

A Bayesian assessment of West Greenland humpback whales

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ABSTRACT

This paper uses the population perturbation caused by the whaling industry during the 19th and 20th centuries to examine whether the population dynamics of the summer aggregation of humpback whales off West Greenland is best described by direct density regulation and an abundance that returns monotonically towards an equilibrium state, or by inertia dynamics that include also delayed density dependence by density dependent selection generating a cyclic population response. When abundance data from the last two decades are combined with the historical catches from 1664 to the present, there is statistically decisive support for the rejection of the density-regulated model as an appropriate model for the long-term dynamics of humpback whales off West Greenland. The dynamics is instead most likely damped cyclic, although the density-regulated, as well as the exponential, model provide good fits for the short-term dynamics of humpback whales during the last two decades. It is suggested that the equilibrium population abundance is between 1,700 (90% CI:1,500 – 2,000) and 2,700 (90% CI:2,300 – 3,100) whales, that the current depletion ratio is between 0.88 (90% CI:0.44 – 1.6) and 1.5 (90% CI:0.71 – 2.4), that the current exponential growth rate is 0.09 (90% CI:0.06 – 0.11), and that the current replacement yield is between 160 (90% CI:72 – 370) and 220 (90% CI:96 – 510) whales per year.

INTRODUCTION

During summer humpback whales *Megaptera novaengliae* in the North Atlantic can be found mainly in the high-latitude feeding aggregations of the Gulf of Maine, the Gulf of St Lawrence, and in waters off West Greenland, Iceland and northern Norway. For the winter the majority of the whales migrate to common low-latitude winter breeding areas in the West Indies and around the Cape Verde Islands. Although humpback whales from different summer aggregations spend the winter in the same area, the summer aggregations are practically isolated from one another with almost no within and between year exchange of adult individuals (Martin et al. 1984; Katona and Beard 1990; Stevick et al. 1999).

The humpback whale in the North Atlantic was often targeted by the pelagic whaling in all summer feeding areas and in the winter breeding areas from the mid 1800s and to early 1900s. With a total estimated take of 30 thousand humpback whales (IWC 2003), which is almost three times the best abundance estimate for the whole North Atlantic from 1992-93 (Stevick et al. 2003), high hunting mortality often led to rapid declines and severe stock depletion after only few years of commercial whaling (Tønnessen and Johnsen 1982).

For the aggregation of humpback whales off West Greenland a local non-mechanised shore-based fishery was well established by the late 1700s (Kapel 1979; Mitchell and Reeves 1983; Reeves and Smith 2002). This hunt continued until 1923 when mechanised whaling by catcher boats were introduced by the Danish authorities. The total annual removal up to 1923 are estimated to an average of 10 humpback whales per year (IWC 2003), with the mechanised local hunt remaining small with an average removal of less than five whales per year from 1924 to 1958 (Kapel 1979), continuing with an average of seven whales until the hunt was closed by the IWC in 1986. A major catch of 327 humpback whales, however, was taken by the Norwegian whaling fleet in only three years from 1922 to 1924, with the fleet failing to find appreciable numbers of humpback whales in the following years (Hjort and Ruud 1929; Jonsgård 1955).

Animal populations, like those of humpback whales, that have experienced a major perturbation of the abundance away from equilibrium often have a population trajectory that over-shoots the equilibrium abundance continuing into a damped population dynamic cycle. Nearly all the population dynamic modelling of perturbed marine mammal populations, however, have been based on the population dynamic model of direct density regulation, which generally have a trajectory that returns monotonically to the carrying capacity given no human imposed mortality (see e.g., Givens et al. 1995; Wade 2002; IWC 2003; Breen et al. 2003; Alvarez-Flores and Heide-Jørgensen 2004; Witting and Born 2005; Winship and Trites 2006). Being the early target of the pelagic whaling industry with only limited hunting since the 1920s, the North Atlantic humpback whale has had one of the longest time-periods to recover from commercial whaling. It is therefore intriguing whether the humpback whale is currently in the process of returning to a stable equilibrium or over-shooting the equilibrium to a smaller or larger extend.

An almost complete monotonic recovery to a stable carrying capacity was predicted for all feeding aggregations of North Atlantic humpback whales by the comprehensive assessment that was carried out by the IWC in 2001/02 (IWC 2002, 2003). This assessment was based on the population dynamic model of direct density dependence, with the model showing poor fits to the data. While the model predicted an almost constant abundance at population dynamic equilibrium for all aggregations, the observed abundance of humpback whales around Iceland has been increasing almost constantly at 11% per year since 1970 (Sigurjónsson and Gunnlaugsson 1990; IWC 2003). The abundance in the Gulf of Maine have also been estimated to increase at 6.5% per year between 1979 and 1991 (Barlow and Clapham 1997), the abundance of the Western North Atlantic to increase at 9.4% per year between 1979 and 1986 (Katona and Beard 1990), the abundance of humpback whales wintering in the West Indies to increase at 3.2% per year between 1979 and 2003 (Stevick et al. 2003), and the abundance off West Greenland to increase by 9.4% per year from 1984 to 2007 (Heide-Jørgensen et al. 2008). This inconsistency between a density-regulated model that predicts an almost steady abundance close to equilibrium and an observed abundance that continues to increase, has also been found for other historically exploited whale stocks like the North Pacific gray whale (Butterworth et al. 2002; Witting 2003).

An abundance that increases steadily at population equilibrium is expected for cyclic population dynamics. Apart from direct density dependence over-compensation in cyclic dynamics requires an additional layer of delayed density dependence. While traditional population dynamic models with delayed density dependence include the delayed term in a non-mechanistic

way, delayed density dependence may be included explicitly by predator-prey interactions. But cyclic dynamics by predator-prey interactions require that the generation time of the predator and the prey is in the same order of magnitude, suggesting that predator-prey interactions is an unrealistic cause for cyclic dynamics in baleen whale populations unless they are severely regulated by killer whales. Delayed density dependence, however, is expected independently of inter-specific interactions for most animal populations owing to the intra-specific mechanism of natural selection by density dependent competitive interactions (Witting 1997, 2000, 2002). This mechanism allows for a cyclic population dynamic response that has become known as inertia dynamics (Ginzburg and Taneyhill 1994; Ginzburg 1998; Witting 1997, 2000, 2002; Ginzburg and Colyvan 2004).

On the time-scale of long-term evolution, selection by density dependent competitive interactions will maintain the life history in a balance between energy allocated into increased reproduction and population dynamic growth versus energy allocated into competitive traits like body mass, with the hypothesis representing the most parsimonious selection mechanism for the evolution of organisms with large body masses (Witting 2002, 2003). When considered on the time-scale of population dynamics, the population dynamic equilibrium is also the evolutionary equilibrium that maintains the life history in a balance, while any abundance perturbation away from equilibrium introduces selection for perturbations in the life history balance. These perturbations show up as delayed density dependence with the potential for a cyclic population dynamic response. Such a delayed density dependence in the life history may reflect not only genetic responses to the selection pressure, but also an epigenetic inheritance response like maternal effects, or a behavioural induced learning response from one generation to the next.

In this paper I analyse the applicability of the hypotheses of population dynamic by direct density dependence (monotonic return to equilibrium) and inertia responses (damped cyclic return to equilibrium) to humpback whales off West Greenland. Given the historical catches of humpback whales off West Greenland and the West Indies it is examined whether dynamics by direct density dependence is consistent with the abundance estimates, or whether a more flexible population model like that of inertia dynamics is required to explain the data. A final aim of the paper is a population dynamic assessment that allows for production estimates and biological recommendations on sustainable removals of West Greenland humpback whales. In doing so I take a precautionary approach by treating the aggregation of humpback whales off West Greenland as an isolated stock, i.e., I apply the stock structure assumption that made the IWC close the hunt on humpback whales in West Greenland in 1986 (IWC 1986).

METHOD

Data

For the large whales off West Greenland the humpback whale is probably the best monitored species. Not only does it have the most estimates of abundance but these estimates also cover the longest period of time.

The first abundance estimate is from photo-identification surveys conducted by the U.S. Ocean Research and Education Society during 1981-83. These surveys produced a Chapman-

Abun	N^m	<i>cv</i>	N^s	<i>cv</i>
Age	1+		1+	
1984	-	-	138	28
1988	357	16	231	11
1989	355	12	-	-
1991	376	19	-	-
1992	348	12	-	-
1993	-	-	873	53
2005	-	-	1158	35
2007	-	-	1020	35

Table 1: The sets with abundance estimates, their *cv* in %, and age component (1+ includes the 1+ age-classes). The sets of abundance estimates include the agreed mark-recapture estimates (N^m), and the index series from aerial surveys (N^s).

modified Petersen mark-recapture estimate of 271 whales (95% CI: 200-342) for the three years combined (Perkins et al. 1984, 1985). Photo-identification surveys based on similar methods were again carried out off West Greenland from 1988 to 1993, resulting in abundance estimates for five years with four of the estimates considered reliable, while a single high estimate from 1990-91 was considered abnormal owing to very few identification matches (Larsen and Hammond 2000, 2004). For the four years combined, this gave an estimate of 360 whales (*cv*:0.07) between 1988 and 1993.

From sighting surveys we have various estimates from 1984 to 2007 (Kingsley and Witting 2001; Heide-Jørgensen et al. 2006a,b; Heide-Jørgensen et al. 2006; Heide-Jørgensen et al. 2008), with an index of uncorrected abundance estimates running from 1984 to 2007, and a fully corrected 2007 estimate of 3,040 whales (95% CI:1,310 – 7,050) (Heide-Jørgensen et al. 2008).

The abundance estimates that are used for the population dynamic modelling in this paper (Table 1) are the mark-recapture estimates from 1988 to 1993, excluding the anomalously high mark-recapture estimate from 1990-91, and the ORES estimate from 1981-83. As the latter surveys did not in all years covered all areas off West Greenland where humpback whales were believed to be abundant, the joint 1981-83 estimate could be both negatively or positively biased (IWC 1985; Hammond 1985), and thus was believed unreliable by IWC (2002). Apart from this is the index time series of uncorrected estimates from aerial surveys from 1984-2007 applied.

In this paper I assume 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. The population dynamic modelling is thus based both on the West Greenland catch history (Table 9) and the catch history from the West Indies (Table 10), with both catch histories being obtained from the IWC database.

Following the assessment in 2001/02 (Friday et al. 2001, 2002; IWC 2002, 2003) it is 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 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.

Population dynamic model

Three different models of population dynamics were applied to the humpback whale data. A model of exponential growth was applied in order to use the simplest realistic population model to estimate the trend and production potential of the population, assuming that a stable yearly production is realistic for humpback whales off West Greenland over the period from 1980 to 2008. A second model of direct density regulation was applied to allow for estimates of the current and historical depletion levels, should the dynamics of West Greenland humpback whales be monotonically returning towards equilibrium. And a third model of inertia dynamics was applied to allow for estimates of depletion levels should the dynamics be damped cyclic.

A sex structured model with catches taken before survival and reproduction

$$\begin{aligned} N_{t+1}^f &= s(N_t^f - c_t^f)b_t\vartheta + s(N_t^f - c_t^f) \\ N_{t+1}^m &= s(N_t^f - c_t^f)b_t(1 - \vartheta) + s(N_t^m - c_t^m) \end{aligned} \quad (1)$$

was applied, where N_t^f and N_t^m is the number of females (f) and males (m) in year t , c^f and c^m the catch of females and males, s the yearly survival rate, ϑ the fraction of females at birth, and the yearly reproduction per female being

$$\begin{aligned} b_t &= b && \text{for constant reproduction,} \\ b_t &= b_{max}[1 - \alpha(N_t/N^*)^\gamma] && \text{for density regulated dynamics, and} \\ b_t &= N_t^{-\gamma}b_{t-1}N_{t-1}^{-\gamma_q}e^\sigma && \text{for inertia dynamics} \end{aligned} \quad (2)$$

with b_{max} being maximal reproduction, $\alpha = (s + s\vartheta b_{max} - 1)/s\vartheta b_{max}$ a scaling parameter, $N_t = N_t^f + N_t^m$ total abundance in year t , N^* the equilibrium abundance in the absence of harvest, $d_t = N_t/N^*$ the depletion ratio in year t , γ density regulation, $\gamma_q = \iota\gamma$ delayed density dependent effects on intrinsic reproduction caused by selection by density dependent competitive interactions (Witting 2000), $\iota = \gamma_q/\gamma$ the degree of inertia given as the ratio of delayed over direct density dependence, and $\sigma = \gamma_q \ln N^*$ a scaling parameter.

The exponential growth rate $r = \lambda - 1$ for populations with constant reproduction is then $r = s + s\vartheta b - 1$, and the corresponding maximum for density regulated dynamics $r_{max} = s + s\vartheta b_{max} - 1$. With catches taken before survival and reproduction, for the case of density regulated dynamics, the maximum sustainable yield level (msyl) and the maximum sustainable yield rate for the total population component (msyr) are estimated numerically from the constraint that the msyl occurs at $\partial \text{sy} / \partial N = 0$, where $(s + sb_{max} - 1)(1 - d^\gamma)(1 + b_{max}(1 - \alpha d^\gamma)) - b_{max}\alpha\gamma d^\gamma = 0$.

Unlike traditional population dynamics, like that of exponentially growing or density regulated populations, where the exponential growth rate is a parameter, the realised and the maximum growth rate are both initial conditions for inertia dynamics (Ginzburg and Taneyhill 1994; Ginzburg 1998; Witting 1997, 2000, 2002; Ginzburg and Colyvan 2004). This implies that

there is no single abundance curve of sustainable yields and, thus, no easily defined maximum 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 of a large suite of both positive and negative numbers.

Assessment models

Only West Greenland catches were applied to the exponential and density-regulated models that were initialised in 1980 to estimate the trend and current production level of the West Greenland summer aggregation. The models of density regulation and inertia dynamics that assumed a pre-harvested population in dynamic equilibrium, applied the complete catch history and were run two times to cover a range of likely historical catches taken from the West Greenland summer aggregation. The first of these runs applied only the West Greenland catch history, while the second run included also 10% of the historical catches taken in the West Indies, which is twice the suggested maximum by the comparison of the abundance estimates from 1992/93. Hence, it is very likely that the true number of historical catches that have been taken from the West Greenland summer aggregation lies somewhat within the limits of these two runs.

In summary, the assessment runs are:

E: Exponential growth; Initialised in 1980.

Da: Density regulation; Pre-harvest equilibrium; WG catches only.

Db: Density regulation; Pre-harvest equilibrium; WG + 10% WI catches.

Dc: Density regulation; Initialised in 1980.

Ia: Inertia dynamics; WG catches only.

Ib: Inertia dynamics; WG + 10% WI catches.

Statistical methods

The population dynamic models were fitted to the abundance 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 the 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.

Prior distributions

The values and prior ranges of the different parameters for all the assessment models are listed in Table 2. Most of the priors were continuous and uniform and, having no evidence of a foetal sex ratio that differs significantly from uniform, a fixed value of 0.5 was applied to the fraction of females at birth.

Model	s	ι	γ	msyr	msyl	r	N_0	N^*	β^i	β^{ii}
E	.96, .028 ^b	-	-	-	-	.03, .14 ^u	.1, .8 ^u	-	.1, 1 ^u	.46, .12 ^b
Da	.96, .028 ^b	-	-	.01, .075 ^u	.5, .7 ^u	-	-	.2, 1.6 ^u	.2, 1 ^u	.46, .12 ^b
Db	.96, .028 ^b	-	-	.01, .06 ^u	.5, .7 ^u	-	-	.8, 2.2 ^u	.3, 1 ^u	.46, .12 ^b
Dc	.96, .028 ^b	-	-	.025, .075 ^u	.5, .7 ^u	-	.15, .75 ^u	1, 40 ^u	.1, 1 ^u	.46, .12 ^b
Ia	.96, .028 ^b	.01, 1 ^u	1e-8, .05 ^u	-	-	-	-	1.4, 2.4 ^u	.2, 1 ^u	.46, .12 ^b
Ib	.96, .028 ^b	.01, 1 ^u	1e-8, .05 ^u	-	-	-	-	2, 3.6 ^u	.1, 1 ^u	.46, .12 ^b

Table 2: **Prior distributions** for the different assesment models. The list of parameters: s is yearly survival, ϑ the fraction of females at birth, ι the level of inertia, γ the density regulation, msyr the maximum sustainable yield rate, msyl the maximum sustainable yield level, r the yearly growth rate given no removals (r_{max} for density regulated dynamics; in 2008 given inertia dynamics), N_0 the abundance in the first year of the iteration (given in thousands), N^* the equilibrium abundance (given in thousands), β^i the bias of abundance estimates \mathbf{N}_{1+}^i , and β^{ii} the bias of abundance estimates \mathbf{N}_{1+}^{ii} . The type of probability distribution is given by superscripts; u =uniform, b =beta, and p a parameter with fixed value. The first number of an entry in the table is the min value if $pd = u$, a fixed parameter value if $pd = p$. The second number is the max value if $pd = u$, and the sd if $pd = b$.

For the population dynamic model of direct density dependence the median of the msyl was set to 0.6 with a uniform prior between 0.5 and 0.7. A uniform prior on the msyr (effectively msyr_{1+}) was set to cover the range from 0.01 to 0.075, with the maximum value corresponding to an agreed maximal growth rate of 0.106 (IWC 2007) assuming a msyl of 0.6.

Having two models (exponential and direct density regulation) with a prior on the growth rate (r and msyr), and one model (inertia) where the growth rate is an initial condition instead of a parameter, the yearly survival rate was chosen as the only demographic parameter with a prior, leaving the birth rate to be determined from the prior on the survival rate and the prior, or the initial condition, on the growth rate.

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 in 1664 or 1750, depending on the applied catch history. The assumption of a pre-harvested population in dynamic equilibrium was also applied to some of the runs for the model with direct density regulation only.

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). I used the West Greenland estimate as an informative prior, applying a Beta distributed prior to the annual survival rate ($a = 49.27$, $b = 2.21$).

The prior range on the level of inertia (ι) in the inertia model was set to cover the complete range from almost no ($\iota = 0.01$) to full inertia ($\iota = 1$) given stable or damped population cycles. An inertia level of zero represents the case with direct density regulation and a monotonic return to population dynamic equilibrium, while an inertia level of one represents the case with neutrally stable cycles given no harvest. Inertia values from one to zero give a continuum of more

and more damped cyclic behaviour, while values above one give unstable cycles that eventually would cause the population to go extinct. The prior ranges on the abundance and the density regulation parameter of the inertia model (γ) were set by trial and error.

The correction factor of the 2007 aerial survey for submerged whales was given as an informative prior for the bias of the index time series of abundance estimates from aerial surveys. With the correction factor adjusted for the non-instantaneous visual sighting process of the aerial surveys, the correction factor was 0.46 with a SD of 0.12 (Heide-Jørgensen et al. 2008), which was applied as a Beta prior ($a = 6.954$, $b = 8.196$). A uniform prior was set by trial and error for the bias of the mark-recapture abundance estimates.

Bayesian integration

The Bayesian integration was obtained by the sampling-importance-resampling routine (Berger 1985; Rubin 1988), where n_1 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_1 , 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

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)} \quad (3)$$

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_1 parameter sets were then re-sampled n_2 times with replacement, with the sampling probability of the i th parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_1} w(\theta_j)} \quad (4)$$

This generates a random sample of the posterior distribution of size n_2 . The resample of the posterior distribution was set to $n_2 = 5000$, and the n_1 sample from the joint prior being between 1000000 and 28000000.

The method of de la Mare (1986) was used to calculate the likelihood L under the assumption that observation errors were log-normally distributed (Buckland 1992). With a bias factor β^x [where $N_t^x = \beta^x N_t$, N_t^x is the point estimate and N_t the iterated abundance of time series \mathbf{N}^x at time t] that is constant over all years, and to be estimated for the abundance of time series one ($\mathbf{N}_{1+}^{\text{i}}$) and the abundance of time series two ($\mathbf{N}_{1+}^{\text{ii}}$) the likelihood function is

$$L = \prod_t \exp \left(- \frac{[\ln(N_{1+,t}^i / \beta^i N_{1+,t})]^2}{2cv_t^2} \right) / cv_t \quad (5)$$

where cv_t is the coefficient of variation of the abundance estimate at time t .

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_1 draws. For example, 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_2 parameter sets, as well the maximum number of occurrences of a unique parameter set in the resample.

Model comparison

The relative likelihoods of the different assessment models can be compared by Bayes factor (Reckhow 1990; Kass and Raftery 1995; Ellison 1996; Wade 2000). Comparing two models Bayes factor is the ratio of the probability of the data given one model over the probability of the data given the other model. Assuming equal prior weight to all models the probability of a model (p) may be calculated as the average likelihood over the prior

$$p_o = \frac{1}{n_1} \sum_{i=1}^{n_1} L(\theta_i) \quad (6)$$

where n_1 is the number of draws from the prior.

A comparison based on Eq. (6) will not necessarily reflect the ability of the models to explain the data. The best explanation of the data is instead provided by the parameterisation in the initial n_1 sample that has the maximum likelihood $p_l = \max[L(\theta_1), L(\theta_2), \dots, L(\theta_{n_1})]$. I therefore provide pair wise model comparisons based on Bayes factor and on the ratio of the maximum likelihood. The p_o and p_l likelihood estimates of the models are furthermore scaled to one across all models in order to reflect the relative probability of the different models.

Probability of meeting the objective

For exponential growth and inertia dynamics the management objective was set to $N_{2013} > N_{2008}$. For density regulated dynamics the management objective was set to $N_{2013} > N_{2008}$ should the abundance be below the msyl, while a total take of 90% of the msy was allowed should the abundance be at or above the msyl.

Given the population dynamic model and the data, the probabilities that this objective be met by future catches are straightforwardly calculated from the Bayesian statistical method applied here. For each parameterisation θ_i of the random sample of the posterior distribution of size n_2 , we have perfect knowledge of the status of the population for that parameterisation. Hence, for a given θ_i -projection with future catches c it can be determined whether the population objectives are met or not. This implies that the probability $p(ob)$ that the objectives be met can be determined by the following sum

$$\begin{aligned} p(ob) &= \sum_{i=1}^{n_2} g(\theta_i, c) / n_2 \\ g(\theta_i, c) &= \begin{cases} 1 & \text{if objective met} \\ 0 & \text{if objective not met} \end{cases} \end{aligned} \quad (7)$$

Model	Sample	Weight	Unique	Max
E	1000000	0.0	3991	7
Da	28000000	0.1	4560	7
Db	28000000	0.5	2783	29
Dc	1000000	0.0	4254	5
Ia	28000000	0.1	2782	11
Ib	28000000	0.3	2217	25

Table 3: **Sampling statistics** for the Bayesian runs of the different assessments models. Sample is the number of draws from the importance function; Weight the maximum importance weight of a draw relative to the total importance weight of all draws (given in percent); Unique the number of unique parameter sets in the resample of 5000 parameter sets; and Max the maximum occurrence of a unique parameter set in the resample.

over the complete random sample of the posterior distribution.

RESULTS

Posterior distributions

The maximum importance weight of a parameter set relative to the total sum of importance weights for all drawn parameter sets in an assessment was smaller than .5% for all assessments. And the number of unique parameter sets in a resample of 5000 parameter sets was not smaller than 2217 for any model, while the maximum occurrences of a unique parameter set in the resample across all models was 29. The model specific statistics are given in Table 3.

The posterior estimates and their 90 % credibility intervals are given in Table 4.

Model comparison

The predicted trajectories of the different models are shown in Figures 1 to 3, and the relative likelihoods of the different models are given in Table 5. Jeffreys (1961) considered Bayes factors above 100 (or below 0.01) to be decisive support for one model over the other, factors between 10 and 100 (or 0.1 and 0.01) to be strong support, factors between 3.2 and 10 (or 0.31 and 0.1) to be substantial support, and factors between 1 and 3.2 (or 0.31 and 1) as not worth more than a bare mention.

Although it can be problematic to compare different models by Bayes factors, we note that the density-regulated and the inertia models have the same number of parameters. These two models may thus be compared. For the case where they make the same initial assumption of a pre-harvested population in population dynamic equilibrium, the pair-wise comparisons between **Da** and **Ia**, and between **Db** and **Ib**, give Bayes factors of 7,100 and 240 in favour of the inertia model. Hence, there is decisive support for the rejection of the density-regulated model as an appropriate model for the historical long-term modelling of the population dynamics of humpback whales off West Greenland. When instead the inertia models are compared to the short-term density-regulated model **Dc** that is initialised in 2008, they have similar Bayes factors

Model		s	b_{max}	ι	γ	msyr	msyl	r	N_0	N^*	β^i	β^{ii}	N_T	d	ry	$Q1$
E	Med.	.96	.26	-	-	-	-	.09	.34	.00	.59	.46	2.6	-	220	-
	5th	.90	.18	-	-	-	-	.06	.24	.00	.33	.26	1.5	-	96	-
	95th	.99	.41	-	-	-	-	.11	.56	.00	.87	.65	5.0	-	510	-
Da	Med.	.96	.17	-	1.9	.03	.58	.04	.84	.84	.67	.53	.65	.83	7.7	10
	5th	.90	.07	-	.98	.01	.51	.02	.53	.53	.41	.33	.51	.51	2.1	8.0
	95th	.99	.39	-	4.2	.07	.68	.12	1.3	1.3	.95	.70	.96	.98	10	22
Db	Med.	.97	.16	-	2.2	.03	.59	.04	1.2	1.2	.73	.55	.82	.70	18	19
	5th	.92	.10	-	.96	.02	.51	.03	.89	.89	.48	.39	.69	.44	11	13
	95th	.99	.27	-	4.6	.04	.69	.07	1.7	1.7	.89	.73	1.0	.92	22	23
Dc	Med.	.96	.26	-	2.3	.05	.60	.09	.34	21	.58	.45	2.5	.13	200	140
	5th	.91	.17	-	1.0	.04	.51	.06	.24	4.0	.34	.27	1.5	.05	83	60
	95th	.99	.42	-	4.4	.07	.69	.11	.55	38	.87	.65	4.7	.62	430	290
Ia	Med.	.98	-	.31	.018	-	-	.07	1.7	1.7	.56	.43	2.3	1.3	160	-
	5th	.93	-	.09	.0047	-	-	.05	1.5	1.5	.34	.28	1.3	.71	72	-
	95th	.99	-	.87	.044	-	-	.09	2.0	2.0	.87	.65	4.0	2.4	370	-
Ib	Med.	.97	-	.33	.016	-	-	.07	2.7	2.7	.57	.44	2.4	.88	190	-
	5th	.93	-	.08	.0038	-	-	.05	2.3	2.3	.34	.28	1.2	.44	68	-
	95th	.99	-	.90	.046	-	-	.10	3.1	3.1	.86	.63	4.2	1.6	380	-

Table 4: **Parameter estimates** for the different assessment models denoted by the labels in Section . The estimates are given by the median and the 90% credibility intervals of the posterior distributions. Abundances (N) are given in thousands, and N_T and d are estimated for 2008.

with values of 0.68 and 0.88 (in favour of the short-term density-regulated model); values that are similar with those of the exponential model that has fewer parameters. Hence, we may conclude that all models are appropriate for a short-term description of the historical dynamics, and that the inertia model is also appropriate for a long-term description given the catch history and the abundance data.

As the life history dynamics of the inertia models implies population dynamic changes in the carrying capacity over time, it is quite reasonable to have an inertia model that can explain the long-term dynamics, while at the same time the density-regulated and exponential models may explain the short-term dynamics, where the carrying capacity and the population dynamic growth rate may not change much.

Model fits

Figures 4 and 5 show the realised prior and posterior distributions for selected parameters of the exponential model, the density-regulated model initialised in 1980, and the two inertia models. All models show well updated posterior distributions for the population dynamic growth rates (r or msyr) and the population abundance, although for the density regulated model there was no data signal on the upper limit to the carrying capacity (not shown in the figure).

The bias parameters on the survey estimates show similar updating for all models. For the informative bias prior on the aerial surveys no updating of the posterior distribution was found,

	E	Da	Db	Dc	Ia	Ib	p_l
E	1	0	0	1	.69	.89	.28
Da	1.2e6	1	38	1e4	7100	9300	0
Db	1.1e5	.1	1	280	190	240	0
Dc	.71	0	0	1	.68	.88	.28
Ia	140	0	0	190	1	1.3	.19
Ib	270	0	0	380	2	1	.25
p_o	.41	0	0	.58	0	0	

Table 5: **Model comparison.** The lower left side of the matrix gives pairwise Bayes factors, and the upper right side gives pairwise maximum likelihood ratios, with the denominators given by the average or maximum likelihood of the model in the left-hand column. The p_l column gives the maximum likelihood and the p_o row the average likelihood of the prior with likelihood normalised to a sum of one across all models.

while for the uninformative prior on the mark-recapture estimates a strong updating was found. The results suggest that the mark-recapture estimates are negatively biased to approximately 58% of the true abundance (**E**, **Dc**, **Ia** and **Ib** models), which is a somewhat smaller bias than the 46% for the uncorrected aerial surveys.

The density dependence (γ) and level of inertia (ι) on the inertia models show some updating of the posterior distribution, although not as strongly as for the abundance and population dynamic growth rates.

Population dynamics

Although there is a high level of uncertainty in the posterior distributions on the level of inertia, they give a relatively well updated median estimate around 0.3, which is similar to the estimate for fin whales off West Greenland (Witting 2008). This shows that the population dynamics of the humpback whales off West Greenland is likely to be damped cyclic on the longer time-scale. The inertia models **Ia** and **Ib** furthermore suggest a population dynamic equilibrium between 1,700 (90% CI:1,500 – 2,000) and 2,700 (90% CI:2,300 – 3,100) whales, and a current depletion ratio between 0.88 (90% CI:0.44 – 1.6) and 1.3 (90% CI:0.71 – 2.4).

From the exponential model and the short-term density-regulated model initialised in 1980, we have an estimated current exponential growth rate of 0.09 (90% CI:0.06 – 0.11) [or multiplication factor of 1.09 (90% CI:1.06 – 1.12) per year], and an estimate of the current msyr of 0.05 (90% CI:0.04 – 0.07), although the long-term applicability of the concept behind the msyr and the msyl is questioned by the lack of long-term fit for the density-regulated model. It is intriguing to see that the short-term dynamics predicted by the two short-term models of exponential and density regulated growth and the long-term model of inertia dynamics are essentially identical (compare top and bottom graph in Figure 1, and bottom graph in Figure 3). All models are also fairly consistent on the current production in the population, estimating that the current yearly replacement yield is between 160 (90% CI:72 – 370; **Ia** model) and 220 (90% CI:96 – 510; **E** model) whales per year.

Catch	p_1	p_2	p_3	p_4	p_5	p_6
2	1.0	1.0	1.0	1.0	1.0	1.0
4	1.0	1.0	1.0	1.0	1.0	1.0
6	1.0	1.0	1.0	1.0	1.0	1.0
8	1.0	.98	1.0	1.0	1.0	1.0
10	1.0	.59	1.0	1.0	1.0	1.0
12	1.0	.32	.98	1.0	1.0	1.0
14	1.0	.24	.97	1.0	1.0	1.0
16	1.0	.17	.88	1.0	1.0	1.0
18	1.0	.12	.65	1.0	1.0	1.0
20	1.0	.08	.40	1.0	1.0	1.0

Table 6: **Catch objective trade-off.** The probability p_i of meeting the management objectives for annual total removals between 2 and 20 individuals in the period 2008 to 2013. The assessment models, denoted by subscript i in p_i , are: 1 = **E**; 2 = **Da**; 3 = **Db**; 4 = **Dc**; 5 = **Ia**; 6 = **Ib**.

Meeting management objectives

Catch	p_1	p_2	p_3	p_4	p_5	p_6
2	1.0	1.0	1.0	1.0	1.0	1.0
4	1.0	.66	1.0	1.0	1.0	1.0
6	1.0	.58	.99	1.0	1.0	1.0
8	1.0	.47	.98	1.0	1.0	1.0
10	1.0	.10	.97	1.0	1.0	1.0
12	1.0	.00	.92	1.0	1.0	1.0
14	1.0	.00	.81	1.0	1.0	1.0
16	1.0	.00	.72	1.0	1.0	1.0
18	1.0	.00	.43	1.0	1.0	1.0
20	1.0	.00	.16	1.0	1.0	1.0

Table 7: **Replacement yeild.** The probability p_i that the replacement is larger than annual total removals between 2 and 20 individuals in the period 2008 to 2013. .

Assuming that the fraction of females in the future catches is 0.50, we calculated the probabilities of meeting the management objectives given the different assessment models. This was done for total removals of 2 to 20 individuals in the period from 2008 to 2013, with the results shown in Table 6.

The probabilities that the replacement yield and the Q1 measure of sustainability for 2008 is larger than annual total removals between 2 and 20 individuals are given in Table 7 and 8. All appropriate models estimated that the probability that the population will continue to increase until 2013 is one even with an annual take of 20 humpback whales per year.

Acknowledgements

Catch	p_1	p_2	p_3	p_4	p_5	p_6
2	-	1.0	1.0	1.0	-	-
4	-	1.0	1.0	1.0	-	-
6	-	1.0	1.0	1.0	-	-
8	-	.95	1.0	1.0	-	-
10	-	.58	.98	1.0	-	-
12	-	.32	.97	1.0	-	-
14	-	.24	.93	1.0	-	-
16	-	.17	.82	1.0	-	-
18	-	.12	.63	1.0	-	-
20	-	.08	.33	1.0	-	-

Table 8: **Q1.** The probability p that Q1 is larger than annual total removals between 2 and 20 individuals in the period 2008 to 2013. .

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Year	m	f	Year	m	f	Year	m	f	Year	m	f	Year	m	f
1750	4	4	1802	4	4	1854	13	13	1906	4	4	1958	0	0
1751	4	4	1803	4	4	1855	13	13	1907	4	4	1959	0	0
1752	4	4	1804	4	4	1856	13	13	1908	4	4	1960	0	1
1753	4	4	1805	4	4	1857	13	13	1909	4	4	1961	0	1
1754	4	4	1806	4	4	1858	13	13	1910	2	2	1962	1	1
1755	4	4	1807	4	4	1859	13	13	1911	6	5	1963	0	0
1756	4	4	1808	4	4	1860	13	13	1912	6	5	1964	0	0
1757	4	4	1809	4	4	1861	13	13	1913	2	2	1965	0	1
1758	4	4	1810	4	4	1862	13	13	1914	2	2	1966	2	2
1759	4	4	1811	4	4	1863	13	13	1915	2	2	1967	2	2
1760	4	4	1812	4	4	1864	13	13	1916	2	2	1968	2	3
1761	4	4	1813	4	4	1865	13	13	1917	2	2	1969	1	2
1762	4	4	1814	4	4	1866	2	2	1918	2	2	1970	0	0
1763	4	4	1815	4	4	1867	2	2	1919	8	6	1971	2	2
1764	4	4	1816	4	4	1868	2	2	1920	1	1	1972	1	2
1765	4	4	1817	4	4	1869	2	2	1921	1	1	1973	5	6
1766	4	4	1818	4	4	1870	2	2	1922	88	57	1974	4	5
1767	4	4	1819	4	4	1871	2	2	1923	95	59	1975	4	5
1768	4	4	1820	4	4	1872	2	2	1924	28	20	1976	4	5
1769	4	4	1821	4	4	1873	2	2	1925	4	4	1977	8	9
1770	4	4	1822	4	4	1874	2	2	1926	6	6	1978	12	12
1771	4	4	1823	4	4	1875	2	2	1927	5	6	1979	7	8
1772	4	4	1824	4	4	1876	2	2	1928	4	5	1980	8	8
1773	4	4	1825	4	4	1877	2	2	1929	5	5	1981	6	6
1774	4	4	1826	4	4	1878	2	2	1930	19	12	1982	6	6
1775	4	4	1827	4	4	1879	2	2	1931	13	10	1983	7	9

Year	m	f	Year	m	f	Year	m	f	Year	m	f	Year	m	f
1776	4	4	1828	4	4	1880	2	2	1932	5	4	1984	8	8
1777	4	4	1829	4	4	1881	2	2	1933	3	2	1985	4	4
1778	4	4	1830	4	4	1882	2	2	1934	2	2	1986	0	0
1779	4	4	1831	4	4	1883	2	2	1935	3	3	1987	0	0
1780	4	4	1832	4	4	1884	2	2	1936	2	3	1988	0	1
1781	4	4	1833	4	4	1885	2	2	1937	8	5	1989	1	1
1782	4	4	1834	4	4	1886	4	4	1938	0	1	1990	0	1
1783	4	4	1835	4	4	1887	4	4	1939	1	1	1991	0	1
1784	4	4	1836	4	4	1888	4	4	1940	0	0	1992	0	1
1785	4	4	1837	4	4	1889	2	2	1941	0	0	1993	0	0
1786	4	4	1838	4	4	1890	4	4	1942	0	0	1994	0	1
1787	4	4	1839	4	4	1891	4	4	1943	0	0	1995	0	0
1788	4	4	1840	4	4	1892	2	2	1944	0	0	1996	0	0
1789	4	4	1841	16	16	1893	6	6	1945	0	0	1997	0	0
1790	4	4	1842	13	13	1894	7	7	1946	2	2	1998	0	1
1791	4	4	1843	13	13	1895	6	6	1947	2	3	1999	0	1
1792	4	4	1844	10	10	1896	2	2	1948	0	1	2000	0	2
1793	4	4	1845	13	13	1897	5	5	1949	1	1	2001	1	1
1794	4	4	1846	13	13	1898	2	2	1950	1	2	2002	2	1
1795	4	4	1847	13	13	1899	5	5	1951	2	3	2003	0	1
1796	4	4	1848	13	13	1900	8	8	1952	0	0	2004	2	1
1797	4	4	1849	13	13	1901	8	8	1953	0	1	2005	2	3
1798	4	4	1850	11	11	1902	8	8	1954	0	0	2006	0	0
1799	4	4	1851	13	13	1903	8	8	1955	0	0	2007	1	1
1800	4	4	1852	13	13	1904	8	8	1956	0	0	2008	-	-
1801	4	4	1853	13	13	1905	4	4	1957	0	0	2009	-	-

Table 9: **Yearly catch** of male (m) and female (f) humpback whales off West Greenland. Data from IWC (2003).

Year	m	f	Year	m	f	Year	m	f	Year	m	f	Year	m	f
1664	2	5	1732	7	19	1800	2	3	1868	123	105	1936	2	3
1665	9	21	1733	7	19	1801	2	3	1869	81	72	1937	2	3
1666	5	12	1734	7	19	1802	2	3	1870	58	52	1938	2	3
1667	7	19	1735	7	19	1803	2	3	1871	53	66	1939	2	6
1668	2	5	1736	7	19	1804	2	3	1872	72	76	1940	0	2
1669	5	12	1737	7	19	1805	2	3	1873	60	67	1941	2	3
1670	5	12	1738	7	19	1806	2	3	1874	78	86	1942	0	2
1671	5	12	1739	7	19	1807	2	3	1875	98	102	1943	0	0
1672	5	12	1740	7	19	1808	2	3	1876	99	101	1944	0	0
1673	5	12	1741	7	19	1809	2	3	1877	93	97	1945	0	0
1674	5	12	1742	7	19	1810	2	3	1878	96	114	1946	0	0
1675	5	12	1743	7	19	1811	2	3	1879	81	85	1947	0	2
1676	5	12	1744	7	19	1812	2	3	1880	86	95	1948	2	4
1677	5	12	1745	7	19	1813	2	3	1881	78	88	1949	0	0
1678	5	12	1746	7	19	1814	2	3	1882	54	74	1950	0	0
1679	0	0	1747	7	19	1815	2	3	1883	65	76	1951	0	0
1680	0	0	1748	11	26	1816	2	3	1884	84	128	1952	0	0
1681	0	0	1749	7	19	1817	2	3	1885	66	97	1953	0	0
1682	0	0	1750	7	19	1818	2	3	1886	94	172	1954	0	0
1683	0	0	1751	2	3	1819	2	3	1887	29	74	1955	0	0
1684	0	0	1752	2	3	1820	2	3	1888	11	28	1956	0	0
1685	7	19	1753	2	3	1821	2	3	1889	16	39	1957	0	0
1686	7	19	1754	2	3	1822	2	3	1890	20	48	1958	3	6
1687	7	19	1755	2	3	1823	2	3	1891	16	38	1959	3	6
1688	7	19	1756	2	3	1824	2	3	1892	13	33	1960	0	2
1689	7	19	1757	2	3	1825	2	3	1893	25	60	1961	0	0
1690	7	19	1758	2	3	1826	7	18	1894	16	38	1962	0	0
1691	4	11	1759	2	3	1827	6	14	1895	18	45	1963	2	4
1692	7	19	1760	2	3	1828	2	5	1896	18	45	1964	0	2
1693	7	19	1761	2	3	1829	3	6	1897	47	114	1965	0	2
1694	7	19	1762	2	3	1830	9	22	1898	8	20	1966	0	0
1695	7	19	1763	2	3	1831	9	20	1899	20	51	1967	2	4
1696	7	19	1764	2	3	1832	15	37	1900	27	68	1968	2	4
1697	7	19	1765	2	3	1833	11	26	1901	38	94	1969	2	4
1698	7	19	1766	2	3	1834	20	50	1902	31	75	1970	4	11

Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>
1699	7	19	1767	2	3	1835	18	43	1903	29	73	1971	2	4
1700	7	19	1768	2	3	1836	16	38	1904	9	23	1972	3	8
1701	7	19	1769	2	3	1837	16	38	1905	7	15	1973	0	2
1702	7	19	1770	2	3	1838	20	48	1906	11	26	1974	0	2
1703	7	19	1771	2	3	1839	13	33	1907	9	25	1975	0	0
1704	7	19	1772	2	3	1840	17	42	1908	13	31	1976	0	2
1705	7	19	1773	2	3	1841	16	40	1909	6	15	1977	0	0
1706	7	19	1774	2	3	1842	16	38	1910	4	11	1978	0	2
1707	7	19	1775	2	3	1843	16	38	1911	4	11	1979	2	5
1708	7	19	1776	2	3	1844	12	29	1912	5	13	1980	1	3
1709	7	19	1777	2	3	1845	14	35	1913	3	8	1981	0	0
1710	7	19	1778	2	3	1846	13	33	1914	2	6	1982	2	3
1711	7	19	1779	2	3	1847	4	11	1915	4	11	1983	0	2
1712	7	19	1780	0	2	1848	20	50	1916	6	15	1984	0	0
1713	7	19	1781	0	2	1849	15	37	1917	3	8	1985	0	0
1714	7	19	1782	0	2	1850	23	37	1918	3	8	1986	0	2
1715	7	19	1783	0	2	1851	19	33	1919	9	20	1987	0	2
1716	7	19	1784	0	2	1852	48	54	1920	9	20	1988	0	2
1717	7	19	1785	0	2	1853	50	61	1921	2	3	1989	0	0
1718	7	19	1786	2	3	1854	42	50	1922	7	19	1990	0	0
1719	7	19	1787	2	3	1855	60	65	1923	5	12	1991	0	0
1720	7	19	1788	2	3	1856	74	77	1924	7	17	1992	0	2
1721	7	19	1789	2	3	1857	60	65	1925	86	23	1993	0	2
1722	7	19	1790	2	3	1858	60	63	1926	60	20	1994	0	0
1723	7	19	1791	2	3	1859	46	48	1927	2	3	1995	0	0
1724	7	19	1792	2	3	1860	39	47	1928	3	8	1996	0	2
1725	7	19	1793	2	3	1861	35	42	1929	2	6	1997	0	0
1726	7	19	1794	2	3	1862	27	30	1930	2	3	1998	0	2
1727	7	19	1795	2	3	1863	42	40	1931	2	6	1999	0	2
1728	7	19	1796	2	3	1864	39	38	1932	2	4	2000	0	2
1729	7	19	1797	0	0	1865	133	111	1933	2	3	2001	0	2
1730	7	19	1798	2	3	1866	134	116	1934	2	3	2002	-	-
1731	7	19	1799	2	3	1867	196	169	1935	2	6	2003	-	-

Table 10: **Yearly catch** of male (*m*) and female (*f*) humpback whales in the West Indies. Data from IWC (2003).

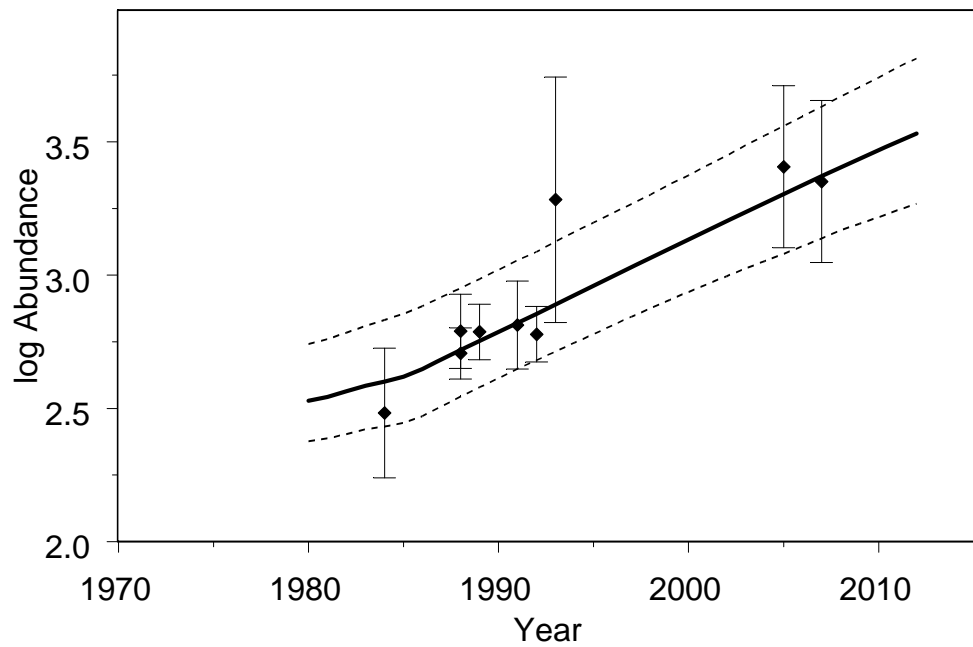
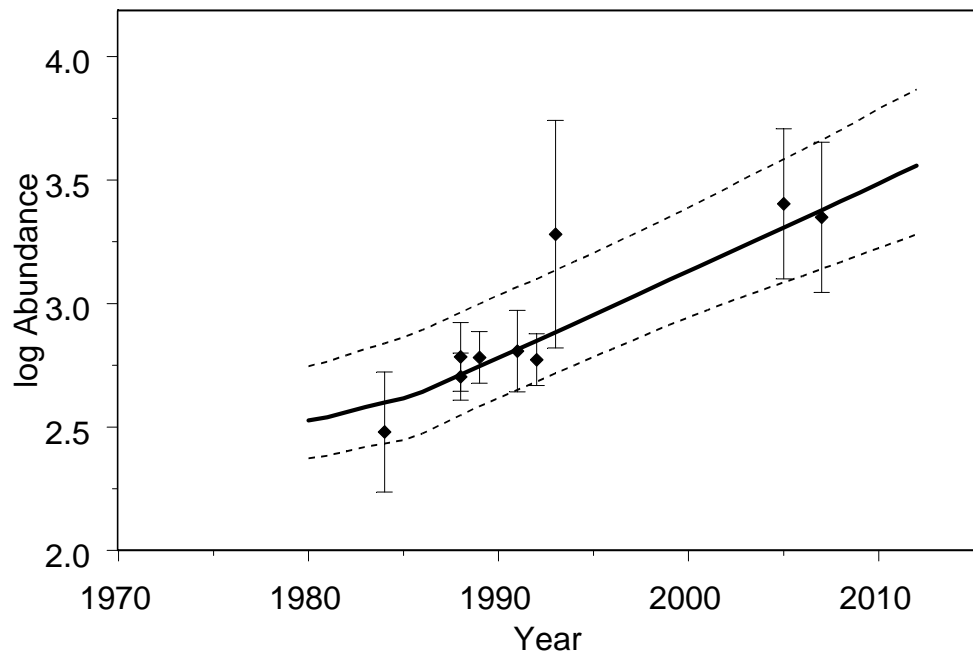


Figure 1: Projections of the median and the 95% credibility intervals of the exponential (top figure) and density-regulated (bottom) models initiated in 1980.

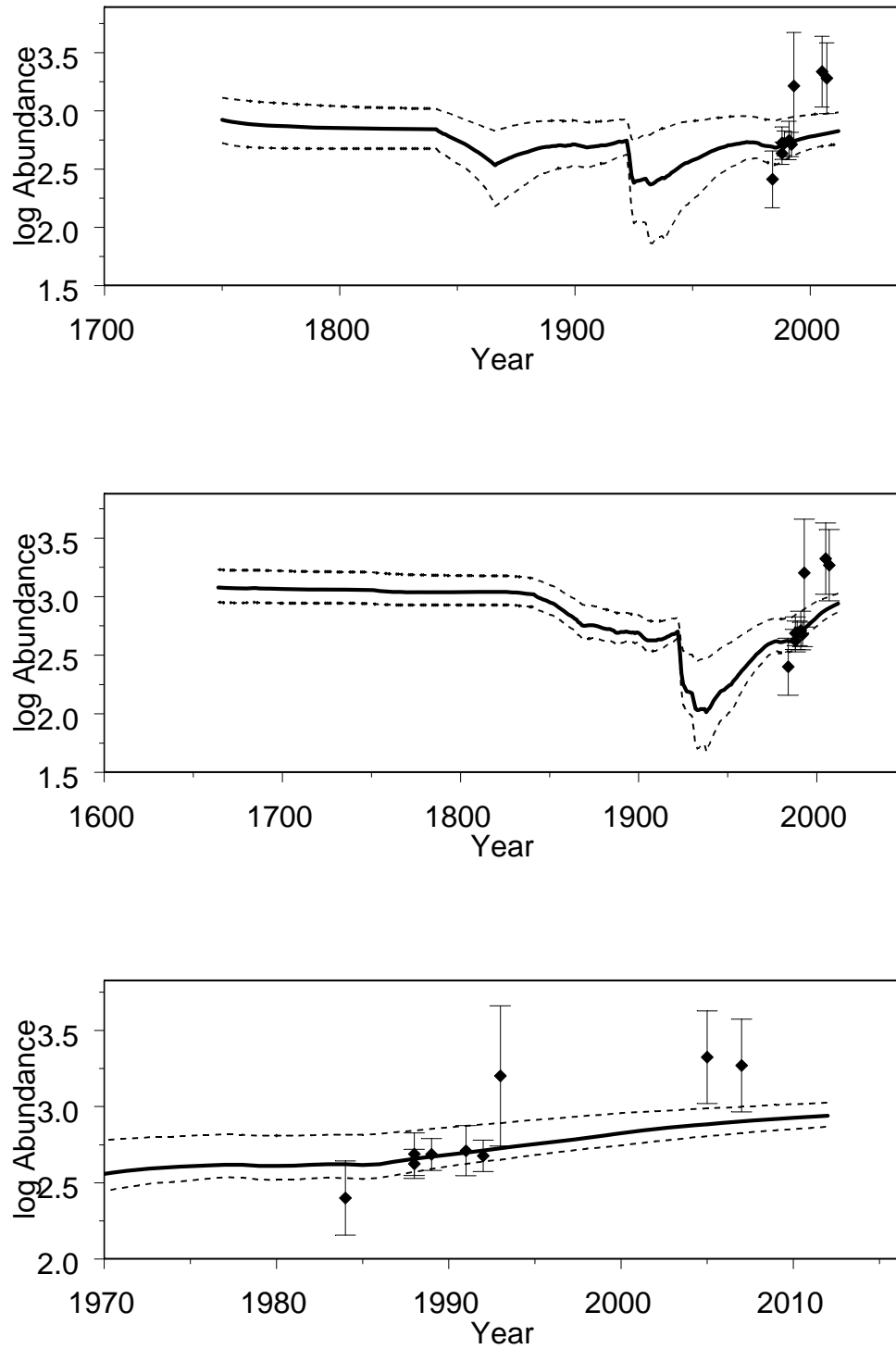


Figure 2: Projections of the median and the 95% credibility intervals of the density-regulated model with a pre-harvested population in equilibrium, given zero (top figure) and ten (middle and bottom) percent of the West Indies catches.

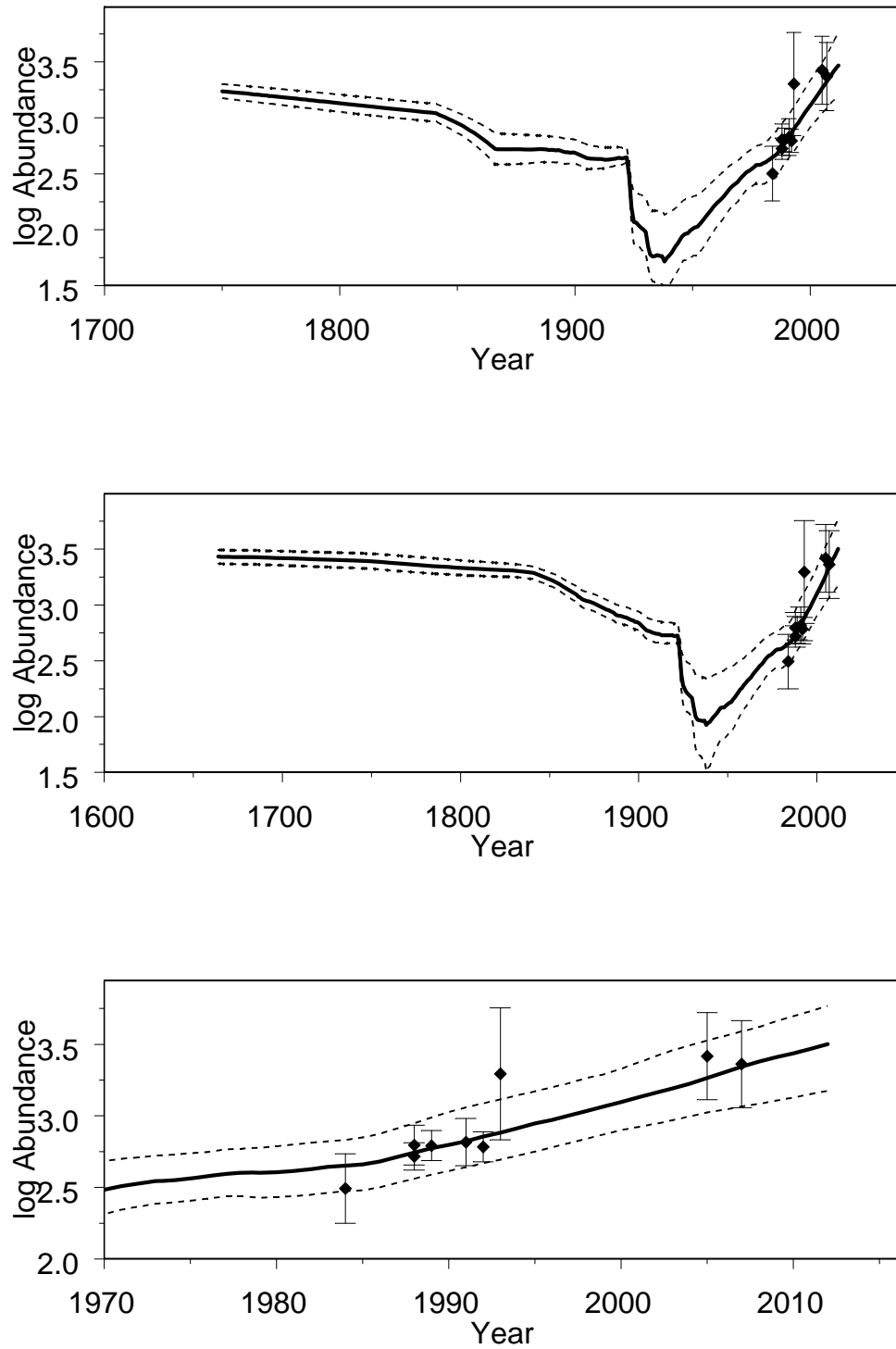


Figure 3: Projections of the median and the 95% credibility intervals of the inertia model with a pre-harvested population in equilibrium, given zero (top figure) and ten (middle and bottom) percent of the West Indies catches.

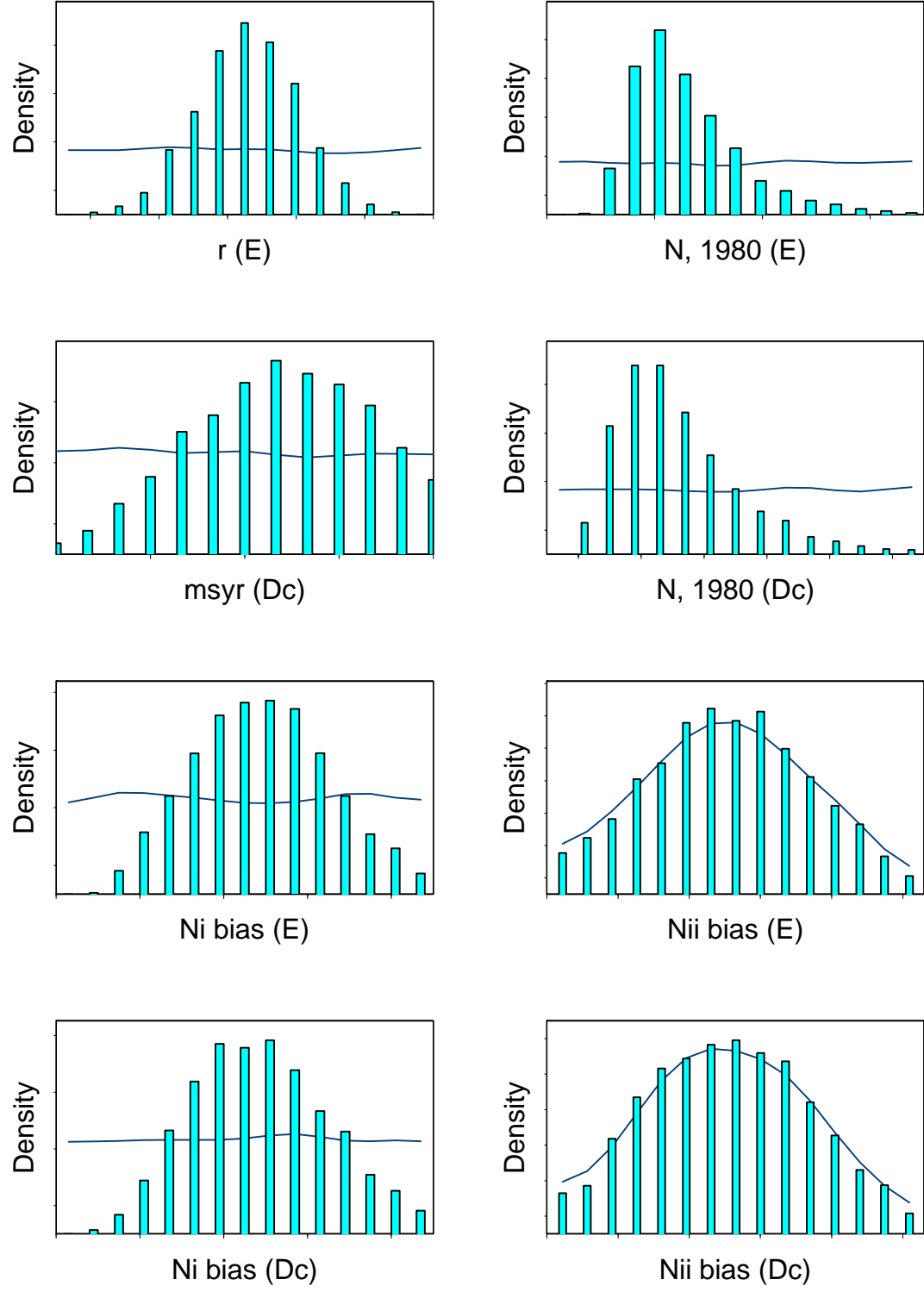


Figure 4: The realised prior (curve) and the posterior (bars) distributions for selected parameters of the exponential (E) and density-regulated (Dc) model initialised in 1980.

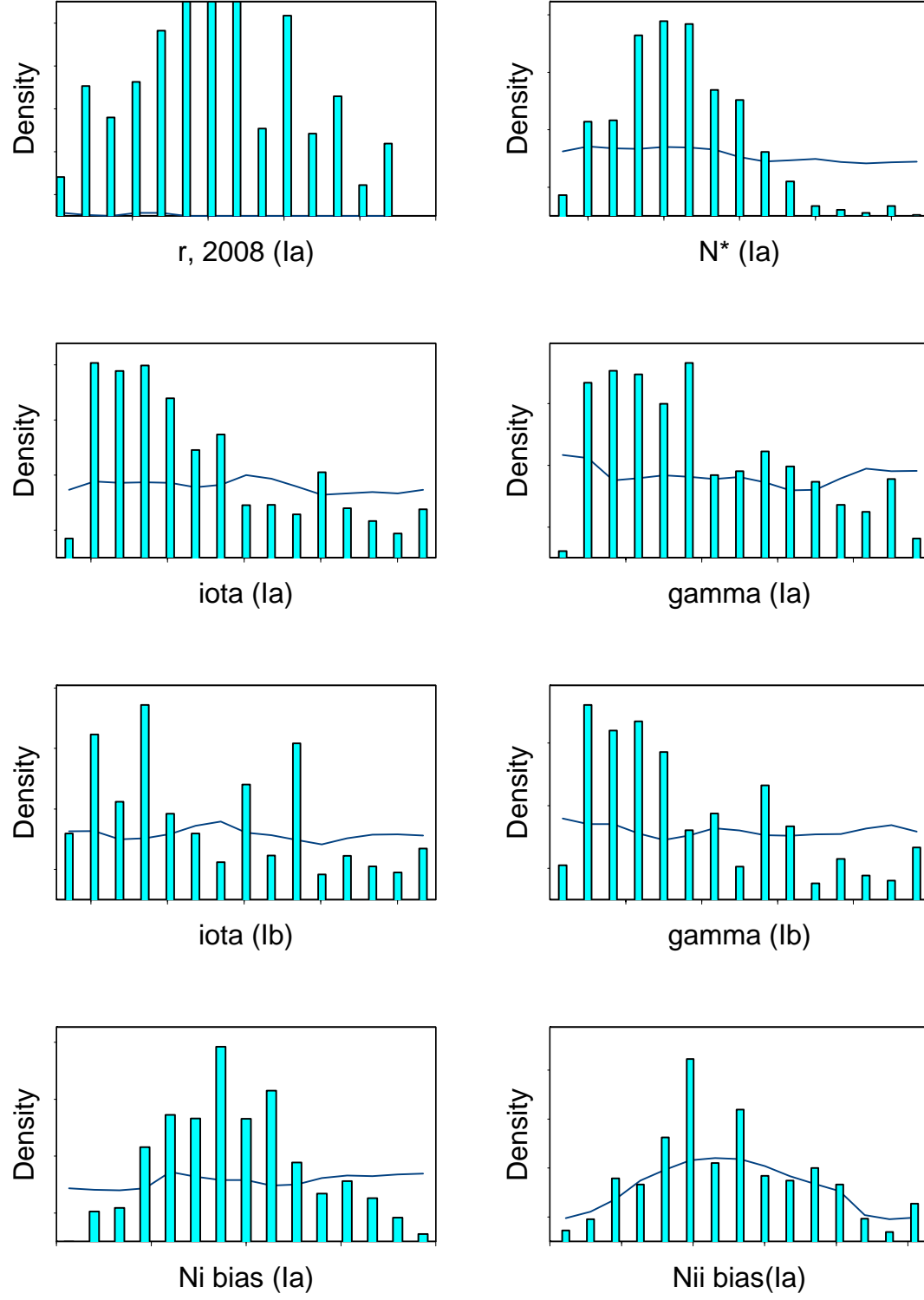


Figure 5: The realised prior (curve) and the posterior (bars) distributions for selected parameters of the two inertia models (Ia and Ib).