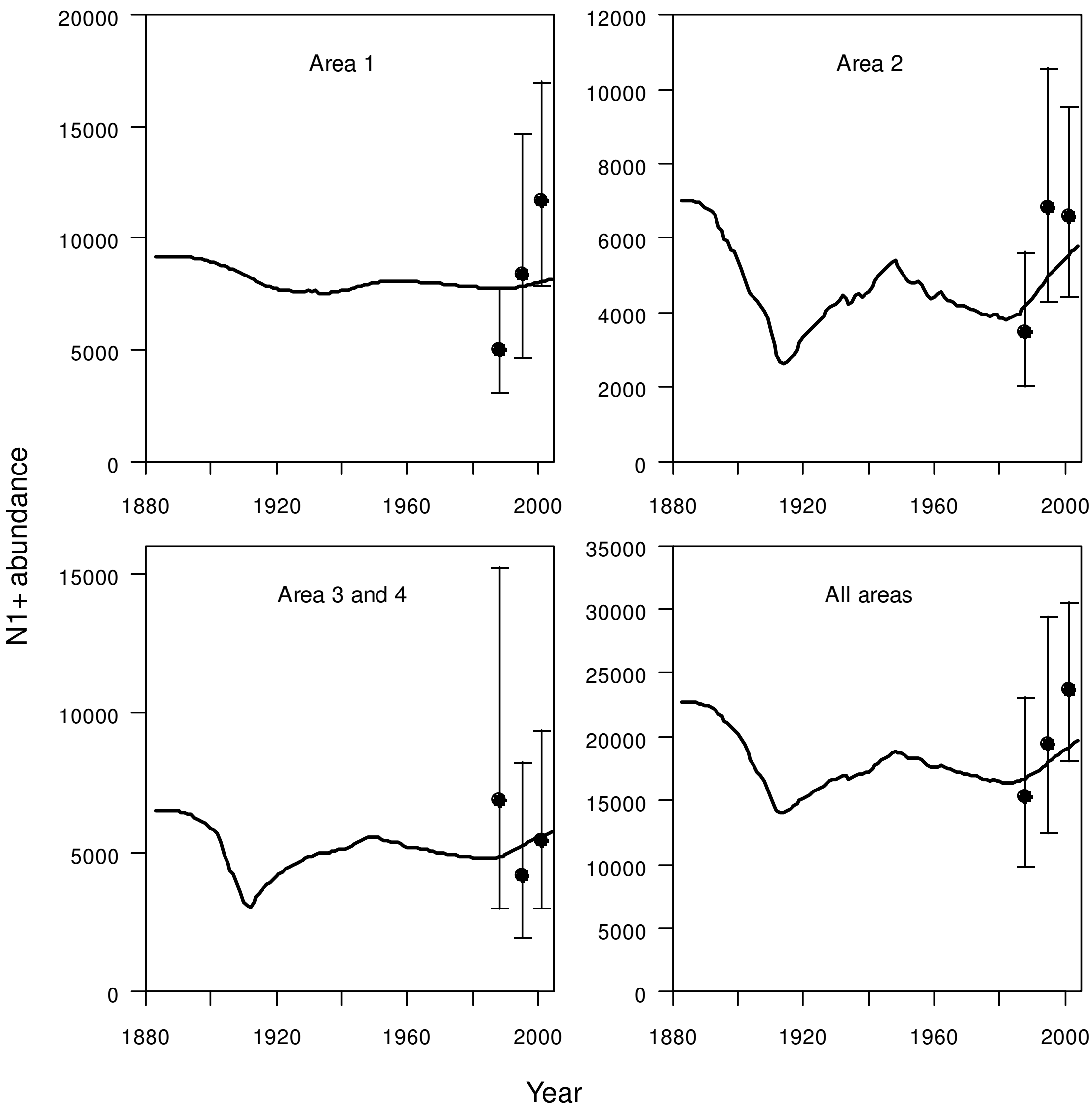

Figure 5. Maximum likelihood model fit to the 1+ abundance trajectories and sighting survey estimates separated into areas for all years, and for all areas combined. The 95% confidence intervals for the sightings estimates are indicated. The model does not reflect the increasing trend seen in the abundance estimates for East Greenland (area 1).

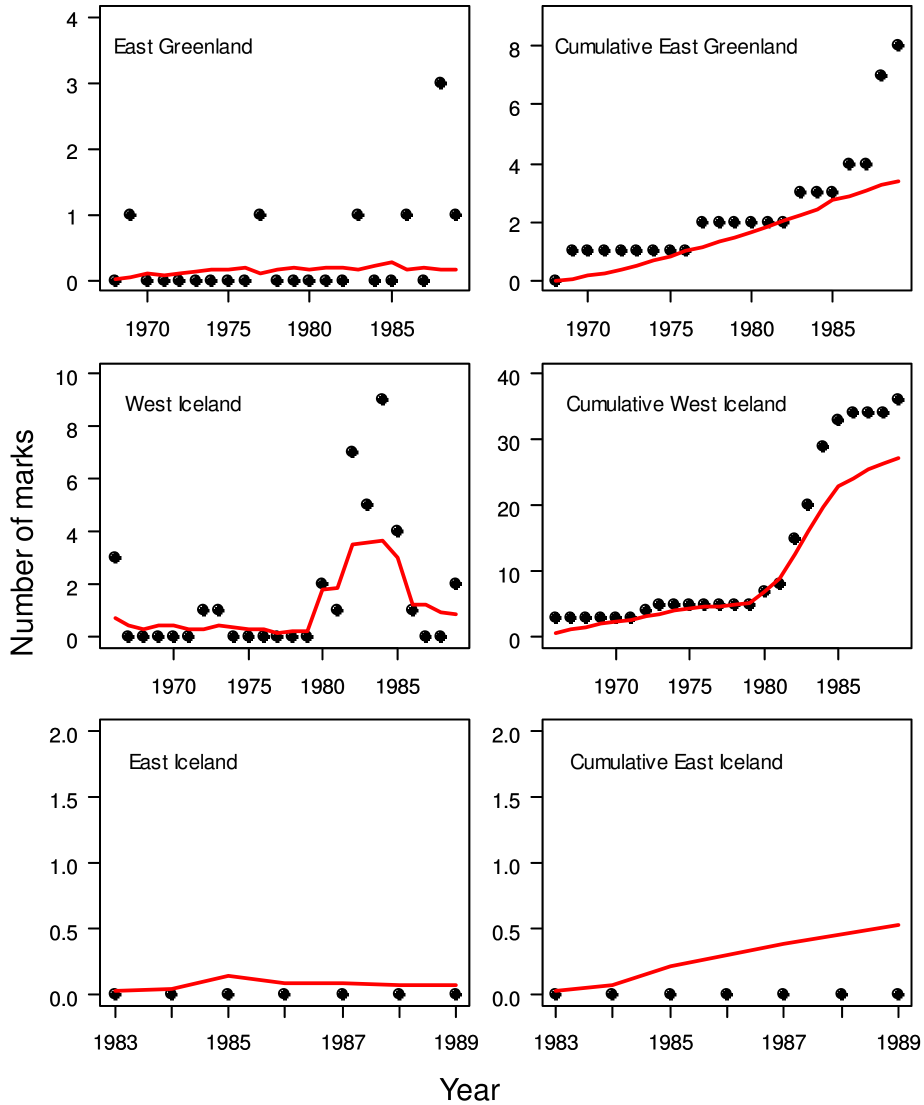

Figure 6. Fit of the base case model (lines) to the mark-recapture data (points). The left panels represent marks and recaptures; the right panels cumulative marks and recaptures. Areas are those in which the fin whales were marked; all recaptures were in West Iceland. No fin whales marked in East Iceland were recaptured.

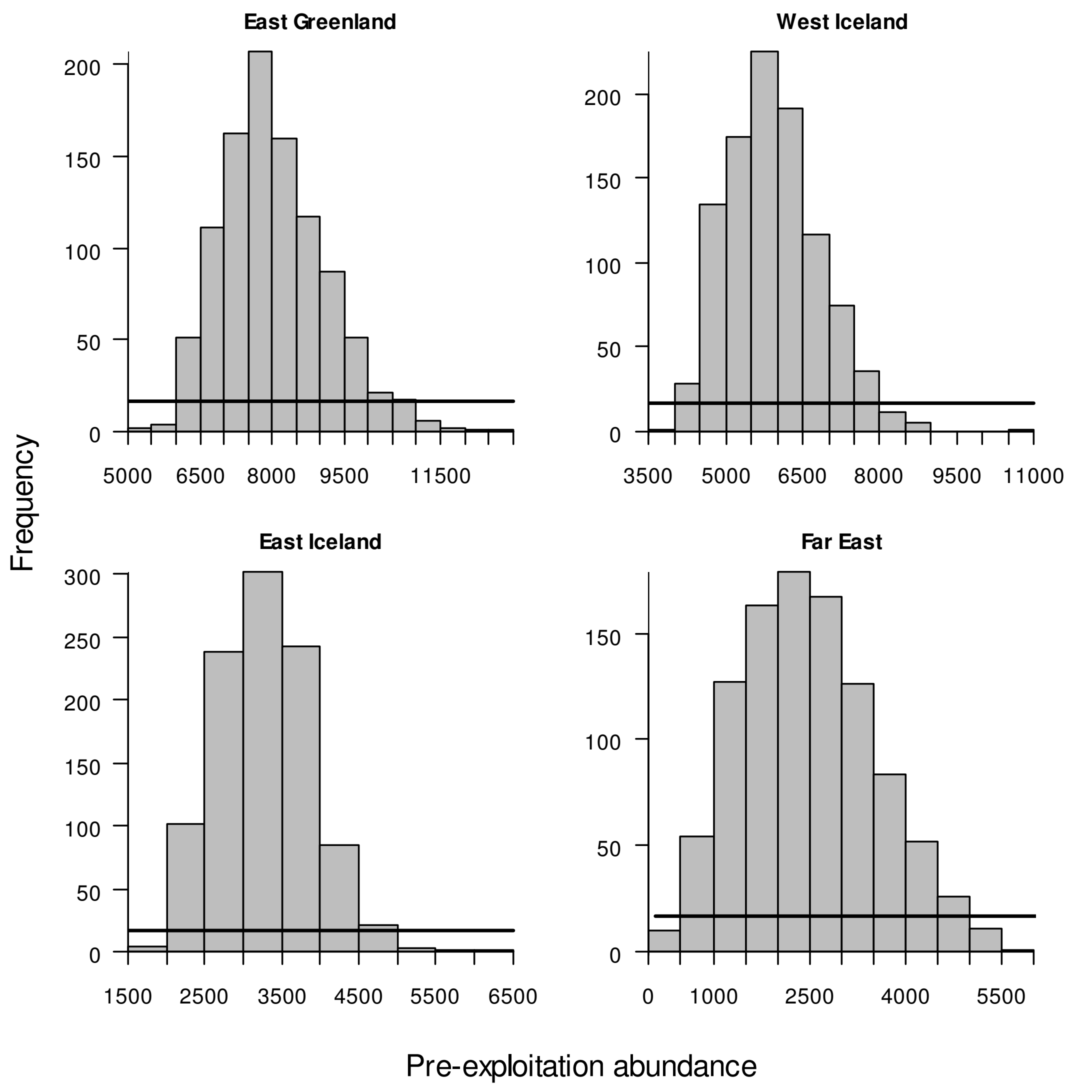

Figure 7. Prior (solid line) and posterior (histogram) distributions for pre-exploitation equilibrium recruited abundance in each of the four areas (parameters K_1 to K_4). The prior distribution was U(100; 30000) but is not shown in full as the horizontal axis has been truncated for clarity.

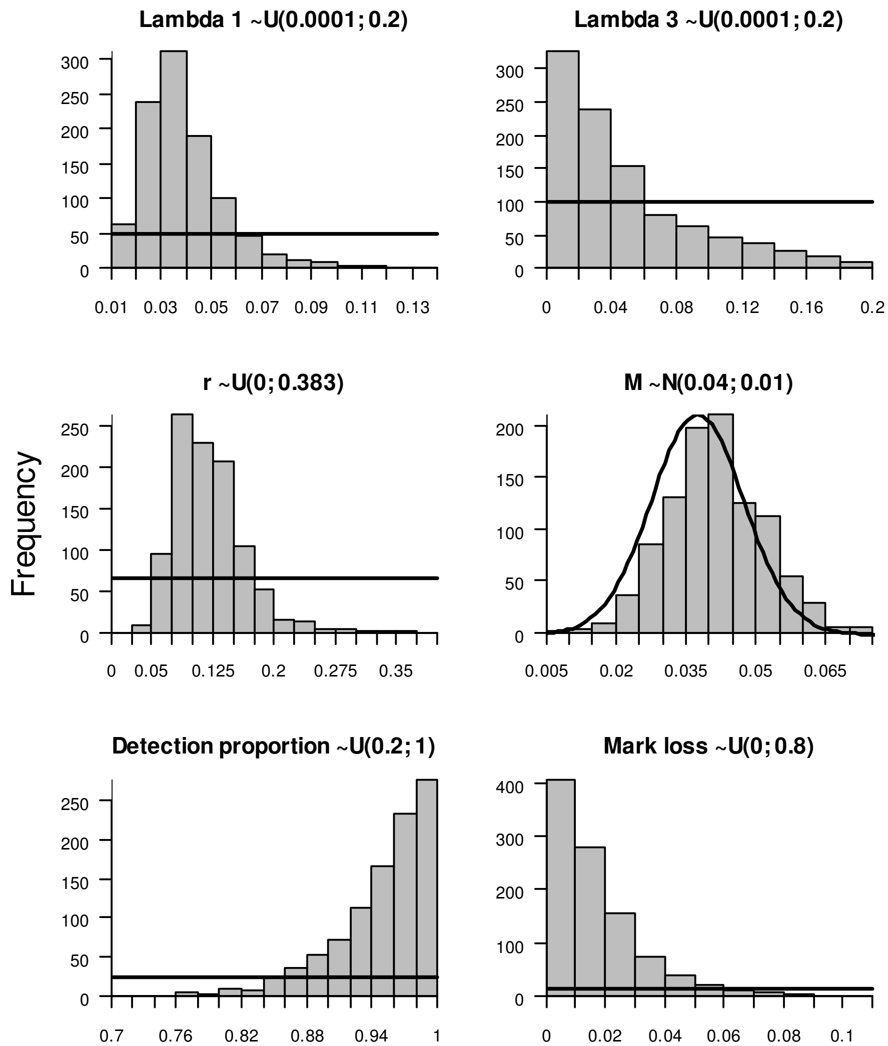

Figure 8. Prior (lines) and posterior (histograms) distributions for the eastward movement rate between area 1 and 2 (λ_1) and between areas 3 and 4 (λ_3), population growth rate parameter (*r*), natural mortality rate (*M*), tag detection proportion (ξ) and mark loss (and mark-associated additional mortality) rate (τ). Values used for prior distributions are shown in the panel captions, note that the horizontal axes are truncated for clarity in some panels.

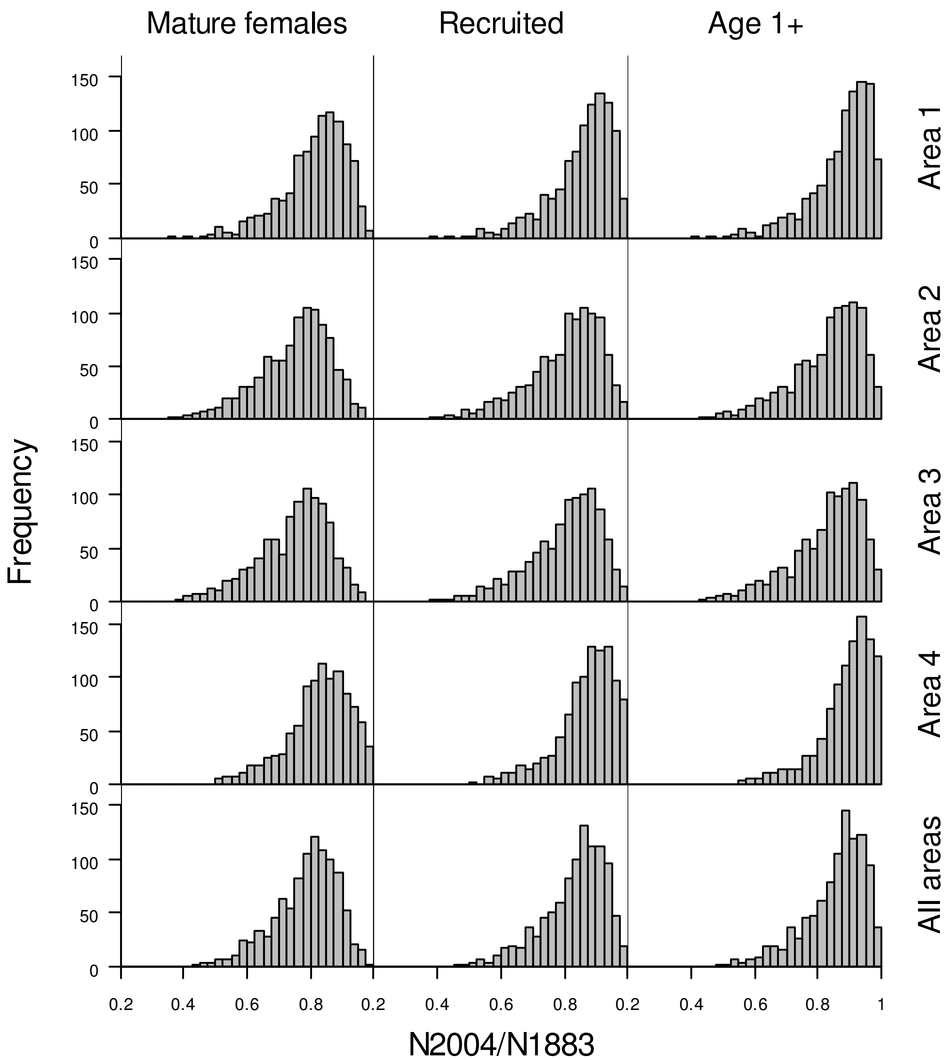

Figure 9. Posterior N_{2004}/N_{1883} ratios (depletions) for mature female, recruited and 1+ populations in each of the four areas and for all areas combined. The population was assumed to be at pre-exploitation equilibrium in 1883.

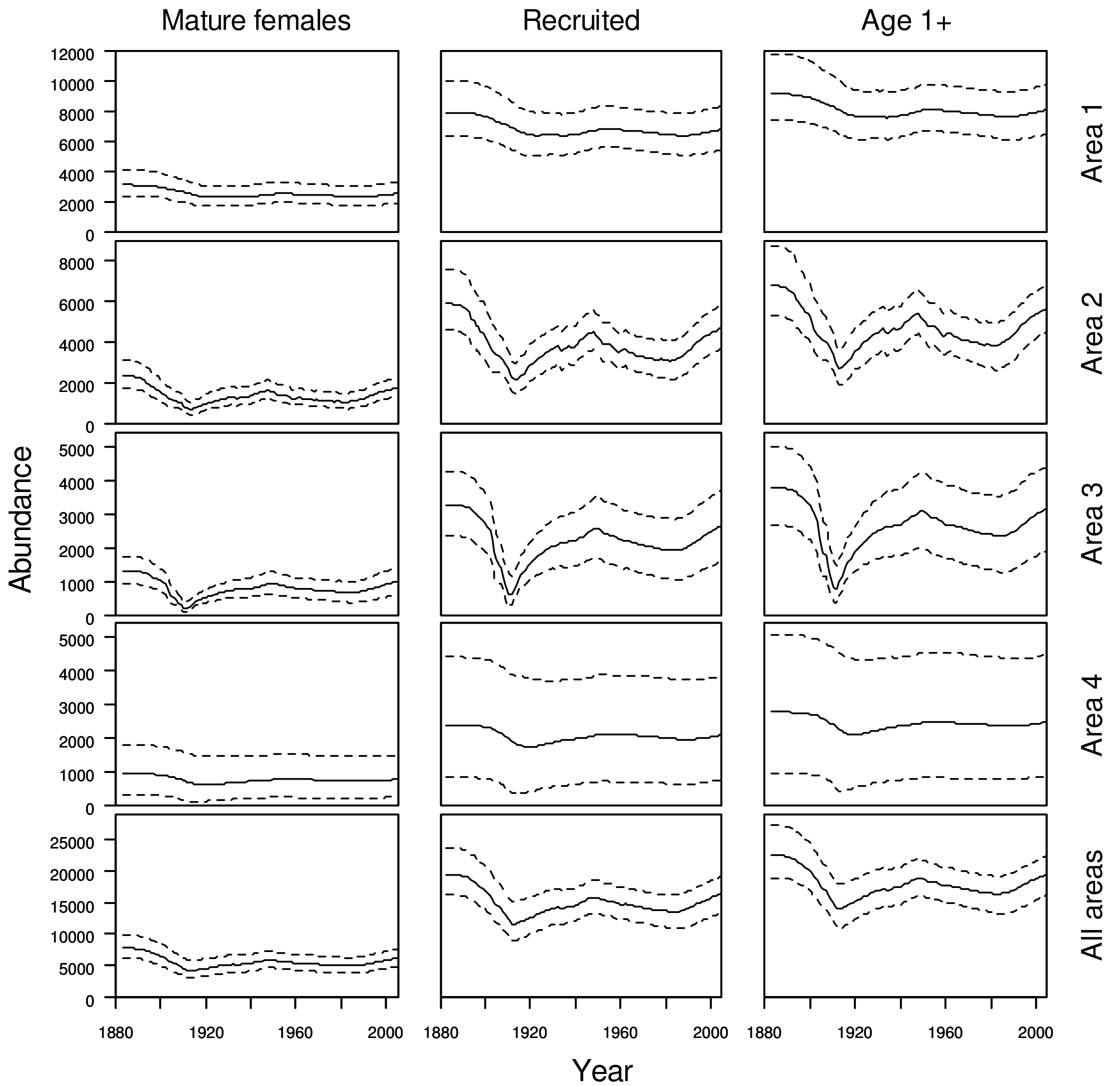

Figure 10. Posterior trajectories for 1+ and recruited (males and females) and mature (females only) abundance in each of the four areas and for all areas combined. The solid line shows the posterior median, and the dashed lines the 90% posterior credibility interval envelope.

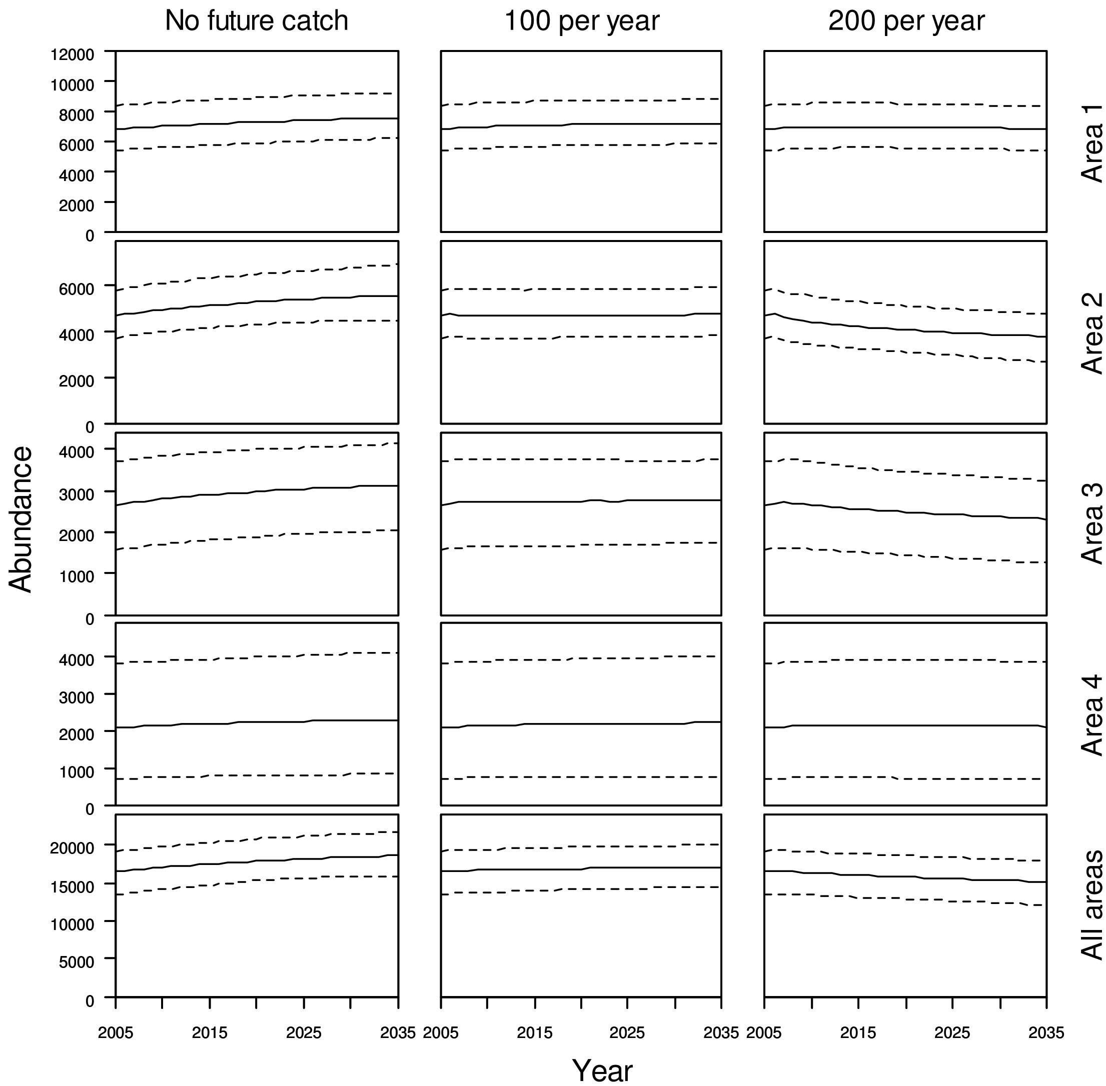

Figure 11. Future projections of recruited abundance in each area given catches of zero, 100 and 200. Catches were assumed to be 54.2% females and to be taken solely from area 2.