On population dynamics of West Greenland humpback whales

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ABSTRACT

We use recent abundance estimates, historical catches starting from 1664, and an age- and sex-structured population model to perform Bayesian assessments of humpback whales (*Megaptera novaeangliae*) in West Greenland. It is examined if the population dynamics is best described by density regulated growth, with perturbed populations returning monotonically towards an equilibrium state, or by inertia dynamics, where populations typically return through damped cycles. For humpback whale there is substantial statistical support for the acceptance of inertia dynamics and the rejection of density regulated growth. It is estimated that the abundance has declined from a population dynamic equilibrium with 2900 (90% CI:1800-5900) individuals in 1664 to a minumum of 1300 (90% CI:230-5100) individuals in 1927. It is expected that the population will increase to a projected abundance estimate of 5200 (90% CI:2400-9000) individuals in 2020 (assuming yearly post 2010 catches of 10). We estimate a 2011 depletion ratio of 1.4 (90% CI:0.68-3.1) and a yearly replacement of 55 (90% CI:-16-220) individuals.

INTRODUCTION

In this paper we build population models in order to examine the population dynamics of humpback whales (*Megaptera novaeangliae*) in West Greenland. The modelling framework is sex and age-structured, and it is used to reconstruct historical trajectories for a shorter (1980 to 2020) and longer (1664 to 2020) time period from abundance and catch data.

The underlying dynamics is assumed to be either unchecked exponential growth, density regulated growth, or inertia dynamics (Ginzburg 1998; Witting 2000, 2002; Ginzburg and Colyvan 2004). Inertia dynamics can show a continuum of behaviour from the monotonic increase of traditional density regulated growth, over damped, to stable cyclic behaviour. Exponential growth is useful for estimating the trend over shorter time periods, while density regulated growth and inertia dynamics are useful for examining the long-term behaviour of populations.

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,

Year	I_a	I_b	N_c
1984	138 (54)	–	–
1988	231 (70)	357 (16)	–
1989	–	355 (12)	–
1991	–	376 (19)	–
1992	–	348 (12)	–
1993	873 (53)	–	–
2005	1160 (35)	–	–
2007	–	–	3270 (50)

Table 1: **Abundance** estimates with cv in parenthesis (given in %). I_a is an index series from aerial surveys. I_b is an index series of mark-recapture estimates. N_c is fully corrected line transect survey from 2007. Data from Larsen and Hammond (2004) and Heide-Jørgensen et al. (2008).

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.

METHOD

Abundance data

The available abundance data are listed in Table 1.

The population dynamic analysis is based on 3 data sets on the summer abundance West Greenland. These are an index series from aerial surveys [denoted I_a, from Heide-Jørgensen et al. (2008)], an index series of mark-recapture estimates [I_b, from Larsen and Hammond (2004)], and a fully corrected line transect estimate from 2007 [N_c, from Heide-Jørgensen et al. (2008)].

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 2 catch histories. These are the West Greenland catches (IWC data base) and the West Greenland catches plus 10% West Indies catches (IWC data base).

By including catches from the West Indies, it is assumed that humpback whales from the West Greenland summer aggregation have been exposed not only to harvest in West Greenland but also to some harvest in the West Indies during winter.

Following the assessment in 2001/02 (Friday et al. 2001, 2002; IWC 2002, 2003) it was recommended that the catches from a given area are allocated to the different summer aggregations in proportion to the aggregations contribution to the number of whales in that area. When the estimate and confidence interval of the West Greenland abundance

M	E	Ds	D	I
$\tilde{p}_0$	.67|.67	.67|.67	.67|.67	.67|.67
$\tilde{p}_1$	.74|.74	.74|.74	.74|.74	.74|.74
$\tilde{p}_2$	.8|.8	.8|.8	.8|.8	.8|.8
$\tilde{p}_3$	.87|.87	.87|.87	.87|.87	.87|.87
$\tilde{p}_4$	.93|.93	.93|.93	.93|.93	.93|.93
$\tilde{p}_5$	1|1	1|1	1|1	1|1
$\tilde{p}_6$	1|1	1|1	1|1	1|1
$\tilde{p}_7$	1|1	1|1	1|1	1|1
$\tilde{p}_8$	1|1	1|1	1|1	1|1
$\tilde{p}_9$	1|1	1|1	1|1	1|1
$\tilde{p}_{10}$	1|1	1|1	1|1	1|1
$\tilde{p}_{11}$	1|1	1|1	1|1	1|1
$\tilde{p}_{12}$	1|1	1|1	1|1	1|1
$\tilde{p}_{13}$	1|1	1|1	1|1	1|1
$\tilde{p}_{14}$	1|1	1|1	1|1	1|1
$\tilde{p}_{15+}$	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.

in 1992/93 (Hammond and Larsen 1985; Hammond 1986) is compared with those for the breeding population in the West Indies in 1992/93 (Stevick et al. 2003) the West Greenland summer aggregation is estimated to contain between two and five percent of the total breeding population. It is therefore likely that it is only a small fraction of the catches in the West Indies that have been taken from the aggregation of humpback whales that spend the summer off West Greenland. Ten percent is included here as the maximum bound on the proportion of West Greenland individuals in the historical catches from the West Indies.

Population dynamics

Three 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 on the short time-scale from 1980 to 2020. 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. A third model of inertia dynamics was applied to allow for estimates of depletion levels should the dynamics be damped to stable cyclic.

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

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

3

M	E	Ds	D	I
$\tilde{c}_0$	0|0	0|0	0|0	0|0
$\tilde{c}_1$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_2$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_3$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_4$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_5$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_6$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_7$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_8$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_9$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{10}$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{11}$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{12}$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{13}$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{14}$	.067|.067	.067|.067	.067|.067	.067|.067
$\tilde{c}_{15+}$	.067|.067	.067|.067	.067|.067	.067|.067

Table 3: **Age-structured catch selectivity.** The catch selectivity $\tilde{c}_a$ for individuals in age-class a, is given $(m|f)$ for males (m) and females (f) seperately. Models (M) are indicated by symbols.

and the number of animals in age-class x be

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

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 $(0 < \tilde{p}_a^g \le 1)$ survival rate, with the sex and age structure of the relative survival rates being given in Table 2. The age and gender specific catches $c_{a,t}^{m/f} = c_t^{m/f} \tilde{c}_a^{m/f}$ 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 the age-specific catch selectivity $(\tilde{c}_a^{m/f})$, as specified separately for males and females in Table 3.

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

$$N_{0,t} = \sum_{a=a_m}^{x} B_{a,t} \tag{3}$$

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

$$B_{a,t} = b_{a,t}\, \tilde{b}_a\, M_{a,t}^f \tag{4}$$

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, $0 < \tilde{b}_a \le 1$ is the relative age-specific birth rate (given in Table 4), and $M_{a,t}^f$ is the number of mature females in age-class a in year t, defined as

$$M_{a,t}^f = \begin{cases} 0 & \text{if } a < a_m \\ N_{a,t}^f & \text{if } a \ge a_m \end{cases} \tag{5}$$

4

M	E	Ds	D	I
$\tilde{b}_m$	1	1	1	1
$\tilde{b}_{m+1}$	1	1	1	1
$\tilde{b}_{m+2}$	1	1	1	1
$\tilde{b}_{m+3}$	1	1	1	1
$\tilde{b}_{m+4}$	1	1	1	1
$\tilde{b}_{m+5}$	1	1	1	1
$\tilde{b}_{m+6}$	1	1	1	1
$\tilde{b}_{m+7}$	1	1	1	1
$\tilde{b}_{m+8}$	1	1	1	1
$\tilde{b}_{m+9}$	1	1	1	1
$\tilde{b}_{m+10}$	1	1	1	1
$\tilde{b}_{m+11+}$	1	1	1	1

Table 4: **Age-structured relative birth rate.** The relative birth rate $\tilde{b}_a$ for females in age-class a. Models (M) are indicated by symbols.

Let $b_{a,t}$ be

$$b_{a,t} = b \quad \text{for exponential growth} \tag{6}$$
$$b_{a,t} = b^* + [b_{\max} - b^*][1 - (\hat{N}_t/\hat{N}^*)^\gamma] \quad \text{for density regulated growth}$$
$$b_{a,t} = \min[b_{\max}, \dot{b}_a(\hat{N}_t/\hat{N}^*)^{-\gamma}] \quad \text{for inertia dynamics}$$

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, $\dot{b}_a$ is the average intrinsic birth rate for females in age-class a, γ is the density dependence parameter, and the abundance component that imposes density dependence is the one-plus component

$$\hat{N}_t = \sum_{a=1}^{x} N_t^f + N_t^m \tag{7}$$

The average intrinsic fecundity rate of newborns, $\dot{b}_{0,t}$, is expected to be a function of the intrinsic fecundity rates of the parents and the natural selection that is imposed by the density dependent ecology. This selection pressure is, in fact, the major reason why we may expect non-negligible sized organisms with sexual reproduction between males and females to exist at all (Witting 2008). Following Witting (2000), we can approximate the selection response as

$$\dot{b}_{0,t+1} = \frac{\sum_{a=a_m}^{x} \tilde{b}_a N_{a,t} \ \min[b_{\max}, \dot{b}_{a,t}(\hat{N}_t/\hat{N}^*)^{-\iota}]}{\sum_{a=a_m}^{x} \tilde{b}_a N_{a,t}} \tag{8}$$

where ι defines the between generation response to the natural selection pressure. This response may include, but is not limited to, genetic driven changes. It may also include responses by epigenetic inheritance, maternal effects, and selection induced between generation changes in the way that the individuals interact with one-another and the environment. Assuming that there is no change in the intrinsic fecundity rate of a cohort

over time, $\dot{b}_{a+1,t+1} = \dot{b}_{a,t}$ and

$$\dot{b}_{x,t+1} = \frac{\dot{b}_{x,t}(p_x^f N_{x,t}^f - c_{x,t}^f) + \dot{b}_{x-1,t}(p_{x-1}^f N_{x-1,t}^f - c_{x-1,t}^f)}{N_{x,t+1}^f} \tag{9}$$

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 $\hat{N}_{\mathrm{msy}}$, also known by the maximum sustainable yield rate (msyr $= $ msy$/\hat{N}_{\mathrm{msy}}$) and the maximum sustainable yield level (msyl $= \hat{N}_{\mathrm{msy}}/\hat{N}^*$). For inertia dynamics, however, the intrinsic growth rate is an initial condition, unlike the fixed parameter for exponential and density regulated growth. For a given abundance, this implies that there is no constant λ to define a constant sustainable yield. Hence, there is no single abundance curve of sustainable yields and, thus, no easily defined maximum of sustainable yield. For any single abundance at a given time the yield that will leave the abundance unchanged for the next generation may, dependent upon initial conditions and time, be any value within a range of both positive and negative numbers.

Assessment models

The population dynamic description is based on the 4 assessment models that are described in this subsection.

Short-term exponnetial growth (E): Short-term (1980-2020) model based on exponnetial growth.

Short-term density regulated (Ds): Short-term (1980-2020) model based on density regulated growth.

Density regulated growth (D): A long-term (1664-2020) model based on density regulated growth.

Inertia dynamics (I): A long-term (1664-2020) model based on inertia dynamics.

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^*	r	b	a_m	ϑ	γ
E	$.1,4^U$	-	$.01,.11^u$	$2.7,2.1^b$	$5,13^u$	$.5$	-
Ds	$.1,4^U$	$.5,100^U$	$.01,.11^u$	$2.7,2.1^b$	$5,7^u$	$.5$	$1.5,5^u$
D	-	$.5,15^U$	$.01,.11^u$	$2.7,2.1^b$	$5,7^u$	$.5$	$1.5,5^u$
I	-	$.5,15^U$	$.01,.11^u$	$2.7,2.1^b$	$5,7^u$	$.5$	$1e\text{-}6,5e\text{-}5^U$

M	ι	c_h	β_a	β_b
E	-	$0,1^u$	$.01,1^U$	$.01,1^U$
Ds	-	$0,1^u$	$.01,1^U$	$.01,1^U$
D	-	$0,1^u$	$.01,1^U$	$.01,1^U$
I	$5e\text{-}5,.0005^U$	$0,1^u$	$.01,1^U$	$.01,1^U$

Table 5: **Prior distributions** for the different models (M). The list of parameters: N_0 is the initial abundance, N^* the population dynamic equilibrium abundance, r the exponential growth rate, b the birth rate, a_m the age of the first reproductive event, ϑ the female fraction at birth, γ the density regulation, ι the inertia, c_h the catch history, and β_i the abundance estimate bias (i: data reference). Abundance is given in thousands. The prior probability distribution is given by superscripts; p: fixed value, u: uniform (min,max), U: log uniform (min,max), and b: beta (a,b).

Prior distributions

The values and prior distributions of the different parameters for all the assessment models are listed in Table 5.

The population dynamic growth rate was given a uniform prior from 0.01 to 0.106 in all models, with the maximum value corresponding to an agreed maximal growth rate (IWC 2007).

The density regulation parameter (γ) was given a uniform prior from 1.5 to 5 in the density regulated models, to mimic a msyl in the range from 0.5 to 0.7. A log uniform prior was set by trial and error for the density regulation (γ) and the inertia (ι) parameters of the inertia model to provide the best long-term fits of the model to the abundance data, given that the population was allowed to overshoot the pre-harvest abundance only once since 1664. For the inertia model the initial condition on the growth rate was set to be zero growth of an assumed population dynamic equilibrium prior to the first catches. The assumption of a pre-harvested population in dynamic equilibrium was also applied to the density regulated model. For the two short-term models of exponential and density regulated growth the projections were initialised with a stable-age structure.

There is no estimate of the age of the first reproductive event (a_m) for humpback whales in West Greenland. There are, however, several estimates from other areas (Clapham 1992; Gabriele et al. 2007; Robbins 2007; Ramp 2008). For North Atlantic humpback whales, Ramp (2008) estimated a_m to exceed 12 years in the Gulf of St. Lawrence, Clapham (1992) estimated it to a range from five to seven years for humpbacks in the Gulf of Maine, and a later estimate from this area obtained an average estimate of seven years, ranging from five to 13 (Robbins 2007).

While density dependence is operating on the birth rate in our model, the age of the first reproductive event is known as one of the more responsive life-history parameters to density-dependent effects (e.g., Eberhardt and Siniff 1977; Gaillard et al. 2000). Thus, in the current model, the parameter is relating to the maximal growth rate, which implies that we for the models of density regulated growth and inertia dynamics should aim for a prior on the minimum age of the first reproductive event to be expected in a population at maximal growth rate. Hence, I apply the estimate of Clapham (1992) as a uniform prior form five to seven years of age to these models. For the exponential model I apply the later estimate from the Gulf of Maine ranging from five to 13 years of age (Robbins 2007).

There is no estimate of the birth rate for humpback females in West Greenland, but estimates exist for other areas. Gabriele et al. (2007) found that adult females in Alaska typically give birth every second to third year, with a documented range from one to six, and a mode every second year. Robbins (2007) found a comparable range for humpbacks in the Gulf of Maine, with a mean estimated annual birth rate of 0.57 and a process variance of 0.042 for 201 adult in the south-west of the area. I applied the latter estimate as an informative beta prior on the birth rate ($a = 2.741$, $b = 2.111$). As for a_m, for density regulated growth and inertia dynamics, the prior on the birth rate should reflect the expected range for the average birth rate among the individuals in a population that increases at its maximum growth rate r_{max}. As West Greenland humpbacks are estimated to increase at a rate faster than humpbacks in the Gulf of Maine (Clapham et al. 2003; Heide-Jørgensen et al. 2008), the prior applied here may be in the lower range of the true value.

The fraction of females at birth was set to 0.5, and no prior was applied to the survival rate. It was instead calculated from the drawn values of the population dynamic growth rate and the other life-history parameters. Nevertheless, Larsen and Hammond (2004) estimated an annual survival rate of 0.957 (SE=0.028) for humpback whales off West Greenland. This is similar to estimates of 0.951 (SE=0.010) and 0.960 (SE=0.008) for the Gulf of Maine feeding aggregation of humpbacks (Buckland 1990; Barlow and Clapham 1997), and an estimate of 0.963 (95% CI:0.944-0.978) for humpbacks in the central North pacific (Mizroch et al. 2004).

In the Gulf of Maine, calf survival was estimated at 0.664 (95% CI:0.517-0.784), and yearly adult survival at 0.991 (95% CI:0.919-0.999) when excluding animals younger than five years of age (Robbins 2007). From age zero to five, yearly survival was found to increase by an approximate straight line. I applied a linear increase in the relative survival rate from age zero ($\tilde{p} = 0.67$) to age five plus ($\tilde{p} = 1$, Table 2).

A log uniform prior was set by trial and error for the bias in the index time series of abundance estimates from aerial surveys and the bias in the mark-recapture abundance estimates.

A uniform prior from zero to one was set on a catch history selection parameter c_h, with the applied catch history $c = c_h(c_H - c_L) + c_L$ representing a linear scaling between the low (c_L) and the high (c_H) catch history (Figure 1).

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

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)} \tag{10}$$

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 ith parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_s} w(\theta_j)} \tag{11}$$

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

The method of de la Mare (1986) was used to calculate the likelihood L under the assumption that observation errors are log-normally distributed (Buckland 1992)

$$L = \prod_i \prod_t \exp\left(-\frac{[\ln(\hat{N}_{i,t}/\beta_i N_t)]^2}{2\mathrm{CV}_{i,t}^2}\right)/\mathrm{CV}_{i,t} \tag{12}$$

where $\hat{N}_{i,t}$ is the point estimate of the ith set of abundance data in year t, $\mathrm{CV}_{i,t}$ 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.

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.

M	n_S	n_R	Weight	Unique	Max
E	400	5	3255	1877	25
Ds	400	5	2931	1645	22
D	800	5	106.3	3165	9
I	2000	5	2525	2475	31

Table 6: **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.

RESULTS

Sample and resample statistics are given in Table 6. The maximum importance weight of a parameter set relative to the sum of importance weights for all the sampled sets was between 10600% (density regulated growth model) and 325000% (short-term exponnetial growth model) across all models. The proportion of unique parameter sets in the resample of a model was between 32% (short-term density regulated model) and 63% (density regulated growth model), and the maximum number of occurrences of a unique paramater set in the resample between 9 (density regulated growth model) and 31 (inertia dynamics model).

Posterior distributions

The realised prior and posterior distributions are shown in Figures 2 to 5. 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 ith 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 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. None of the models failed to pass the minimum criterion for acceptence (details given for each model below).

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

abundance data.

For the **short-term exponnetial growth** (E) model in Figure 2 the updating of the initial abundance (N_0) is substantial (49%); the prior is wider than the posterior, especially to the left. The exponential growth rate (r) is substantially (29%) updated; the parameter is badly defined to the right where the posterior is wider than the prior. The life-history parameters (p, b, a_m) have a substantial (27%) updating. The updating of the yearly survival (p) is substantial (40%); the parameter is not well defined to the right where the prior is slightly narrower than the posterior. The birth rate (b) is substantially (32%) updated; the prior is slightly narrower than the posterior to the right. The updating of the age of the first reproductive event (a_m) is very weak (10%), and the parameter is not well defined to the left where the prior is slightly narrower than the posterior. There is hardly any (6%) updating of the catch history (c_h); the prior is slightly narrower than the posterior to the left. The abundance estimate bias (β_a) is strongly (64%) updated; the parameter is well defined, the posterior is only slightly narrower than the prior, especially to the left. The updating of the abundance estimate bias (β_b) is strong (63%); the parameter is well defined, the posterior is narrower than the prior, especially to the left.

For the **short-term density regulated** (Ds) model in Figure 3 there is a substantial (45%) updating of the initial abundance (N_0); the prior is wider than the posterior, especially to the left. The updating of the population dynamic equilibrium abundance (N^*) is substantial (38%); the parameter is not well defined to the right where the prior is slightly narrower than the posterior. There is a substantial (29%) updating of the exponential growth rate (r), and the parameter is not well defined to the right where the prior is slightly narrower than the posterior. The maximum sustainable yield rate (msyr) has a substantial (30%) updating; the prior is slightly narrower than the posterior to the right. The updating of the life-history parameters (p, b, a_m) is substantial (26%). The yearly survival (p) is substantially (39%) updated, and the posterior is slightly wider than the prior to the right. The birth rate (b) has a substantial (30%) updating; the prior is slightly narrower than the posterior to the right. The age of the first reproductive event (a_m) is hardly (7%) updated, and the posterior is slightly wider than the prior in both ends. The density regulation (γ) has hardly any (6%) updating, and the prior is slightly narrower than the posterior to the left. The maximum sustainable yield level (msyl) is hardly (6%) updated, and the parameter is not well defined because the prior is slightly narrower than the posterior in both ends. There is hardly any (6%) updating of the catch history (c_h), and the prior is slightly narrower than the posterior to the left. The updating of the abundance estimate bias (β_a) is strong (64%), and the parameter is strongly defined to the left where the prior is very clearly wider than the posterior. The abundance estimate bias (β_b) has a strong (60%) updating; the posterior is slightly narrower than the prior, especially to the left.

For the **density regulated growth** (D) model in Figure 4 the population dynamic equilibrium abundance (N^*) is strongly (52%) updated; it is clear that the prior is wider than the posterior, especially to the left. The updating of the exponential growth rate (r) is very weak (5%), and the posterior is not well updated in both ends. The maximum

sustainable yield rate (msyr) is not (5%) updated; the prior is not well updated in both ends. The updating of the life-history parameters (p, b, a_m) is very weak (6%). The yearly survival (p) is not (4%) updated; the parameter is not well defined to the right where the prior is slightly narrower than the posterior. There is hardly any (8%) updating of the birth rate (b), and the prior is slightly wider than the posterior to the left. The updating of the age of the first reproductive event (a_m) is non existing (5%), and the posterior is slightly wider than the prior to the left. There is no (4%) updating of the density regulation (γ); the prior is slightly narrower than the posterior to the left. The updating of the maximum sustainable yield level (msyl) is non existing (3%), and the posterior is slightly wider than the prior to the left. The catch history (c_h) is not (4%) updated, and the prior is slightly narrower than the posterior in both ends. The abundance estimate bias (β_a) has a strong (61%) updating, and the parameter is strongly defined, the posterior is clearly narrower than the prior, especially to the left. The updating of the abundance estimate bias (β_b) is strong (64%); the parameter is strongly defined, the prior is very clearly wider than the posterior in both ends.

For the **inertia dynamics** (I) model in Figure 5 the population dynamic equilibrium abundance (N^*) has a strong (64%) updating, and the parameter is strongly defined, it is very clear that the posterior is narrower than the prior in both ends. The updating of the exponential growth rate (r) is very weak (9%); the posterior is not well updated in both ends. There is hardly any (12%) updating of the life-history parameters (p, b, a_m). The updating of the yearly survival (p) is weak (21%); the prior is slightly narrower than the posterior to the right. There is hardly any (8%) updating of the birth rate (b), and the parameter is not well defined to the left where the prior is slightly narrower than the posterior. The age of the first reproductive event (a_m) is hardly (7%) updated; the posterior is slightly wider than the prior in both ends. The updating of the density regulation (γ) is non existing (4%), and the parameter is not well defined to the left where the prior is slightly narrower than the posterior. The inertia (ι) has hardly any (11%) updating, and the posterior is slightly wider than the prior to the left. The catch history (c_h) is hardly (9%) updated; the prior seems not to be well updated in both ends. There is a strong (59%) updating of the abundance estimate bias (β_a), and it is clear that the posterior is narrower than the prior, especially to the left. The abundance estimate bias (β_b) is strongly (58%) updated; it is very clear that the prior is wider than the posterior in both ends.

Parameter estimates

The posterior parameter estimates and their 90% credibility intervals are given in Table 7. 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 **short-term exponnetial growth** (E) model provides the following updated

M		N_0	N^*	r	msyr	p	b	a_m	γ	ι	msyl
	$x_{.5}$	.8	-	.055	-	.98	.81	7.3	-	-	-
	$x_{.05}$	.36	-	.026	-	.96	.51	5.2	-	-	-
$^+$E	$x_{.95}$	2.3	-	.076	-	.99	.97	12	-	-	-
	$x_{.5}$	.79	15	.059	.048	.98	.79	5.8	3.2	-	.64
	$x_{.05}$	.32	2.9	.029	.021	.95	.48	5.1	1.7	-	.55
$^+$Ds	$x_{.95}$	2.3	86	.081	.068	.99	.97	6.9	4.8	-	.69
	$x_{.5}$	-	3.3	.045	.037	.97	.74	5.9	3.2	-	.64
	$x_{.05}$	-	1.5	.014	.011	.94	.38	5.1	1.7	-	.55
$^+$D	$x_{.95}$	-	7.4	.079	.066	.99	.96	6.9	4.8	-	.69
	$x_{.5}$	-	2.9	.051	-	.98	.76	5.9	7.4e-6	.00014	-
	$x_{.05}$	-	1.8	.016	-	.95	.38	5.1	1.2e-6	5.6e-5	-
$^+$I	$x_{.95}$	-	5.9	.079	-	.99	.97	6.9	4.1e-5	.0004	-

M	c_h	N_t	d_t	β_a	β_b
	.48	4.3	-	.29	.25
	.04	2	-	.12	.099
$^+$E	.94	9.6	-	.71	.57
	.49	3.8	.28	.32	.26
	.045	1.8	.042	.13	.1
$^+$Ds	.94	8.6	.98	.73	.62
	.5	3.2	.99	.18	.11
	.047	1.5	.94	.073	.049
$^+$D	.95	7.3	1	.46	.25
	.46	4.6	1.4	.17	.12
	.062	2.1	.68	.075	.052
$^+$I	.94	8.2	3.1	.49	.37

Table 7: **Parameter estimates** for the different models (M). Estimates are given by the median ($x_{.5}$) and the 90% credibility interval ($x_{.05}$ - $x_{.95}$) of the postreior distributions. Abundance is given in thousands. The selected models are indicated a superscript $+$.

parameter estimates: a initial abundance (N_0) estimate of 800 (90% CI:360-2300); the abundance estimate bias (β_a) was estimated to 0.29 (90% CI:0.12-0.71); the abundance estimate bias (β_b) is 0.25 (90% CI:0.099-0.57).

The updated parameter estimates in the **short-term density regulated** (Ds) model are: a initial abundance (N_0) estimate of 790 (90% CI:320-2300); the estimate of the abundance estimate bias (β_b) is 0.26 (90% CI:0.1-0.62).

The **density regulated growth** (D) model has the following updated parameter estimates: the population dynamic equilibrium abundance (N^*) was estimated to 3300 (90% CI:1500-7400); the estimate of the abundance estimate bias (β_a) is 0.18 (90% CI:0.073-0.46); an estimate of 0.11 (90% CI:0.049-0.25) for the abundance estimate bias (β_b).

The **inertia dynamics** (I) model provides the following updated parameter estimates: a population dynamic equilibrium abundance (N^*) estimate of 2900 (90% CI:1800-5900);

the abundance estimate bias (β_a) was estimated to 0.17 (90% CI:0.075-0.49); the estimate of the abundance estimate bias (β_b) is 0.12 (90% CI:0.052-0.37).

Population dynamics

The estimated population dynamic trajectories are shown in Figure 6.

Relating to long-term dynamics, the **inertia dynamics** (I) model is substantially ($K = 3.64$) supported by Bayes factor over the **density regulated growth** (D) model. The **inertia dynamics** (I) model describes the long-term population dynamics from 1664 to 2020. The abundance declined from a population dynamic equilibrium of 2900 (90% CI:1800-5900) individuals in 1664 to a minumum with 1300 (90% CI:230-5100) individuals in 1927. It can be expected that the population increase to a projected abundance estimate with 5200 (90% CI:2400-9000) individuals in 2020 (assuming an average post 2010 catch of 10 per year). For 2011 it is estimated that the depletion ratio is 1.4 (90% CI:0.68-3.1), that the abundance is 4600 (90% CI:2100-8200) individuals, and that the yearly replacement is 55 (90% CI:-16-220). From 2006 to 2011 the population had on average increased by 67 individuals per year.

Relating to short-term dynamics, the **short-term density regulated** (Ds) model is hardly ($K = 2.89$) supported by Bayes factor over the **short-term exponnetial growth** (E) model. The **short-term density regulated** (Ds) model estimates the short-term population trajectory from 1980 to 2020. An estimate of 15000 (90% CI:2900-86000) individuals was obtained for the population dynamic equilibrium. The population has declined from an initial abundance of 790 (90% CI:320-2300) individuals in 1980 to a minumum of 780 (90% CI:300-2300) in 1981. It is expected that the abundance will increase to a projected population of 5400 (90% CI:2300-13000) in 2020 (assuming an average post 2010 catch of 10 per year). The depletion ratio in 2011 is estimated to 0.28 (90% CI:0.042-0.98), with an abundance of 3800 (90% CI:1800-8600) and a yearly replacement of 160 (90% CI:11-490) individuals. From 2006 to 2011 the population had on average increased by 143 individuals per year.

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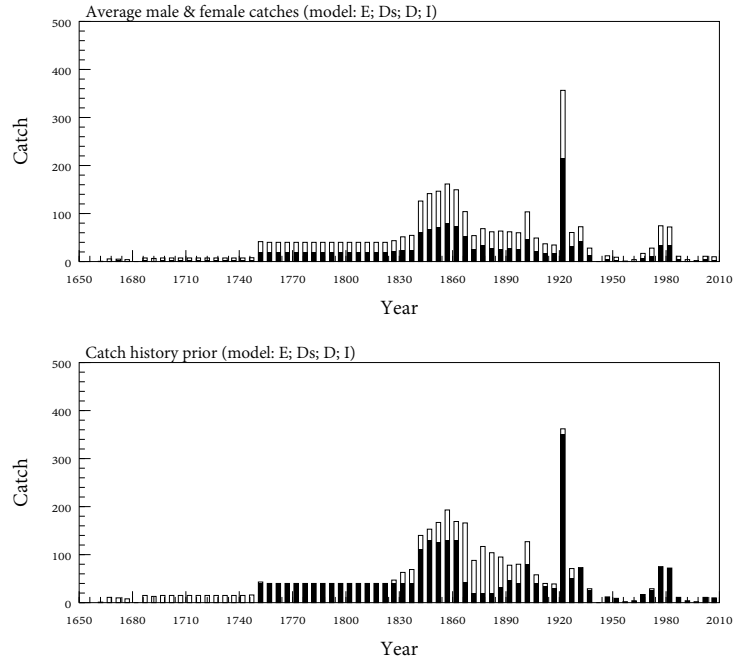
Figure 1: The historical catches of males (solid bars) and females (open bars), and prior range in total catches (minimum by solid bars; maximum by open bars). Data from IWC (data base).

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

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

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

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

Figure 6: The projected median and 90% credibility interval of the different models.

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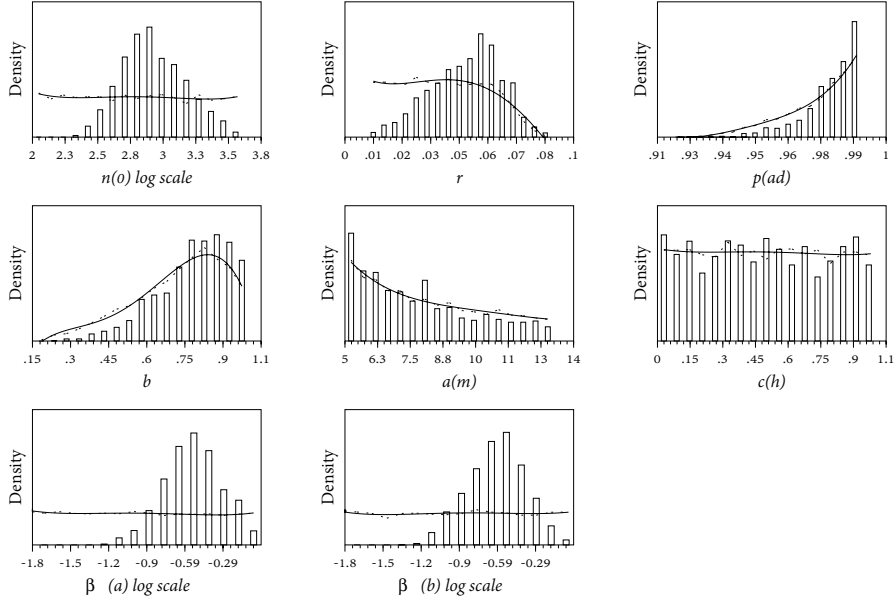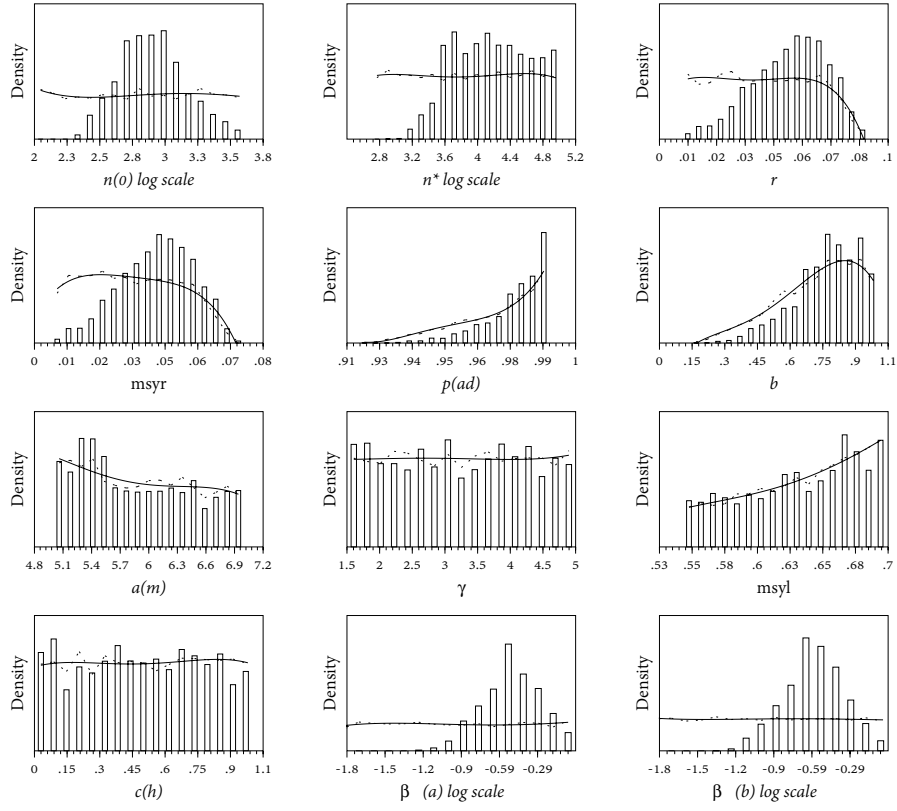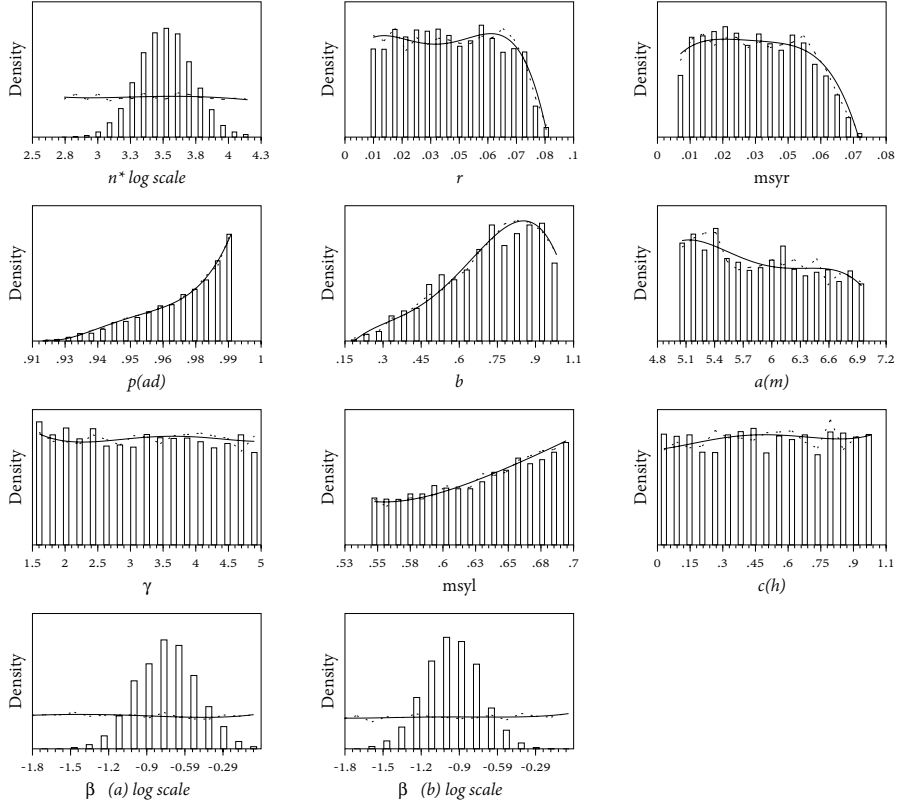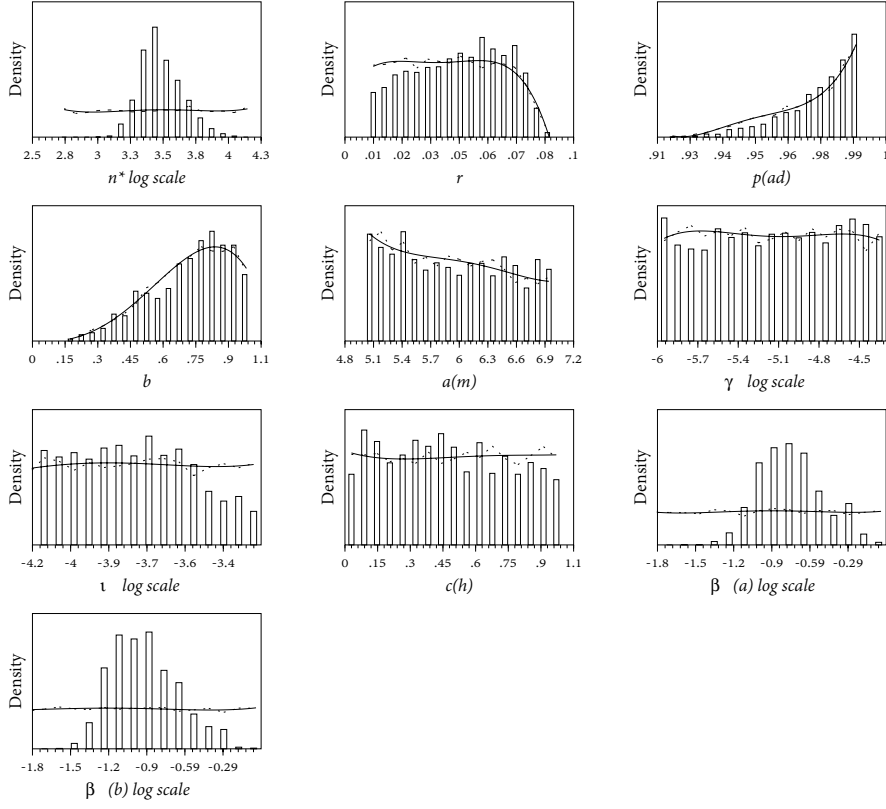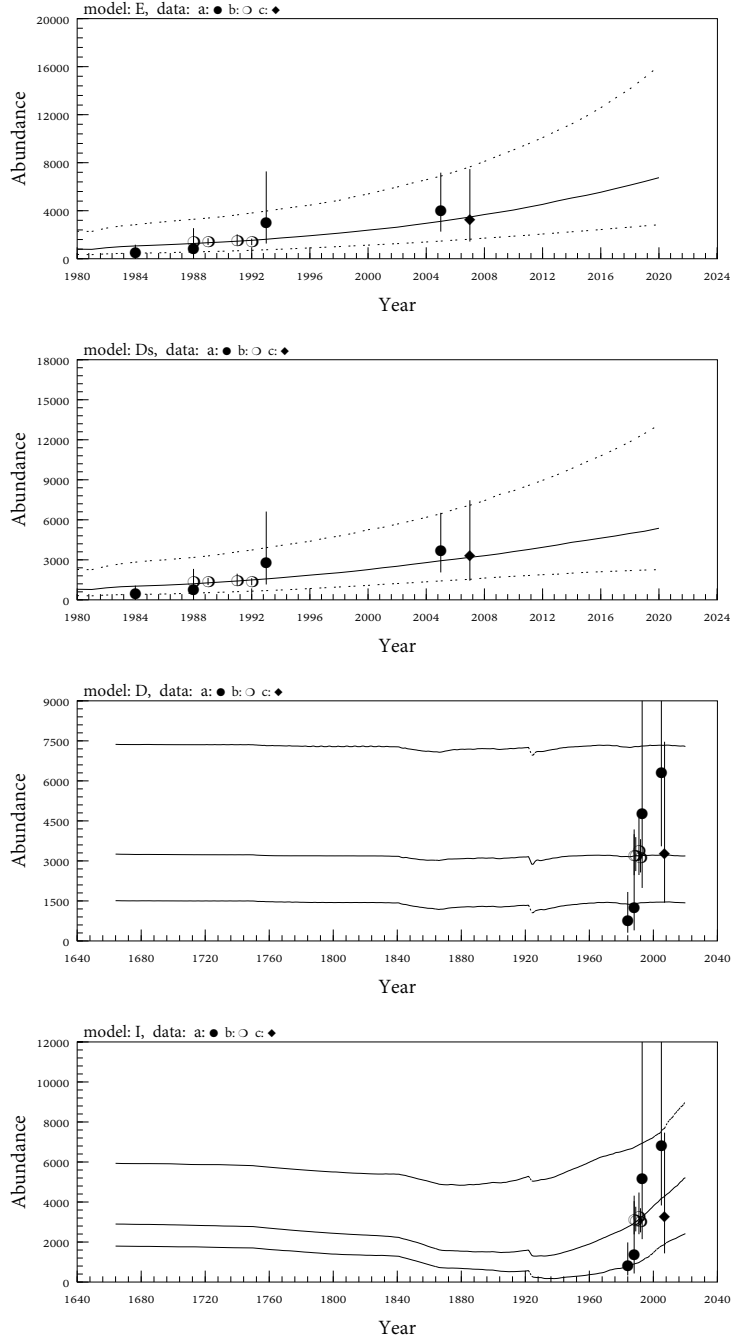
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On population dynamics of West Greenland humpback whales

Lars Witting

This supplement to IWC/SC/63/AWMP2 gives correlation matrixes for the parameters in the different models, and it also lists the applied catch histories.

Par	N_0	r	p	b	a_m	c_h	N_t	β_a	β_b
N_0	1	-	-	-	-	-	-	-	-
r	-0.63	1	-	-	-	-	-	-	-
p	-0.4	0.58	1	-	-	-	-	-	-
b	-0.38	0.59	-0.084	1	-	-	-	-	-
a_m	0.23	-0.45	0.09	-0.062	1	-	-	-	-
c_h	-0.0077	0.03	0	0.02	-0.028	1	-	-	-
N_t	0.56	0.17	0.11	0.1	-0.064	0.02	1	-	-
β_a	-0.63	0.22	0.12	0.12	-0.1	0.02	-0.66	1	-
β_b	-0.74	0.42	0.24	0.23	-0.2	0	-0.65	0.85	1

Table 1: **Parameter correlation matrix** for model E.

Par	N_0	N^*	r	msyr	p	b	a_m	γ	msyl	c_h	N_t	d_t	β_a
N_0	1	-	-	-	-	-	-	-	-	-	-	-	-
N^*	0.01	1	-	-	-	-	-	-	-	-	-	-	-
r	-0.55	-0.11	1	-	-	-	-	-	-	-	-	-	-
msyr	-0.55	-0.11	0.97	1	-	-	-	-	-	-	-	-	-
p	-0.43	-0.04	0.66	0.64	1	-	-	-	-	-	-	-	-
b	-0.31	-0.11	0.66	0.64	-0.087	1	-	-	-	-	-	-	-
a_m	0.07	0.01	-0.22	-0.2	-0.0042	-0.054	1	-	-	-	-	-	-
γ	-0.05	-0.017	0.01	0.25	0.05	-0.018	0.03	1	-	-	-	-	-
msyl	-0.048	-0.018	0.01	0.25	0.05	-0.016	0.03	0.99	1	-	-	-	-
c_h	0.01	-0.032	-0.049	-0.051	-0.013	-0.047	0.01	-0.0091	-0.016	1	-	-	-
N_t	0.49	0.18	0.14	0.13	0.06	0.11	-0.053	0.01	0.01	-0.048	1	-	-
d_t	0.19	-0.7	0.23	0.22	0.09	0.2	-0.09	-0.01	-0.01	0.02	0.04	1	-
β_a	-0.63	-0.037	0.22	0.23	0.18	0.12	-0.025	0.05	0.05	-0.0039	-0.63	-0.19	1
β_b	-0.73	-0.024	0.39	0.4	0.29	0.24	-0.049	0.07	0.07	-0.009	-0.6	-0.24	0.84

Table 2: **Parameter correlation matrix** for model Ds.

Par	N^*	r	msyr	p	b	a_m	γ	msyl	c_h	N_t	d_t	β_a	
N^*	1	-	-	-	-	-	-	-	-	-	-	-	-
r	-0.023	1	-	-	-	-	-	-	-	-	-	-	-
msyr	-0.02	0.99	1	-	-	-	-	-	-	-	-	-	-
p	-0.041	0.7	0.69	1	-	-	-	-	-	-	-	-	-
b	0.01	0.6	0.6	-0.11	1	-	-	-	-	-	-	-	-
a_m	0.03	-0.15	-0.14	-0.001	-0.032	1	-	-	-	-	-	-	-
γ	-0.0054	-0.0019	0.15	0.02	-0.026	0.01	1	-	-	-	-	-	-
msyl	-0.0037	-0.0011	0.15	0.03	-0.032	0	0.99	1	-	-	-	-	-
c_h	-0.0052	0.02	0.02	0.04	-0.011	0.01	-0.029	-0.027	1	-	-	-	-
N_t	1	-0.00019	0	-0.02	0.02	0.02	0	0	-0.0076	1	-	-	-
d_t	0.19	0.43	0.44	0.38	0.18	-0.0098	0.19	0.2	-0.041	0.24	1	-	-
β_a	-0.7	-0.01	-0.013	-0.00053	-0.019	-0.023	-0.0065	-0.0078	-0.0063	-0.7	-0.29	1	-
β_b	-0.77	-0.011	-0.014	-0.0048	-0.015	-0.021	-0.0093	-0.01	-0.0081	-0.77	-0.34	0.88	

Table 3: **Parameter correlation matrix** for model D.

Par	N^*	r	p	b	a_m	γ	ι	c_h	N_t	d_t	β_a	β_b
N^*	1	-	-	-	-	-	-	-	-	-	-	-
r	0.2	1	-	-	-	-	-	-	-	-	-	-
p	0.3	0.67	1	-	-	-	-	-	-	-	-	-
b	-0.018	0.7	-0.045	1	-	-	-	-	-	-	-	-
a_m	-0.011	-0.15	0	-0.024	1	-	-	-	-	-	-	-
γ	-0.037	0.03	0.03	0	-0.011	1	-	-	-	-	-	-
ι	-0.27	0.24	0.4	-0.036	0.04	0.04	1	-	-	-	-	-
c_h	0.18	0.04	0.03	0.02	0.02	0.01	-0.1	1	-	-	-	-
N_t	0.43	0.18	0.16	0.07	-0.057	-0.069	0.15	0.15	1	-	-	-
d_t	-0.43	0.02	-0.09	0.09	-0.05	-0.027	0.39	-0.05	0.59	1	-	-
β_a	-0.4	0.02	0.04	0.01	0.03	0.01	0.08	-0.022	-0.67	-0.3	1	-
β_b	-0.43	0.12	0.11	0.08	0.04	-0.014	0.18	-0.0023	-0.63	-0.24	0.86	1

Table 4: **Parameter correlation matrix** for model I.

Year	m	f	Year	m	f	Year	m	f	Year	m	f	Year	m	f
1980	8	8	1989	1	1	1998	0	1	2007	1	1	2016	-	-
1981	6	6	1990	0	1	1999	0	1	2008	1	2	2017	-	-
1982	6	6	1991	0	1	2000	0	2	2009	0	0	2018	-	-
1983	7	9	1992	0	1	2001	1	1	2010	4	6	2019	-	-
1984	8	8	1993	0	0	2002	2	1	2011	-	-	2020	-	-
1985	4	4	1994	0	1	2003	0	1	2012	-	-			
1986	0	0	1995	0	0	2004	2	1	2013	-	-			
1987	0	0	1996	0	0	2005	2	3	2014	-	-			
1988	0	1	1997	0	0	2006	0	0	2015	-	-			

Table 5: **West Greenland catches.** West Greenland catches. Used in models E (lower limit on catch prior), Ds (lower limit on catch prior), D (lower limit on catch prior), and I (lower limit on catch prior). Data from IWC (data base).

Year	m	f	Year	m	f	Year	m	f	Year	m	f	Year	m	f
1980	8	8	1989	1	1	1998	0	1	2007	1	1	2016	-	-
1981	6	6	1990	0	1	1999	0	1	2008	1	2	2017	-	-
1982	6	6	1991	0	1	2000	0	2	2009	0	0	2018	-	-
1983	7	9	1992	0	1	2001	1	1	2010	4	6	2019	-	-
1984	8	8	1993	0	0	2002	2	1	2011	-	-	2020	-	-
1985	4	4	1994	0	1	2003	0	1	2012	-	-			
1986	0	0	1995	0	0	2004	2	1	2013	-	-			
1987	0	0	1996	0	0	2005	2	3	2014	-	-			
1988	0	1	1997	0	0	2006	0	0	2015	-	-			

Table 6: **West Greenland and West Indies catches.** West Greenland and 10% West Indies catches. Used in models E (upper limit on catch prior), Ds (upper limit in catch prior), D (upper limit in catch prior), and I (upper limit in catch prior). Data from IWC (data base).