

Assessment runs for harbour porpoise in West Greenland

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ABSTRACT

I use an abundance estimate from 2007, historical catches starting from 1975, age-structure data from three periods, and an age- and sex-structured population model with exponential or density regulated growth to perform Bayesian assessment runs for harbour porpoises (*Phocoena phocoena*) in West Greenland. These runs combine two different availability corrections of the abundance estimate, with three different estimates of the historical catches, to provide initial runs that inform on the possible population dynamics of harbour porpoises in West Greenland.

INTRODUCTION

In this paper we build population models in order to examine the population dynamics of harbour porpoises (*Phocoena phocoena*) in West Greenland. The modelling framework is sex and age-structured, and it is used to reconstruct the historical trajectories from 1975 to 2020 based on abundance, catch and age-structure data. The underlying dynamics is assumed to be either unchecked exponential growth or density regulated dynamics.

Our modelling is based on Bayesian statistics (Berger 1985; Press 1989), which is particularly useful when faced with limited or uncertain information. Major data uncertainties are often associated with life-history estimates, imprecise abundance estimates, additional variation in time-series of abundance estimates, and catch histories with uncertain loss and reporting rates. Our description of the dynamics aim to incorporate these uncertainties, and we use Bayes factor ratios in an attempt to identify the population dynamic model/s that provide the best description of the dynamics.

At the end we recalculate the uncertainty into management related estimates, including a trade-off space between assumed future catches and the probabilities of fulfilling a specified management objective. The method is useful in the sense that it integrates uncertainties on many factors into a single one-dimensional trade-off space with particular reference to management issues.

Year	N_a	N_b
2007	275000 (39)	50500 (39)

Table 1: **Abundance** estimates with CV in parenthesis (given in %). N_a is a zero meter depth corrected abundance estimate. N_b is a one meter depth corrected abundance estimate. Data from Heide-Jørgensen (2013) and Heide-Jørgensen et al. (2013).

METHOD

Abundance data

The available abundance data are listed in Table 1.

The population dynamic analysis is based on 2 data sets on the summer abundance West Greenland. These are a 2007 estimate based on zero meter depth availability correction [denoted N_a , from Heide-Jørgensen et al. (2013)] and a 2007 estimate based on a one meter depth availability correction [N_b , from Heide-Jørgensen (2013)].

Age structure

The population dynamic models are also fitted to 3 distributions of the age-structure. These are an age structure of the catches from 1989 [Lockyer et al. (2003); 67 individuals; data subscript c], an age structure of the catches from 1995 [Lockyer et al. (2003); 103 individuals; data subscript d], and an age structure of the catches from 2009 [Heide-Jørgensen et al. (2011); 84 individuals; data subscript e].

The age-structures are shown in Figure 9, and they are assumed to be random samples of the catch.

Catch data

Catch histories are shown in Figure 1, and listed in full length in the supplement part of the paper.

The population dynamic analysis is based on 3 catch histories. These are a low catch history (Nielsen and Heide-Jørgensen 2013), a high catch history (Nielsen and Heide-Jørgensen 2013), and a medium catch history (Nielsen and Heide-Jørgensen 2013).

The low catch history uses the reported catches from 1955 to 1980, together with the reported catches from 1993 to 2012, with the 2011 and 2012 catch corrected for animals not reported in Maniitsoq. The 2012 catch is also corrected for expected catches in October to December (which were not included in the date), and the 2013 catch is assumed to be the same as in 2012. The two series (1955 to 1980, and 1993 to 2012) are combined by a straight line between a 1981 catch assumed to be equal to the average catch from 1976 to 1981, and a 1992 catch assumed to be equal to the average catch from 1993 to 1997.

The high catch history applies a 1.8 multiplication factor to the reported catches from 1993 to 2012, and it scales all the catches from 1995 to 1980 by a factor, obtained by assuming that the average catch from 1976 to 1980 is equal to the average catch from

M	\tilde{p}_0	\tilde{p}_1	\tilde{p}_2	\tilde{p}_3	\tilde{p}_4	\tilde{p}_5	\tilde{p}_6	\tilde{p}_7	\tilde{p}_8	\tilde{p}_9	\tilde{p}_{10+}
e0	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1
e1	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1
e1x	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1
d0	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1
d1	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1
d1x	-	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1

Table 2: **Age-structured relative survival.** The relative survival \tilde{p}_a of age-class a , is given ($m|f$) for males (m) and females (f) seperatedly. Models (M) are indicated by symbols, and - indicate that $\tilde{p}_0 \leq 1$ is a prior with $p_0 = \tilde{p}_0 p_1$.

1993 to 1997. All the catches from 1981 to 1992 are also set to this average. The 2012 catch is also corrected for expected catches in October to December, and the 2013 catch is assumed to be the same as in 2012.

The medium catch history uses the reported catches from 1955 to 1980, together with estimated catches from 1993 to 2012, obtained by multiplying the reported catches by 1.8 to correct for unreported animals. The 2012 catch is also corrected for expected catches in October to December, and the 2013 catch is assumed to be the same as in 2012. The two series (reported 1955 to 1980, and estimated 1993 to 2012) are combined by a straight line between a 1981 catch assumed to be equal to the average reported catch from 1976 to 1981, and a 1992 catch assumed to be equal to the average estimated catch from 1993 to 1997.

Population dynamics

Two different models of population dynamics were applied. A model of exponential growth was used as the simplest realistic population model to estimate trends and production potentials, assuming that a stable yearly production is realistic. A second model of density regulated growth was applied to allow for estimates of current and historical depletion levels, should the population dynamics under constant environmental conditions be monotonically returning towards equilibrium.

Let x be the maximum lumped age-class. Let the number $N_{a,t+1}^{m/f}$ of males (m) and females (f) in age-classes $0 < a < x$ in year $t + 1$ be

$$N_{a+1,t+1}^{m/f} = p_a^{m/f} N_{a,t}^{m/f} - c_{a,t}^{m/f} \quad (1)$$

and the number of animals in age-class x be

$$N_{x,t+1}^{m/f} = p_x^{m/f} N_{x,t}^{m/f} + p_{x-1}^{m/f} N_{x-1,t}^{m/f} - c_{x,t}^{m/f} - c_{x-1,t}^{m/f} \quad (2)$$

where $p_a^{m/f}$ is the age specific survival rate of males/females, and $c_{a,t}^{m/f}$ is the age specific catch of males/females in year t . The age and gender (g) dependent survival rates $p_a^g = p \tilde{p}_a^g$ are given as a product between a survival scalar p and a relative ($0 < \tilde{p}_a^g \leq 1$) survival rate, with the sex and age structure of the relative survival rates being given in Table 2. The age

M	\tilde{b}_m	\tilde{b}_{m+1}	\tilde{b}_{m+2}	\tilde{b}_{m+3}	\tilde{b}_{m+4}	\tilde{b}_{m+5}	\tilde{b}_{m+6}	\tilde{b}_{m+7}	\tilde{b}_{m+8}	\tilde{b}_{m+9}	\tilde{b}_{m+10+}
e0	1	1	1	1	1	1	1	1	1	1	1
e1	1	1	1	1	1	1	1	1	1	1	1
e1x	1	1	1	1	1	1	1	1	1	1	1
d0	1	1	1	1	1	1	1	1	1	1	1
d1	1	1	1	1	1	1	1	1	1	1	1
d1x	1	1	1	1	1	1	1	1	1	1	1

Table 3: **Age-structured relative birth rate.** The relative birth rate \tilde{b}_a for females in age-class a . Models (M) are indicated by symbols.

and gender specific catches $c_{a,t}^{m/f} = c_t^{m/f} \tilde{c}_{a,i}^{m/f}$ in year t is given as a product between the total catch of males/females ($c_t^{m/f}$), as specified by the catch history, and an age-specific catch selectivity against the take of younger individuals

$$\tilde{c}_{a,i}^{m/f} = \frac{1 - e^{s_i a}}{1 - e^{s_i a_{s,i}}} \quad (3)$$

where a is age, $s_i \neq 0$ the selectivity parameter for data age-structure distribution i (convex selection when $s_i < 0$, concave when $s_i > 0$, and approximately linear when $s_i \approx 0$), and $a_{s,i} - 1$ the last age-class with selection, i.e., $\tilde{c}_{a,i}^{m/f} = 1$ for $a \geq a_{s,i}$. Each age-structure i gives an estimate s_i for the year of the age-structure, and s_t over time is then determined as a linear function between the s_i estimates.

The number of females and males in age-class zero is $N_{0,t}^f = \vartheta N_{0,t}$ and $N_{0,t}^m = (1 - \vartheta)N_{0,t}$, where ϑ is the fraction of females at birth, and

$$N_{0,t} = \sum_{a=a_m}^x B_{a,t} \quad (4)$$

where a_m is the age of the first reproductive event and $B_{a,t}$, the number of births from females in age class a , is

$$B_{a,t} = b_{a,t} \tilde{b}_a M_{a,t}^f \quad (5)$$

where $b_{a,t}$ is the birth rate in year t for age-class a females should they be at their age-specific reproductive peak, $0 < \tilde{b}_a \leq 1$ is the relative age-specific birth rate (given in Table 3), and $M_{a,t}^f$ is the number of mature females in age-class a in year t , defined as

$$M_{a,t}^f = \begin{cases} 0 & \text{if } a < a_m \\ N_{a,t}^f & \text{if } a \geq a_m \end{cases} \quad (6)$$

Let $b_{a,t}$ be

$$\begin{aligned} b_{a,t} &= b && \text{for exponential growth} \\ b_{a,t} &= b^* + [b_{max} - b^*][1 - (\hat{N}_t/\hat{N}^*)^\gamma] && \text{for density regulated growth} \end{aligned} \quad (7)$$

where b is a constant birth rate, b^* is the birth rate at population dynamic equilibrium (assuming zero catch and equilibrium denoted by $*$), b_{max} is the maximal birth rate, γ is

the density dependence parameter, and the abundance component that imposes density dependence is the one-plus component

$$\hat{N}_t = \sum_{a=1}^x N_t^f + N_t^m \quad (8)$$

Given a stable age-structure and no catch, let, for a traditional model of exponential or density regulated growth, λ be a constant defined by $\hat{N}_{t+1} = \lambda\hat{N}_t$. The sustainable yield is then $sy = \hat{N}(\lambda - 1)$, and for the density regulated model there is an optimum $\partial sy / \partial \hat{N} = 0$; the maximum sustainable yield (msy) at \hat{N}_{msy} , also known by the maximum sustainable yield rate ($msyr = msy / \hat{N}_{msy}$) and the maximum sustainable yield level ($msyl = \hat{N}_{msy} / \hat{N}^*$).

Assessment models

The population dynamic description is based on the 6 assessment models that are described in this subsection.

Exponential growth (e0): With the high abundance estimate based on zero depth correction, and a uniform catch prior ranging from the low to the high catch history.

Exponential growth (e1): With the low abundance estimate based on one meter depth correction, and catches fixed at the medium catch history.

Exponential growth (e1x): With the low abundance estimate based on one meter depth correction, and catches fixed at the low catch history.

Density regulated growth (d0): With the high abundance estimate based on zero depth correction, and a uniform catch prior ranging from the low to the high catch history.

Density regulated growth (d1): With the low abundance estimate based on one meter depth correction, and catches fixed at the medium catch history.

Density regulated growth (d1x): With the low abundance estimate based on one meter depth correction, and catches fixed at the low catch history.

Statistical methods

The assessment models were fitted to data by projecting the population under the influence of the historical catches, with the initial abundance reflecting, dependent upon the model, a pre-harvested population in dynamic equilibrium or an abundance prior for the first year of the iteration. A Bayesian statistical method (e.g, Berger 1985; Press 1989) was used, and posterior estimates of model parameters and other management related outputs were calculated. This implied an integration of the product between a prior distribution for each parameter and a likelihood function that links the probability of the data to the different parameterisations of the model.

M	N_0	N^*	p	p_0	b	a_m	ϑ	γ
e0	10,1000 ^U	-	.75,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	-
e1	5,300 ^U	-	.75,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	-
e1x	1,300 ^U	-	.7,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	-
d0	10,800 ^U	100,2000 ^U	.7,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	1.5,5 ^u
d1	5,400 ^U	50,1000 ^U	.7,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	1.5,5 ^u
d1x	5,400 ^U	50,1000 ^U	.7,.9 ^u	.7,.9 ^u	.85,1 ^u	3,5 ^u	.5	1.5,5 ^u

M	c_h	s_c	s_d	s_e	$a_{s,c}$	$a_{s,d}$	$a_{s,e}$
e0	0,1 ^u	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u
e1	-	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u
e1x	-	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u
d0	0,1 ^u	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u
d1	-	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u
d1x	-	-1,.6 ^u	-1,.6 ^u	-0.7,.7 ^u	0,5 ^u	0,4 ^u	2,8 ^u

Table 4: **Prior distributions** for the different models (M). The list of parameters: N_0 is the initial abundance, N^* the population dynamic equilibrium abundance, p the yearly survival, p_0 the first year survival, b the birth rate, a_m the age of the first reproductive event, ϑ the female fraction at birth, γ the density regulation, c_h the catch history, s_i the age-structured selectivity (i : data reference), and $a_{s,i}$ the maximum age with age-structured selectivity (i : data reference). Abundance is given in thousands. The prior probability distribution is given by superscripts; p : fixed value, u : uniform (min,max), and U : log uniform (min,max).

Prior distributions

The values and prior distributions of the different parameters for all the assessment models are listed in Table 4.

Bayesian integration

The Bayesian integration was obtained by the sampling-importance-resampling routine (Jeffreys 1961; Berger 1985; Rubin 1988), where n_s random parameterisations θ_i ($1 \leq i \leq n_1$) are sampled from an importance function $h(\theta)$. This function is a probability distribution function from which a large number, n_s , of independent and identically distributed draws of θ can be taken. $h(\theta)$ shall generally be as close as possible to the posterior, however, the tails of $h(\theta)$ must be no thinner (less dense) than the tails of the posterior (Oh and Berger 1992). For each drawn parameter set θ_i the population was projected from the first year with a harvest estimate to the present. For each draw an importance weight, or ratio, was then calculated

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)} \quad (9)$$

where $L(\theta_i)$ is the likelihood given the data, and $h(\theta_i)$ and $p(\theta_i)$ are the importance and prior functions evaluated at θ_i . In the present study the importance function is set to

the joint prior, so that the importance weight is given simply by the likelihood. The n_s parameter sets were then re-sampled n_r times with replacement, with the sampling probability of the i th parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_s} w(\theta_j)} \quad (10)$$

This generates a random sample of the posterior distribution of size n_r .

The log likelihood ($\ln L = \ln L_n + \ln L_a$) was given as a sum between an abundance ($\ln L_n$) and an age-structured ($\ln L_a$) component. The method of de la Mare (1986) was used to calculate the abundance component under the assumption that observation errors are log-normally distributed (Buckland 1992)

$$\ln L_n = \sum_i \sum_t -[\ln(\hat{N}_{i,t}/\beta_i N_t)]^2/2\text{CV}_{i,t}^2 - \ln \text{CV}_{i,t} \quad (11)$$

where $\hat{N}_{i,t}$ is the point estimate of the i th set of abundance data in year t , $\text{CV}_{i,t}$ is the coefficient of variation of the estimate, N_t is the simulated abundance, and β_i a bias term with is set to one for absolute abundance estimates. Following Punt (2006), the age-structure was assumed to be a multinomially distributed, with

$$\ln L_a = \sum_i n_i \sum_a \hat{c}_{i,t,a} \ln(c_{t,a}/\hat{c}_{i,t,a}) \quad (12)$$

where i denote the i th set of age-structured data (which were sampled in year t), n_i is the number of individuals in the sample, $\hat{c}_{i,t,a}$ the observed fraction of individuals in age class a in year t , and $c_{t,a}$ the fraction simulated by the model.

If the importance function is adequately specified, the mean of the importance sample for each parameter should approach the mean from the true posterior distribution, given a sufficiently large sample. To illustrate whether the sampled posterior quantities can be assumed to be representative of the true posterior distribution, convergence diagnostics were calculated. One such diagnostic is the maximum importance weight of a parameter set relative to the total summed importance weight over all n_s draws. McAllister et al. (2001) suggest that the maximum importance weight needs to have dropped below 1% of the total sum. And in line with Wade (2002), we also calculated the total number of unique parameter sets in the resample of n_r parameter sets, as well the maximum number of occurrences of a unique parameter set in the resample.

Models that are based on the same data are compared by Bayes factor K (Jeffreys 1961; Kass and Raftery 1995), in order to investigate if some models provide better descriptions of the data than others. The factor is calculated here as the ratio of the harmonic means of the likelihoods in the posterior distributions of the two models.

RESULTS

Sample and resample statistics are given in Table 5. The maximum importance weight of a parameter set relative to the sum of importance weights for all the sampled sets was

M	n_S	n_R	Weight	Unique	Max
e0	500	1	0.783	710	9
e1	500	1	1.928	474	24
e1x	500	1	0.2853	495	28
d0	500	1	0.601	717	8
d1	1000	1	1.197	661	17
d1x	500	1	1.767	646	20

Table 5: **Sampling statistics** for the different models (M). The number of parameter sets in the sample (n_S) and the resample (n_R), the maximum importance weight of a draw relative to the total importance weight of all draws, the number of unique parameter sets in the resample, and the maximum number of occurrences of a unique parameter set in the resample. n_S and n_R are given in thousands.

between 28.5% (Exponential growth model) and 193% (Exponential growth model) across all models. The proportion of unique parameter sets in the resample of a model was between 47.4% (Exponential growth model) and 71.7% (Density regulated growth model), and the maximum number of occurrences of a unique parameter set in the resample between 8 (Density regulated growth model) and 28 (Exponential growth model).

Posterior distributions

The realised prior and posterior distributions are shown in Figures 2 to 7. With n being the number of bin intervals for the distributions, and $p_{r,i}$ and $p_{s,i}$ being density weight of the prior and the posterior at the i th bin, $u = \frac{1}{n} \sum_{i=1}^n \frac{|p_{s,i} - p_{r,i}|}{p_{s,i} + p_{r,i}}$ gives the updating of the posterior by the data, with $u = 0$ representing no updating and complete overlap between the two distributions, and $u = 1$ representing no overlap and a complete updating. Apart from being well updated a successful posterior should also be well bounded, with the posterior/prior weight-ratio ($w_i = p_{s,i}/p_{r,i}$) at the lower ($i = 0$) and upper ($i = n$) limits of the distributions approaching zero.

Because of the type of biological information available in abundance and age-structured data, it is only for the abundance parameters (N_0, N^*) that we will set up some minimum criterion for an acceptable model. Only models with a well updated posterior ($w_i < 0.5$ and $u > 15\%$) for the abundance will be taken as an acceptable description of a population. Owing to the presence of absolute abundance estimates, we should expect well updated abundance parameters.

Relating to the other parameters, we cannot expect the posterior distributions of the life-history parameters (p, p_0, b, a_m) to be well updated by the available data, but we might expect some updating of the growth rate parameters (r , msyr) because of the age-structured data.

The abundance estimates for the **Exponential growth** (e0) model in Figure 2 could not be accepted. It is weakly (23%) updating the initial abundance (N_0), and the parameter is not well defined to the right where the posterior is slightly wider than the

prior.

The abundance parameters for the **Exponential growth** (e1) model in Figure 3 is not acceptable. It has a substantial (33%) updating of the initial abundance (N_0), and the parameter is strongly defined to the left where the posterior is very clearly narrower than the prior.

The abundance estimates for the **Exponential growth** (e1x) model in Figure 4 could not be accepted. It is strongly (52%) updating the initial abundance (N_0), but the prior is slightly narrower than the posterior to the right.

The **Density regulated growth** (d0) model in Figure 5 was accepted. The initial abundance (N_0) has a substantial (40%) updating, and the parameter is strongly defined, the posterior is very clearly narrower than the prior in both ends. There is a substantial (41%) updating of the population dynamic equilibrium abundance (N^*); the posterior is slightly wider than the prior to the right. The updating of the exponential growth rate (r) is weak (22%); the prior is slightly narrower than the posterior to the left. The maximum sustainable yield rate (msyr) is substantially (25%) updated; the posterior is slightly wider than the prior to the left. The life-history parameters (p , p_0 , b , a_m) have a strong (52%) updating. There is a substantial (48%) updating of the yearly survival (p); the parameter is badly defined to the left where it is clear that the prior is narrower than the posterior. The first year survival (p_0) has a substantial (47%) updating, and the parameter is badly defined to the right where the posterior is wider than the prior. The updating of the birth rate (b) is substantial (34%); the parameter is badly defined to the right where the prior is narrower than the posterior. The age of the first reproductive event (a_m) has a strong (79%) updating, but the parameter is badly defined to the left where it is clear that the posterior is wider than the prior. The updating of the density regulation (γ) is very weak (10%), and the parameter is not well defined to the right where the prior is slightly narrower than the posterior. The maximum sustainable yield level (msyl) is hardly (12%) updated; the parameter is not well defined to the right where the posterior is slightly wider than the prior. There is hardly any (10%) updating of the catch history (c_h); the parameter is not well defined because the posterior is slightly wider than the prior in both ends. The age-structured selectivity (s_c) has a weak (20%) updating, and the parameter is not well defined to the left where the prior is slightly narrower than the posterior. There is a weak (16%) updating of the age-structured selectivity (s_d); the parameter is not well defined to the left where the posterior is slightly wider than the prior. The age-structured selectivity (s_e) has a weak (24%) updating; the parameter is somewhat defined, the prior is slightly wider than the posterior in both ends. The maximum age with age-structured selectivity ($a_{s,c}$) is hardly (14%) updated, and the posterior seems not to be well updated in both ends. The updating of the maximum age with age-structured selectivity ($a_{s,d}$) is weak (20%); the posterior is not well updated in both ends. There is a substantial (29%) updating of the maximum age with age-structured selectivity ($a_{s,e}$), and the parameter is well defined to the right where the prior is slightly wider than the posterior.

The abundance parameters for the **Density regulated growth** (d1) model in Figure 6 is acceptable. The initial abundance (N_0) is strongly (56%) updated; the posterior is

very clearly narrower than the prior in both ends. The population dynamic equilibrium abundance (N^*) has a weak (21%) updating, and the parameter is not well defined to the right where the posterior is slightly wider than the prior. The exponential growth rate (r) is substantially (25%) updated, and the prior is slightly narrower than the posterior to the left. The maximum sustainable yield rate (msyr) has a weak (19%) updating; the parameter is not well defined because the prior is slightly narrower than the posterior in both ends. The life-history parameters (p , p_0 , b , a_m) are strongly (50%) updated. There is a substantial (49%) updating of the yearly survival (p), and the parameter is well defined to the right where the prior is only slightly wider than the posterior. The updating of the first year survival (p_0) is substantial (43%), and the posterior is wider than the prior to the right. The birth rate (b) has a substantial (30%) updating, and the parameter is badly defined to the right where the prior is narrower than the posterior. There is a strong (79%) updating of the age of the first reproductive event (a_m), but the posterior is wider than the prior to the left. The updating of the density regulation (γ) is very weak (9%), and the parameter is not well defined because the posterior is slightly wider than the prior in both ends. There is hardly any (15%) updating of the maximum sustainable yield level (msyl), and the prior is not well updated in both ends. The age-structured selectivity (s_c) is weakly (23%) updated; the parameter is badly defined to the left where the posterior is wider than the prior. The updating of the age-structured selectivity (s_d) is very weak (11%), and the prior is not well updated in both ends. The age-structured selectivity (s_e) is substantially (42%) updated, and the posterior is narrower than the prior, especially to the left. The updating of the maximum age with age-structured selectivity ($a_{s,c}$) is weak (18%), and the prior is slightly narrower than the posterior in both ends. There is a weak (21%) updating of the maximum age with age-structured selectivity ($a_{s,d}$), and the prior seems not to be well updated in both ends. The updating of the maximum age with age-structured selectivity ($a_{s,e}$) is substantial (33%); the parameter is strongly defined to the left where it is very clear that the posterior is narrower than the prior.

The abundance estimates for the **Density regulated growth** (d1x) model in Figure 7 was accepted. The initial abundance (N_0) is strongly (55%) updated; the prior is very clearly wider than the posterior in both ends. The population dynamic equilibrium abundance (N^*) has a weak (22%) updating; the posterior is slightly wider than the prior to the right. The exponential growth rate (r) is weakly (22%) updated, and the prior is narrower than the posterior to the left. The updating of the maximum sustainable yield rate (msyr) is very weak (10%), and the parameter is badly defined to the left where the prior is narrower than the posterior. There is a strong (51%) updating of the life-history parameters (p , p_0 , b , a_m). The yearly survival (p) is substantially (47%) updated, and the parameter is badly defined to the left where it is clear that the posterior is wider than the prior. There is a substantial (47%) updating of the first year survival (p_0); it is clear that the prior is narrower than the posterior to the right. The birth rate (b) has a substantial (35%) updating; the prior is narrower than the posterior to the right. The updating of the age of the first reproductive event (a_m) is strong (77%), but the parameter is badly defined to the left where the posterior is wider than the prior. The density regulation (γ) is hardly

(12%) updated; the posterior is not well updated in both ends. There is hardly any (15%) updating of the maximum sustainable yield level (msyl), and the prior is slightly narrower than the posterior to the right. The updating of the age-structured selectivity (s_c) is weak (19%); the prior is narrower than the posterior to the left. The age-structured selectivity (s_d) has a weak (16%) updating, and the prior is slightly narrower than the posterior to the left. The age-structured selectivity (s_e) is substantially (37%) updated, and the posterior is narrower than the prior in both ends. The maximum age with age-structured selectivity ($a_{s,c}$) has a weak (16%) updating, and the prior is only slightly wider than the posterior to the right. The maximum age with age-structured selectivity ($a_{s,d}$) is weakly (19%) updated; the parameter is well defined to the right where the posterior is slightly narrower than the prior. The maximum age with age-structured selectivity ($a_{s,e}$) has a weak (24%) updating; the posterior is narrower than the prior to the left.

Parameter estimates

The posterior parameter estimates and their 95% credibility intervals are given in Table 6. When the posterior distributions are not well updated from the realised prior, the estimates are given basically by the priors that go into the modelling. Only parameter estimates that are based on a well updated ($w_i < 0.5$ and $u > 15\%$) posterior distribution are considered below.

The updated parameter estimates in the **Density regulated growth** (d0) model are: an estimate of 130000 (95% CI:22000-440000) for the initial abundance (N_0); an estimate of the age-structured selectivity (s_e) of -0.021 (95% CI: $-0.61-0.62$).

The **Density regulated growth** (d1) model has the following updated parameter estimates: an estimate of 57000 (95% CI:16000-150000) for the initial abundance (N_0); the age-structured selectivity (s_e) is 0.043 (95% CI: $-0.42-0.5$).

The updated parameter estimates in the **Density regulated growth** (d1x) model are: the estimate of the initial abundance (N_0) is 45000 (95% CI:12000-110000); an estimate of the age-structured selectivity (s_e) of 0.0035 (95% CI: $-0.54-0.53$).

Population dynamics

The estimated population dynamic trajectories are shown in Figure 8.

The data can hardly differentiate between the 3 models. Nevertheless, it is the **Density regulated growth** (d1x) model that achieves most support. Relative to the other models, the **Density regulated growth** (d1x) model is hardly ($K = 1.12$) supported by Bayes factor over the **Density regulated growth** (d1) model and hardly ($K = 1.5$) supported over the **Density regulated growth** (d0) model. The **Density regulated growth** (d1x) model estimates the population trajectory from 1975 to 2020. The abundance of the population dynamic equilibrium was estimated to 300000 (95% CI:73000-930000) individuals. The population increased from an initial abundance of 45000 (95% CI:12000-110000) in 1975 to a maximum with 52000 (95% CI:24000-90000) individuals in 1995. It is expected that the abundance will decline to a projected population in 2020

with 24000 (95% CI:0-150000) individuals (assuming a post 2013 catch of 3042 per year). The depletion ratio in 2014 is estimated to 0.12 (95% CI:0.026-0.59), with an abundance of 37000 (95% CI:10000-110000) and a yearly replacement of 880 (95% CI:−300-9600) individuals. From 2009 to 2014 the population had on average declined by 1263 individuals per year.

Future catches

The trade-off space between future catches from 2014 to 2018 and the probability of meeting a specified management objective is shown in Table 7, for yearly catches between 600 to 4000. The management objective is assumed to be $N_{2018} > N_{2014}$.

M		N_0	N^*	r	msyr	p	p_0	b	a_m	γ	msyl
-e0	$x_{.5}$	130	-	.035	-	.82	.87	.96	3.3	-	-
	$x_{.025}$	21	-	-0.034	-	.77	.76	.87	3	-	-
	$x_{.975}$	900	-	.12	-	.89	.9	1	3.5	-	-
-e1	$x_{.5}$	45	-	.048	-	.84	.86	.95	3.3	-	-
	$x_{.025}$	13	-	-0.021	-	.77	.76	.86	3	-	-
	$x_{.975}$	250	-	.12	-	.9	.9	1	3.5	-	-
-e1x	$x_{.5}$	50	-	.029	-	.82	.87	.96	3.2	-	-
	$x_{.025}$	11	-	-0.037	-	.76	.76	.87	3	-	-
	$x_{.975}$	270	-	.11	-	.89	.9	1	3.5	-	-
+d0	$x_{.5}$	130	810	.035	.031	.82	.86	.96	3.2	3.4	.65
	$x_{.025}$	22	250	.0008	.00067	.79	.76	.87	3	1.6	.55
	$x_{.975}$	440	1900	.11	.1	.89	.9	1	3.5	4.9	.7
+d1	$x_{.5}$	57	290	.04	.035	.83	.86	.96	3.3	3.3	.64
	$x_{.025}$	16	87	.0013	.001	.79	.76	.87	3	1.5	.55
	$x_{.975}$	150	960	.11	.099	.89	.9	1	3.7	4.9	.7
+d1x	$x_{.5}$	45	300	.037	.032	.82	.87	.96	3.3	3.3	.64
	$x_{.025}$	12	73	.0013	.001	.79	.76	.87	3	1.6	.55
	$x_{.975}$	110	930	.11	.097	.89	.9	1	3.7	4.9	.7

M	c_h	N_t	d_t	\dot{r}_t	ry_t	s_c	s_d	s_e	$a_{s,c}$	$a_{s,d}$	$a_{s,e}$
-e0	.5	320	-	.034	11000	-0.47	-0.47	-0.072	2.1	1.7	4.3
	.028	140	-	-0.036	-6100	-0.97	-0.98	-0.58	.15	.15	2.4
	.97	750	-	.12	77000	.46	.5	.63	4.8	3.9	7.5
-e1	-	27	-	.047	1100	-0.45	-0.23	.046	2.3	1.7	5.6
	-	2.5	-	-0.049	-770	-0.96	-0.96	-0.41	.14	.15	3.3
	-	100	-	.63	10000	.46	.54	.53	4.9	3.9	7.7
-e1x	-	35	-	.021	680	-0.41	-0.3	-0.016	1.9	1.7	5.1
	-	6.2	-	-0.06	-1000	-0.97	-0.95	-0.52	.18	.26	2.7
	-	110	-	.11	10000	.52	.56	.51	4.9	3.7	7.8
+d0	.45	310	.41	.027	7800	-0.49	-0.44	-0.021	2.1	1.7	4.1
	.032	150	.13	-0.0013	-310	-0.98	-0.97	-0.61	.21	.11	2.4
	.97	620	.98	.099	52000	.51	.54	.62	4.8	3.8	7.5
+d1	-	24	.083	.036	760	-0.5	-0.3	.043	2.1	1.7	5.6
	-	2.8	.0075	-0.026	-400	-0.98	-0.95	-0.42	.089	.14	3.2
	-	79	.41	.56	7200	.53	.55	.5	4.9	3.8	7.7
+d1x	-	37	.12	.025	880	-0.49	-0.37	.0035	2	1.8	5
	-	10	.026	-0.018	-300	-0.97	-0.97	-0.54	.15	.14	2.7
	-	110	.59	.11	9600	.51	.5	.53	4.7	3.8	7.8

Table 6: **Parameter estimates** for the different models (M). Estimates are given by the median ($x_{.5}$) and the 95% credibility interval ($x_{.025}$ - $x_{.975}$) of the postreior distributions. Abundance is given in thousands. The selected models are indicated a superscript + and rejected models by superscript -.

M	⁻ e0	⁻ e1	⁻ e1x	⁺ d0	⁺ d1	⁺ d1x
ϑ	0.5	0.5	0.5	0.5	0.5	0.5
600	0.71	0.6	0.56	0.92	0.56	0.64
900	0.71	0.55	0.5	0.9	0.48	0.56
1200	0.69	0.48	0.44	0.88	0.42	0.49
1500	0.68	0.44	0.4	0.85	0.36	0.44
1800	0.67	0.41	0.37	0.82	0.29	0.36
2100	0.66	0.38	0.34	0.79	0.25	0.33
2400	0.65	0.36	0.31	0.77	0.21	0.29
2700	0.65	0.34	0.29	0.75	0.18	0.27
3000	0.64	0.3	0.28	0.73	0.17	0.23
3300	0.63	0.25	0.26	0.72	0.14	0.2
3600	0.62	0.21	0.25	0.7	0.11	0.18
3900	0.62	0.18	0.17	0.68	0.1	0.16

Table 7: **Catch objective trade-off.** The probability of meeting management objectives for the different models (M), given annual total removals between 600 and 4000 individuals in the period 2014 to 2018. ϑ gives the assumed female fraction in the removals. Selected models are indicated a superscript + and rejected models by superscript -.

REFERENCES

- Berger, J. O. 1985. *Statistical decision theory and Bayesian analysis*. Second ed. Springer-Verlag, New York.
- Buckland, S. T. 1992. Proposal for standard presentation of abundance estimates. *Report of the International Whaling Commission* 42:235.
- De la Mare, W. K. 1986. Fitting population models to time series of abundance data. *Report of the International Whaling Commission* 36:399–418.
- Heide-Jørgensen, M. P. 2013. Correction of at-surface abundance of harbour porpoises in West Greenland based on detection to 1 m depth. *NAMMCO/SC/20/HP/WP1*. Available from the North Atlantic Marine Mammal Commission (<http://www.nammco.no/>) .
- Heide-Jørgensen, M. P., M. Iversen, N. H. Nielsen, C. Lockyer, H. Stern and M. H. Ribergaard 2011. Harbour porpoises respond to climate change. *Ecology and Evolution* doi:10.1002/ece3.51.
- Heide-Jørgensen, M. P., N. H. Nielsen and K. B. Zinglensen 2013. Revised abundance estimate of harbour porpoise in West Greenland. *NAMMCO/SC/20/HP07*. Available from the North Atlantic Marine Mammal Commission (<http://www.nammco.no/>) .
- Jeffreys, H. 1961. *Theory of probability*. 3rd edition ed. Clarendon Press, Oxford.
- Kass, R. E., and A. E. Raftery 1995. Bayes factor. *Journal of the American Statistical Association* 90:773–795.
- Lockyer, C., M. P. Heide-Jørgensen, J. Jensen and M. J. Walton 2003. Life history and ecology of harbour porpoises (*Phocoena phocoena*) from West Greenland. *NAMMCO Scientific Publications* 5:177–194.
- McAllister, M. K., E. K. Pikitch and E. A. Babcock 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1871–1890.
- Nielsen, N. H., and M. P. Heide-Jørgensen 2013. Catch statistics for harbour porpoises in West Greenland including correction for unreported catches. *NAMMCO/SC/20/HP06*. Available from the North Atlantic Marine Mammal Commission (<http://www.nammco.no/>) .
- Oh, M. S., and J. O. Berger 1992. Adaptive importance sampling in Monte Carlo integration.. *Journal of Statistics and Computer Simulation* 41:143–168.
- Press, S. J. 1989. *Bayesian statistics: principles, models, and applications*. John Wiley, New York.
- Punt, A. E. 2006. Assessing the Bering-Chukchi-Beaufort Seas stock of bowhead whales using abundance data together with data on length or age. *The Journal of Cetacean Research and Management* 8:127–137.
- Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. pp. 395–402, In: J. M. Bernardo, M. H. DeGroot, D. V. Lindley, and A. M. Smith (eds.) *Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, 1–5 June 1987*. Clarendon Press, Oxford.
- Wade, P. R. 2002. A Bayesian stock assessment of the Eastern pacific gray whale using abundance and harvest data from 1967–1996. *The Journal of Cetacean Research and Management* 4:85–98.

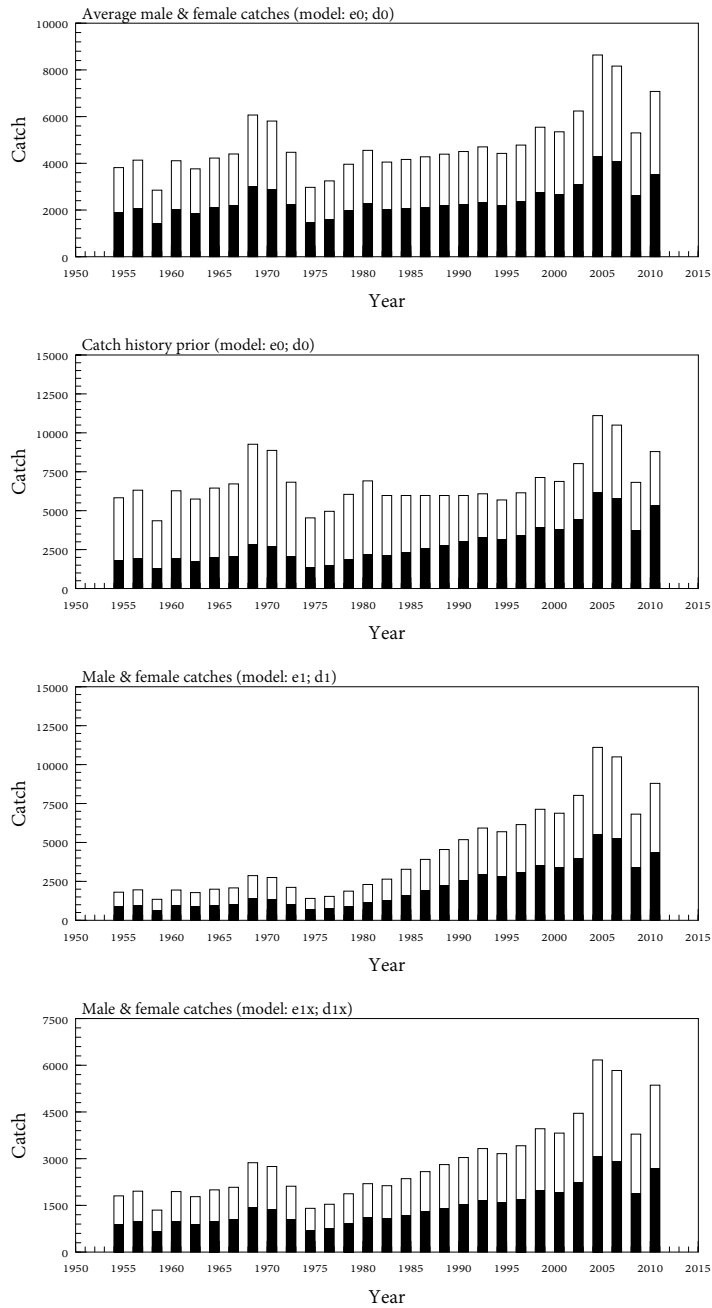


Figure 1: The historical catches of males (solid bars) and females (open bars), and prior range in total catches (minimum by solid bars; maximum by open bars). Data from Nielsen and Heide-Jørgensen (2013).

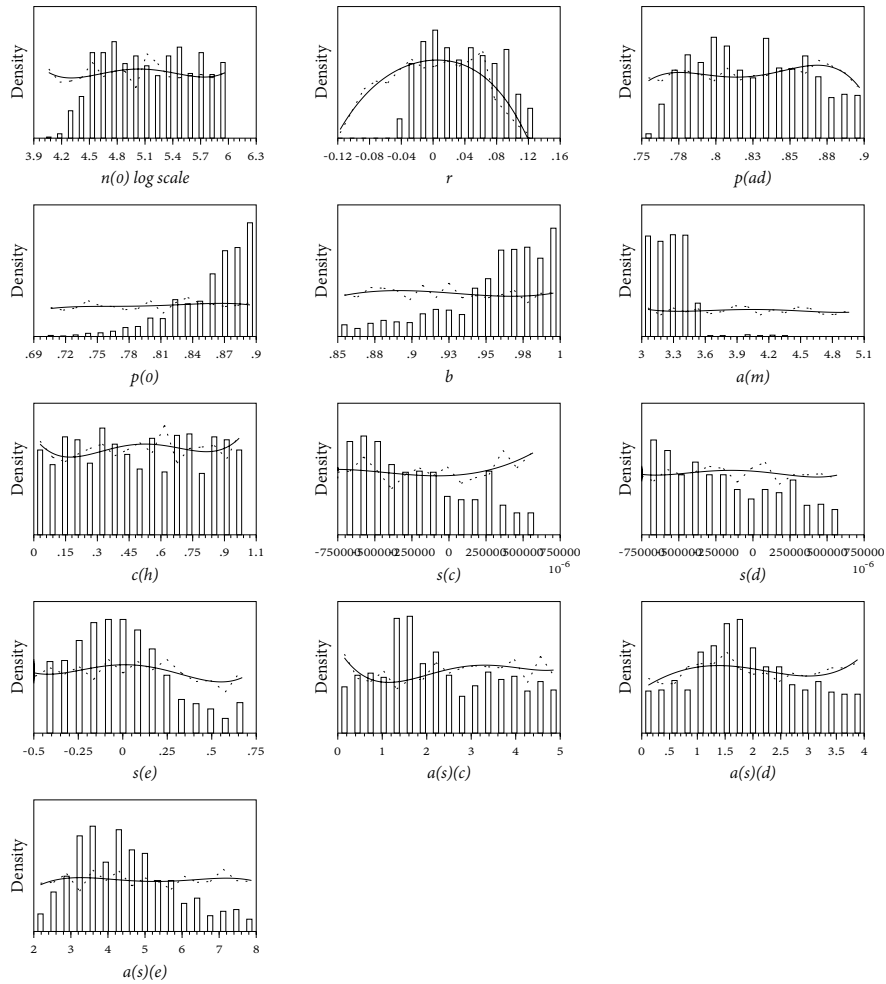


Figure 2: Realised prior (curve) and posterior (bars) distributions for model e0.

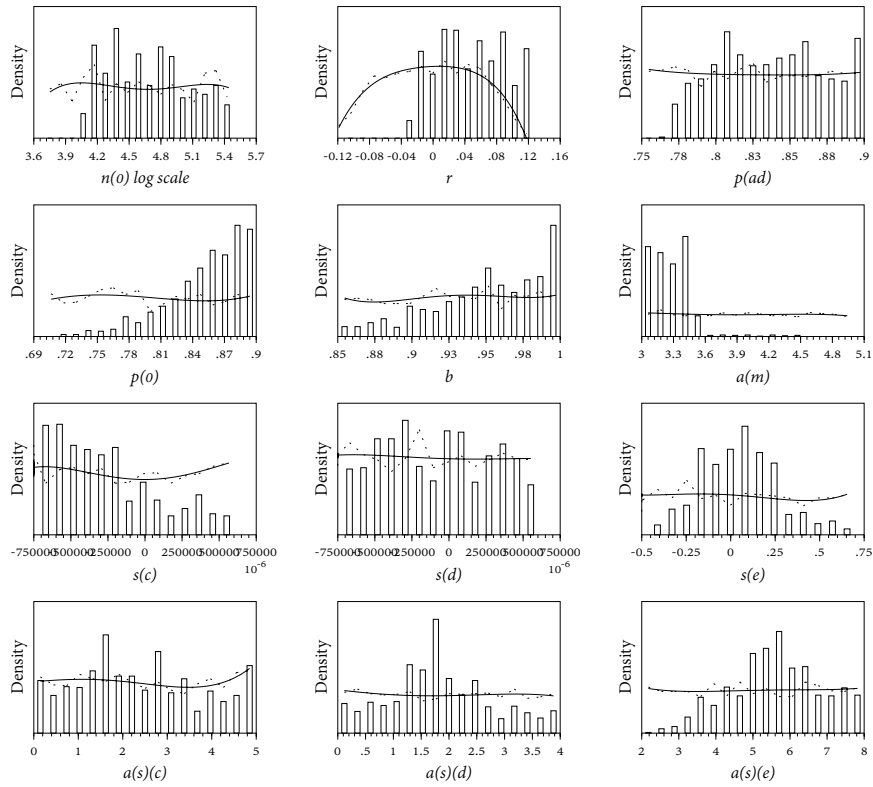


Figure 3: Realised prior (curve) and posterior (bars) distributions for model e1.

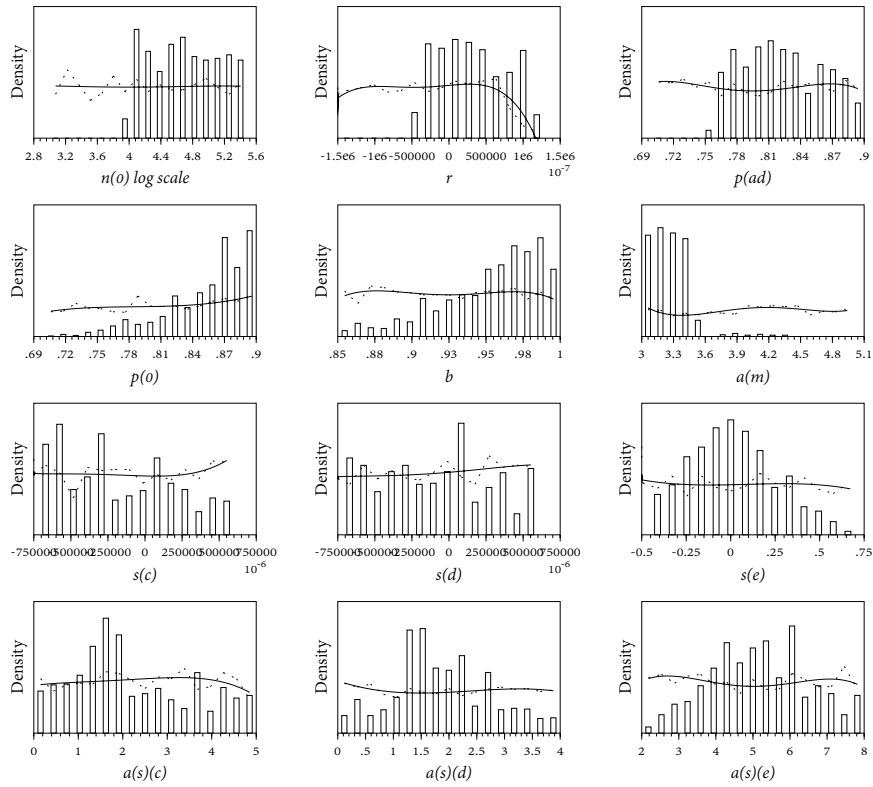


Figure 4: Realised prior (curve) and posterior (bars) distributions for model e1x.

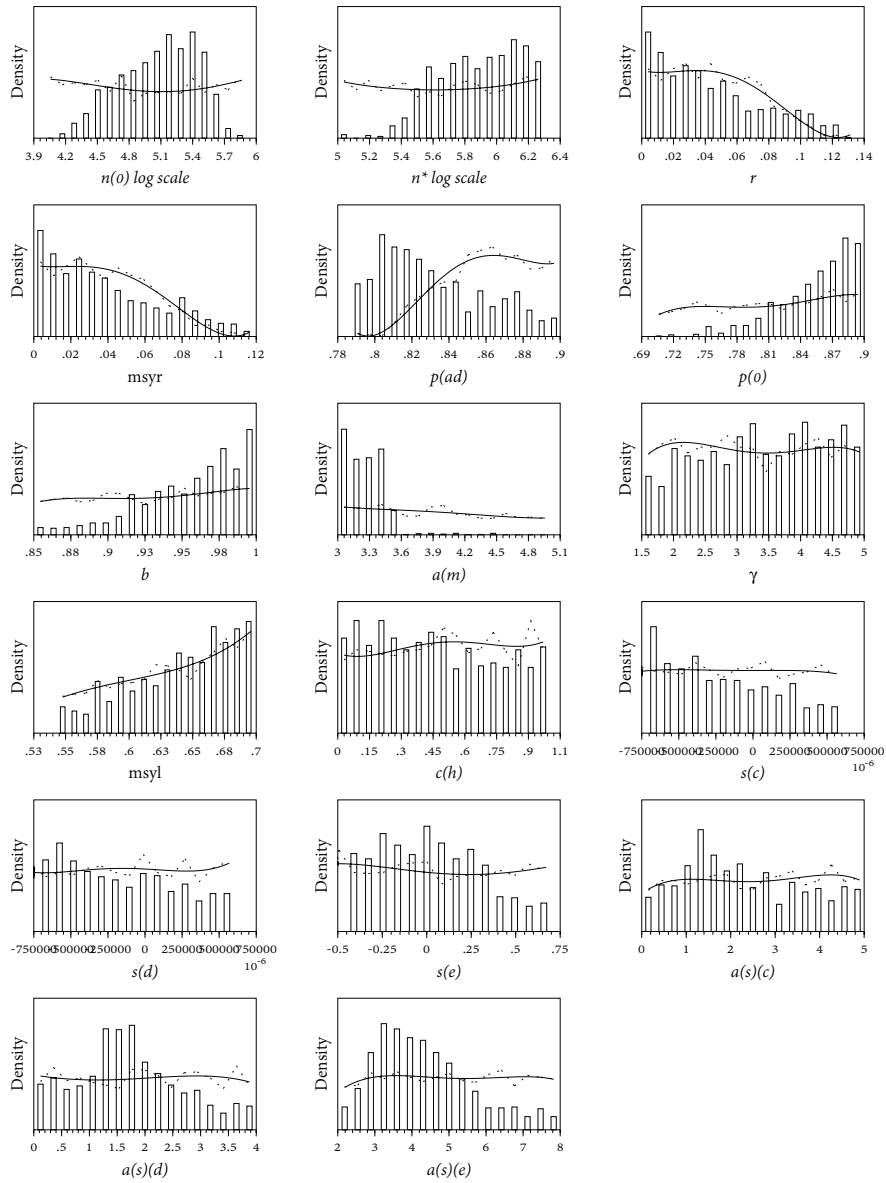


Figure 5: Realised prior (curve) and posterior (bars) distributions for model d0.

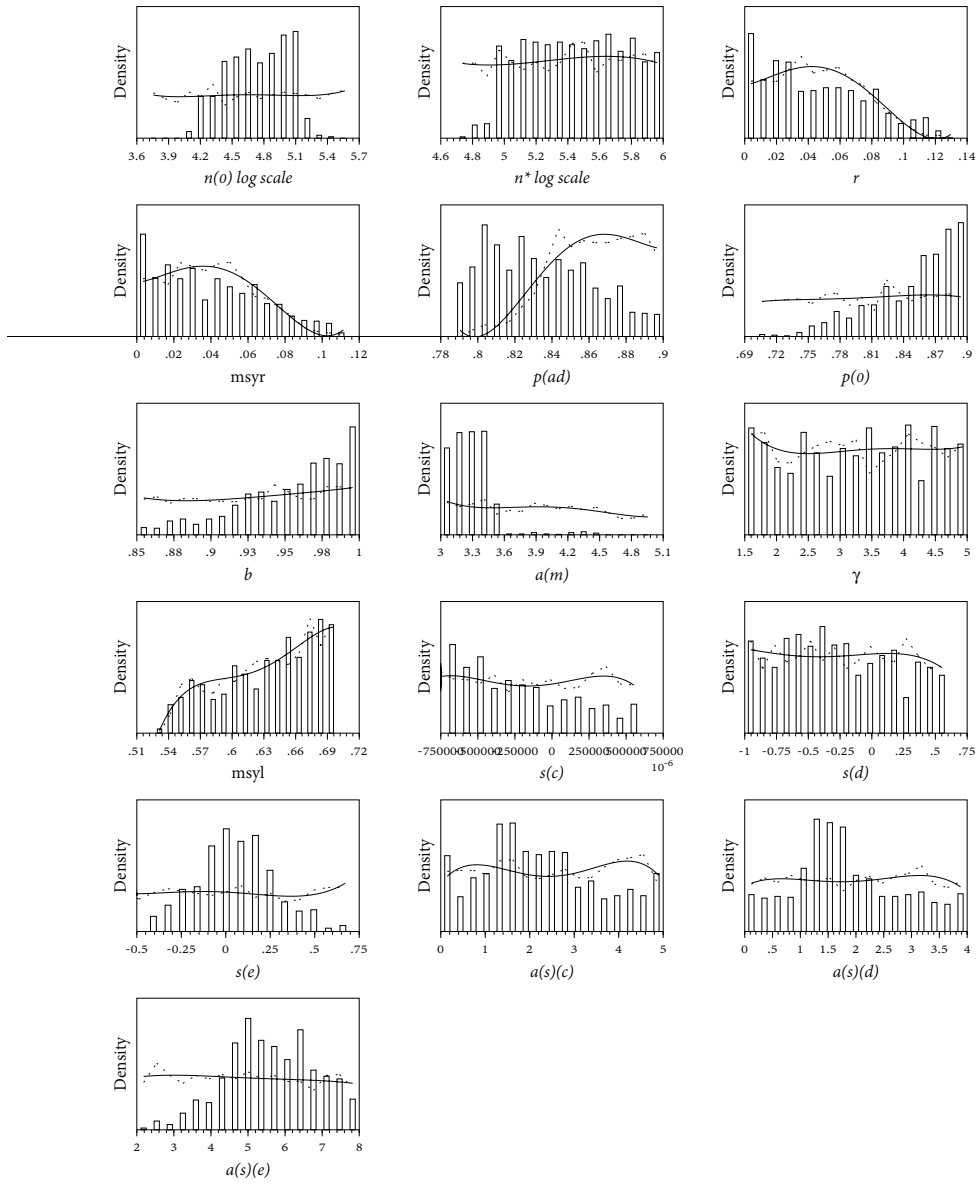


Figure 6: Realised prior (curve) and posterior (bars) distributions for model d1.

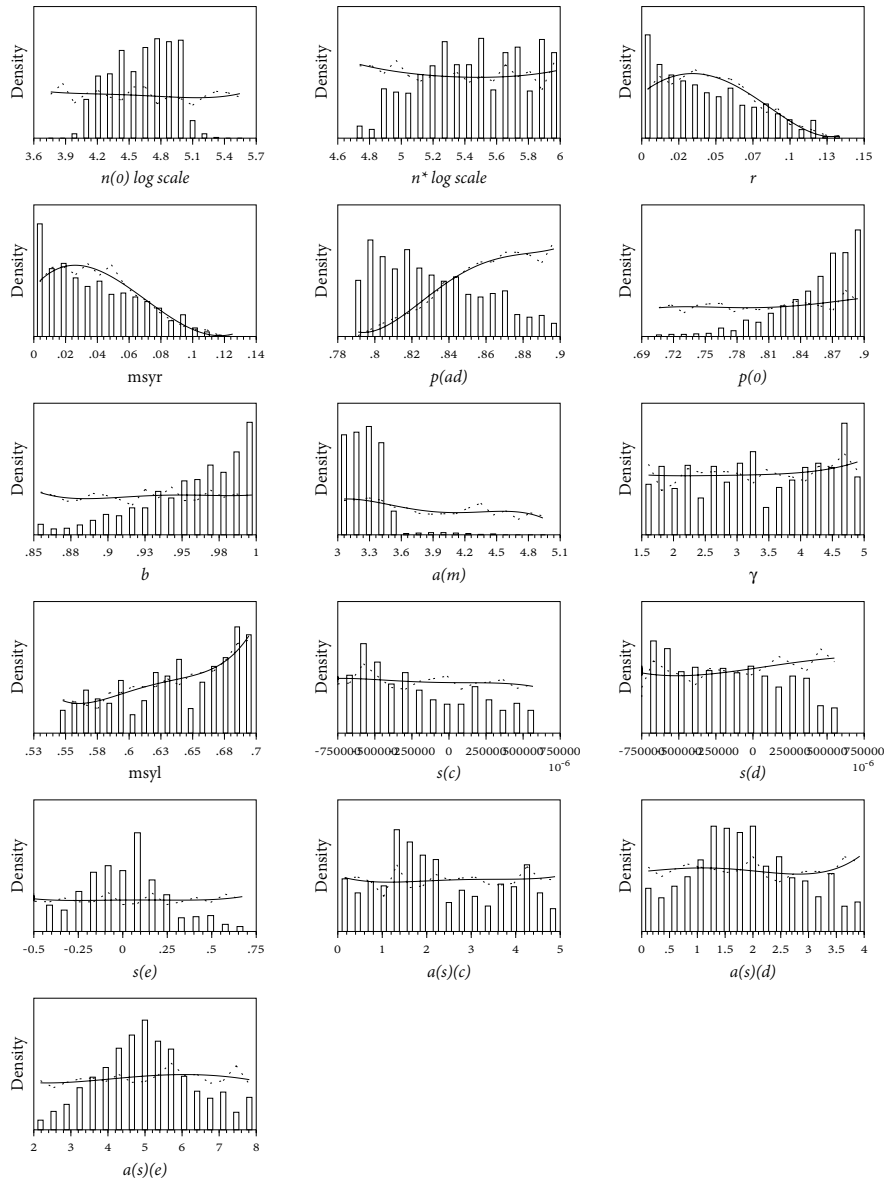


Figure 7: Realised prior (curve) and posterior (bars) distributions for model d1x.

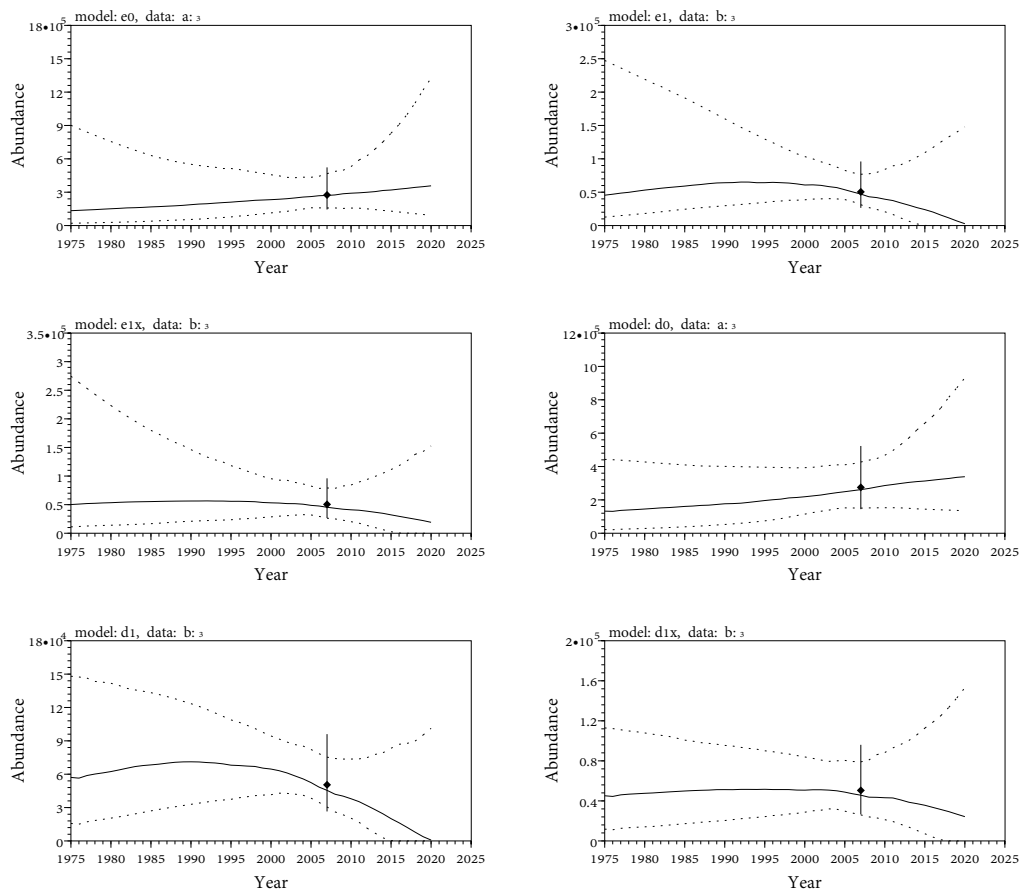


Figure 8: The projected median and 95% credibility interval of the different models.

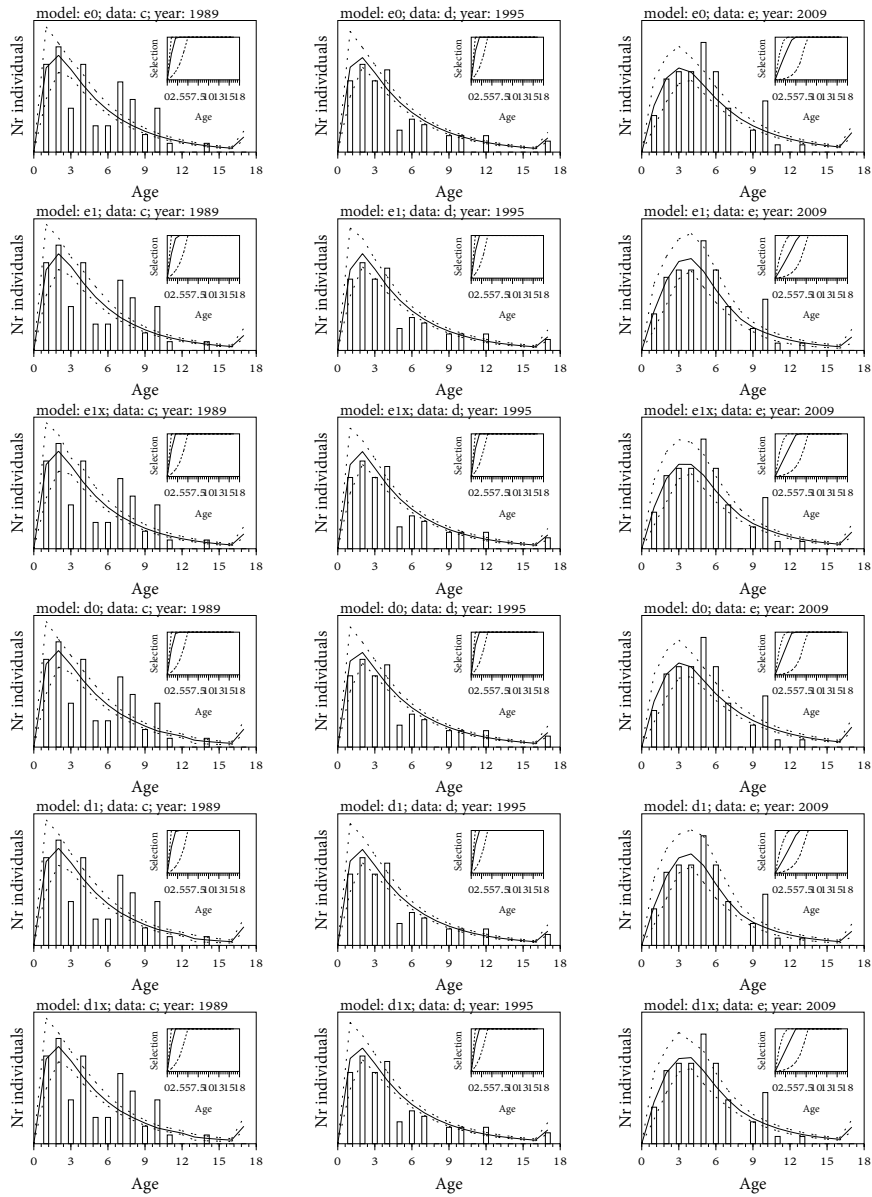


Figure 9: Model fit to age-structure. Data are given by bars, and models by the median estimate (solid curve) and the 95% credibility interval (dashed curves). Inserts show the estimated median and credibility intervals of the age-structured harvest selection. Data from Lockyer et al. (2003) and Heide-Jørgensen et al. (2011).