

Assessment update for West Greenland fin whales

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ABSTRACT

This paper uses the population perturbation caused by the whaling industry during the 20th century to examine whether the population dynamics of fin whales off West Greenland is best described by direct density regulation and an abundance that returns monotonically towards an equilibrium, or by inertia dynamics that include also delayed density dependence by density dependent selection generating a cyclic population response. Having only three reliable abundance estimates, the abundance data will not directly reveal the dynamics. But, when combined with the historical catches, it is shown that there is statistically strong support for the rejection of the density-regulated model as an appropriate model for the long-term dynamics of fin whales off West Greenland. The dynamics is instead most likely damped cyclic, although the density-regulated, as well as the exponential, models provide good fits for the short-term dynamics of fin whales during the last two decades. The equilibrium population abundance is estimated to 2,000 (90% CI:1,400 – 3,700) whales, the 2008 depletion ratio to 1.5 (90% CI:0.67 – 3.5), and the exponential growth rate to 0.07 (90% CI:0.03 – 0.12). The probability that the population will continue to increase with an annual catch of 20 whales per year is estimated to 96%.

INTRODUCTION

The population dynamic history of fin whales (*Balaenoptera physalus*) off West Greenland is like that of many other marine mammals characterised by a brief period of heavy exploitation. For fin whales off West Greenland the catch started in the 1920s, with the Norwegian fleet taking 109 fin whales in 1922-24 and 333 whales in 1931-33, and combined with the hunt of the Greenland Office a total of 1014 fin whales were taken between 1922 and 1939. The whaling activity resumed by the Greenland Office after World War II, and continued until it was unprofitable catching a total of 324 fin whales between 1946 and 1958. Since then the Greenlanders have taken relatively few fin whales with a total of 385 being taken during approximately 50 years; with an average of 16 whales per year from 1989 to 1999, and ten per year since 2000.

While animal populations with strongly perturbed abundances often show complex dynamics like population cycles, nearly all the population dynamic models that are used for assessments of perturbed marine mammal populations are based on direct density regulation showing a monotonic return to an equilibrium abundance given that the environment is stable (e.g., Givens et al. 1995; Wade 2002; Breen et al. 2003; Alvarez-Flores and Heide-Jørgensen 2004; Witting and Born 2005; Winship and Trites 2006). Although direct density regulation may generate fluctuating or even chaotic dynamics if the density dependence is sufficiently strong and generations

are non-overlapping, these fluctuations typically have a period of only two generations and show little resemblance with the majority of observed complex dynamics where the population dynamic period usually takes more than four generation (Turchin and Taylor 1992; Witting 1997; Ginzburg and Colyvan 2004).

One likely reason for the continued use of direct density regulated models for marine mammal populations is the lack of time series of abundance estimates that are sufficiently long to document whether the dynamics is cyclic or monotonically returning to equilibrium. Among whales, the eastern Pacific gray whale is probably the best monitored population with more than 20 estimates of abundance since 1968 (Rugh et al. 2005), with the data showing an almost steadily increasing population with no clear sign of cyclic dynamics. But when analysed in relation to the catch history the hypothesis of direct density regulation is unable to explain the continued increase in gray whale abundance unless the carrying capacity today is at least 2.5 times larger than the historical level (Butterworth et al. 2002). The dynamics of the gray whale data, however, is consistent with the hypothesis of a damped population cycle by inertia dynamics (Witting 2003; Punt et al. 2004) suggesting a period in the order of 200 years. This apparent inconsistency between the observed dynamics and the hypothesis of direct density regulation may also include other species of marine mammals. For the humpback whale, e.g., the observed increase in abundance around Iceland is much stronger than predicted by direct density regulation and the known catch history (IWC 2003), and the catch history and abundance trend for humpback whales off West Greenland is more consistent with cyclic dynamics than with a monotonic return to equilibrium (Witting 2008).

In this paper I analyse the applicability of the population dynamic hypotheses of direct density regulation (monotonic return to equilibrium) and inertia dynamics (damped cyclic return to equilibrium) to fin whales off West Greenland. Apart from direct density dependence does inertia dynamics include an additional layer of delayed density dependence that induces a cyclic population response to a perturbed abundance (Ginzburg and Taneyhill 1994; Ginzburg 1998; Witting 1997, 2000, 2002; Ginzburg and Colyvan 2004). While traditional population dynamic models with delayed density dependence include the delayed term in a non-mechanistic way, does the delayed density dependent effects of inertia dynamics represent an expected response from natural selection by the density dependent competitive interactions in populations with varying abundance (Witting 1997, 2000, 2002). This response may reflect not only genetic responses to the selection pressure, but also epigenetic inheritance responses as maternal effects, or across generational culturally induced responses to the density dependent changes in the intra-specific competitive interactions.

For fin whales off West Greenland there are only three reliable abundance estimates. These estimates will not reveal population dynamics by themselves, but given the historical catches of fin whales off West Greenland it is examined whether direct density regulation is consistent with the abundance estimates, or whether a more flexible population model like that of inertia dynamics is required to explain the relationship between the catch history and the recent abundance estimates.

Considering fin whales off West Greenland we note that the geographical boundaries of the population that supports the harvest have never been determined. Based on the absence of

Year	N^{1+}	cv
1988	1096	35
2005	3218	43
2007	4656	46

Table 1: The abundance estimates (N^{1+}), and their cv in % .

evidence a working group on North Atlantic fin whales in Oslo in 1976 concluded that the fin whales off West Greenland could be treated as an independent management unit, separate from the East Greenland-Iceland, the Nova Scotia and the Newfoundland-Labrador management units (IWC 1977). Later reviews have continued failing to resolve the stock structure issue for North Atlantic fin whales (IWC 1979, 1992, 2006; NAMMCO 2000, 2003), with the most recent studies indicating that a relatively large exchange of individuals may occur between areas (Berube et al. 2006; Danielsdottir et al. 2006; Skaug et al. 2006), with up to 20% of the whales in a given location being classified as immigrants (Berube et al. 2006).

Looking within the West Greenland management area recent evidence from satellite tracking (Heide-Jørgensen et al. 2003) have shown not only inshore-offshore movements of fin whales, but also movements between two of the major hunting grounds in West Greenland, suggesting that there are no stock-structuring within the West Greenland area. In this paper I make the conservative assumption that the abundance estimates from the West Greenland surveys are estimates of the total population that supports the harvest.

METHOD

Data

Only recently have surveys conducted off West Greenland found a relatively large number of fin whales. A corrected estimate of 980 ($cv : 0.48$) fin whales off West Greenland for 2002/2004 (Witting and Kingsley 2005) is similar to an earlier estimate of 1,100 (95% CI: 520-2,100) fin whales in 1987-88 (IWC 1992), and larger than an estimate of 178 (95% CI: 26-382) fin whales in 1993 (Larsen 1995). Two surveys off West Greenland in 2005, however, found more fin whales with an estimate of 1,850 (95% CI: 855-3990) whales from a ship survey (Heide-Jørgensen et al. 2006), and a corrected estimate of 3,220 (95% CI: 1,430-7,240) whales from an aerial survey (Heide-Jørgensen et al. 2007). An additional aerial survey in 2007 provided an estimate of 4,660 (95% CI: 1,980-10,950) fin whales (Heide-Jørgensen et al. 2008).

The abundance estimate from 1993 was not considered a reliable estimate of the number of fin whales summering off West Greenland because of a complete lack of survey effort in some survey blocks and a low coverage in other survey blocks that are important for fin whales (Larsen 1995). The estimate from 2002/04 was also not agreed by the IWC SC because it was based on a photo survey that apparently failed to detect the presence of minke whales (IWC 2006). And for the two surveys in 2005, the estimate from the aerial survey was agreed by the IWC SC, while the estimate from the shipboard survey was not accepted because the survey effort in the SW block was poor and concentrated in a small part of the block (IWC 2007). Owing to the

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>
1922	7	7	1940	0	0	1958	2	6	1976	4	5	1994	11	11
1923	10	10	1941	0	0	1959	0	1	1977	6	7	1995	9	3
1924	47	47	1942	0	0	1960	0	0	1978	4	4	1996	8	11
1925	15	15	1943	0	0	1961	0	0	1979	3	4	1997	6	7
1926	12	12	1944	0	0	1962	0	0	1980	6	7	1998	2	9
1927	8	14	1945	0	0	1963	0	0	1981	3	4	1999	4	5
1928	12	12	1946	26	21	1964	0	1	1982	4	5	2000	3	4
1929	10	14	1947	29	22	1965	0	1	1983	4	4	2001	3	5
1930	12	15	1948	10	11	1966	0	0	1984	5	5	2002	4	9
1931	161	140	1949	5	16	1967	0	0	1985	3	6	2003	3	6
1932	32	34	1950	18	18	1968	1	2	1986	5	4	2004	6	7
1933	13	11	1951	8	7	1969	0	0	1987	4	5	2005	1	12
1934	12	12	1952	4	12	1970	0	0	1988	4	5	2006	4	7
1935	9	14	1953	6	10	1971	0	0	1989	7	7	2007	7	5
1936	6	9	1954	17	5	1972	0	1	1990	11	8	2008	-	-
1937	124	148	1955	14	8	1973	1	1	1991	8	10	2009	-	-
1938	4	3	1956	17	11	1974	2	3	1992	8	14	2010	-	-
1939	1	2	1957	11	10	1975	1	1	1993	2	12	2011	-	-

Table 2: **Yearly catch** of male (*m*) and female (*f*) West Greenland fin whales. Data from IWC data base and the Greenland Home Rule Government.

different status of the abundance estimates, the population dynamic modelling is carried out on a limited set of abundance estimates that includes only the three aerial estimates from 1988/89, 2005, and 2007 (Table 1).

The catch data obtained from the IWC database and the Greenland Home Rule Government are given in Table 2.

Population dynamic model

Three different models of population dynamics were applied to the fin 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 fin whales off West Greenland over the relatively short period from 1985 to 2008. A second model of direct density regulation was also applied to allow for estimates of the current and historical depletion levels, should the dynamics of West Greenland fin whales be monotonically returning towards an equilibrium state. 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

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

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

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

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 $\sigma = \gamma \ln N^*$ 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

Considering the three models of exponential growth, density regulated and inertia dynamics the following four assessment runs were made:

E: Assuming exponential growth.

Da: Assuming density regulation and a pre-harvested population in equilibrium.

Db: Assuming density regulation.

I: Assuming inertia dynamics and a pre-harvested population in equilibrium.

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

Model	s	ϑ	ι	γ	msyr	msyl	r	N_0	N^*
E	.9, .99 ^u	.5 ^p	-	-	-	-	-.02, .18 ^u	.2, 3 ^u	-
Da	.9, .99 ^u	.5 ^p	-	-	.015, .35 ^l	.5, .7 ^u	-	-	1, 5 ^u
Db	.9, .99 ^u	.5 ^p	-	-	.015, .35 ^l	.5, .7 ^u	-	.3, 3.8 ^u	1, 30 ^u
I	.9, .99 ^u	.5 ^p	.01, 1 ^u	1e-8, .2 ^u	-	-	-	-	1, 5 ^u

Table 3: **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), and N^* the equilibrium abundance (given in thousands). The type of probability distribution is given by superscripts; u =uniform, l =ln normal, and p a parameter with fixed value. The first number of an entry in the table is the min value if $pd = u$, the mode if $pd = l$, and a fixed parameter value if $pd = p$. The second number is the max value if $pd = u$, and the sd of the corresponding normal distribution if $pd = l$.

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 3. All priors are continuous and most of them also uniform and, having no evidence of a foetal sex ratio that differ significantly from even, a fixed value of 0.5 was applied to the fraction of females at birth.

For the case of direct density regulation the median of the msyl was set to 0.6 having a uniform prior between 0.5 and 0.7. An informative log normal prior [$\ln \text{msyr}_{1+}$ $N(-4.220, 0.345^2)$, with a median estimate around 1.5%] was applied to the msyr to reflect an estimate of the msyr from an assessment of fin whales between East Greenland and Iceland (Branch and Butterworth 2006; IWC 2008).

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 the zero growth of an assumed population dynamic equilibrium prior to the first catches in 1922.

No significant new information on biological parameters in North Atlantic fin whales appears to have been published since Lockyer and Sigurjonsson's (1992) study on biological parameters in fin whales caught southeast of Iceland (see review by Lockyer 2006). Their analysis suggested a total annual mortality rate in mature females between 0.088 and 0.013, with fishing mortality between 0.002 and 0.09 and mortality rates of males being slightly smaller. For the present study I applied a uniform prior from 0.90 to 0.99 to annual survival.

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.

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 500000 and 3000000.

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)

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

where $N_{1+,t}$ is the projected and $N_{1+,t}^i$ the point estimate of the observed 1+ abundance at time t , and 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

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

over the complete random sample of the posterior distribution.

Model	Sample	Weight	Unique	Max
E	500000	0.0	4857	3
Da	3000000	0.0	4999	2
Db	500000	0.0	4924	3
I	3000000	0.0	4951	3

Table 4: **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.

Model		s	b_{max}	ι	γ	msyr	msyl	r	N_0	N^*	N_T	d	ry	$Q1$
E	Med.	.94	.27	-	-	-	-	.07	1.0	.00	4.4	-	320	-
	5th	.90	.14	-	-	-	-	.03	.53	.00	2.5	-	75	-
	95th	.99	.42	-	-	-	-	.12	2.0	.00	7.8	-	870	-
Da	Med.	.94	.17	-	2.3	.01	.60	.02	2.7	2.7	2.3	.86	12	21
	5th	.90	.07	-	1.1	.01	.51	.01	2.0	2.0	1.6	.72	11	13
	95th	.99	.27	-	4.6	.03	.69	.04	3.8	3.8	3.3	.95	13	39
Db	Med.	.95	.17	-	2.1	.02	.59	.03	1.8	17	2.9	.18	66	49
	5th	.91	.08	-	1.0	.01	.51	.01	1.2	4.4	1.9	.08	26	21
	95th	.99	.28	-	4.5	.03	.69	.05	2.7	29	4.3	.63	160	110
I	Med.	.96	-	.30	.056	-	-	.02	2.0	2.0	3.1	1.5	73	-
	5th	.91	-	.06	.012	-	-	.00	1.4	1.4	2.0	.67	11	-
	95th	.99	-	.89	.17	-	-	.06	3.7	3.7	5.0	3.5	280	-

Table 5: **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.

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 0% for all assessments. And the number of unique parameter sets in a resample of 5000 parameter sets was not smaller than 4857 for any model, while the maximum occurrences of a unique parameter set in the resample across all models was 3. The model specific statistics are given in Table 4.

The posterior estimates and their 90 % credibility intervals are given in Table 5.

Model comparison

The predicted trajectories of the different models are shown in Figures 1 to 2, and the relative likelihoods of the different models are given in Table 6. Jeffreys (1961) considered Bayes factors

	E	Da	Db	I	p_l
E	1	.03	.99	.99	.33
Da	8.6	1	35	35	.01
Db	2	.24	1	1	.33
I	5.7	.67	2.8	1	.33
p_o	.56	.07	.28	.1	

Table 6: **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.

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** gives a Bayes factor of 35 in favour of the inertia model. Hence, there is strong support for the rejection of the density-regulated model as an appropriate model for the historical long-term modelling of the population dynamics of fin whales off West Greenland. When instead the inertia model is compared to the short-term density-regulated model **Db** that is initialised in 1985, they have a similar Bayes weight (a Bayes factor of one); a weight that is similar with that of the exponential model that has fewer parameters. Hence, all three types of dynamics are appropriate for the short-term description of the historical dynamics, and the inertia model is also appropriate for a long-term description given the catch history and the recent abundance estimates.

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

Figure 3 shows the realised prior and posterior distributions for selected parameters of the exponential model, the density-regulated model initialised in 1985, and the inertia model. 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 density dependence (γ) and level of inertia (ι) on the inertia model show some updating

Catch	p_1	p_2	p_3	p_4
2	1.0	1.0	1.0	.98
4	1.0	1.0	1.0	.97
6	1.0	1.0	1.0	.97
8	1.0	1.0	1.0	.96
10	1.0	.99	1.0	.95
12	1.0	.97	1.0	.95
14	1.0	.91	1.0	.94
16	.99	.81	.99	.93
18	.99	.70	.99	.92
20	.99	.57	.98	.91

Table 7: **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 = **I**.

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 distribution on the level of inertia, it gives a relatively well updated median estimate of 0.3, which is similar to the level of inertia that is estimated for humpback whales off West Greenland (Witting 2008). This shows that the population dynamics of the fin whale off West Greenland is likely to be damped cyclic on the longer time-scale. The inertia model furthermore suggests a population dynamic equilibrium of 2,000 (90% CI:1,400 – 3,700) whales, and a 2008 depletion ratio of 1.5 (90% CI:0.67 – 3.5).

From the exponential model and the short-term density-regulated model initialised in 1985, we have an estimated current exponential growth rate of 0.07 (90% CI:0.03 – 0.12) [or multiplication factor of 1.07 (90% CI:1.03 – 1.13) per year], and an estimate of the current msyr of 0.02 (90% CI:0.01 – 0.03), 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.

Meeting management objectives

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 7.

For the short-term exponential and density-regulated models, and the long-term inertia model, the probability of fulfilling an objective of an increasing population for a total removal of 20 fin whales per year are 0.99, 0.98 and 0.91.

Catch	p_1	p_2	p_3	p_4
2	1.0	1.0	1.0	.98
4	1.0	1.0	1.0	.97
6	1.0	1.0	1.0	.97
8	1.0	1.0	.99	.96
10	1.0	.98	.99	.95
12	1.0	.56	.99	.95
14	1.0	.01	.99	.94
16	.99	.00	.99	.93
18	.99	.00	.98	.92
20	.99	.00	.98	.91

Table 8: **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. .

Catch	p_1	p_2	p_3	p_4
2	-	1.0	1.0	-
4	-	1.0	1.0	-
6	-	1.0	1.0	-
8	-	1.0	1.0	-
10	-	.99	1.0	-
12	-	.97	1.0	-
14	-	.91	1.0	-
16	-	.81	.99	-
18	-	.70	.98	-
20	-	.57	.96	-

Table 9: **Q1.** The probability p that Q1 is larger than annual total removals between 2 and 20 individuals in the period 2008 to 2013. .

Comparing with 2007 assessment

The 2007 assessment for fin whales off West Greenland (Witting 2007) used the same population dynamic models, lacked the 2007 abundance estimated, and did not find statistical support for a rejection of the long-term dynamics of the density-regulated model. In 2007 the inertia model estimated approximately the same equilibrium [2,400 (90% CI:1,600 – 3,200) compared with a current estimate of 2,000 (90% CI:1,400 – 3,700)], while the estimated exponential growth rate was lower in 2007 [0.03 (90% CI:–0.02 – 0.08) compared with a current estimate of 0.07 (90% CI:0.03 – 0.12)]. In result, the average probability that the population will increase with a catch level of 20 whales per year has increased from 69% in the 2007 assessment to 96% in the current assessment.

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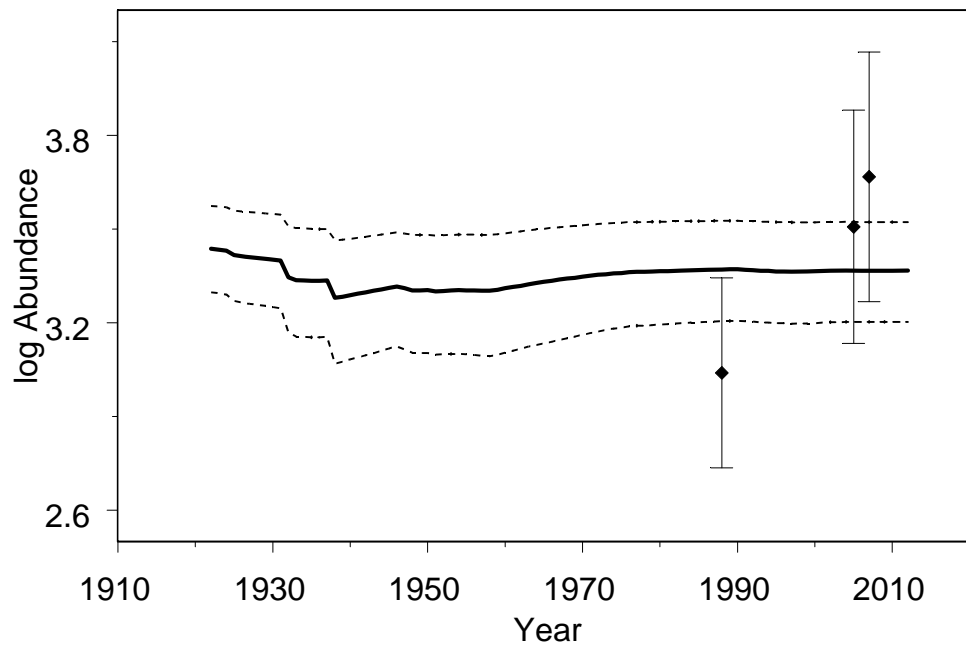
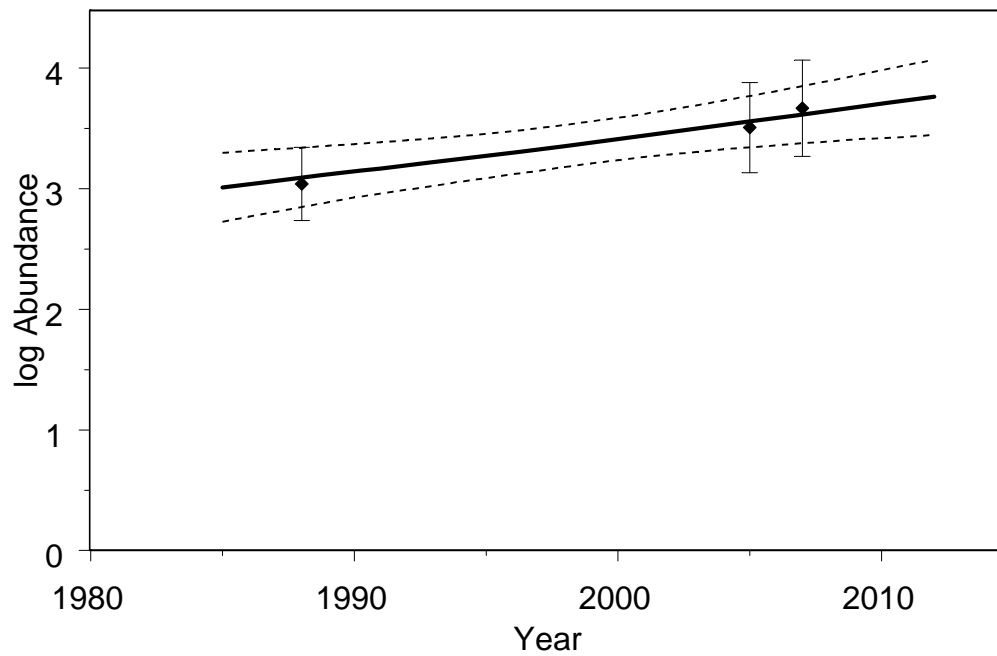


Figure 1: The estimated trajectory (median and 90% credibility interval) for West Greenland fin whales given exponential growth (top figure) and density regulated dynamics with a pre-harvested population in equilibrium (bottom figure).

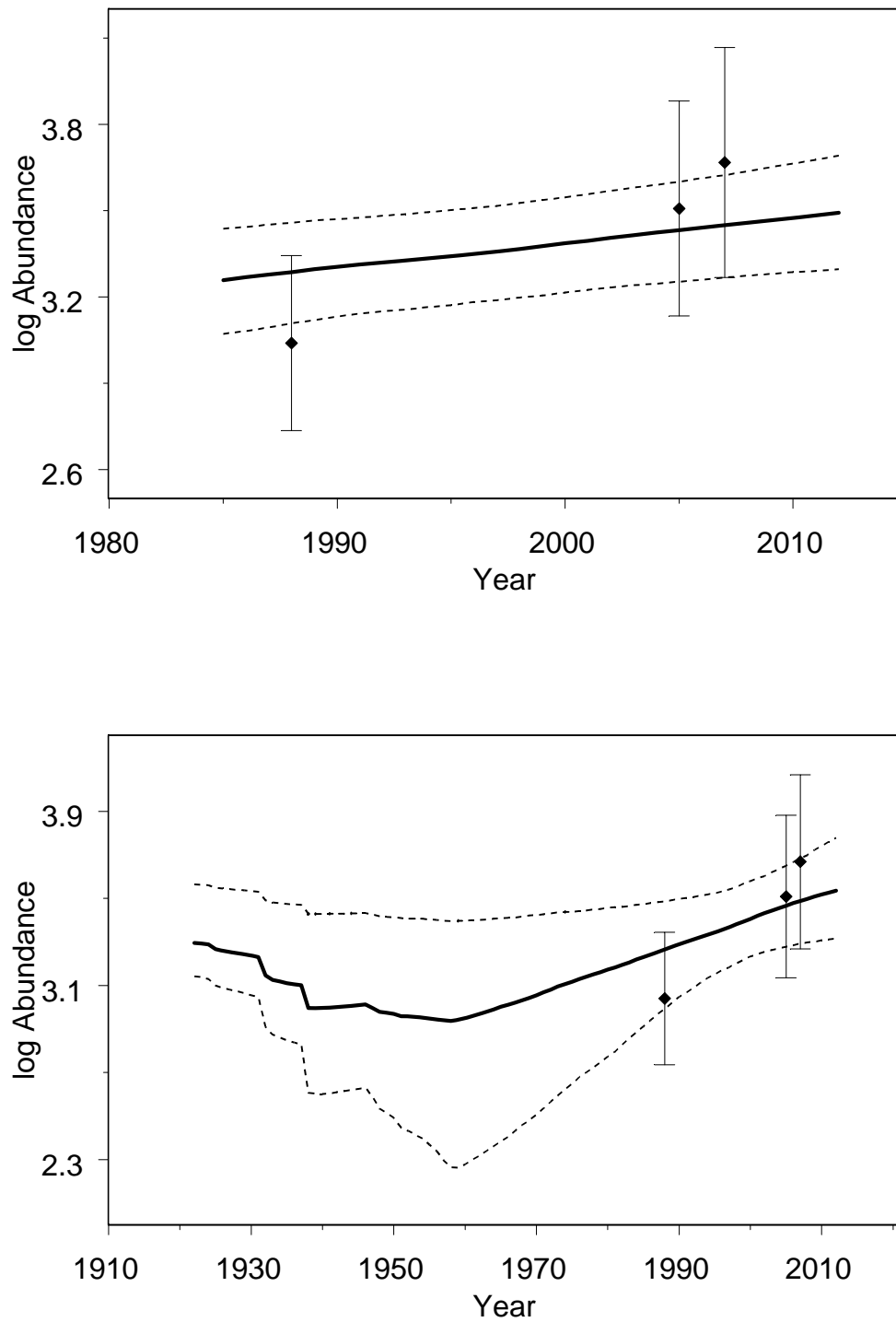


Figure 2: The estimated trajectory (median and 90% credibility interval) for West Greenland fin whales given density regulated (top) and inertia (bottom) dynamics.

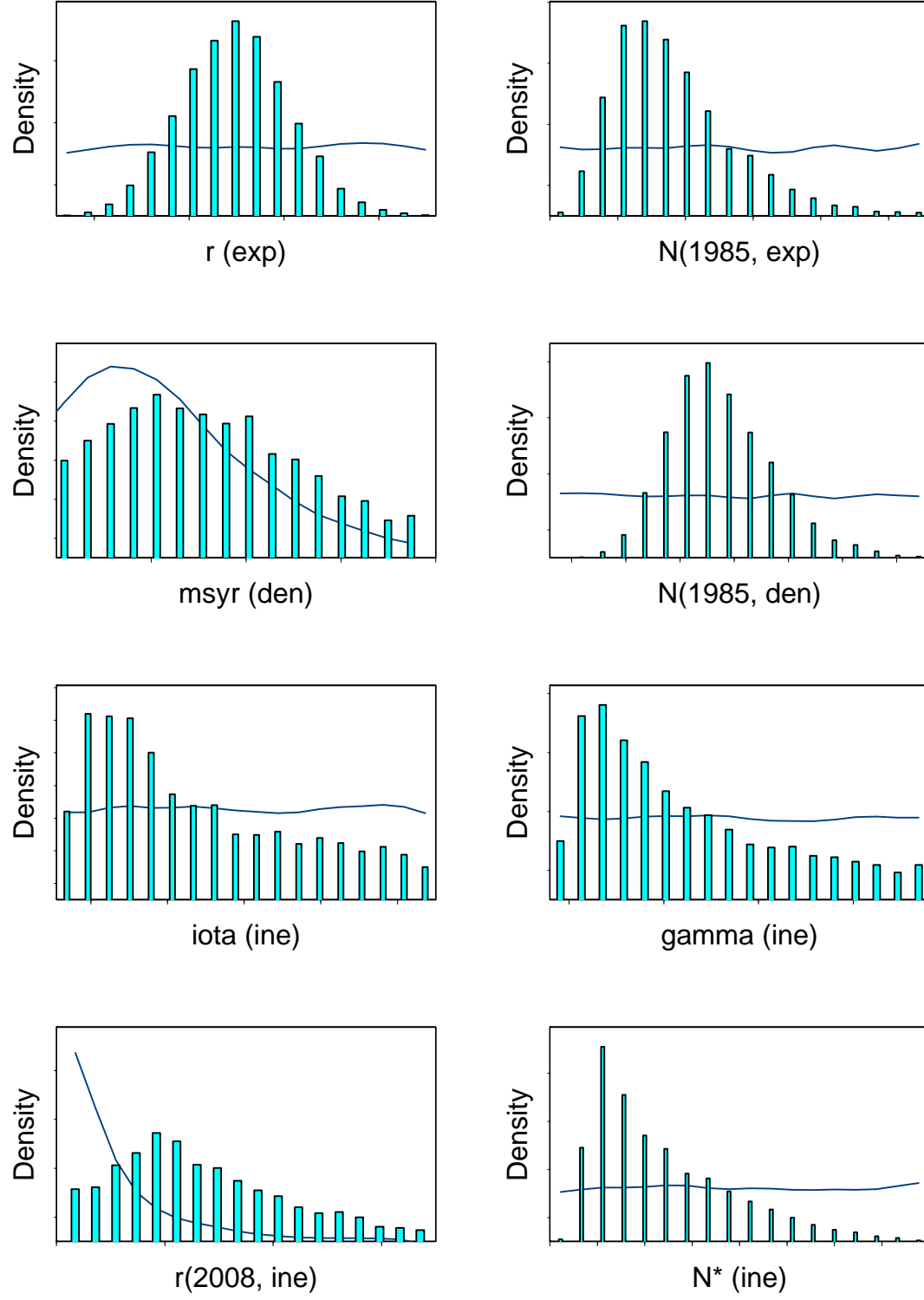


Figure 3: The realised prior (curves) and posterior (bar) distributions for selected parameters, for the exponential (*exp*), density regulated (*den*), and inertia (*ine*) population dynamic models.