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Model Estimates of Cumberland Sound beluga (*Delphinapterus leucas*) population size and total allowable removals

Marianne Marcoux[1] and M.O. Hammill[2]

[1]Fisheries and Oceans Canada
501 University Crescent
Winnipeg, Manitoba, R3T 2N6

[2]Fisheries and Oceans Canada
850 route de la mer,
Mont-Joli, Québec, G5H 3Z4

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ABSTRACT

The subsistence harvest of Pangnirtung, Nunavut, is directed towards a single stock of belugas (*Delphinapterus leucas*) in Cumberland Sound, which forms a separate stock among belugas in the Canadian Eastern Arctic. A population model incorporating updated information on harvest statistics (1920–2015) was fitted to four aerial survey estimates using Bayesian methods, resulting in a current estimated population of 1,000 (rounded to the nearest 100) animals. The management objective is to achieve a population of 5,000 animals by 2091. This could be expressed as an interim target of 1,235 animals within a decade (2026). At current reported harvest levels of 41 animals, the probability of the population declining over a 10-year period is 1. The probability that the population would increase to the interim target was 0.3, 0.25 and 0.1 for reported harvests of 0, 6, and 25 animals respectively.

Estimations modélisées de la taille de la population de béluga de la baie Cumberland (*Delphinapterus leucas*) et des prélèvements totaux autorisés.

RÉSUMÉ

La récolte de subsistance effectuée à Pangnirtung (Nunavut) vise un seul stock de bélugas (*Delphinapterus leucas*) dans la baie Cumberland, qui constitue un stock distinct parmi les bélugas présents dans l'est de l'Arctique canadien. Un modèle de population intégrant des données actualisées sur les statistiques de récolte (1920-2015) a été ajusté à quatre estimations tirées de relevés aériens à l'aide de méthodes bayésiennes, ce qui a donné une population estimée actuellement à 1 000 animaux (à une centaine près). L'objectif de gestion est de parvenir à une population de 5 000 individus d'ici 2091. Il pourrait s'exprimer sous la forme d'un objectif intermédiaire de 1 235 animaux d'ici dix ans (2026). Aux niveaux de récolte déclarés actuellement (41 animaux), la probabilité d'un déclin de la population sur une période de 10 ans est de 1. La probabilité que la population atteigne l'objectif intermédiaire est de 0,3, de 0,25 et de 0,1 pour des récoltes déclarées de 0, 6 et 25 animaux respectivement.

INTRODUCTION

Belugas (*Delphinapterus leucas*) in Cumberland Sound (CS) form a separate summering stock among belugas based on genetic and satellite telemetry evidence (de March et al. 2002, 2004, Richard and Stewart 2009, Turgeon et al. 2012). In the summer, belugas from the CS stock may be found throughout Cumberland Sound, with large aggregations occurring particularly in Clearwater Fiord located in the northwest corner of the Sound (Fig. 1; Richard and Stewart 2009).

Commercial whaling in CS between 1868 and 1939, appears to have reduced the population (Mitchell and Reeves 1981) from a historical estimate of 8,500 (Standard Error [SE] = 400; rounded to the nearest 100; DFO 2005) to probably less than 1,000 individuals in the 1970s (Brodie et al. 1981). Aerial surveys and cliff observations conducted between 1979 and 1984 estimated between 400 and 600 individuals at the surface (Richard and Orr 1986). More recent aerial surveys, conducted in 1990, 1999, and 2009, estimated population numbers of approximately 1,000, 2,000, and 700 individuals, respectively. In 2004, the CS beluga population was designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004).

CS belugas are also hunted for subsistence by Pangnirtung Inuit. Since the early 1980s, the subsistence harvest has been managed under a quota system (Richard and Pike 1993). To effectively manage this population, up-to-date abundance estimates are necessary. However, the most recent attempts at abundance estimation have been largely unsuccessful. An aerial survey in 2005 was not completed due to inclement weather conditions, while large confidence intervals make the 2009 abundance estimate unreliable. The most recent aerial survey of CS beluga was completed in 2014 (Marcoux et al. 2016).

A historical population estimate of 8,500 animals was produced by fitting a population model to aerial survey counts (1990 and 1999) and reported harvest data, as part of a Recovery Potential Analysis (RPA) of four beluga stocks (DFO 2005). If a recovery target is set at 70% of the estimated historical population, then the recovery population would be 5,900 (DFO 2005). In subsequent discussions with stakeholders, the management objective set for CS belugas was to increase population abundance to a recovered size of 5,000 animals by 2091 (Fig. 2, DFO Unpublished report). The objective of this study is to provide an updated abundance estimate of beluga whales in CS and advice to co-managers on the probability of the CS beluga population increasing to the identified recovery objective of 5,000 animals by 2091, under different levels of harvest.

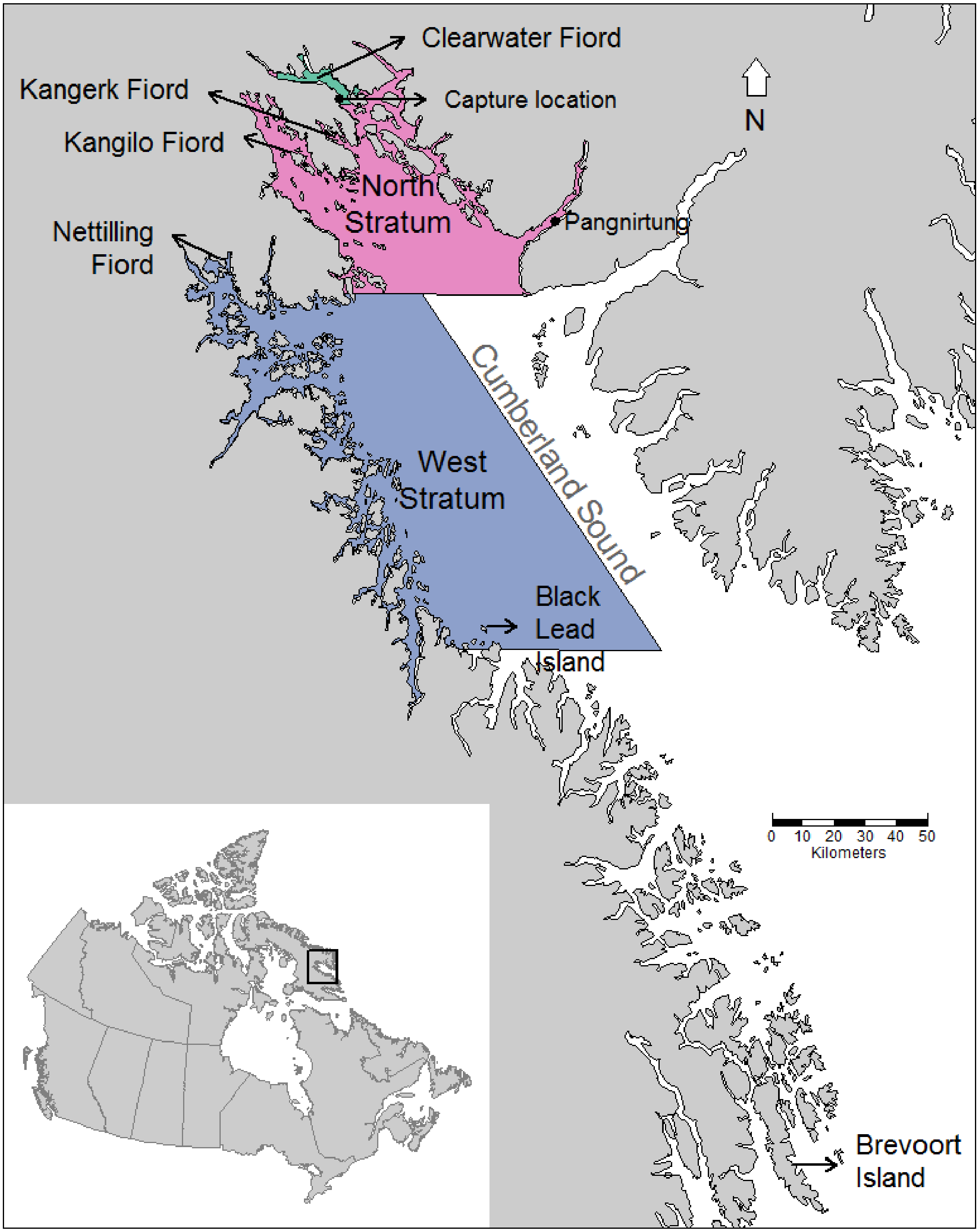

Figure 1. Location of strata for Cumberland Sound beluga aerial surveys as well as capture location for belugas equipped with satellite transmitters in 2006–2007.

METHODS

A model was fitted by MCMC Bayesian methods to a time series of aerial survey (1980–2014) to provide insights into the population trend since 1920, estimates of current population size and future trajectories under different harvest scenarios.

AERIAL SURVEYS

Nine aerial surveys have been flown between 1980 and 2014 over CS (Table 1) (Richard and Orr 1986, Richard 1991, 2013, Marcoux et al. 2016). However, many of the early surveys focussed mainly on Clearwater Fiord (Fig. 1); at the time it was thought that all animals were concentrated in the Fiord during the survey period. In 1990, aerial surveys were extended outside of Clearwater Fiord to survey a North stratum, and a West stratum was included starting in 1999. In some years these two strata accounted for an additional 500 animals outside of Clearwater Fiord (Table 1; Richard 2013, Marcoux et al. 2016). In this assessment different model runs were completed using different combinations of survey estimates to evaluate their impact on current estimates of population abundance and trend.

Near surface abundance estimates $N_{surface}$ were corrected to account for belugas that were diving and were unavailable to be seen by observers (availability bias) using:

$$N_{survey} = C_a \times N_{surface}$$

Where: N_{survey} is the corrected number of belugas estimated by the survey, and

C_a is the availability bias correction factor for belugas that were unavailable to be seen by the survey observers (i.e., they were diving).

The availability bias correction factors calculations were the same as the ones in Marcoux et al. (2016). In short, satellite linked time depth recorder tags (SPLASH tags, Wildlife Computers) were deployed on belugas to transmit daily information on their location and diving behaviour. Three female belugas were captured and tagged in 2006 and 2007 following methods described in Orr et al. (2001). Dive data were summarized in 6-hour time periods. We calculated weighted averages to determine the average time belugas spent in 0–1, 0–2, 0–3, 0–4, and 0–6 m depth bins during daytime. The availability bias correction factor, C_a, was calculated by:

$$C_a = 1/proportion\ spent\ in\ depth\ bin$$

Surface estimates of previous surveys were corrected the following way. For estimates of the North and West strata, it is assumed that belugas can be seen to depths up to 5 m (Richard et al. 1994, Richard 2013). Thus, an average of the C_a for dive depths bin 0–4 m and 0–6 m located in the North and West strata was used ($C_a = 2.54$, coefficient of variation [CV] = 0.050). During the 2014 photographic survey of Clearwater Fiord, the water was very murky on some photographs (defined as when only belugas at the surface could be seen in the photographs). To give an indication of the effect of murkiness, sometimes it was possible to observe a beluga “disappear” in consecutive photos as it swam from an area of less murky water to an area of increasingly murky water (see Fig. 5 in Marcoux et al. 2016). When the water was very murky, as in Clearwater Fiord, we used a correction factor based on the proportion of time spent in the 0–1 m dive depth bin (C_a = 4.46, CV = 0.117). For photos where the water was not murky (i.e., the entire body of belugas below the surface could be seen), we used the correction factor based on the 0–2 m depth bin (C_a = 2.06, CV = 0.056). For the 2014 photographic survey, an average of 21.5% (standard deviation = 1.65%) of the photos were murky (Table 5 in Marcoux et al. 2016). Information about the murkiness in the photos was also available for the 2009 photographic survey. Therefore, we calculated a weighted average of the 0–1 m and 0–2 m.

Table 1. Estimates of Cumberland Sound beluga abundance within Clearwater Fiord, the area of main concentration, the estimated number of animals outside the fiord and the total. Surface estimates (Surf) are number of animals estimated at the surface, the factor to adjust the counts for animals not at the surface (Ca), estimates adjusted for animals below the surface (Corr), and coefficient of variation (CV). Note that no CVs were calculated for the earlier surveys. Complete photographic coverage refers only to Clearwater Fiord. Surveys outside of Clearwater fiord were normally visual surveys.

Year	**Clearwater Fiord**			**Outside Clearwater Fiord**			**Total**			**% outside**	**Survey method**	**Survey coverage**	**Reference**
	Surf	C_a	Corr	Surf	C_a	Corr	Surf	Corr	CV				
1980	40	4.46	178	251	2.54	637	291	815		78	non-systematic aerial visual and photographic	Clearwater, Kangilo Fiords	Richard and Orr 1986
1981	206	4.46	919	20	2.54	50	226	969		5	non-systematic aerial visual	Clearwater, Kangilo Fiords, west coast of Cumberland Sound	Richard and Orr 1986
1982	276	4.46 and 2.06	1054	66	2.54	177	345	982		18	non-systematic aerial visual and photographic	Clearwater, Kangerk, Kangilo Fiords, northern part of Nettiling Fiord, west coast of Cumberland Sound	Richard and Orr 1986
1985	398	4.46	1775	0	2.54	0	398	1775		0	systematic photo and visual	Clearwater Fiord, West stratum	Richard 1991
1986	485	4.46 and 2.06	1102	2	2.54	5	487	1107		0	systematic and non-systematic visual and photographic	Clearwater Fiord, North stratum	Richard 1991
1990	459	2.57	1180	0	2.54	0	459	1180	0.10	0	complete photographic and visual systematic.	Clearwater Fiord, North stratum	Richard 2013
1999[1]	749	2.57	1924	137	2.54	347	885	2270	0.09	15	complete photographic, visual systematic	Clearwater Fiord, North and West strata	Richard 2013
2009	118	2.57	303	215	2.54	546	333	849	0.38	64	complete photographic, visual systematic	Clearwater Fiord, North and West strata	Richard 2013
2014	228	4.46 and 2.06	603	215	2.54	548	444	1151	0.21	48	complete photographic, visual systematic	Clearwater Fiord, North and West strata	Marcoux et al. 2016

[1] Based on two surveys that covered both Clearwater Fiord and the area outside of Clearwater Fiord. In 1999, there were three surveys of Clearwater Fiord and two surveys outside of Clearwater. The third survey of Clearwater has not been used because of concerns that an unknown number of animals may have been outside of the Fiord on that day. If the third survey had been included the final corrected average estimate would be slightly lower at 2,051 animals, CV = 0.1.

correction factor based on the proportion of photos with murky (21.5%) and non-murky water (78.5%). For survey years where we could not find information about water murkiness (1990 and 1999), we applied a correction factor based on the average proportion of photos in 2009 and 2014 with and without murky water ($C_a = 2.57$, CV = 0.069). Lastly, surveys from 1980 to 1986 included information about water murkiness. Accordingly, surface estimates were corrected with the correction factor based on the 0–1 m bin for murky water and with the correction factor based on the 0–2 m bin for non-murky water (Table 1).

HARVEST RECORDS

Reported harvest data (1868–2014) were obtained from a variety of sources (Table 2). All animals reported harvested were assumed to belong to the CS stock. Data were not continuous, and in the earlier part of the series the data gaps are large (Fig. 2). After 1920, data were only missing for the year 1944. Thus, we initiated our analyses with the year 1920, and interpolated a value for 1944 using the mean harvests from years 1942, 1943, 1945, and 1946. Harvest data since 2004 were not available, as well as for the most recent year, 2015. Therefore we used the established quota (n = 41) as an estimated harvest for those years (Fig. 2).

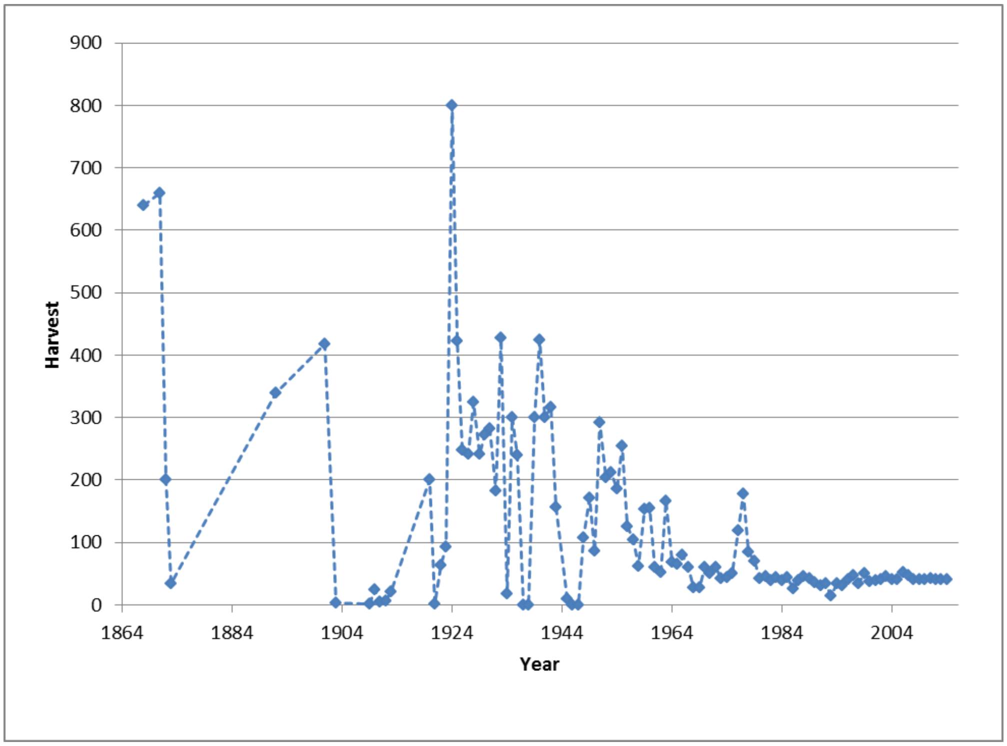

Figure 2. Reported harvests of Cumberland Sound belugas from 1864–2014. Data from several years were missing prior to 1920. Harvest data for several years were not available since 2004, therefore we used the established quota (n = 41) as an estimated harvest for those years. The model was only fitted to data from 1960–2015.

Table 2. Reported harvests and quotas of Cumberland Sound belugas 1923–2014. Data for 1923 to 1972 are from Stewart (2004 unpubl. rep.); 1973–1976 are from the Planning Committee for the Co-Management of Southeast Baffin Beluga (1994 unpubl. rep.), and 1977–2014 from DFO harvest statistics unpublished data. There was no reported harvest for several years since 2004. In those years, it was assumed that the entire quota was taken.

Year	Reported landed	Year	Reported landed	Year	Reported landed	Quota
1868	640	1945	10	1980	43	
1871	660	1946	0	1981	45	
1872	200	1947	0	1982	40	
1873	35	1948	107	1983	44	
1892	340	1949	171	1984	40	
1901	418	1950	87	1985	44	
1903	4	1951	292	1986	26	
1909	1	1952	204	1987	40	
1910	25	1953	213	1988	46	
1911	5	1954	186	1989	42	
1912	6	1955	255	1990	36	
1913	21	1956	125	1991	31	35
1920	200	1957	104	1992	35	35
1921	1	1958	62	1993	15	35
1922	63	1959	153	1994	35	35
1923	93	1960	155	1995	31	35
1924	800	1961	60	1996	41	35
1925	422	1962	52	1997	47	35
1926	248	1963	167	1998	35	35
1927	242	1964	69	1999	50	35
1928	325	1965	65	2000	37	35
1929	242	1966	80	2001	39	35
1930	272	1967	60	2002	41	41
1931	283	1968	28	2003	46	41
1932	183	1969	27	2004		41
1933	427	1970	60	2005		41
1934	18	1971	50	2006	52	41
1935	300	1972	61	2007	48	41
1936	240	1973	43	2008		41
1937	0	1974	44	2009		41
1938	0	1975	50	2010		41
1939	300	1976	120	2011	42	41
1940	424	1977	178	2012		41
1941	300	1978	85	2013		41
1942	317	1979	70	2014		41
1943	157			2015		41

MODEL SPECIFICATION

A stochastic stock-production model, assuming density dependence acting on the population growth rate, was fitted by MCMC Bayesian methods to the aerial survey and reported harvest data. We sought to separate the observation error (associated with data collection and abundance estimation) from the process error (arising from natural variability in population dynamics). To this end, we developed a hierarchical state-space model that considers survey data to be the outcome of two distinct stochastic processes: a state process and an observation process (de Valpine and Hastings 2002).

The state process describes the underlying population dynamics and the evolution of the true stock size over time, using a discrete formulation of the Pella-Tomlinson model (Pella and Tomlinson 1969, Innes and Stewart 2002). Population size in each year N_t (from 1920 to 2015) is a multiple of the previous year's, with removals deducted:

$$N_t = N_{t-1} + N_{t-1} \cdot (\lambda_{max} - 1) \cdot \left(1 - \left(\frac{N_{t-1}}{K}\right)^{\theta}\right) \cdot \varepsilon_p - R_t$$

Where: λ_{max} is the maximum growth rate or rate of population increase,

K is the environmental carrying capacity,

θ defines the shape of the density-dependent function,

ε_p is a stochastic term for the process error,

R_t are the removals for that year, calculated as reported catches, C_t, that are corrected for the proportion of animals that were struck and lost, $S\&L$:

$$R_t = C_t \cdot (1 + S\&L)$$

The observation process describes the relationship between true population size and observed data. In our model, aerial survey estimates S_t are linked to population size N_t by a multiplicative error term, ε_{S_t}:

$$\ln(S_t) = \ln(N_t) + \varepsilon_{S_t}$$

The model was fitted to the aerial survey (1980–2014) to provide population estimates and trends for the years 1920–2015 and included harvest data (1920–2015). However, plots of the degree of autocorrelation against time lag identified significant levels of autocorrelation that did not diminish with time for the variables: carrying capacity K, starting population (N1920), and Struck and Lost ($S\&L$)(Appendix 1, Fig. 2). Cross-correlation was also observed between $S\&L$, N1920, N2015 and K (Appendix 1, Fig. 3). Visual checking of the chains indicated some clumping, suggesting that some chains had not reached a stationary distribution (Geweke's diagnostic, Geweke 1992, Z-scores >1.96). Significant autocorrelation will not have much impact on estimates of the mean, but will overestimate the precision of the estimates and could affect estimates from the tails of the distributions. No improvement (reduction in autocorrelation) was observed after increasing the number of runs, burn-in or thinning. The significant autocorrelation and serial correlation indicated that there was not enough information in the data to properly update the priors for K, $S\&L$ and N1920 and/or some problems with the data (see Discussion). Outputs from this full model are shown in Appendix 1. It was suspected that there might be problems with the catch-history data (see Discussion). The model was re-run using the 1960–2014 harvest data and fitted to the survey data corrected for animals not visible at the surface. In a separate run, the model was also re-parameterized by setting θ, the shaping parameter that governs the form of the density-dependent relationship, to θ = 1. The following runs were examined using the survey series from Table 1, and harvest data from Table 2 (Fig. 2):

1) All survey data from 1980–2014 with 1960–2015 catch history
2) All survey data from 1980–2014 with 1960–2015 catch history, but estimates from surveys flown prior to 1990 were increased by 25%, and it was assumed that the CV around the estimate was 50%
3) Survey data from 1985–2014 with 1960–2015 catch history
4) Survey data from 1990–2014 with 1960–2015 catch history
5) Survey data from 1985–2014 with 1960–2015 catch history and theta fixed ($\theta = 1$).
6) Survey data from 1990–2014 with 1960–2015 catch history and theta fixed ($\theta = 1$).

PRIORS

Traditional knowledge, information from modelling of Eastern Hudson Bay belugas (Doniol-Valcroze et al. 2013) and initial runs of the full model were used to formulate prior distributions for the random variables included in the model (Table 3). The maximum rate of population increase (λ_{max}) was set as a fixed value at λ_{max} = 1.04 (Wade 1998). The shaping parameter θ was allowed to vary between 1 and 7, and in a separate run was also fixed to θ = 1. The initial runs of the full model suggested that the starting population most likely lay between 2,000–15,000 animals and that carrying capacity (k) probably lay between 5,000 and 15,000 animals.

Reported harvests underestimate the number of belugas killed because some animals are wounded or killed but cannot be recovered. The loss rates in beluga hunts are not known exactly, and may vary with location (Clearwater Fiord vs outer Clearwater Fiord) and by season, but in two years $S\&L$ was reported to be 16% (DFO harvest statistics unpublished data).

In the literature, $S\&L$ ranges from around 0.2 for shallow water hunts up to 0.6 for deep-water hunting, e.g., along ice edges (Seaman and Burns 1981). Heide-Jørgensen and Rosing-Asvid (2002) calculated a struck-and-lost factor of 0.29 for Greenland, not including unreported catches. Innes and Stewart (2002) estimated a correction factor that accounted for $S\&L$ and whales not reported in Baffin Bay at 0.41 belugas per beluga landed. Since there are no data on $S\&L$ rate for Cumberland Sound, we used the $S\&L$ factor from the eastern Hudson Bay assessment: a moderately informative prior following a Beta(3, 4) distribution, with a median of 0.42 and quartile points at 0.29 and 0.55. This is a change from previous assessments of eastern Hudson Bay beluga, in which the $S\&L$ correction was given a log-normal prior with quartile points at 0.43 and 0.85 and a median value of 0.61, as there was little support in published reports for these high values (Doniol-Valcroze et al. 2013).

The stochastic process error terms ε_{p_t} were given a log-normal distribution with a zero location parameter. The precision parameter for this log-normal distribution was assigned a moderately informative prior following a Gamma(1.5, 0.001) distribution. These parameters were chosen so that the resulting error multiplier would have quartiles of 0.98 and 1.02 reflecting our belief that beluga stock dynamics are not highly variable.

The uncertainty associated with each aerial survey was poorly estimated. Therefore, they were incorporated into the fitting process only by guiding the formulation of the prior distribution of the survey error. The survey error term ε_{s_t} followed a log-normal distribution with a zero location parameter. Its precision parameter was given a moderately informative prior following a Gamma(2.5, 0.4) distribution. These parameters were chosen so that the resulting CV of the survey estimates would have quartiles Q_1 and Q_3 of 0.35 and 0.55, which are approximately equivalent to the range of what we consider to be a plausible CV for the survey abundance estimates (e.g., Table 6 in Gosselin et al. 2014).

Table 3. Prior distributions, parameters and hyper-parameters used in the population model. "dist." denotes a hyper-parameter with its own prior distribution.

Parameters	Notation	Prior distribution	Hyper-parameters	Values
Survey error (t)	ε_{st}	Log-normal	μ_s	0
			τ_s	*dist.*
Precision (survey)	τ_s	*Gamma*	α_s	*2.5*
			β_s	*0.4*
Process error (t)	ε_{pt}	Log-normal	μ_p	0
			τ_p	*dist.*
Precision (process)	τ_p	Gamma	α_p	1.5
			β_p	0.001
Density dependence shape function	θ	Fixed		1
Struck-and-lost	$S\&L$	Beta	α_{sl}	3
			β_{sl}	4
Initial population	N_{1960}	Uniform	N_{upp}	9000
			N_{low}	500
Carrying capacity	K	Gamma	α	8
			β	0.0015
Lambda	λ			1.04

PARAMETER ESTIMATION AND MODEL DIAGNOSTICS

We obtained posterior estimates of all the parameters using a Gibbs sampler algorithm implemented in JAGS (Plummer 2003). Results were examined using packages R2jags and coda developed in the R programming language (R Core Team 2013). With any Markov Chain Monte Carlo (MCMC) simulation, it is important to check convergence of the sampled values to their stationary distribution (Brooks et al. 2004; King et al. 2010). Initial runs of the code were made to investigate convergence and mixing (i.e., the extent and spread with which the parameter space was explored by the chain), as well as autocorrelation (see results with autocorrelation in Appendix 1).

We visually inspected the Geweke plots and tested for mixing of the chains using Geweke's test of similarity between different parts of each chain (Geweke 1996). For convergence between chains we used the Brooks-Gelman-Rubin (BGR) diagnostic, which compares the width of 80% Credible Interval (CI) of pooled chains with the mean of widths of the 80% CI of individual chains (Brooks and Gelman 1998). The relative contributions of the parameters to the model were examined by estimating the p_D value, which corresponds to the 'effective' number of parameters being fitted (Spiegelhalter et al. 2002).

FUTURE PROJECTIONS AND MANAGEMENT OBJECTIVES

The impact of harvesting was examined in three ways. First, the draft *Species at Risk Act* (SARA) Recovery Plan for CS belugas identified the management objective of allowing the population to increase to 5,000 animals by 2091 (DFO Unpublished report). If the current population size is approximately 1,000 animals, then to reach this recovery target in 75 years would require an average instantaneous annual rate of increase of approximately 0.021 (Fig. 3). We suggest that, rather than projecting into the future 75 years, interim targets be identified to more easily evaluate progress towards the recovery objective. If we assume an average instantaneous annual rate of increase of approximately 0.021, then after 10 years the population should increase to about 1,235 animals (Fig. 3). Thus, in a first analysis, we examined the probability of achieving this management assuming different harvest levels over a 10-year period.

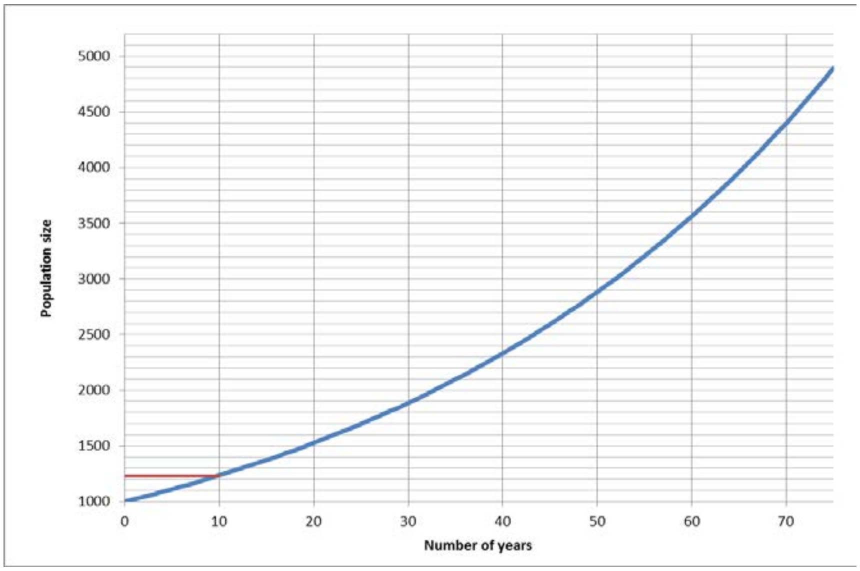

Figure 3. The expected change in the population if it is to reach the recovery objective of 5,000 belugas in 75 years, assuming a 2015 abundance estimate of approximately 1,000 belugas. Year 75 is 2091 assuming an average instantaneous rate of increase of 0.0214. The red line identifies the expected population size (N = 1,235) within 10 years, if the population is to recover to 5,000 animals after 75 years.

In a second analysis, the sustainable yield was estimated. The sustainable yield is the number of animals that could be removed annually, over a ten-year period that would maintain a constant population. We used different catch levels and expressed the impacts of these harvests as the probability of causing a decline in the population over a period of 10 years.

In a third analysis, we estimated Potential Biological Removal (PBR) levels assuming a Recovery Factor (F_R) of 0.5 (Wade 1998).

The PBR threshold is calculated as:

$$PBR = N_{min} \cdot 0.5 \cdot R_{max} \cdot F_R$$

Where: R_{max} is the maximum rate of population increase. The default value for cetaceans is 0.04,

F_R is a recovery factor (between 0.1 and 1), and

N_{min} is the estimated population size using the 20-percentile of the log-normal distribution (Wade 1998).

We used the model estimate for the population size in 2015 to calculate N_{min} because the model estimate uses information from multiple surveys. This method also takes into account the uncertainties associated with the different surveys.

PBR is an estimate of total removals from the population that includes harvested animals, animals killed and not recovered, non-reported harvests and other types of human-induced mortality. The Total Allowable Landed Catch (TALC) is therefore:

TALC = PBR - (animals killed but not recovered + non-reported harvests + bycatch + ship strikes, etc.)

RESULTS

The model incorporated harvest data (1960–2015) and was fitted to different combinations of aerial survey (1980–2014) estimates of abundance. A few runs also examined the impact of using a shorter harvest data time series (1980–2014; not shown in this document) and if theta was fixed ($\theta = 1$), instead of allowing the model to estimate θ. Detailed results with respect to model fitting are presented in Appendix 2. Each chain for the variables carrying capacity (K), population size in 2015 (N_{2015}), process error, initial population size (N_{1960}), and $S\&L$ rate showed rapid convergence (Appendix 2). The overall BGR statistics for the five variables were close to 1 also indicating convergence of the chain. The amount of autocorrelation among values for carrying capacity (K), the starting population (N_{1960}), and $S\&L$ was considerably reduced using the 1960–2014 catch series. Cross-correlation was observed between K, $S\&L$, N_{1960} and the N_{2015} (Appendix 2).

All model runs provided a similar view; the population has been declining since 1960 (Fig. 4). The surveys flown during the 1980s are considered to be negatively biased since coverage of the areas outside of Clearwater Fiord was incomplete. This applied particularly to the 1980–82 surveys, whereas the 1985 and 1986 surveys appear to have provided considerably improved coverage of the North and West strata. We examined the estimated change in the population using the 1980–2014 survey time series and in a second run, we increased the 1980–1986 surveys by 25%, which is the mean proportion of the herd that has been observed outside of Clearwater Fiord from the historical time series of surveys (Table 1). These runs estimated a higher starting population in 1960, but as in other runs the population declined to about 1,000 in 2015 (Fig. 4). Using the surveys flown only since 1990, the population may have declined from 3,000 or more animals in 1960, to about 1,500 or more animals at the beginning of the 1980s (Fig. 4 and green line in Fig. 5). Since then the population has declined to approximately 1,000 animals in 2015. There was little updating of model priors for many of the parameters (e.g., theta, S&L, see Appendix 2). With only four surveys since 1989, there was too little information for fitting the model and updating the model priors. Therefore we fixed theta to $\theta = 1$, which resulted in a starting population of 3,100 animals in 1960 and an estimated population of 1,000 in 2015 (Table 5, Fig. 4, 5).

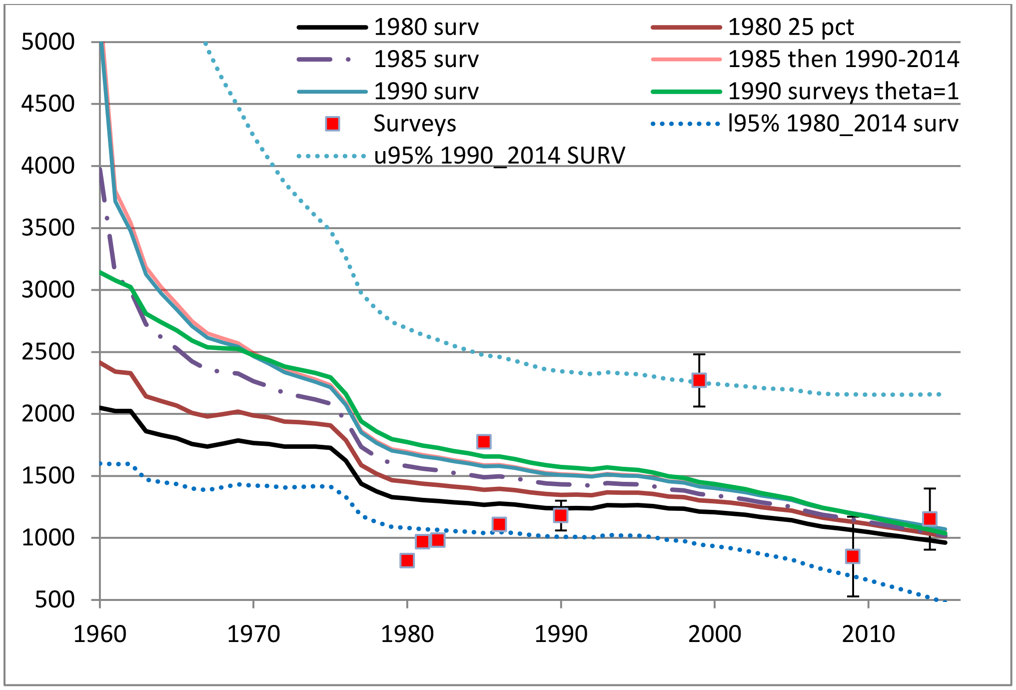

Figure 4. Estimated changes in abundance of Cumberland Sound beluga determined after fitting the population model to different estimates of abundance from aerial surveys flown between 1980–2014.The squares represent survey estimates ± 95% Confidence Limits [CL], where estimated. The dotted lines represent the lower 95% Credibility Limit from fitting the model to the 1980–2014 time series. The upper 95% Credibility Limit is from fitting the model to the 1990–2014 survey time series. The different runs were fitting to: 1) the 1980–2014 surveys (1980 surv); 2) the 1980–2014 surveys, where the 1980–1986 surveys were adjusted upwards by 25% (1980 25 pct); 3) the 1985–2014 surveys (1985 surv); 4) the 1985 and 1990 to 2014 surveys (1985 then 1990–2014); 5) 1990 to 2014 surveys (1990 surv); and 6) 1990 to 2014 surveys with $\theta = 1$ (1990 surveys theta = 1).

Table 5. Potential Biological Removal (PBR) estimates from the 2014 survey and from the model estimate (median) of the 2015 population from the different runs used to fit the model. In the run (+25%), pre-1990 survey estimates were increased by 25%.

Method	Survey data included	2015 Estimate	SE	CV	95% Credibility Interval	N_{min}	**PBR**
Model	1980–2014	1000	310	0.31	500–1700	704	7.0
Model	1980–2014+25%	1000	310	0.31	500–1800	788	7.9
Model	1985–2014	1000	340	0.34	500–1800	774	7.7
Model	1990–2014	1100	450	0.41	500–2200	763	7.6
Model theta fixed	1990–2014	1000	390	0.39	500–2000	765	7.7

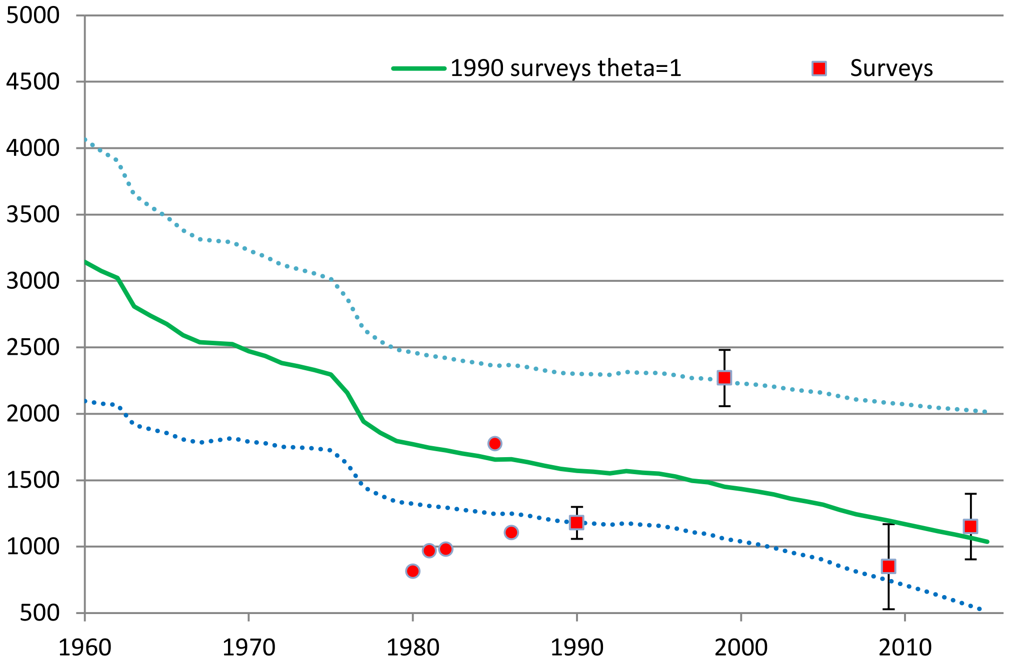

Figure 5. Model estimates of Cumberland Sound beluga abundance from preferred model fitted to aerial survey estimates flown in 1990, 1999, 2009 and 2014 corrected for animals at the surface (red squares with ± SE), and assuming θ of 1. Solid line shows the median estimates and dashed lines show 95% Credibility Intervals. Earlier surveys that only covered Clearwater Fiord 1980–1986 (red dots) were not used for this model fitting.

As indicated above, all model runs pointed to a 2015 abundance estimate of approximately 1,000 animals. Under the SARA management scenario of allowing the CS beluga stock to increase to 1,239 animals within 10 years, the probability of success is only 0.32 if no harvesting occurs, 0.25 if six animals are removed annually, 0.1 if the reported harvest is 25 animals and 0 if the reported harvest is 41 animals (Table 6, Fig. 6).

Table 6. Probability (P) that the population, subjected to different levels of reported harvest, will increase to the management objective of 1,235 animals within 10 years.

Reported Harvest level	P
25	0.1
17	0.15
10	0.20
6	0.25
1	0.30
0	0.32

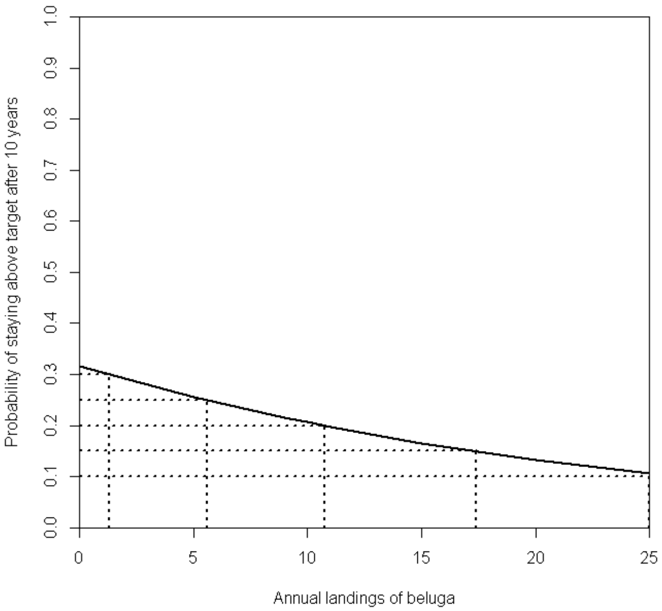

Figure 6. Probability of the Cumberland Sound beluga stock reaching the recovery estimate of 1,235 whales after 10 years of different reported harvest levels estimated by a stochastic Bayesian stock-production model (θ = 1) as a function of the number of reported belugas removed from the stock every year. Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of reaching the target level of 1,235 whales (y-axis).

If the management objective is sustainable yield, then the probability of population decline after 10 years is approximately 0.2 for a reported removal of two animals, 0.95 for a reported harvest of five animals and 1 if the reported harvest is 41 animals (Fig. 7).

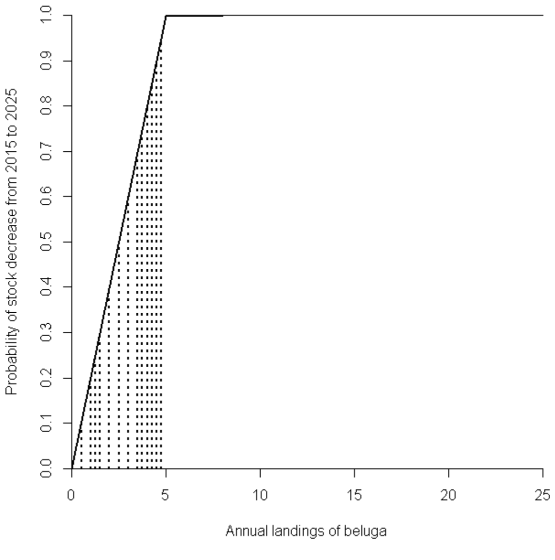

Figure 7. Probability of the Cumberland Sound beluga stock decreasing from the 2014 abundance estimate after 10 years of harvest, estimated by a stochastic Bayesian stock-production model (θ = 1) as a function of the number of reported belugas removed from the stock every year. Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of decline (y-axis).

Based on our model estimates for the 2015 population size, and a recovery factor (F_R) = 0.5, the PBR equation produces a removal threshold that varied from seven using the 1980 to 2014 time series, to eight using the other model runs that fitted to surveys flown during 1985 and later (Table 4). The PBR estimate from the 2014 aerial survey alone is ten animals.

DISCUSSION

In this study we fitted a discrete formulation of the Pella-Tomlinson model to recent aerial survey data (1980–2014), as well as a time series of reported catch data (1960–2015) using Bayesian methods (Pella and Tomlinson 1969, Innes and Stewart 2002). The preferred model was the formulation that was fitted to the 1990–2014 aerial survey data, with a fixed shaping parameter of $\theta = 1$. The estimated starting population after hunting (rounded to the nearest 100) in 1960 was 3,100 animals, which declined to a current (2015) population estimate of 1,000 animals (rounded to the nearest 100).

The surveys completed prior to 1990 were re-examined for possible inclusion in the model fitting. Overall, they had little impact on our current understanding of the population, but they did have some impact on estimates of early population size. The 1981, 1982 and 1983 survey estimates are all below estimates of population trend obtained by fitting to the 1990–2014 surveys (Fig. 4). Prior to 1990, it was thought that most belugas were distributed within the Clearwater Fiord area, so coverage outside of this area was irregular and often limited to coastal areas. Also, the very early surveys did not provide complete photographic coverage of Clearwater Fiord. The surveys flown in 1985 and 1986 appeared to provide more extensive systematic coverage outside of Clearwater Fiord, but whales appear to have been detected within a very restricted area and no estimate of survey variance was provided (Richard et al. 1990). Overall, these early surveys are likely negatively biased and should not be included in any future analysis, other than to provide support for a minimum population size estimate. In 1990, based on recommendations from hunters, the survey coverage was first extended to other parts of CS and the extended coverage has continued since then (Kilabuk 1998, Richard 2013). The number of whales outside of Clearwater Fiord has varied, ranging from 23% in 1999 to 60% in 2009 of the total population estimate (Richard 2013) underlining the importance of surveying areas outside of Clearwater Fiord.

The 2015 abundance estimates for CS belugas are much lower than those used in a previous Recovery Potential Assessment (RPA) of CS belugas (DFO 2005). In that exercise, a population model was fitted to two years of aerial survey data (1990 and 1999) and a harvest data series extending back to 1852, using a Pella-Tomlinson model fitted using Bayesian methods (Alvarez-Flores 2005, unpublished report). The 1999 survey abundance estimate was much higher than the 1990 survey, suggesting an increase in abundance (Fig. 4). Consequently the model used in the RPA estimated a 2002 population size of 2,000 animals (95% CI=1,500–2,600; rounded to the nearest 100). The model projected that the population would increase with harvest levels of up to 41 animals per year, with a 0.6 probability of reaching the recovery objective of 5,000 animals in 80 years (Alvarez-Flores 2005, unpublished report). Since then there have been two additional aerial surveys of CS belugas, both have returned abundance estimates that are much lower than those produced by the 1999 survey. Fitting our model to the additional data reduced the estimate of 2002 abundance to 1,400 animals (CI = 1,000–2,200; rounded to the nearest 100). This value is 30% lower than the previous estimates of CS beluga abundance, but still within the 95% Credibility Interval of the RPA (DFO 2005). More importantly, even if there is no harvest the model predicts a 0.3 probability of reaching the recovery target (1,235 animals in 10 year). For a harvest of only 5 animals per year, the probability that the population will decline in 10 years is close to 1, and the probability of achieving the interim 10 year recovery objective of 1,235 animals is only about 0.26.

The four aerial surveys of CS belugas (1990 to 2014; Table 1) produced sequential abundance estimates that cannot be explained by our current understanding of the dynamics of beluga populations (Richard 2013). The large increase in estimated population size observed between the 1990 and 1999 surveys is not possible biologically, since beluga populations are thought to only be capable of a maximum rate of increase of about 4% per annum, if not hunted (Richard 2013). In addition, the severe decline implied by the 1999 and 2009 population estimates would be only possible if hunting mortality was substantially larger (~180 belugas/year) than is presently reported (mean of 43 belugas/year) or there are important sources of mortality acting on CS belugas that are not taken into account (Richard 2013). Another factor, which might contribute to the marked increases or declines observed between surveys may be due to a larger sampling error than previously thought. If some small groups escape detection on some surveys or are detected on others, than this can have a significant impact on survey estimates of abundance.

Beluga aerial survey estimates of abundance are normally characterized by high CVs, implying considerable uncertainty (e.g., Gosselin et al. 2009, 2014). This is thought to be a consequence of trying to estimate the abundance of small populations of animals that tend to be highly aggregated in their behaviour. In contrast, the CVs of the CS beluga aerial surveys appear to be remarkably small (most are less than 20%). It is likely that the precision of the CS abundance estimate is poorly estimated. One factor contributing to the small CV is that the main contributor to the estimate is a total count of animals in Clearwater Fiord estimated by aerial photography, which has a small variance associated with it. In 1990, 1999 and 2009, the only term contributing to the calculated variance of the estimate for Clearwater Fiord was the variance associated with the correction factor for availability bias (animals that were not visible to be counted because they were diving). In 2014, the variance in the counts between photos was also included in the calculation of the variance for the total abundance of belugas in Clearwater Fiord. However, this variance is small given the large number of photos. In addition, the variance associated with the availability of animals at the surface is likely underestimated. Belugas are social animals that show socially-driven behaviour. Diving patterns of individuals in the same group may be correlated which will increase the uncertainty associated with survey estimates of abundance. Future effort should consider temporal correlation in dive pattern among individuals.

There is a need to build a time series of abundance estimates based on a survey design that covers the entire summer range of CS belugas (inside and outside Clearwater Fiord). The number of whales outside of Clearwater Fiord accounted for 23–60% of the total population estimate, in 1999 and 2009, respectively (Richard 2013). The variation in the proportion of beluga outside Clearwater Fiord during the time of the survey (August) needs to be better understood. Location data from eight belugas equipped with satellite transmitters in 1998–1999 and 2006–2007 showed that these belugas spent most of their time in Clearwater Fiord in August (their 95th percentile fixed-kernel range was limited to Clearwater Fiord; Richard and Stewart 2009). However, these belugas were tagged within Clearwater Fiord (Fig. 1) and might not represent the entire population.

The photographic aerial surveys used in this study include uncertainties that should be addressed in future surveys. These include, a measure of intra- and inter-photo-reader counts; within and between photo-readers' assessment of the percentage of glare in photos and of water turbidity (murkiness). Alternatively, automated methods could be used to calculate glare and water turbidity. In addition, measurement of water turbidity (e.g., Secchi disk measurement) at the same time as surveys are conducted might help to resolve this issue. Lastly, the use of tags with better depth resolution would greatly improve the precision of the availability bias corrections used in surveys.

We examined changes in the CS beluga population assuming that their dynamics could be described using a density-dependent population model. The model estimated K, θ, initial population size, $S\&L$ and the 2015 population using the catch history time series and fitting to the aerial survey abundance estimates. The different model runs all indicated that the population has declined over the last 55 years, and all runs converged to a 2015 population of approximately 1,000 animals. However, for many runs there was little to no updating of the priors, considerable cross-correlation among parameters and in all runs there is considerable uncertainty associated with parameter estimates (see Appendix 2). Therefore, it is recommended that parameter estimates of K, S&L, and the starting population not be used outside of this analysis.

The high level of uncertainty in the model is due to both a lack of data and some inconsistencies within the available data. First, with four surveys, there was not enough information in the data to inform model parameter estimation. Secondly, as outlined above, the differences between the very high 1999 aerial survey estimate and much lower 1990 and 2009 estimates cannot be accounted for by what is known about the dynamics of this population and reported harvests. The high level of autocorrelation in the parameter chains was an indication that model convergence was hard to attain. To reduce some of the autocorrelation observed among model parameters, we used a shortened harvest time series (1960–2014). The impact of including different start dates with harvest data was examined in a cursory fashion and it appeared that as harvests from earlier periods were included, difficulties with model fit increased. This suggests that there are some problems with the earlier harvest data or changes in harvesting practices occurred, meaning that applying a single $S\&L$ value to the entire time series may not be appropriate. In addition to these difficulties, harvest data were not available for many years. In these cases, it was assumed that the entire quota was taken, but the amount and direction of bias compared to true harvests is not known. Lastly, $S\&L$ rates were only reported for two years. Better $S\&L$ statistics would contribute to improving model fitting.

Given the high level of uncertainty, the shaping parameter for the density dependent relationship was also fixed to θ = 1, which sets the region of maximum productivity at 50% of K. This is at the lower end of a range of maximum productivity of 50–85% that has been identified for marine mammals (Taylor and DeMaster 1993, Wade 1998). Other studies of modeling beluga population trajectories have noted the difficulty in setting θ (e.g., Innes and Stewart 2002, Alvarez-Flores and Heide-Jørgensen 2004). Most beluga populations have been heavily exploited and are currently much closer to the lower tail of the population curve (their historic minimums), than at the upper end of the curve (much closer to K) where θ would be expected to play a more important role in shaping the dynamics of the population. Fixing θ = 1 has little impact on our advice, compared to fixing a different parameter such as $S\&L$. Fig. 8 shows that at current low levels of abundance, there is little difference (less than 4%) between models in the population trajectories under other assumptions using different shaping parameters, or assuming exponential growth over the next decade.

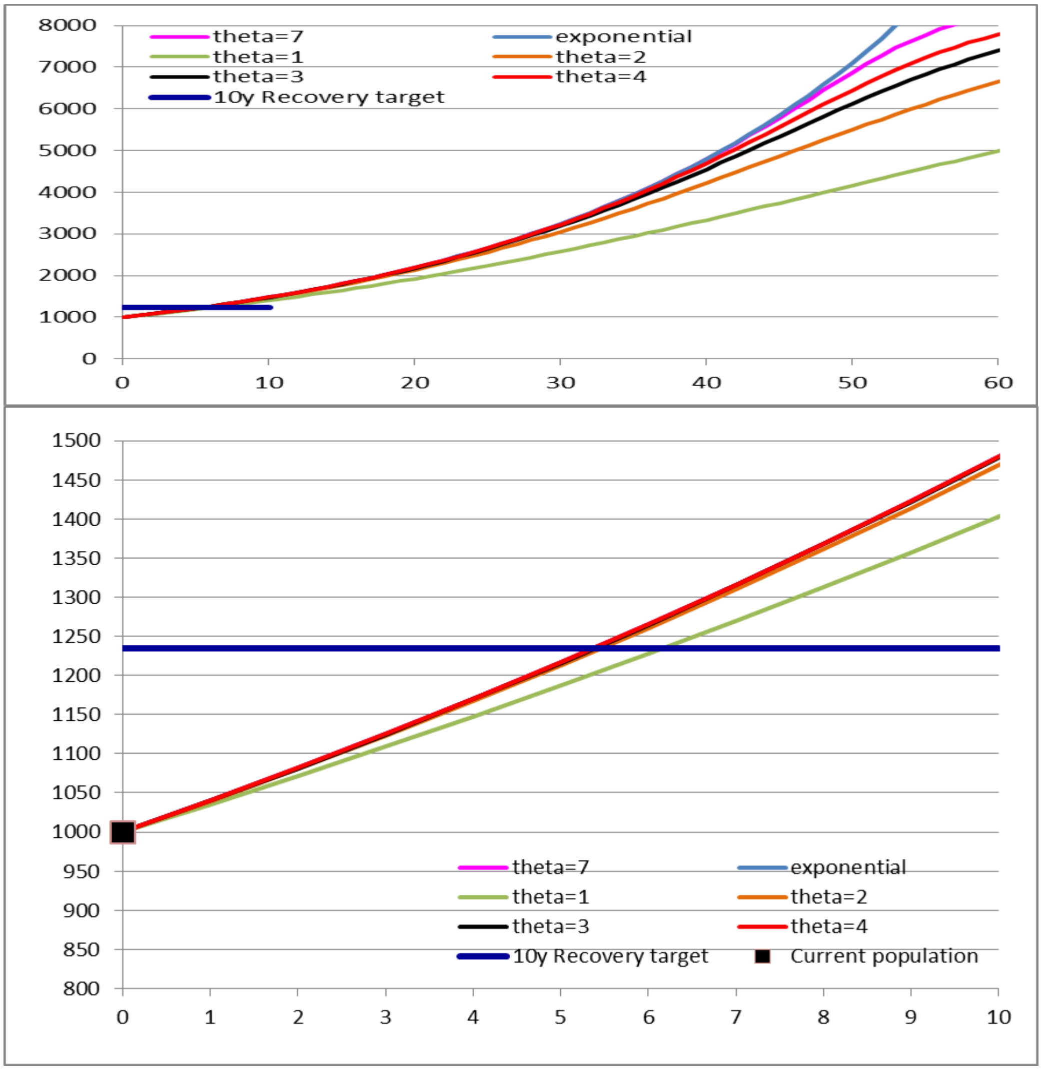

Figure 8. Trajectories for a population starting at a current population of 1,000 animals (square), and assuming no harvest with an instantaneous rate of increase of 0.04. The population was allowed to increase exponentially or subject to density-dependent regulation with K=8400 and θ =1, 2, 3, 4 or 7. The blue line represents the 10 year interim recovery target of 1,235 animals. The type of model has little impact on future population trends over the first 10 years.

The management objective for this stock is for the population to increase to 5,000 animals by 2091. To achieve this objective, the population should reach an interim target population of 1,235 animals within the next 10 years. This management objective will not be achieved at current harvest levels. However, the population model indicates that even under scenarios of 0 harvest, the probability of achieving the management objective is only 0.32. This high level of uncertainty in achieving the management objective even when there is no hunting is due to a combination of a limited time series of survey estimates for a species that is difficult to survey, as well as uncertainty in $S\&L$ and reported harvests.

We provide estimates of PBR that are estimated from the 2014 aerial survey and from the 2015 model estimate of abundance. One of the advantages of the PBR method is that it only requires a single point estimate of abundance, to be able to calculate the PBR level. However, if several survey estimates are available, then it may be difficult to decide which survey provides the best estimate upon which to base the PBR calculation. Also, the variability in the survey estimates will result in PBR estimates that will fluctuate much more than would be expected given the dynamics of beluga populations. For example estimating PBR from the 1990, 1999, 2009 or 2014 survey estimates would have resulted in highly variable PBR numbers, which are unlikely given the expected dynamics of beluga populations. Instead, when several estimates of abundance are available it is recommended that a population model be fitted to the abundance data, and the PBR be calculated from the model estimate of abundance. This approach makes greater use of the available information with respect to the dynamics of beluga populations, harvest data, and multiple abundance indices and will tend to result in a more stable estimate of PBR.

PBR estimates, which do not take into account other sources of human-induced mortality were less than or equal to eight, assuming a recovery factor of 0.5, which DFO has used as a standard in the past for populations considered as ‘threatened’ by COSEWIC. Assuming $S\&L$ levels and non-reporting are on average 0.42, the Total Allowable Harvest, would be five. It is clear that additional surveys, and improved harvest data are needed to reduce uncertainty related to our understanding of the status of this population. Nonetheless some reduction in harvest levels is needed to contribute to population recovery.

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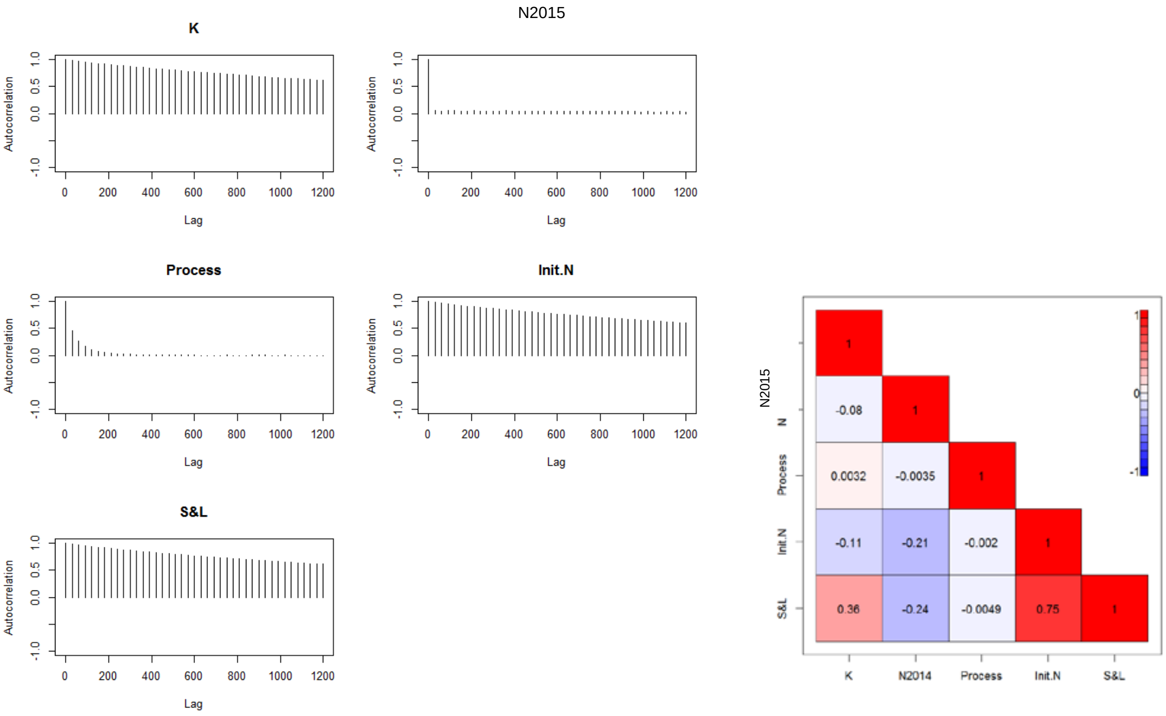
APPENDIX 1

Detailed output from model run to examine abundance trends of Cumberland Sound beluga using the 1920–2015 harvest data and survey from 1990 to 2014.

Appendix 1. Table 1. Model outputs for Cumberland Sound beluga stock model using all aerial survey and harvest data from 1920–2014 with $\theta = 1$. The mean, standard deviation (SD), median (50th Q), 25th and 75th quantiles (25th Q, 75th Q), 95% credibility intervals (2.5%CI, 97.5%CI) are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (surv), starting population (Startpop), struck and loss (S&L), and population size in 2015 (N2015). $\hat{R}$ is the Brooks-Gelman-Rubin statistics; values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation.

Parameter	Mean	SD	2.5%CI	25th Q	50th Q	75th Q	97.5%CI	$\hat{R}$	n.eff
K	9424	2141	6686	7791	8803	10644	14446	1.004	930
K.prior	10001	2887	5247	7499	10001	12500	14747	1.001	200000
Theta	1.92	0.57	1.04	1.42	1.89	2.41	2.94	1.001	32000
Theta. prior	2.00	0.58	1.05	1.50	2.00	2.50	2.95	1.001	250000
Deviance	135.9	2.0	133.6	134.5	135.4	136.8	141.1	1.001	6400
Prec. process	1497.0	1222.5	109.3	605.5	1181.6	2046.3	4666.0	1.001	39000
Prec. process. prior	1503.9	1229.6	106.4	605.8	1185.7	2062.6	4689.9	1.001	200000
Prec. surv	6.88	2.73	2.61	4.89	6.53	8.48	13.15	1.001	47000
Prec. surv prior	6.25	3.95	1.04	3.34	5.45	8.28	16.03	1.001	250000
Startpop	7662	1136	5597	6869	7591	8399	10051	1.004	1200
Startpop. prior	8485	3756	2318	5225	8494	11730	14668	1.001	200000
Struck. and .lost	0.25	0.14	0.04	0.14	0.23	0.33	0.56	1.004	1000
Struck. and .lost. prior	0.33	0.18	0.05	0.19	0.31	0.45	0.72	1.001	250000
Population 2015	1196	332	639	970	1165	1384	1943	1.001	9300



Appendix 1 Figure 1. Autocorrelation plots showing evidence for autocorrelation within each chain for the Cumberland Sound beluga stock model using the full model which attempted to estimate θ, K, N2015, init_N, and S&L. The model was fitted to all aerial survey data and harvest data between 1920 and 2015. Variables shown include carrying capacity (K), 2015 population estimate (N2015), process error (Process), initial population size (init.N) and struck and lost (S&L). Cross-correlation among model parameters carrying capacity (K), 2015 population estimate (N2015), process error (Process), initial population size (Init.N), and struck and lost (S&L) for the Cumberland Sound beluga stock model runs that included all survey data and reported harvests from 1920–2014 (θ = 1).

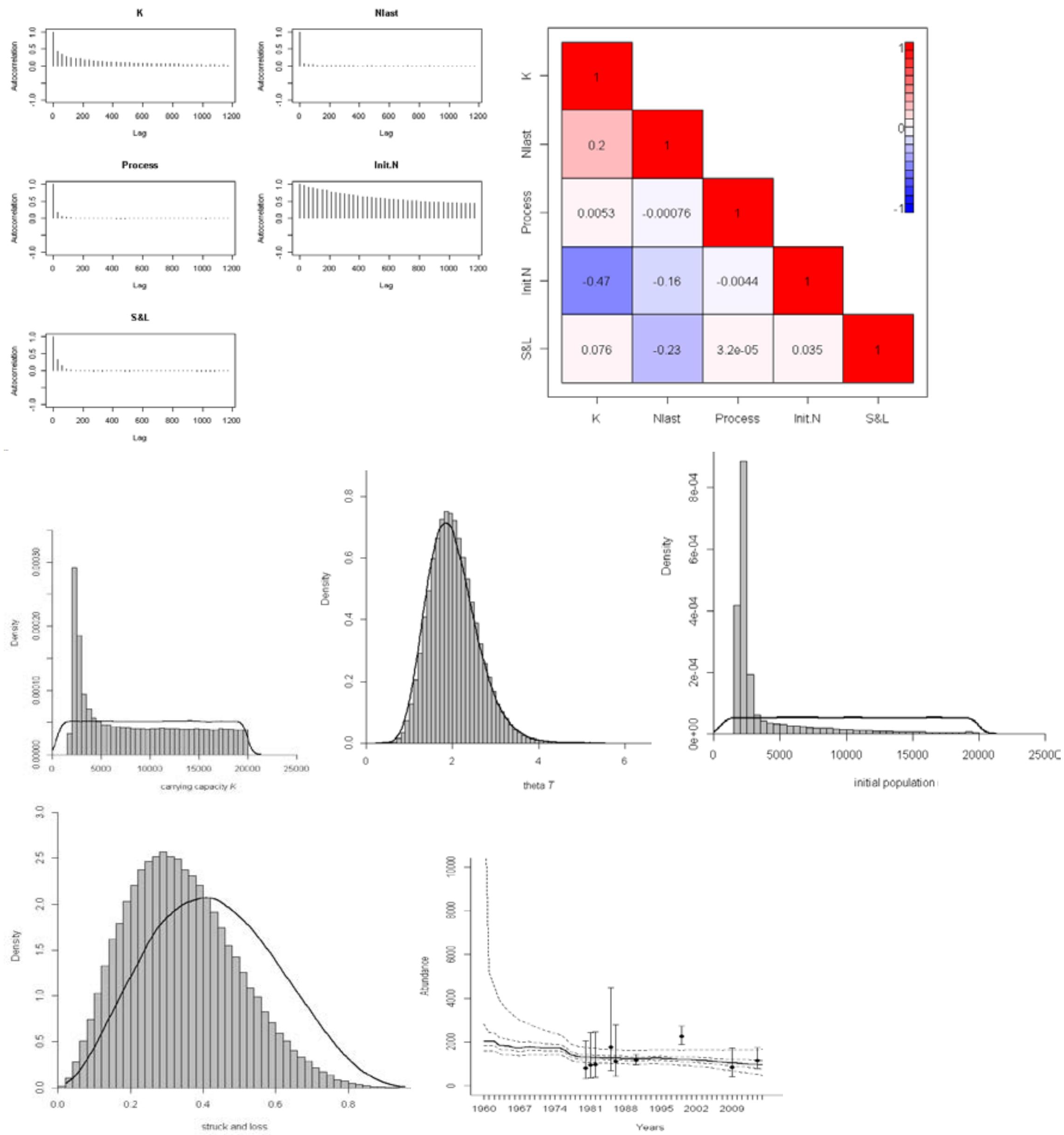
APPENDIX 2

Detailed outputs from different model runs to examine abundance trends of Cumberland Sound beluga using the 1960–2015 catch history and different combinations of aerial survey abundance estimates.

Appendix 2. Table 1, Figure 1. Model outputs using 1980–2014 surveys .
Appendix 2. Table 2, Figure 2. Model outputs using 1980–2014 surveys, with pre-1990 survey estimates increased by 25%.
Appendix 2. Table 3, Figure 3. Model outputs using 1985–2014 surveys .
Appendix 2. Table 4, Figure 4. Model outputs using 1990–2014 surveys
Appendix 2. Table 5, Figure 5. Model outputs using 1985–2014 surveys, with θ = 1.
Appendix 2. Table 6, Figure 6. Model outputs using 1990–2014 surveys, with θ = 1.

Appendix 2 Table 1. Model outputs for Cumberland Sound beluga stock using 1960–2015 catch history and 1980–2014 surveys. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.

	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	8657	5750	2047	2959	7469	13661	19356	1.001	87000
K.prior	10246	5627	997	5367	10259	15096	19511	1.001	200000
Theta	2.03	0.55	1.10	1.64	1.98	2.37	3.26	1.001	200000
Theta.prior	2.00	0.58	1.03	1.59	1.95	2.35	3.28	1.001	180000
Deviance	135.4	2.5	132.1	133.6	134.9	136.8	141.501	1.001	150000
Process	1495	1219	105	606	1179	2055	4645	1.001	52000
Process .prior	1497	1218	107	607	1184	2051	4646	1.001	200000
Survey	7	3	3	5	7	9	14	1.001	95000
Survey. prior	6	4	1	3	5	8	16	1.001	200000
Start	3607	3284	1773	2037	2268	3022	14635	1.001	11000
Start.prior	10247	5627	996	5388	10230	15123	19519	1.001	200000
S&L	0.34	0.15	0.09	0.23	0.33	0.44	0.67	1.001	200000
S&L.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	200000
N2015	990	307	479	779	961	1165	1681	1.001	53000

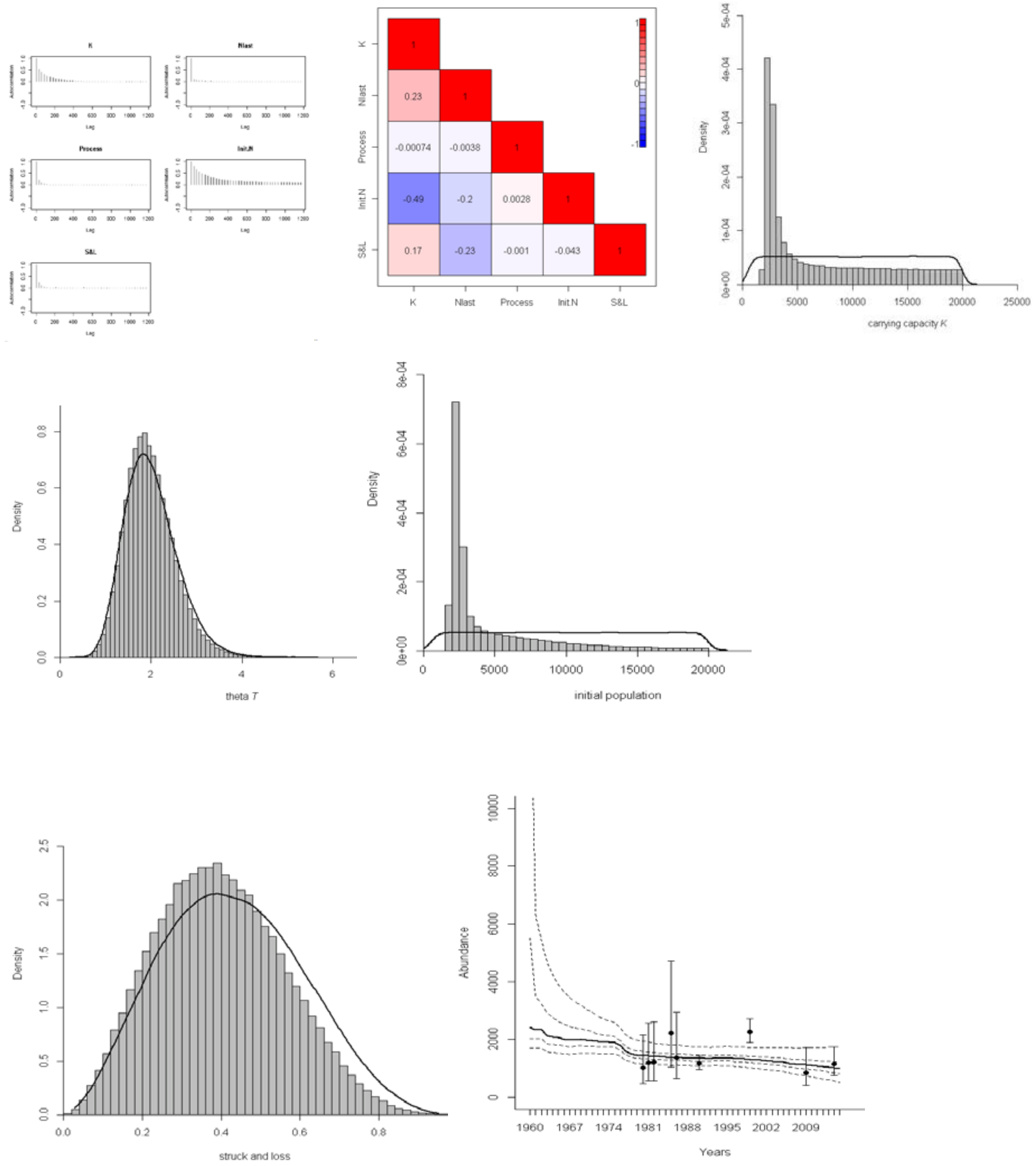


	K	Nlast	Process	Init.N	S&L
K	1				
Nlast	0.2	1			
Process	0.0053	-0.00076	1		
Init.N	-0.47	-0.16	-0.0044	1	
S&L	0.076	-0.23	3.2e-05	0.035	1

Appendix 2. Figure 1. The model was fitted to all aerial survey data 1980–2014. Plots show change in autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, theta, initial population and S&L. Population estimates show survey estimates (Mean ± 95% confidence intervals), median (solid line) estimate, 2.5th, 25th, 75th, and 97.5th quantiles (dashed lines).

Appendix 2. Table 2. Model outputs for Cumberland Sound beluga stock using all 1980 to 2014 surveys with 1960–2015 catch history. Estimates from surveys flown prior to 1990 were increased by 25%, and it was assumed that the cv around the estimate was 50%. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ *is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.*

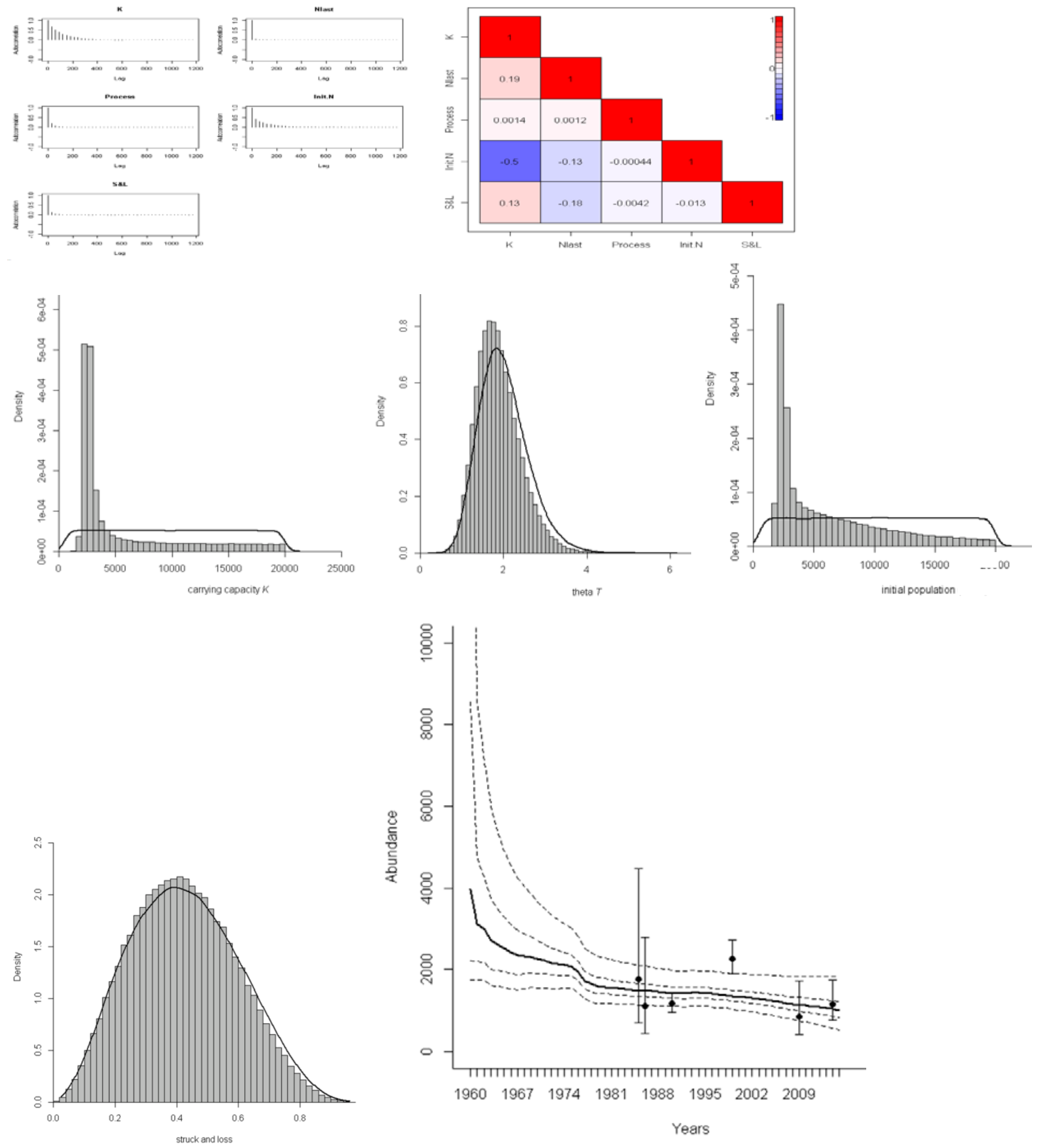
	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	7019	5497	2065	2550	4098	11098	19092	1.001	24000
K.prior	10265	5626	997	5390	10278	15145	19510	1.001	80000
Theta	1.97	0.54	1.07	1.60	1.92	2.30	3.18	1.001	76000
Theta.prior	2.00	0.58	1.04	1.59	1.94	2.35	3.28	1.001	170000
Deviance	136	2	133	134	135	137	142	1.001	190000
Process	1497	1226	108	604	1175	2052	4655	1.001	110000
Process .prior	1499	1222	110	608	1182	2050	4662	1.001	160000
Survey	8	3	3	6	7	10	15	1.001	200000
Survey. prior	6	4	1	3	5	8	16	1.001	200000
Start	4678	3916	1896	2259	2654	5736	16393	1.001	35000
Start.prior	10242	5632	991	5362	10225	15118	19510	1.001	110000
S&L	0.40	0.16	0.11	0.28	0.39	0.51	0.73	1.001	200000
S&L.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	190000
N2015	1047	312	532	833	1015	1222	1758	1.001	130000



Appendix 2. Figure 2. Model outputs for Cumberland Sound beluga stock using all aerial survey data 1980–2014, with the 1980–1986 estimates increased by 25% to account for possible animals outside Clearwater Fiord. Plots show autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, theta, starting population and S&L. Population estimates show aerial survey (Mean ± 95% confidence intervals), and model estimates median (solid line) estimate, 2.5th, 25 th, 75 th, and 97.5 th quantiles (dashed lines).

Appendix 2. Table 3. All 1985 to 2014 surveys with 1960–2015 catch history. A 50% CV was assumed for the 1985 and 1986 surveys. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.

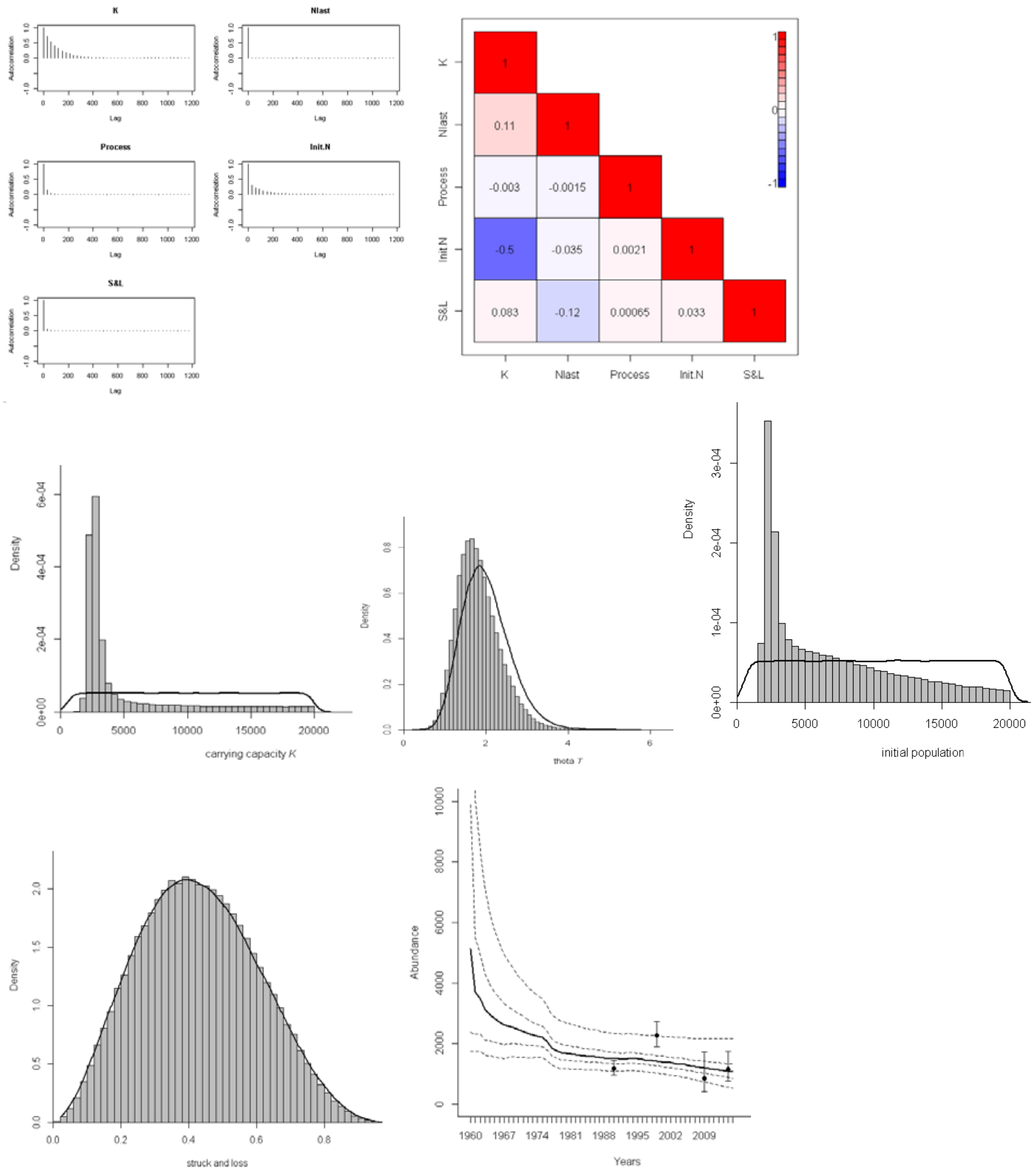
	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	5591	4922	2034	2465	2900	7122	18617	1.001	17000
K.prior	240	5624	981	5369	10255	15111	19499	1.001	150000
Theta	1.87	0.52	1.02	1.50	1.81	2.18	3.06	1.001	200000
Theta.prior	2.00	0.58	1.03	1.59	1.95	2.35	3.29	1.001	200000
Deviance	90.9	2.1	88.5	89.5	90.4	91.8	96.3	1.001	200000
Process	1494	1216	107	602	1179	2052	4631	1.001	200000
Process .prior	1502	1225	109	607	1183	2053	4674	1.001	200000
Survey	7	3	2	5	7	9	15	1.001	200000
Survey. prior	6	4	1	3	5	8	16	1.001	200000
Start	6177	4650	1942	2469	4195	8771	17984	1.001	20000
Start. prior	248	5623	981	5394	10251	15113	19505	1.001	88000
S&L	0.42	0.17	0.12	0.30	0.42	0.54	0.76	1.001	150000
S&L.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	84000
N2015	1060	340	526	833	1018	1236	1844	1.001	200000



Appendix 2, Figure 3. The model was fitted to all aerial survey data 1985–2014. Plots show reduction in autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, theta, starting population and S&L. Population estimates show aerial survey (Mean ± 95% confidence intervals), and model estimates median (solid line) estimate, 2.5th, 25th, 75th, and 97.5th quantiles (dashed lines).

Appendix 2. Table 4. All 1990 to 2014 surveys with 1960–2015 catch history. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ *is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.*

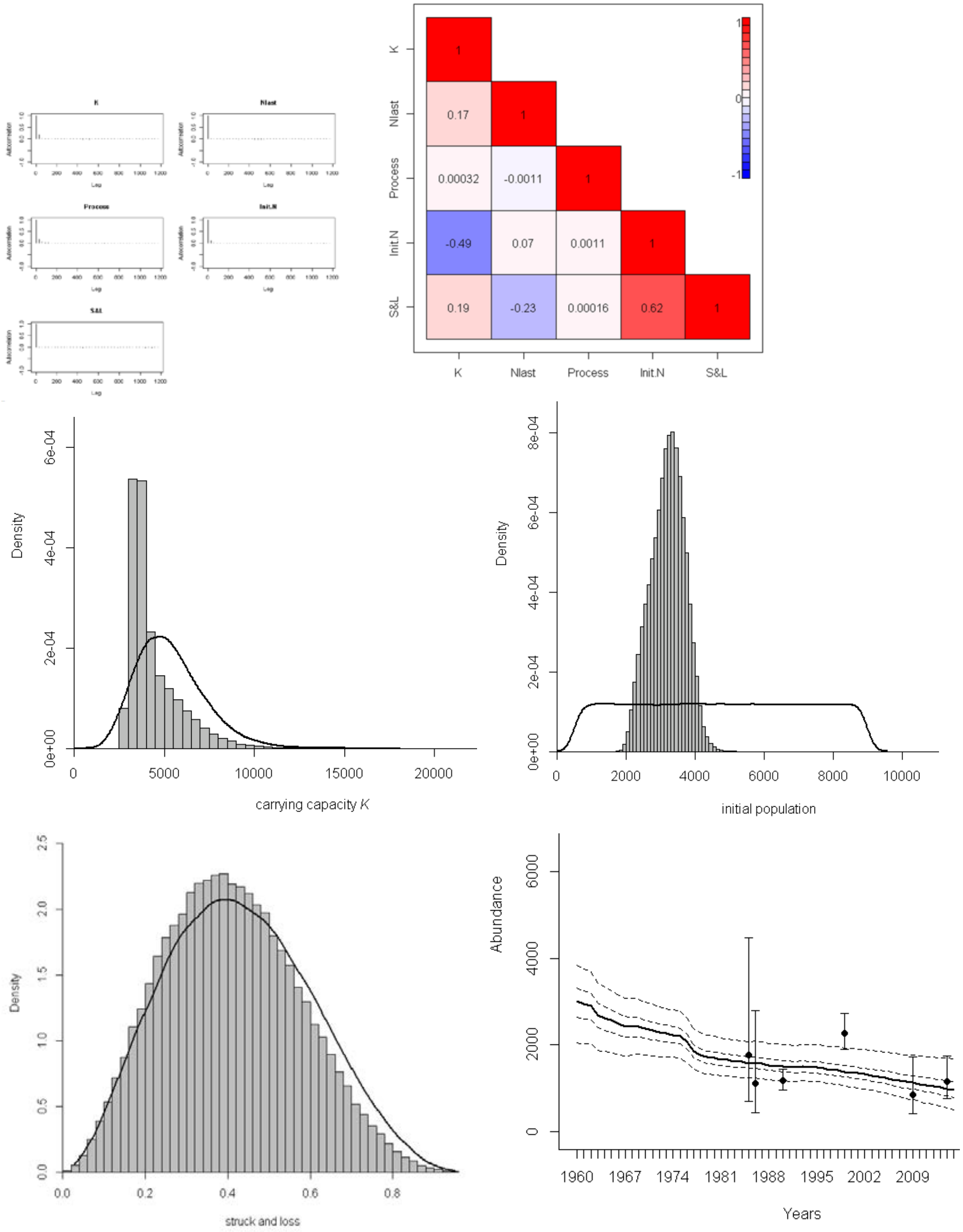
	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	5100	4568	2035	2483	2857	5260	18294	1.001	49000
K.prior	10249	5623	1004	5369	10239	15115	19508	1.001	200000
Theta	1.81	0.52	0.97	1.44	1.75	2.12	3.00	1.001	90000
Theta.prior	2.00	0.58	1.03	1.59	1.94	2.35	3.28	1.001	180000
Deviance	61.4	1.9	59.4	60.0	60.8	62.1	66.6	1.001	200000
Process	1497	1222	109	602	1181	2052	4663	1.001	110000
Process .prior	1500	1224	107	608	1184	2051	4660	1.001	200000
Survey	7	3	2	4	6	8	14	1.001	200000
Survey. prior	6	4	1	3	5	8	16	1.001	200000
Start	6931	4899	1946	2617	5358	10111	18400	1.001	200000
Start.prior	10263	5632	990	5390	10272	15134	19508	1.001	200000
S&L	0.43	0.17	0.12	0.30	0.42	0.55	0.77	1.001	140000
S&L.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	200000
N2015	1138	445	521	860	1069	1327	2159	1.001	110000



Appendix 2. Figure 4. The model was fitted to 1990–2014 aerial survey data . Plots show reduction in autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, theta, initial population and S&L. Population estimates show aerial survey (Mean ± 95% confidence intervals), and model estimates median (solid line) estimate, 2.5th, 25th, 75th, and 97.5th quantiles (dashed lines).

Appendix 2. Table 5. Model fitted to 1985–2014 surveys, using 1960–2015 catch history. In this run theta was fixed, with theta=1. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.

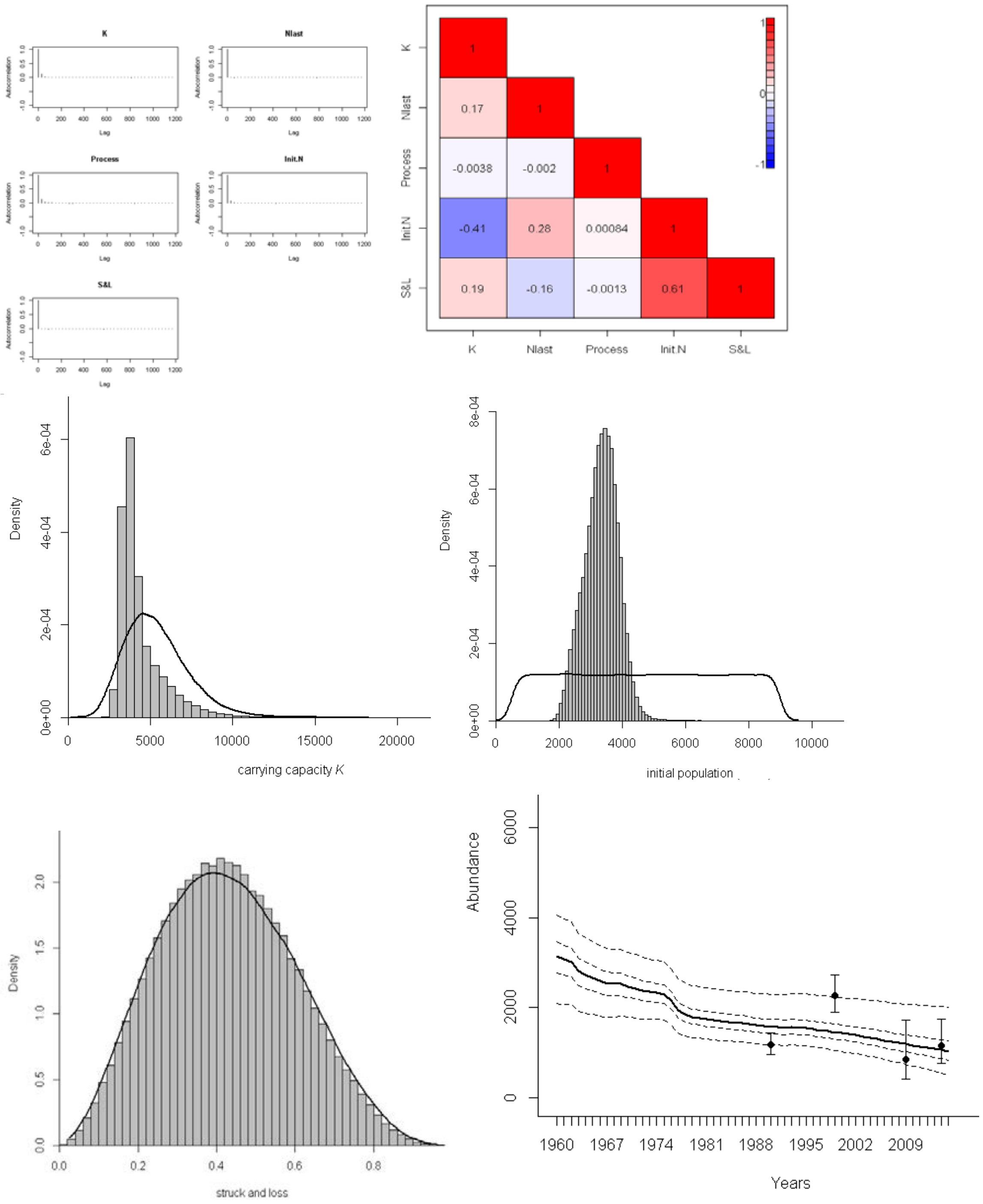
	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	4359	1422	2936	3413	3822	4905	8223	1.001	90000
K.prior	5332	1882	2300	3974	5112	6448	9628	1.001	200000
Deviance	91	2	89	90	90	92	96	1.001	100000
Process	1500	1225	106	608	1183	2055	4684	1.001	98000
Process .prior	1497	1216	108	608	1183	2052	4638	1.001	100000
Survey	74	33	23	49	69	93	152	1.001	79000
Survey. prior	62	39	10	33	54	83	160	1.001	200000
Start	3204	489	2249	2862	3230	3552	4107	1.001	79000
Start.prior	4750	2452	714	2625	4746	6871	8787	1.001	200000
S&L	041	017	012	029	040	052	074	1.001	200000
S&L.prior	043	018	012	030	042	055	078	1.001	170000
N2015	1001	301	508	798	968	1164	1685	1.001	200000



Appendix 2. Figure 5. The model was fitted to all aerial survey data 1985–2014. In this run theta was fixed, with theta = 1. Plots show reduction in autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, starting population and S&L. Population estimates show aerial survey (Mean ± 95% confidence intervals), and model estimates median (solid line) estimate, 2.5th, 25th, 75th, and 97.5th quantiles (dashed lines).

Appendix 2. Table 6. Model fitted to 1990–2014 surveys, using 1960–2015 catch history. In this run theta was fixed, with theta = 1. The mean, standard deviation (SD), 2.5th , 25th, 50th, 75th and 97.5th quantiles are given for the following model parameters and their priors: carrying capacity (K), process error (process), survey precision (survey), starting population (Start), struck and lost (S&L), and population size in 2015 (N2015). $\hat{R}$ *is the Brooks-Gelman-Rubin statistic; values near 1 indicate convergence of chains. N.eff is the number of effective runs after considering autocorrelation.*

	Mean	SD	2.5%	25%	50%	75%	97.5%	$\hat{R}$	n.eff
K	4334	1325	2973	3488	3884	4727	8031	1.001	56000
K.prior	5331	1885	2310	3967	5112	6448	9630	1.001	200000
Deviance	61.3	1.9	59.4	59.9	60.7	62.0	66.3	1.001	200000
Process	1497	1225	109	603	1178	2051	4674	1.001	120000
Process .prior	1500	1223	110	610	1184	2052	4676	1.001	200000
Survey	6. 6	3. 3	1. 8	4. 1	6. 0	8. 4	14. 5	1.001	150000
Survey. prior	6. 2	3. 9	1. 0	3. 3	5. 4	8. 3	15. 9	1.001	200000
Start	3335	531	2286	2978	3359	3700	4320	1.001	63000
Start.prior	4746	2454	714	2611	4752	6873	8786	1.001	200000
S&L	0. 43	0. 17	0. 12	0. 30	0. 42	0. 55	0. 77	1.001	87000
S&L.prior	0. 43	0. 18	0. 12	0. 30	0. 42	0. 55	0. 78	1.001	200000
N2015	1094	387	512	840	1037	1279	2015	1.001	120000



Appendix 2. Figure 6. The model was fitted to all aerial survey data 1990–2014. In this run theta was fixed, with theta = 1. Plots show reduction in autocorrelation, cross correlation and priors (lines), posterior (histograms) for K, starting population and S&L. Population estimates show aerial survey (Mean ± 95% confidence intervals), and model estimates median (solid line) estimate, 2.5th, 25th, 75th, and 97.5th quantiles (dashed lines).